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Biophysical control of whole tree transpiration under an urban environment in Northern China

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SUMMARY

Urban reforestation in China has led to increasing debate about the impact of urban trees and forests on water resources. Although transpiration is the largest water flux leaving terrestrial ecosystems, little is known regarding whole tree transpiration in urban environments. In this study, we quantified urban tree transpiration at various temporal scales and examined the biophysical control of the transpiration pattern under different water conditions to understand how trees survive in an urban environment. Concurrent with microclimate and soil moisture measurements, transpiration from *Cedrus deodara*(Roxb)Loud., *Zelkova schneideriana* Hend.-Mazz., *Euonymus bungeanus* Maxim., and *Metasequoia glyptostroboides* Hu et cheng was measured over a 2-year period using thermal dissipation probe (TDP) techniques. The average monthly transpiration rates reached 12.78 ± 0.73 (S.E.) mm, 1.79 ± 0.16 mm, 10.18 ± 0.55 mm and 19.28 ± 2.24 mm for *C. deodara*, *Z.schneideriana*, *E. bungeanus* and *M. glyptostroboides*, respectively. Transpiration rates from *M. glyptostroboides* reported here may need further study as this species showed much higher sap flows and greater transpiration fluctuation under different environmental conditions than other species. Because of deep soil moisture supply, summer dry spells did not reduce transpiration rates even when tree transpiration exceeded rainfall. While vapor pressure deficit (*VPD*) was the dominant environmental factor on transpiration, trees controlled canopy conductance effectively to limit transpiration in times of water stress. Our results provide evidence that urban trees could adopt strong physiological control over transpiration under high evaporative demands to avoid dehydration and can make use of water in deeper soil layers to survive summer dry spells. Moreover, urban trees have the ability to make the best use of precipitation when it is limited, and are sensitive to soil and air dryness.

1. Introduction

China, the most populous country in the world, has experienced rapid urbanization as the country's economy has expanded in recent years. To improve urban eco-environments and provide amenable living conditions, urban forestry has been developing very quickly for the past decade. In addition, high water consumption for urban grass irrigation in water stressed cities has led to the implementation of urban forestry practices to reduce the high cost of open green space and increase ecological and environmental services and functions of urban lands (Li et al., 2007; Shi et al., 2003; Zhang, 2008). However, world wide research on forest water relations indicate that forest trees use more water than shorter crops like shrub and grassland under natural conditions (Huxman et al., 2005; Jackson et al., 2005; Lubczynski and Gurwin, 2005; Zhang et al., 2001). As the result, water yield can be reduced by afforestation in grass covered watersheds and increased in forested watersheds by deforestation (Bosch and Hewlett, 1982; Jackson et al., 2005; Zhang et al., 2001).

Most of our current understanding of water use by trees was derived from studies under natural conditions or from physiological research in laboratories (Chu et al., 2009; Chuang et al., 2006) with leaf-level gas exchange measurements (Zeppel et al., 2008), paired watershed hydrological experiments (Bosch and Hewlett, 1982; Jackson et al., 2005; Zhang et al., 2001), sap flux measurements (Ewers et al., 2008; Martin et al., 2001; Tang et al., 2006), and non-destructive eddy covariance ecosystem evaportranspiration measurements (Fisher et al., 2007; Granier et al., 2000; Law et al., 2002; Testi et al., 2004; Villalobos et al., 2000; Williams et al., 2004). While transpiration from trees in natural conditions is well studied, our understanding of water use in urban trees is limited (Chu et al., 2009; Chuang et al., 2006).

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Tree transpiration rate is largely controlled by biological factors such as tree size and leaf area index, and environmental factors such as incident radiation, vapor pressure deficit (*VPD*), wind speed, and soil moisture availability (David et al., 2004; Ewers et al., 2008; Hernández-Santana et al., 2008; Komatsu et al., 2006; Oren and Pataki, 2001; Tang et al., 2006; Tognetti et al., 2005, 2009; Wullschleger et al., 2000). These biophysical factors affect transpiration at multiple temporal and spatial scales. Plant water use and tree transpiration rates can be increased in response to rainfall (Mitchell et al., 2009) and reduced during periods of low soil water availability (Gazal et al., 2006; Luis et al., 2005). Studies have shown that stand transpiration increases in years of higher precipitation (Macfarlane et al., 2010; Zeppel et al., 2008). Mean daily transpiration of an olive plantation was higher under wet conditions both as a result of increased rainfall and fully irrigated treatments than when soil water was limited (O'Grady et al., 2008; Tognetti et al., 2009). Low soil water availability can increase the hydraulic resistance between the soil and root system, prevent water movement from soil to plant leaves, and trigger stomatal closure, thus reducing the transpiration rate (Meinzer et al., 1993; Sala and Tenhunen, 1996; Tognetti et al., 2009). Under such conditions, plants adopt conservative water use strategies (Tognetti et al., 2009) and appear to exploit water reserves from deeper soil layers (David et al., 2004; Hernández-Santana et al., 2008; Thomas et al., 2006).

In addition to soil water availability, stomatal activities are also regulated by radiation, *VPD*, and the combined effect of these environmental variables. Transpiration rates increase exponentially with *VPD* until a certain threshold at which stomata close to keep water potential above a critical level (Hernández-Santana et al., 2008). Such constraint can help to avoid embolism, which causes the collapse of conductive system (Bush et al., 2008). Since stomata regulate plant water use, tree transpiration rates may be limited even if soil water availability is not a problem (Hernández-Santana et al., 2008). Under such a condition, the hydraulic resistance sets the maximum transpiration rate (Hogg and Hurdle, 1997).

Hysteresis between transpiration and environmental variables as well as the nocturnal water movement are widely observed. For example, O'Grady et al. (2008) reported that hysteresis between transpiration and *VPD* was more evident under increased *VPD* conditions regardless of the soil moisture. It is estimated that nocturnal sap flow is responsible for about 2–8% of seasonal total woodland evapotranspiration in semi-arid environment (Mitchell et al., 2009).

Most prior research on tree transpiration focused on understanding the biophysical control of whole tree transpiration under natural conditions. In an urban environment, however, there are distinctly different conditions that may impact tree transpiration such as the "heat island" phenomenon, irrigation, decreased evaporation due to pavement, and potential water sources from sewage. Moreover, planted urban trees are widely scattered and thus are considered isolated or rowed plants (Zhang et al., 1997). Consequently, urban vegetation is expected to exhibit a unique set of complex hydrological behaviors. To our knowledge, urban tree water relations have not been well studied (Bush et al., 2008; Chu et al., 2009; Hagishima et al., 2007). Understanding plant water relations is of great importance in developing economical and efficient irrigation schedules (Fernández et al., 2008; Villalobos et al., 2000). Therefore, quantifying the water use of different tree species and understanding their biophysical control under an urban environment is necessary to increase the ecological and environmental benefits of urban forests through efficient management practices.

To answer these questions, we measured microclimate and transpiration from four tree species in an urban park located in northern China, including *Cedrus deodara*(Roxb)Loud, *Zelkova schneideriana* Hend.-Mazz., *Euonymus bungeanus* Maxim, and *Metasequoia glyptostroboides* Hu et cheng. Our specific objectives were to: (1) quantify the whole tree transpiration of these four urban tree species, (2) explore the biophysical control of tree transpiration under an urban environment, and (3) elucidate the survival strategies that urban trees adopt in times of low water availability.

2. Methods

2.1. Site description and tree selection

The study was conducted in Laodong Park, Dalian City (38°54′N, 121°37′E), Liaoning Province, China. Under a temperate maritime climate, the mean annual temperature is 10.2 °C and the mean annual precipitation ranges from 550–800 mm, most of which falls in summer.

The study site is located in a 350 m^2 plot located in the north side of the park consisting of *Cedrus deodara*(Roxb)Loud., *Zelkova schneideriana* Hend.-Mazz., *Euonymus bungeanus* Maxim, and *Metasequoia glyptostroboides* Hu et cheng. Three trees of each species were selected with diameter of breast height (DBH) distribution well represented (Table 1). Trunks of sampled trees were bored to measure sapwood area. Tree transpiration and microclimate measurements took place from June 25th 2008 to October 17th 2009.

2.2. Sap flow measurement

Tree transpiration was estimated from sap flux density (*Js*), measured continuously using thermal dissipation probes (TDPs) (Dynamax, Houston, TX, USA). The 30 mm probes were used in all trees except Z_1 and Z_2 where the shallow sapwood thickness required the use of 20 mm probes. Each sensor consisted of a pair of needle-shaped probes with thermocouples. The upper probe was powered to constant heat by a 12 V storage cell and the lower probe served as an unheated reference, reflecting the sap temperature. Upward sap flow removes energy from the heated probe, generating temperature differences between the two probes. Based on the energy conservation principle, sap flux density can be calculated according to standard calibration for the TDP method (Granier, 1987; Otieno et al., 2005; Tang et al., 2006):

$$Js = 0.0119\,K^{1.231} \tag{1}$$

where *K* is a parameter derived from

$$K = (\Delta T_m - \Delta T)/\Delta T \tag{2}$$

Js: Sap flux density (g cm^{-2} s^{-1}), ΔT_m: maximum temperature difference between sensors during a day (°C) ΔT: temperature difference between sensors at any given time (°C) and whole tree transpiration rate (*E*) on hourly scale (g h^{-1}) then can be calculated as

$$E = Js \times As \times 3600 \tag{3}$$

where *As* is the sapwood area (cm^2), 3600 is the conversion factor from seconds to hours. Canopy transpiration rate (*Ec*) in millimeter was calculated by dividing the total sap flow by crown area to facilitate comparison with rainfall measurements.

A 5 cm^2 square of bark was removed at a height of 1.3 m to expose the cambium and mount the probes to the trunk. After installation, the probes were sealed with silicon foam to prevent rain water infiltration and shielded with aluminum foil to insulate thermal influences from outside. The output from the probes was read at 10 s intervals, and recorded as half-hourly average from measurements on a CR1000 data logger (Campbell Scientific, Inc., Logan, UT, USA).

Table 1
Characteristics of all sampled trees for sap flow measurement.

Species	Tree no.	DBH (cm)	Projected crown area (m^2)	Tree height (m)	Sapwood area (cm^2)
Cedrus deodara	C1	13.6	10.18	6.1	26.42
	C2	17.2	16.61	6.7	30.19
	C3	21	22.9	8.3	45.36
Zelkova schneideriana	Z1	10	13.85	4.7	11.34
	Z2	14.2	18.1	5.3	20.11
	Z3	17.6	24.63	5.9	25.52
Metasequoia glyptostroboides	M1	24.6	7.07	12.9	50.27
	M2	18.8	5.31	11.6	43.01
	M3	14.6	2.01	10.3	16.62
Euonymus bungeanus	E1	16.6	22.90	6.3	66.48
	E2	13.5	34.21	5.4	51.53
	E3	10.4	47.78	5.2	36.32

2.3. Canopy conductance and decoupling coefficient

Meteorological data were collected using an automatic weather system WeatherHawk (Campbell Scientific, Logan, UT, USA). The station was mounted by a 2-m cross arm outward from a 15 m high roof to avoid influence of concrete on temperature readings. The canopy conductance (Gc) can be calculated by applying Penman–Monteith equation (Lu et al., 2003; Zeppel et al., 2008):

$$\lambda E = \frac{\Delta R_n + 3600\rho C_p VPD Ga}{\Delta + [\gamma(1 + Ga/Gc)]} \tag{4}$$

where λ is the latent heat of vaporization of water (2.39 MJ kg^{-1}), E is in the unit of (mm h^{-1}), Δ is the ratio of the saturated vapor pressure to temperature (kPa $°C^{-1}$), R_n is the net radiation (MJ m^{-2} h^{-1}), estimated from the regression equation $R_n = 0.7965 * Rs\text{-}57.64$ (Zeppel et al., 2008) (Rs is the total radiation, MJ m^{-2} h^{-1}), 3600 is the conversion factor from seconds to hours, ρ is air density (kg m^{-3}), C_p is the specific heat of air (1.013 MJ kg^{-1} $°C^{-1}$), VPD is the vapor pressure deficit (kPa), γ is the psychrometer constant (0.066 kPa $°C^{-1}$), Ga is the aerodynamic conductance (m s^{-1}) and calculated from Eq. (5) according to (Mielke et al., 1999).

$$Ga = \frac{k^2 * u}{\left[\ln\left(\frac{Z-d}{Z_0}\right)\right]^2} \tag{5}$$

where k is von Karman's constant, 0.41, u is the wind speed above the canopy (m s^{-1}), Z is the reference height to record wind (m), Z_0 is roughness height (usually 0.1 h and h is the canopy height) and d is the displacement height (0.7 h). The wind speed above the canopy was measured as 30 min averages, therefore, stability effects were included and the corrections not required.

By comparing correlation coefficients as suggested by Martin et al. (2001), we determined that J_s lagged behind solar radiation by 30 min, and led VPD by 30 min. The Gc then was calculated using R_n 30 min ahead Js and VPD 30 min behind Js.

Stomatal control of whole tree transpiration is commonly described by a decoupling coefficient (Ω) which reflects the extent to which the tree canopy is coupled with the ambient atmosphere (Kumagai et al., 2004). The decoupling coefficient (Ω) ranges from zero to one (Kumagai et al., 2004; Wullschleger et al., 2000). Plants that are well coupled with the atmosphere have Ω approaching zero, meaning stomatal control is strong. When Ω approaches one, plants are decoupled from the atmosphere. Stomatal control of transpiration is decreased in the latter case, and tree transpiration is controlled more by solar radiation (Wullschleger et al., 2000).The decoupling coefficient can be calculated following Kumagai et al. (2004):

$$\Omega = \frac{1 + \Delta/\gamma}{1 + \Delta/\gamma + Ga/Gc} \tag{6}$$

The relative importance of equilibrium energy (E_{eq}) and imposed energy (E_{imp}) (Komatsu et al., 2006; Kumagai et al., 2004) was calculated according to

$$E = \Omega E_{eq} + (1 - \Omega)E_{imp} \tag{7}$$

$$E_{eq} = \frac{\Delta}{\Delta + \gamma}\frac{R_n}{\lambda} \tag{8}$$

$$E_{imp} = GcVPD\frac{\rho C_p}{\lambda\gamma} \tag{9}$$

2.4. Soil water measurement

Volumetric soil water content (θ, m^3 m^{-3}) was monitored and recorded every 30 min with ECH2O soil moisture monitors (Deca-

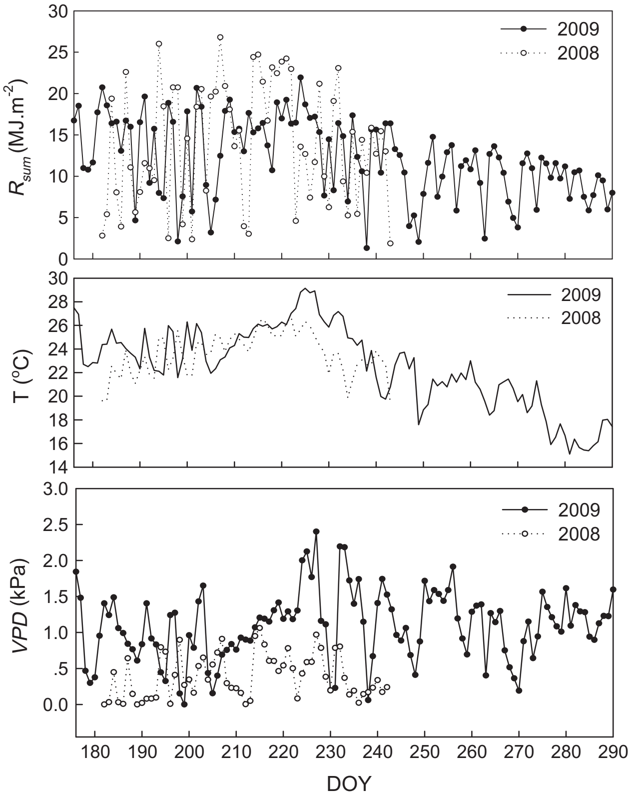

Fig. 1. Daily accumulated solar radiation (R_{sum}), average air temperature (T), and averaged vapor pressure deficit (VPD) in 2008 and 2009. Data missed in 2008 were due to instrument failure.

gon Devices Inc., Pullman, WA, USA). Two sets of soil moisture monitors were deployed, one under crown and the other in open space. Soil moisture sensors were installed vertically through soil profile to the depth of 100 cm at 25 cm interval, and the relative extractable water (*REW*, unit less) (Pataki and Oren, 2003; Zeppel et al., 2008) was calculated by using averaged θ across layers as:

$$REW = \frac{\theta - \theta_{\min}}{\theta_{\max} - \theta_{\min}} \tag{10}$$

where $\theta_{\max}$ and $\theta_{\min}$ are the maximum and minimum soil water content θ measured during the observation period respectively, Since transpiration was the major cause of soil water depletion, soil moisture accumulation (*SMA*) was used to describe rainfall retained in the soil. Based on the idea of soil moisture depletion (Oren and Pataki, 2001), *SMA* was calculated as cumulative rainfall minus transpiration. Overland runoff was not considered because no slope factor was involved. The *SMA* was set to zero when transpiration exceeded rainfall during a specific period.

3. Results

3.1. Climatic condition and soil water availability

Seasonal variations of the solar radiation, air temperature, and *VPD* in 2008 and 2009 There was no significant difference in daily solar radiation between the same time of the year in 2008 and 2009 (Fig. 1, *Sig.* = 0.975, *n* = 61, Paired-Sample T test). The maximum solar radiation recorded was 26.8 and 21.9 $\mathrm{MJ^{-1}\,m^{-2}\,d^{-1}}$ in 2008 and 2009, respectively. However, average daily air temperature, *T*, and *VPD* were significantly different between the same period of the 2 years (*Sig.* = 0, *n* = 61, Paired-Sample T test). Mean daily air temperature was 23.5 °C in 2008 and 24.7 °C in 2009. Daily averaged *VPD* in 2009 (1.09 kPa) was significantly higher (Fig. 1, *Sig.* = 0, *n* = 61, Paired-Sample T test) than that in 2008 (0.39 kPa).

Rainfall totals were 234.7 mm and 432.5 mm during the study period from July 1st to October 17th for 2008 and 2009, respectively (Table 2). The combined effect of rainfall and evapotranspiration was reflected in the soil moisture dynamics (Fig. 2a and b). Rainfall was less frequent but more intense in a single event

Table 2
Comparison between monthly rainfall and total transpiration of all sampled trees from July 1st to October 17th in 2008 and 2009.

Year	2008			2009		
Month	Rainfall (mm)	E_{tot}[a] (mm)	% of rainfall by E_{tot}[b]	Rainfall (mm)	E_{tot} (mm)	% of rainfall by E_{tot}
July	105.20	46.03	43.75	265.25	60.01	22.62
August	114.70	46.52	40.56	106.75	47.05	44.07
September	14.80	44.54		60.50	39.45	65.21
October[c]	0.00	16.92		0.00	27.50	
Total	234.70	154.01	65.62	432.5	174.01	40.23

[a] E_{tot} means total transpiration of all sampled trees (gap-filled).

[b] The percentages of rainfall by E_{tot} were not calculated for the months when E_{tot} exceeded rainfall.

[c] E_{tot} in October included 17 days after which the sap flow measurement stopped. The 17-day totals should be counted to represent the monthly transpiration in October since trees sap flow activity became trivial after this date.

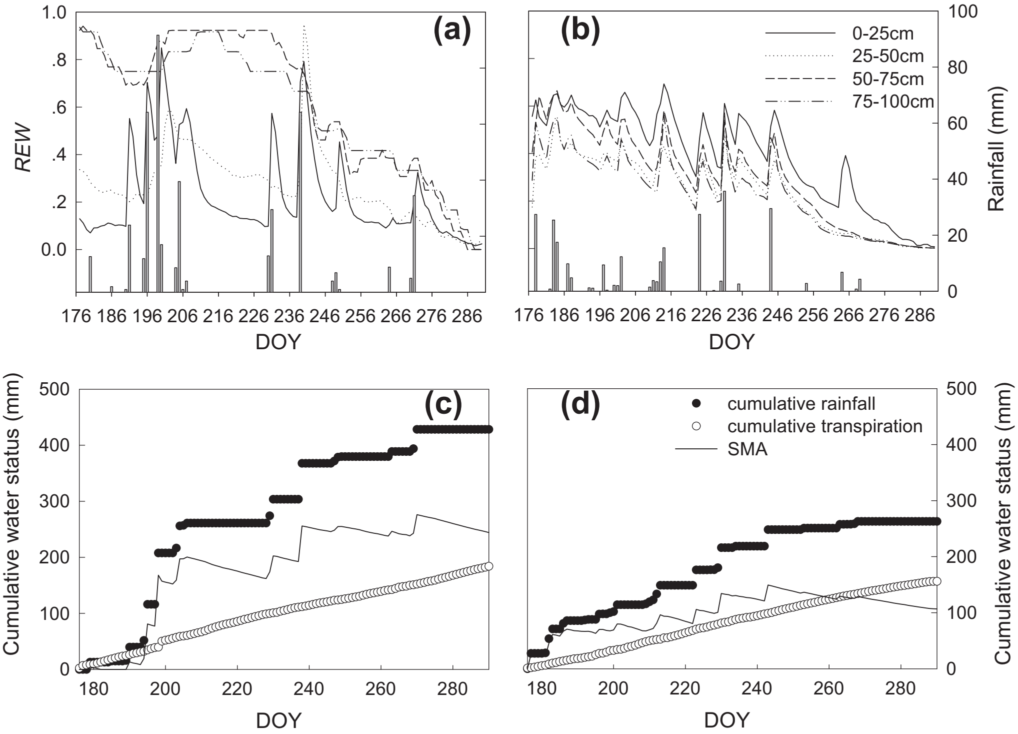

Fig. 2. Rainfall and relative extractable water (*REW*) in different soil layers from June 25th to October 17th in 2009 (a) and 2008 (b). The cumulative rainfall, and transpiration by all sampled trees were presented along with soil moisture accumulation (*SMA*) during experimental periods in 2009 (c) and 2008 (d).

in 2009 than in 2008 (Fig. 2a and b). Since the top soil was exposed to rain water and evaporation, soil moisture in the upper layer increased quickly after rainfall events but also decreased rapidly thereafter. As a result, soil moisture of shallow layers tended to be highly variable in both years. However, soil water content of deeper soil layers was seasonally stable in 2009 when higher intensity rainfall events contributed to more infiltrated water (Fig. 2a and b). Larger vertical soil *REW* gradients were observed in 2009 than in 2008.

The soil water condition was more favorable for tree use in 2009 as soil-profile-average *REW* reached 0.43 ± 0.01 (mean ± S.E.) compared to only 0.29 ± 0.01 in 2008. Although the total amount of

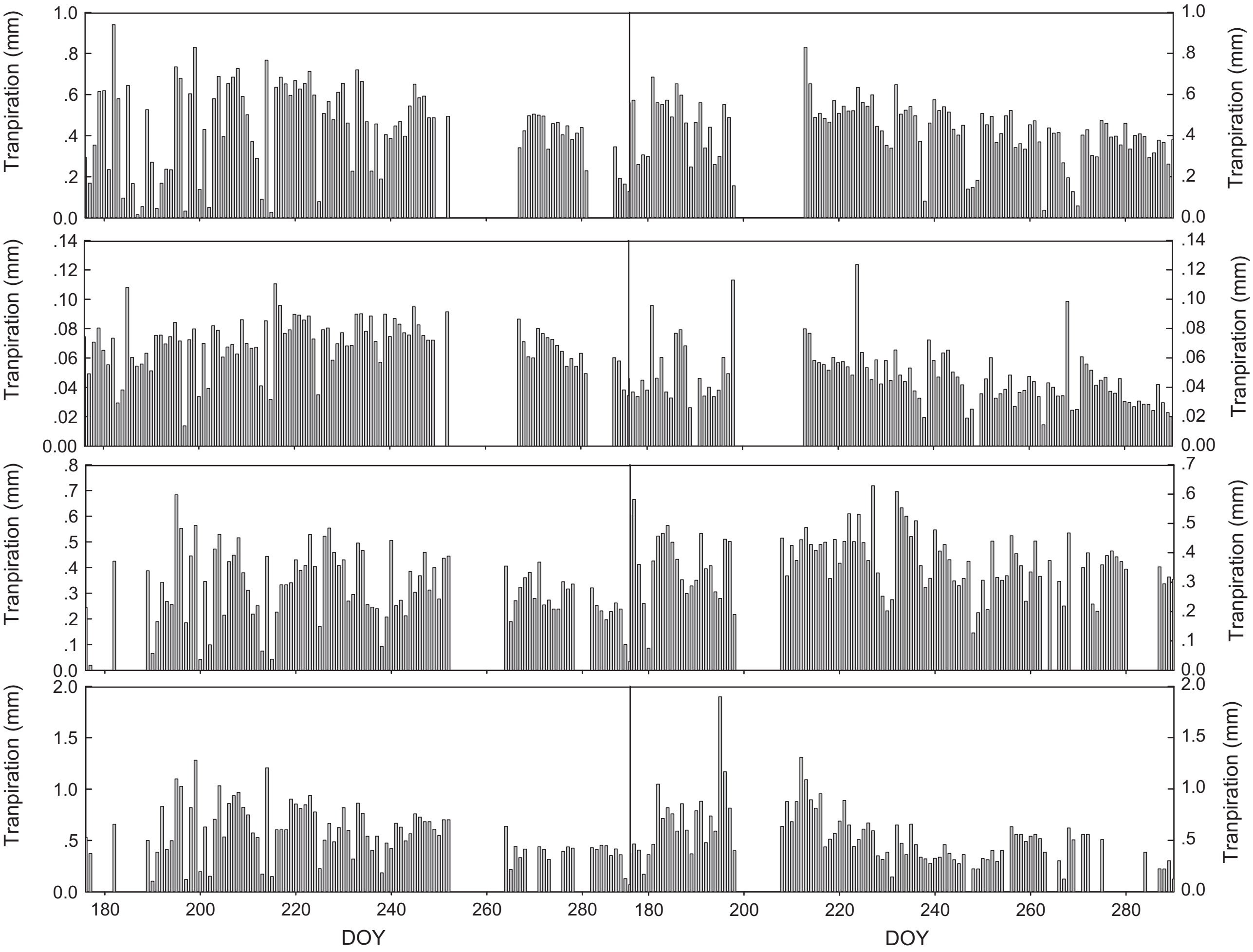

Fig. 3. Daily transpiration during the study periods in 2008 (left panels) and 2009 (right panels). From top to bottom are *Cedrus deodara*, *Zelkova schneideriana*, *Euonymus bungeanus* and *Metasequoia glyptostroboides* in sequence. Missing data were due to equipment malfunctions.

Table 3
Stepwise regression equations between daily whole tree transpiration (E_{day}) and daily averaged *VPD*, daily averaged radiation (R_{ave}), and daily total radiation (R_{sum}) for each sampled tree in 2009.

Species	Tree no.	Regression model[a]	R^2
Cedrus deodara	C1	$E_{day} = 179.617 + 40.125\ R_{ave} + 245.068 VPD$	0.939
	C2	$E_{day} = 493.894 + 84.767\ R_{ave} + 605.133 VPD$	0.886
	C3	$E_{day} = 1309.4 + 146.71\ R_{ave} + 1271.525 VPD$	0.912
Zelkova schneideriana	Z1	$E_{day} = 56.037\ R_{sum} - 202.614$	0.563
	Z2	$E_{day} = 674.447 + 21.685\ R_{ave} - 213.36 VPD$	0.561
	Z3	$E_{day} = 185.79 + 32.536\ R_{ave} + 203.741 VPD$	0.821
Metasequoia glyptostroboides	M1	$E_{day} = 484.359 + 98.326 R_{sum}$	0.174
	M2	$E_{day} = 270.229 + 209.665 VPD$	0.294
	M3	$E_{day} = 46.603 + 10.117\ R_{sum}$	0.338
Euonymus bungeanus	E1	$E_{day} = 1899.486 VPD + 210.013\ R_{ave} - 423.45$	0.919
	E2	$E_{day} = -29.115 + 3213.360\ R_{ave} + 2041.021 VPD$	0.667
	E3	$E_{day} = 854.687 + 36.096\ R_{ave} + 272.863 VPD$	0.683

[a] Regression models were derived from 2009 dataset using daily transpiration amount (E_{day}, g d^{-1}), daily averaged *VPD* (kPa) and daily averaged radiation (R_{ave}, MJ m^{-2}) or sum of daily radiation (R_{sum}, MJ m^{-2}). Equations were significant at $P = 0.05$ level.

water transpired by all trees was significantly higher in 2009 than in 2008 (*Sig.* = 0, *n* = 230, One-way ANOVA), soil water accumulation in 2009 was significantly higher than in 2008 (*Sig.* = 0, *n* = 230, One-way ANOVA) (Fig. 2c and d).

3.2. Monthly Transpiration Variation

Daily transpiration rates are shown in Fig. 3 for four species (data gap due to the power or rainfall-induced equipment failure). Monthly estimates for total transpiration by all trees are also reported in Table 2 with missing data gap-filled by regression models developed by field data using solar radiation (daily sum and average) and *VPD* (Table 3).

Day-to-day transpiration variations within each month were appreciable (Fig. 3). There was no significant difference (*Sig.* = 0.564, One-way ANOVA) between the average daily transpiration in 2008 and 2009 after the summer season (DOY 244). The average daily transpiration for August, September and October was 1.51 ± 0.01(S.E.) mm d^{-1}, 1.39 ± 0.08 mm d^{-1} and 1.31 ± 0.31 mm d^{-1}, respectively. There was no distinct transpiration reduction during the short non-rainfall period in summers in any species (Figs. 2 and 3). Soil water depletion during this period in 2009 to *REW* = 0.215 (averaged among layers) did not cause a reduction in transpiration. For both years, daily transpiration was significantly correlated with climate variables ($R^2_{VPD} > 0.66$, $P < 0.05$; $R^2_{radiation} > 0.61$, $P < 0.05$) but not with soil moisture content (θ_{soil}) ($P > 0.302$). The linear regression equations for calculating whole tree transpiration for all trees were derived on the basis of incident solar radiation and *VPD* (Table 3).

Gap-filled daily transpiration enabled us to examine the role of transpiration in the rainfall budget during the whole measurement period in 2008 and 2009 (Table 2). The average monthly transpiration reached 12.78 ± 0.73 (S.E.) mm, 1.79 ± 0.16 mm, 10.18 ± 0.55 mm, and 19.28 ± 2.24 mm for *Cedrus deodara*, *Zelkova schneideriana*, *Euonymus bungeanus* and *Metasequoia glyptostroboides*, respectively. Inter-annual variation in monthly *E* ranged from 16.92 mm in 2008 to 60.01 mm in 2009. Total transpiration by all trees increased with increasing cumulative precipitation but trees used a smaller percentage of rainfall in the wetter year 2009 than in the drier year 2008.

3.3. Daily transpiration, canopy conductance and decoupling coefficient

On a daily basis, tree transpiration demonstrated a similar pattern regardless of soil water conditions. *Js* rose from nearly zero at

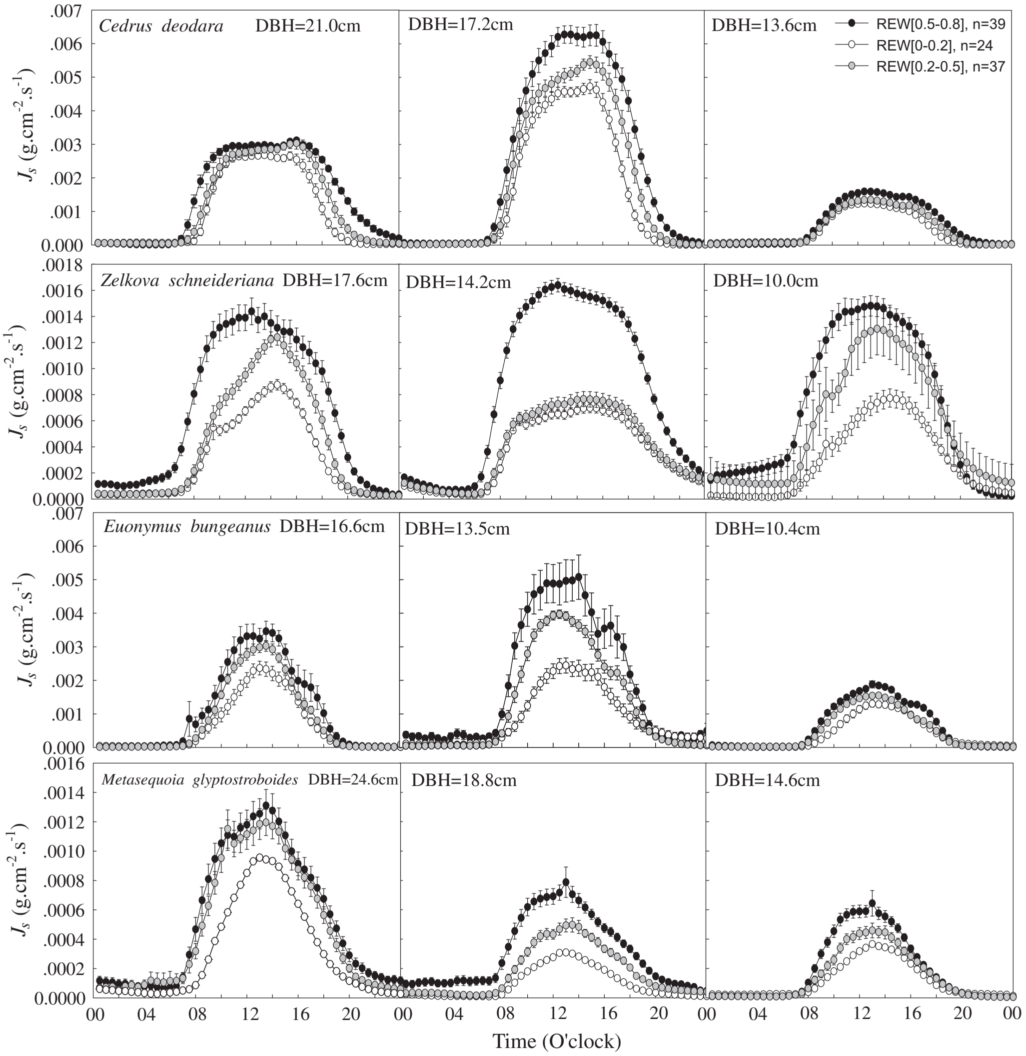

Fig. 4. Averaged diurnal sap flow (*Js*) (mean ± 1 S.E.) of each sampled tree under different soil water conditions ranked by relative extractable water (*REW*) of sampled days (*n*) pooled from 2009.

0700 to 0800 and remained elevated from 1000 to 1400, then began to decline (Fig. 4). However, tree transpiration was more intense and prolonged when soil water was less limiting (Fig. 4).

Nocturnal sap flow was frequently observed and was significantly correlated with the amount of diurnal sap flow (Fig. 5 and Table 4) as well as *VPD* (except in the case of *Euonymus bungeanus*) (Fig. 6). Nocturnal sap flow by the sampled species tended to be lower than 1 kg d^{-1} except for *Metasequoia glyptostroboides* in 2009 (Table 4). Also, this species exhibited the largest S.D. The species-specific averaged ratio of nocturnal to diurnal sap flow were 11.05 ± 2.08% (S.E. among individuals within same species), 20.01 ± 1.34%, 9.98 ± 0.05%, and 25.1 ± 14.04% for *Cedrus deodara*, *Zelkova schneideriana*, *Euonymus bungeanus* and *Metasequoia glyptostroboides*, respectively.

We evaluated the canopy conductance, *Gc*, and coupling state of the trees under contrasting *REW* conditions (Fig. 7) when *VPD* was relatively high (>1.2 kPa). The *Gc* and Ω exhibited similar patterns, substantiating the theory that plants exert strong physiological control over water losses, with Ω less than 0.2 during most of the daytime. Under greater water stress (*REW* < 0.2), *Gc* reached a maximum at about 0900 and then gradually decreased afterwards, peaking before *R* and *VPD*. However, response of *Gc* and Ω to *VPD* was more coupled under wet soil conditions. The Ω remained at a constant magnitude regardless of soil water condition (*Sig.* = 0.229, Paired-Samples T test) for all species as did the daily average *Gc* by *Euonymus bungeanus* (*P* = 0.356, Paired-Samples T test). However, canopy conductance of the other three species increased significantly (*P* < 0.004, Paired-Samples T test) under wetter soil conditions. Transpiration rates more closely followed the diurnal pattern of canopy conductance (Fig. 7) as soil water condition improved.

3.4. VPD and soil moisture influences

Low Ω indicated that *VPD* exerted more influence than incident radiation on tree transpiration under this urban environment. The relationship between midday canopy conductance and *VPD* indicated progressive stomatal closure (Fig. 8). Clockwise hysteresis existed between sap flow and *VPD*, and the extent of this hysteresis increased with increasing daily average *VPD* regardless of soil water conditions (Fig. 9). During nighttime hours, *VPD* exerted major influences in the absence of solar radiation. Mean nighttime sap

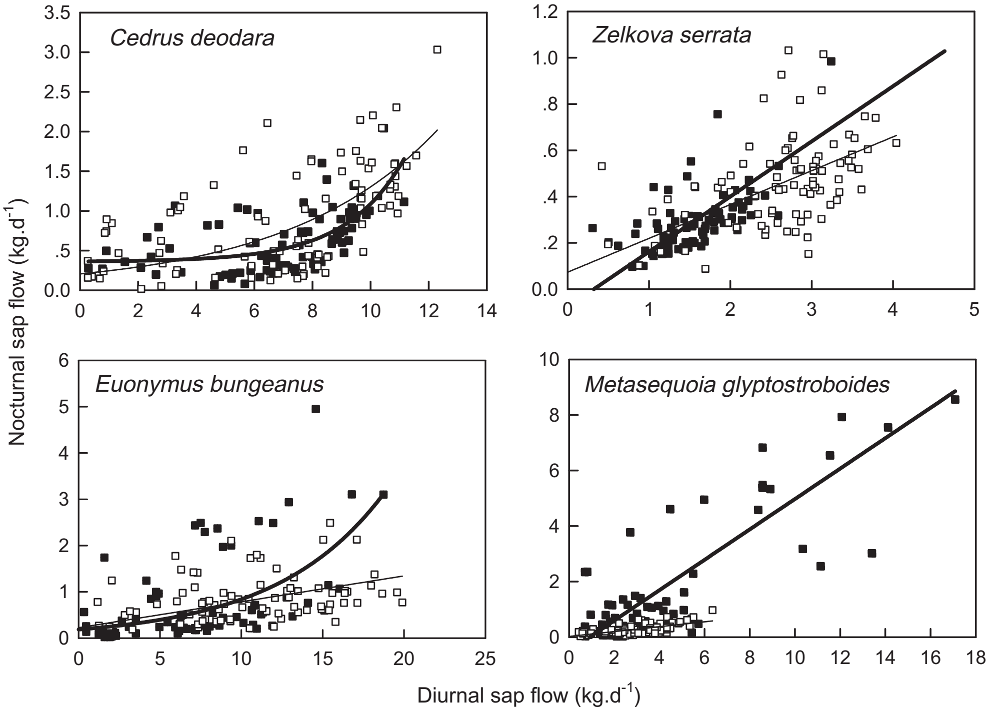

Fig. 5. Relationship between daily nocturnal and diurnal sap flow during the study periods in 2008 and 2009. Open squares and thin lines represent original values and trends for 2008 while filled squares and thick lines for 2009.

Table 4
Species-accumulated nocturnal sap flow and its percentage as of the diurnal transpiration and the correlation coefficient between nocturnal and daytime water uptake for 2008 and 2009.

Species	2008			2009		
	Nocturnal sap flow mean ± S.D. (kg d^{-1})	% of diurnal transpiration	Correlation coefficient between nocturnal and diurnal sap	Nocturnal sap flow mean ± S.D. (kg d^{-1})	% of diurnal transpiration	Correlation coefficient between nocturnal and diurnal sap
Cedrus deodara	0.89 ± 0.64	13.13	0.618**	0.62 ± 0.37	8.97	0.484**
Zelkova schneideriana	0.46 ± 0.19	18.67	0.529**	0.28 ± 0.13	21.36	0.632**
Euonymus bungeanus	0.87 ± 0.50	9.93	0.430**	0.72 ± 0.94	10.04	0.519**
Metasequoia glyptostroboides	0.28 ± 0.18	11.06	0.624**	1.54 ± 2.08	39.14	0.855**

S.D.: standard deviation.
** *P* = 0.01, *n* = 102.

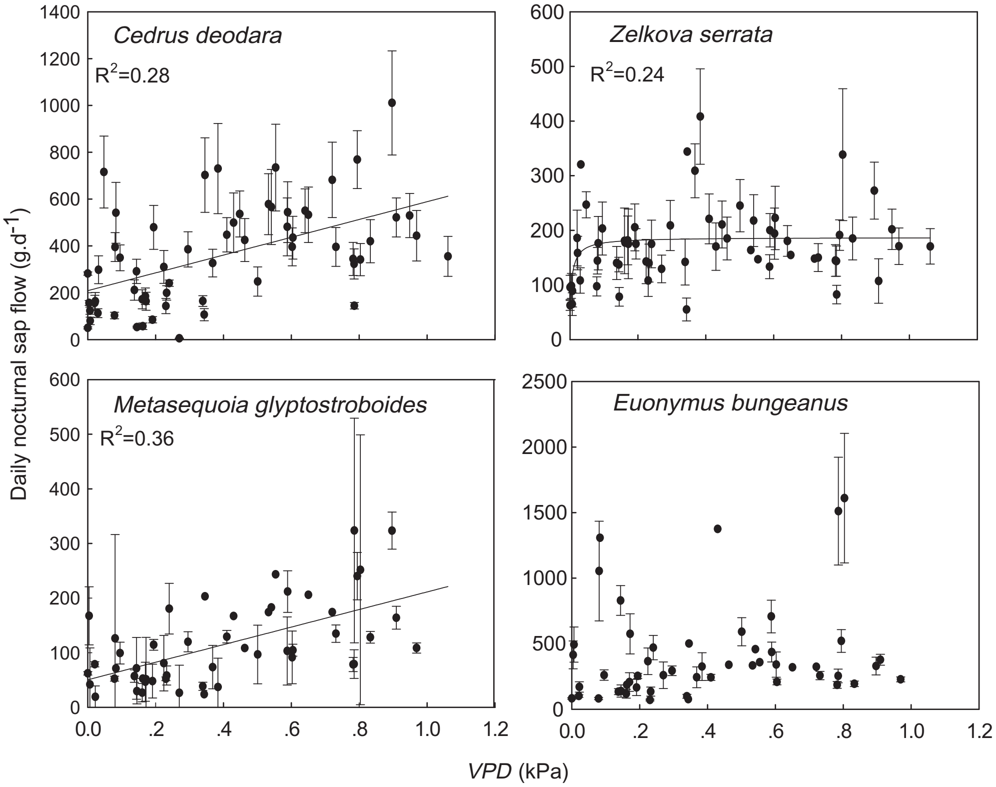

Fig. 6. Relationship between daily nocturnal sap flow (from 19:00 p.m. to 5:30 a.m. next morning) and averaged *VPD* by different species during summer (July and August) in 2008. Data shown are the average value of all trees in each species with standard error bars.

flow by three out of four species exhibited statistically significant responses to *VPD* (Fig. 6). Nocturnal sap flow of two coniferous species *Cedrus deodara* and *Metasequoia glyptostroboides* was more closely related to nocturnal *VPD* than that of *Zelkova schneideriana*. By contrast, *Euonymus bungeanus* failed to show a significant relationship between nighttime sap flow and *VPD*.

The effect of soil moisture on transpiration became apparent under different *REW* ranges (Fig. 4). The magnitude of transpiration decreased as the soil desiccated. Moreover, differences in soil moisture triggered variation in daily *Gc* patterns with peak hours occurring earlier under low *REW* than that under high *REW* (Fig. 7).

4. Discussion

4.1. Physiological and environmental control on tree transpiration

The low day time Ω (<0.2) for all sampled individuals indicates that these urban trees adopted conservative water strategies during times of low soil water availability. One implication of low Ω ($\sim$0) is that trees were well coupled with the atmosphere and able to exert effective stomatal control over transpiration in response to environmental stresses. Stomatal variations caused corresponding changes in transpiration throughout the day. The *Gc* increased and sap flow began when total solar radiation reached $\sim$0.05 MJ m^{-2}. At higher levels of solar radiation, *Gc* and transpiration rapidly increased because of the relatively low stomatal control (i.e. increasing Ω under low *VPD*) until *VPD* reached $\sim$1.5 kPa (Fig. 7). After the peak in *Gc* and transpiration, canopy conductance declined as stomatal control increased (decreasing Ω). This physiological process imposed a hydraulic limit in the sap flow path (Hogg and Hurdle, 1997) and minimized excessive water losses under high evaporative demands.

Efficient stomatal control enables plants to regulate water use based on the level of soil water availability (Mediavilla and Escudero, 2004). Dry spells in 2009 not only occurred frequently but also lasted longer during the summer rainy season than in 2008. Soil water available for transpiration was reduced because of higher evaporative loss to the air. Under such circumstances, control of stomatal conductance enables urban trees to avoid excessive water loss (Tognetti et al., 2009) and ensures safe water potential (Hogg and Hurdle, 1997). Otherwise, cavitations (Bush et al., 2008; Cochard et al., 2002) and irreversible loss of xylem function (Bush et al., 2008) will occur. Given the strong stomatal control by urban trees over transpiration, reducing stomatal conductance or leaf area (Smith and Jarvis, 1998) by choosing species with low stomatal conductance or intervention practices such as pruning can be an efficient way to conserve water resources in urban forests.

The relative importance of radiation and *VPD* on transpiration can also be explained by Ω (Eqs. (8) and (9)). The Ω approaching one suggests tree transpiration is increasingly dependent on *R* whilst low Ω (near zero) suggests transpiration is increasingly dependent on *VPD* (Martin et al., 2001; Wullschleger et al., 2000). The low Ω observed in our study indicated that the dominant factor in determining transpiration of urban trees was VPD. Stomas gradually opened at sunrise, and transpiration increased rapidly because of the relatively weak stomatal control over transpiration (increasing Ω). The coupling began to increase when *VPD* reached $\sim$1.5 kPa, and *Gc* declined afterwards. The influence of radiation on transpiration was consequently diminished and shifted to *VPD*.

4.2. Hysteresis and nocturnal sap flow

Hysteresis between sap flow and microclimate variables has been widely reported (O'Brien et al., 2004; O'Grady et al., 2008; Zeppel et al., 2004). We found that urban trees showed more hysteresis at higher daily average *VPD*. One explanation for this is that resistance increased in the soil–plant-atmosphere continuum pathway on a diurnal basis (Zeppel et al., 2004). However, hyster-

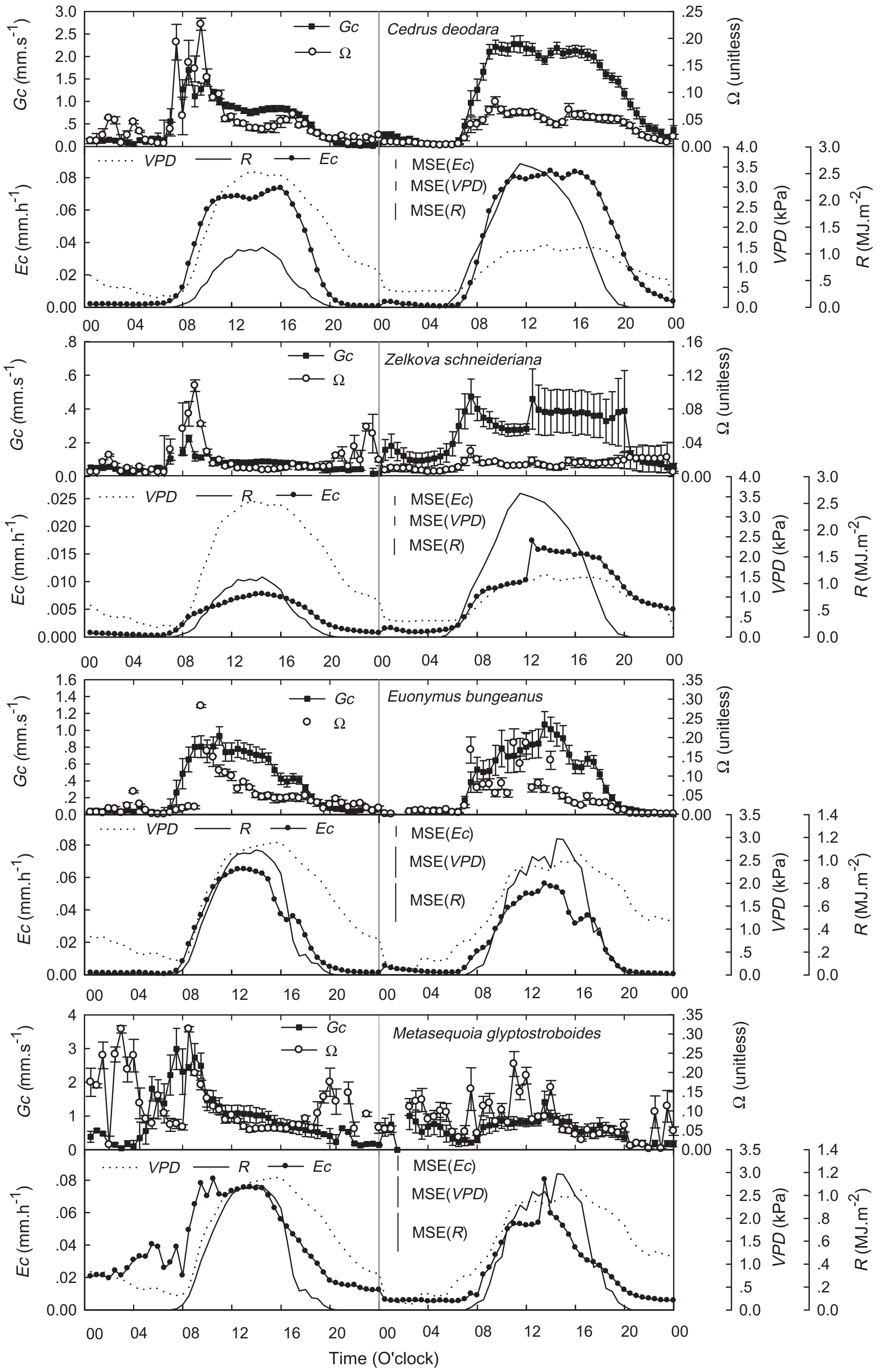

Fig. 7. Diurnal patterns of canopy transpiration (*Ec*), canopy conductance (*Gc*) and decoupling coefficient (Ω) of four species along with concurrent *R* and *VPD* under high evaporative demand (average daily *VPD* > 1.2 kPa) and decreasing soil water stress (*REW* = [0–0.2] on the left and [0.5–0.8] on the right). As values were averaged from five sampled days, it was inconvenient to mark the standard errors at each specific hour for *Ec*, *VPD* and solar radiation. Therefore, standard errors of each hour ($n = 5$ replicates) throughout the day were averaged to be mean standard errors (MSE) (Tognetti et al., 2005), and presented as single bars for the sake of graphic clarity.

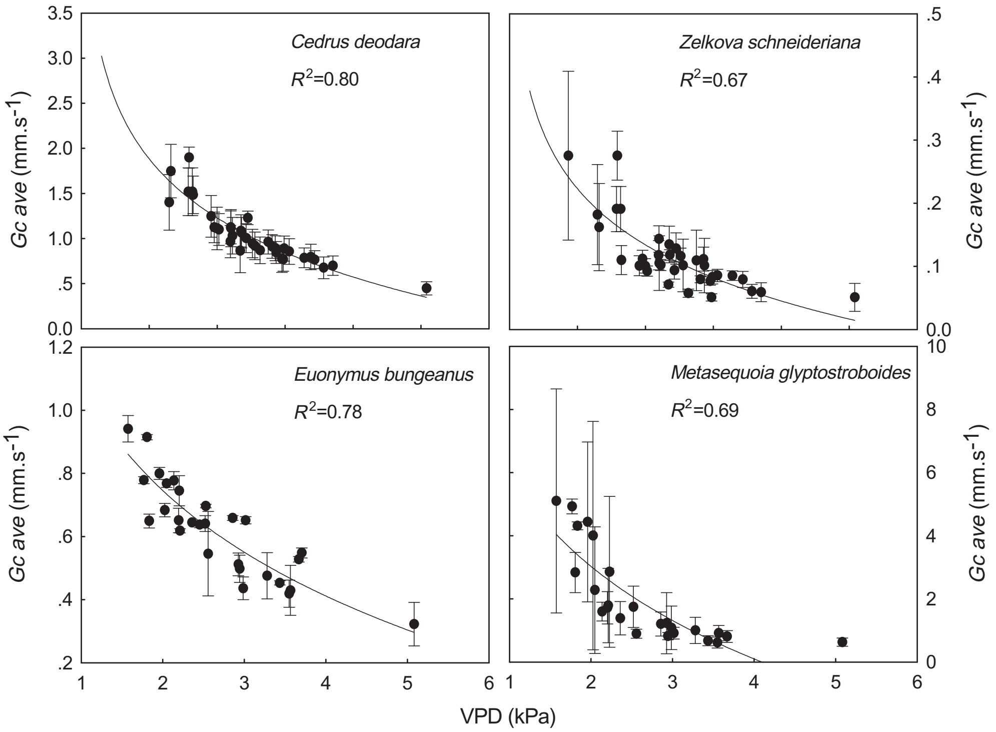

Fig. 8. Relationship between species-averaged canopy conductance (Gc_{ave}) (±1 S.E.) and *VPD* at midday (12:00 am) for 24 days in 2009.

esis was observed both during dry spells in the summer rain season in 2009 when *REW* was high (>0.5) and September and October in 2008 and 2009 when there was no rainfall and *REW* was below 0.1 (heavy dry as ranked by Kumagai et al. (2004)). Moreover, time lag between sap flow and *VPD* became longer when *VPD* increased even under unstressed soil moisture conditions. Therefore, the time lag was not systemically related to soil moisture. Stomatal conductance can be decreased significantly by excessive water loss and leaf water potential reduction even under ideal water conditions (Brodribb and Holbrook, 2006). Therefore, hysteresis can be seen as a way of self-protection for plants to avoid the overlapping of peak transpiration and peak *VPD,* thus preventing excessive extraction of water from the stem.

Nocturnal sap flow has been widely observed for many tree species (Fisher et al., 2007; Snyder et al., 2003). Caspari et al. (1993) and Phillips et al. (2003) reported that nocturnal sap flow did not necessarily mean nighttime transpiration since it was integral to replenishing water within the tree lost by daytime transpiration. Alternatively, nocturnal sap flow might be used for transpiration when it was positively correlated with *VPD* (Fisher et al., 2007; Green et al., 1989; Hogg and Hurdle, 1997). We found close correlation between diurnal and nocturnal sap flow (Fig. 5, Table 4), indicating water replenishment by nocturnal water uptake. Three out of four species showed nocturnal transpiration, though the coefficient of determination was low due to the coexistence of nighttime water replenishment and transpiration (Fig. 6).

Daily nighttime water uptake of *Metasequoia glyptostroboides* during the observation increased from 0.24 kg d^{-1} in 2008 to 1.54 kg d^{-1} in 2009, which was higher than any of the other three species. In addition, the large standard deviation of nocturnal sap flow of this species indicated fluctuation of nighttime water uptake under different environments. These abnormalities cannot be explained convincingly through available experimental and literature information. As a result, these data should be used with discretion. Further study of transpiration behavior for this species in the urban environment is necessary.

In urban areas, nighttime stomatal opening has important implications for air pollutant intake (Musselman and Minnick, 2000; Takahashi et al., 2005). For example, ozone absorption was proved to continue in darkness (Matyssek et al., 1995) and it represented up to 9% of daily ozone uptake (Grulke et al., 2004).This can be pernicious for plants since detoxification of reactive oxygen species is non-viable without photosynthetic electron transport at night (Matyssek et al., 1995).

4.3. Soil water and rainfall budget

Though cumulative transpiration of all species (E_{tot}) was significantly different between a relatively dry (2008) and a wet year (2009), transpiration in rain season (July and August) failed to show significant differences between the two years (*Sig.* = 0.476, *n* = 62, Paired-samples T-test, Table 2). Moreover, transpiration increased from 2008 to 2009 disproportionately to precipitation. A reduction of 45.7% in rainfall could trigger an 11.5% decrease in transpiration, while a 84.3% rainfall increase brought only a 13.0% increase in transpiration (Table 2), indicating that urban trees regulate water loss during both drought and in well-watered conditions.

Access to water at depth using deep or expansive lateral root systems is an important strategy for plants to survive summer droughts (Bucci et al., 2008; David et al., 2004; Thomas et al., 2006; Vincke and Thiry, 2008). In our study, short periods of no rainfall did not significantly reduce transpiration during the rainy seasons (Figs. 2 and 3). The only possible source for replenishment in our study was available water in deeper layers due to the absence of artificial irrigation. *Zelkova schneideriana* and *Euonymus bungeanus* are deep rooted species, while the other two are shallow rooted and the individuals we studied developed a large lateral root colony due to their age. The use of deep soil water was also reflected in Fig. 2 which showed that the *REW* of the 50–100 cm soil layer dropped dramatically to that of the 0–50 cm soil layer in October 2009 when there was no rainfall.

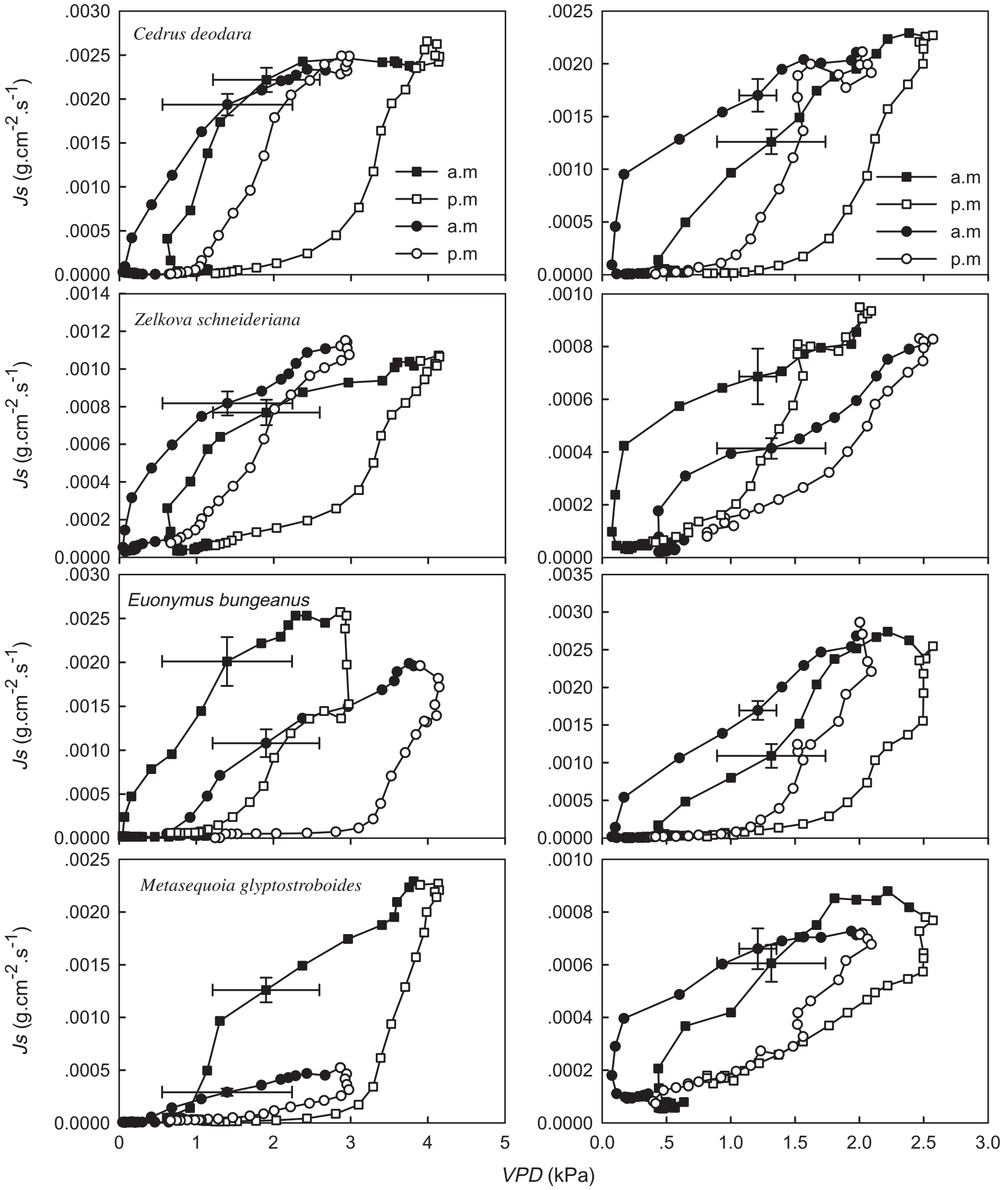

Fig. 9. Hysteresis between sap flow and *VPD* for different species under contrasting soil water conditions in 2009. On the left column *REW* = [0–0.2] with average *VPD* being 2.2 kPa (squares) and 1.3 kPa (circles), while *REW* = [0.5–0.8] with *VPD* being 1.3 kPa (squares) and 0.8 kPa (circles) on the right. The filled symbols stand for values in the morning and the open for in the afternoon. Bars representing mean standard error were given for clarity. Data of 4 days were pooled.

4.4. Comparison with natural plants

The urban trees evaluated in this study exhibited similar responses to those in the natural environment. All trees showed strong stomatal regulation over canopy transpiration. The Ω for conifers in our study was approximately 0.25, similar to their natural counterparts (Jassal et al., 2009). However, Ω for two broadleaf tree species in our study rarely exceeded 0.25, lower than the reported Ω range from 0.27 to 0.67 of broadleaf trees in natural temperate forests (Hinckley et al., 1994; Magnani et al., 1998; Meinzer et al., 1993). Contrasting ambient conditions between the natural and the urban environment determined the level of coupling between plants and the atmosphere since morphological differences would vary little for the same species. Urban constructions change the intensity and frequency of air turbulence which influences Ω through air conductance. Thus urban plants are subjected to volatile atmospheric conditions. Proactive physiological control aids plants in stabilizing their inner water status for normal biomechanical activities.

Increases in transpiration accompanying larger rainfall events are a frequently observed phenomenon for plants in the natural environment (Mitchell et al., 2009; O'Grady et al., 2008; Tognetti et al., 2009). However, we found that there was only a slight enhancement in urban tree transpiration during the study year with more rainfall. Such a difference may be related to more favorable water conditions under urban than natural environment. Urban trees suffer little water competition due to low density, therefore scattered urban trees have access to enough water even during years with lower rainfall. As a result, transpiration only increases from 154.01 mm to 174.01 mm in response to a 197.8 mm rainfall increase (Table 2), indicating that conservative strategies for water consumption may be adopted by urban trees even under sufficient water supply under rapidly changing urban environmental drivers. Scattered and distributed urban trees do not have mature stand structure and canopy stratification (Baker and Wilson, 2000; Roberts et al., 1993), which potentially influences whole tree transpiration.

5. Conclusions

The two broadleaf species evaluated in this study exhibited a higher level of control over canopy conductance than the average level observed in the natural environment. Moreover, transpiration by the sampled urban tree cluster was relatively stable under dramatically different rainfall regimes than would be the transpiration in the natural environment. As a result, transpiration from the urban trees accounted for a larger percentage of rainfall during drier year. Since transpiration from *Metasequoia glyptostroboides* was highly variable in response to different environmental conditions, further study on this species is needed. Our study suggests that vapor pressure deficit (*VPD)* is a major environmental controller over urban tree transpiration. Canopy conductance decreased logarithmically with increasing *VPD* and the nocturnal transpiration was significantly correlated with *VPD*. Urban trees exhibited efficient stomatal control over transpiration when the atmosphere evaporative demand became large (i.e. increasing risks of being over dehydrated) regardless of soil moisture conditions. Prolonged time lag between peak transpiration and *VPD* served as a strategy to avoid excessive water loss. In addition, nocturnal water uptake played an important role in replenishing the tree stems from diurnal water loss. The robust root system also contributed to the survival through water stress by facilitating access to accumulated moisture in the deeper soil layers during drought. As a result, summer dry spells did not necessarily trigger the transpiration reduction.

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