Urban Tree Species Show the Same Hydraulic Response to Vapor Pressure Deficit across Varying Tree Size and Environmental Conditions

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Abstract

Background: The functional convergence of tree transpiration has rarely been tested for tree species growing under urban conditions even though it is of significance to elucidate the relationship between functional convergence and species differences of urban trees for establishing sustainable urban forests in the context of forest water relations.

Methodology/Principal Findings: We measured sap flux of four urban tree species including Cedrus deodara, Zelkova schneideriana, Euonymus bungeanus and Metasequoia glyptostroboides in an urban park by using thermal dissipation probes (TDP). The concurrent microclimate conditions and soil moisture content were also measured. Our objectives were to examine 1) the influence of tree species and size on transpiration, and 2) the hydraulic control of urban trees under different environmental conditions over the transpiration in response to VPD as represented by canopy conductance. The results showed that the functional convergence between tree diameter at breast height (DBH) and tree canopy transpiration amount ($E_c$) was not reliable to predict stand transpiration and there were species differences within same DBH class. Species differed in transpiration patterns to seasonal weather progression and soil water stress as a result of varied sensitivity to water availability. Species differences were also found in their potential maximum transpiration rate and reaction to light. However, a same theoretical hydraulic relationship between $G_c$ at VPD = 1 kPa ($G_{c,ref}$) and the $G_c$ sensitivity to VPD (−d$G_c$/dlnVPD) across studied species as well as under contrasting soil water and $R_s$ conditions in the urban area.

Conclusions/Significance: We concluded that urban trees show the same hydraulic regulation over response to VPD across varying tree size and environmental conditions and thus tree transpiration could be predicted with appropriate assessment of $G_{c,ref}$.

Introduction

Establishing urban forest/trees is widely accepted as one of the critical approaches to combat the rapid urbanization associated environmental, ecological, and human health problems [1–3]. The potential impact of urban forest/tree development on water resources availability is questioned due to the projected more severe water stress for urban area under global climate change [4,5] and world-wide reorganization of reduced water yield at watershed scale from increased forest coverage due to land conversion, industry plantation, and forest ecological restoration programs [6,7]. Our current understanding on forest/tree and water relations under urban environment is very limited [8]. Therefore, it is vital for assessing accurately the role vegetation may play in affecting urban water budget by understanding the eco-physiological response and environmental control of tree water use in urban environments [9].

Practically, tree species selection is of significance for the urban forest development from the water resources management viewpoint as observed species differences in controlling transpiration rate [10–12] add variability to the water flux leaving ecosystems and consequently to the hydrological cycle under natural environment [13,14]. These differences can lead to a substantial spatial heterogeneity of canopy transpiration [15] and the amount of stand transpiration [16,17]. For example, Fraxinus excelsior showed a greater tendency in enhancing transpiration towards the edge than Quercus robur did in natural mixed deciduous woodland stands [18]. Annual stand-scale transpiration from bamboo forest is higher than that from the coniferous forests in western Japan [19]. Dynamically, stand transpiration can be significantly enhanced during succession as species shift from woodland oaks and elms to Savanna oaks [20]. Therefore, it is highly probable that species differences in transpiration would influence local hydrology [6,20–24].
Despite the convincing evidence of species effects on transpiration rates, analysis of the relationship between transpiration and tree size or hydrological control [25-27] have revealed the convergence in functioning across plant species. Meinzer et al. found that variation in diameter at breast height (DBH) accounted for 91\% of the variation in total daily sap flux in the outermost 2 cm of sapwood by comparing 24 different species in a Panamanian rain forest [28]. Thus, the examination of species influence on transpiration is complicated by structural factors such as root, leaf and sapwood area. Regulation of canopy conductance ($G_c$) exerts a major control over plants transpiration. Stomatal closure is a well known mechanism to regulate plant water status and avoid fatal xylem cavitation under decreasing humidity [29]. Despite the fact that vulnerability to cavitation is highly species specific [30], a synthesis showed that the stomatal response to VPD can be described by a proportionate relationship between the $G_c$ sensitivity to VPD ($-dG_c/dhVPD$ or $-m$) and $G_c$ at VPD = 1 kPa ($G_{rest}$) across 40 species and this relationship was theoretically verified [27]. The theoretical underpinnings suggests that for isohydric species that regulate minimum leaf water potential to prevent excessive cavitation, hydraulic control over transpiration and the ratio between $G_c$ sensitivity to VPD and $G_{rest}$ should be the same despite varying $G_{rest}$ between species.

Urban areas tend to exhibit higher air temperature (e.g. “heat island” phenomena), more complex wind turbulence, and increased evaporative demand than the adjacent rural areas due to dense buildings and road system pavement. In addition, urban trees are usually planted in isolation or in rows. These characteristics may induce varied energy partitioning and thus microclimatic difference from natural forest stands. A natural question to ask is “Are there any differences for urban trees from that of natural forest in transpiration control?” as the tree hydraulic control tends to be related to the originating habitat [27]. Therefore, our study was conducted to explore the functional convergence across urban tree. Specifically, our objectives are to examine 1) the influence of tree species and size on transpiration, and 2) the hydraulic control of urban trees over the transpiration in response to VPD as represented by canopy conductance under different environmental conditions.

**Materials and Methods**

**Site description and tree selection**

The study was conducted in Laodong Park (38°54’N, 121°37’E), Dalian City, Liaoning Province, China. The temperate maritime climate is characterized by mean annual temperature ranging from 8°C–10°C and mean annual precipitation 550–800 mm with 60%–70% in summer.

The study plot is a man-made tree patch located in the north side of the park consisting of Cedrus deodara (Roxb.) Loud., Zelkova schneideriana Hend.-Mazz., Euonymus buxifolius Maxim, and Meta-squama gilgastoboides Hu et Cheng. The trees were originally planted with varying sizes to meet the aesthetic demand. Therefore, the DBH distribution is not the result of growth competition. Due to the restriction from park management, three trees were selected for each species with different DBHs. Trunks of sampled trees were bored to measure the sapwood. It was easy to distinguish the sapwood from heartwood by color difference contrasted by water content (Table 1, also see [31]).

**Sap flow Measurement and Canopy Conductance**

Sap flux ($J_i$) of individual trees was measured continuously from June 25th to October 17th in 2009 using thermal dissipation probes (Dynamax, USA) [32]. A square of 5 cm×5 cm bark at a height of 1.3 m was removed to expose the cambium and the probes were installed. Thirty mm probes were used in all trees except two smaller Z. schneideriana trees whose shallow sapwood required the use of 20 mm probes. After the installation, the probes were sealed with silicon foam to prevent rain water infiltration and shielded with aluminum foil to insulate external thermal influences. The output from the probes was recorded as half-hourly average from measurements made at 10 s intervals and stored in a CR1000 data logger (Campbell Scientific, Inc., Logan, UT, USA). The sensors, the heaters and the data loggers were all powered by a 700 mA storage cell. Sap flux can be calculated according to standard calibration for the TDP method based on temperature differences between the two probes [32]:

$$J_i = 0.0119 \times \left[ (\Delta T_m - \Delta T) / \Delta T \right]^{1.23}$$  (1)

where $J_i$ is sap flux density ($g \text{ cm}^{-2} \text{ s}^{-1}$), $\Delta T_m$ is the maximum temperature difference between sensors during a day ($°C$), $\Delta T$, Temperature difference between sensors at any given time ($°C$). This equation works well for non-porous species [33], and we acknowledge the existence of limitations when using it for ring-porous species due to non-uniform sap flow [34,35]. However, given the small sapwood width for our studied trees, we assume the radial velocity gradient is not steep. Moreover, the contact between the probes and non-conducting xylem will give rise to greater errors [34], therefore, the sap flux density of only one depth was examined. Studies show good agreement between sap flux calculated by this equation and other independent transpiration measurements for ring-porous trees [36].

Daily canopy transpiration ($E_c$, mm $d^{-1}$) then can be calculated as

$$E_c = \sum_{i=1}^{24} J_i \times A_i / A_c$$  (2)

Where $A_i$ is the sapwood area ($cm^2$) and $A_c$ is the crown area ($m^2$), $i$ stands for the sequence of daily hours..

Canopy conductance ($G_c$) was calculated by using measured canopy transpiration and Penman-Monteith equation [37]:

$$\lambda E = \frac{\Delta R_n + 3600 \rho C_p \text{VPD} G_a}{\Delta + \left[ (1 + G_s / G_c) \right]}$$  (3)

Where $\lambda$ is the latent heat of vaporization of water (2.39 MJ kg$^{-1}$), $\Delta$ 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 $R_n = 0.7965 \times R_{s} - 57.64$ (recommended by Zeppel et al. [37]), $R_{s}$ is the total radiation, MJ m$^{-2}$ h$^{-1}$, $\rho$ 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), $\gamma$ is the psychrometer constant (0.066 kPa °C$^{-1}$). The constant 3600 is time conversion factor from second to hour. The unit of $E$ here is m$^3$ m$^{-2}$ h$^{-1}$.

**Meteorology and Soil Moisture Content Measurement**

Meteorological data were collected using an automatic weather system Weather-Hawk (Campbell Scientific, Logan, UT, USA) mounted at the height of 15 m and 5 m away from the sampled trees. Volumetric soil water content ($\theta$, m$^3$ m$^{-3}$) was measured by two sets of ECH2O (Decagon Devices Inc., Pullman, WA, USA). The measurement was made at 25 cm, 50 cm, 75 cm, and 100 cm of soil profile. Relative extractable water (REW, unitless)
The slope between radiation (W m\(^{-2}\)) and VPD vapor pressure deficit (kPa). The modified Jarvis model is

\[ E_{c,HI} = a \times \frac{R_e}{R_c + b} + \frac{1}{1 + \frac{c - VPD}{d}} \]  

where \( E_{c,HI} \) is hourly canopy transpiration (mm h\(^{-1}\)), \( R_e \) total radiation (W m\(^{-2}\)), and VPD vapor pressure deficit (kPa). Parameter \( a \) is a maximum modeled canopy transpiration under ideal environmental conditions, \( b \) describes light saturation level, \( c \) and \( d \) reflect plants response to VPD with \( c \) being interpreted as VPD level when half of maximum \( E_{c,HI} \) is reached and \( d \) as the slope between \( E_{c,HI} \) and VPD.

To estimate the average canopy stomatal sensitivity to VPD, we employed the simplified formula used by Oren et al. [27]:

\[ G_c = -m \times \ln VPD + G_{cref} \]  

where \( G_c \) is canopy conductance, an estimate of average stomatal conductance over the canopy (mm s\(^{-1}\)) [43], \( -m \) is the slope of \( G_c \) versus lnVPD (i.e. \( -d G_c / d \ln VPD \)), which quantifies the sensitivity of average canopy stomatal conductance to VPD. \( G_{cref} \) is reference canopy conductance when VPD = 1 kPa and can be used as surrogate for \( G_{max} \) [43].

### Statistical analysis

All statistical analysis was performed using SPSS (Version 16.0, Chicago, IL). Curve fitting was run through SigmaPlot (version 10.0, Systat Software, California, USA) and parameters of individual trees were analyzed among species or environmental condition ranks via one-way ANOVA. ANOVA analysis was employed to test the existence of significant differences among groups, and the multiple comparisons of the results were performed by LSD post-hoc test.

In this study, we first tested the assumption that the relationship between \(-m \) and \( G_{cref} \) defined by Eq. (6) follows 0.6 slope [27] across the studied species, and then quantified \( G_c \) responses to VPD using boundary line analysis between \( G_{cref} \) and \( \theta \) as described by Schäfer et al. [44].

### Results

#### Micrometeorology and soil water condition

Statistics of the averaged daily VPD, daily total solar radiation, and daily air temperature for July, August, and September, 2009 is shown in Table 2. There were significant differences in daily total solar radiation between the three months (P<0.001, n=92, One-way ANOVA) with September lower than the other two. Averaged daily VPD was significantly higher in August than in July (P=0.000, LSD post-hoc test) and September (P=0.024, LSD post-hoc test). Total rainfall was 492.5 mm from July 1\(^{st}\) to September 31\(^{st}\) with several intensive rainfall events. Soil moisture content in the upper layer depleted more quickly than deeper layers below 50 cm which maintained stable during several dry spells between the rain events (Fig. 1A).

#### Canopy transpiration and its relationship with DBH

Transpiration varied considerably among the individuals both across and within species. The averaged daily total canopy transpiration was different across the species (Fig. 1B). Canopy transpiration of C. deodara and E. bungeanus was similar and did not show continuous decline as summer passed by. By contrast, Z. schneideriana showed decreasing canopy transpiration which was lower than the other species. Similarly, transpiration of M. glyptostroboidea decreased throughout the observation period but recovered a little in September from transpiration decrease in August (Fig. 1B). On a daily scale, \( J_{\delta} \) of different species followed similar pattern but varied in magnitude under different soil water conditions of similar \( R_e \) and VPD (Fig. 1C).

Individually, average daily transpiration rate ranged from 0.07 mm d\(^{-1}\) by the smallest E. bungeanus tree to 0.20 mm d\(^{-1}\) by the largest C. deodara tree. It could be partially ascribed to the dependence of water use on tree size (Fig. 2). However, there were considerable species-specific differences in canopy transpiration as indicated by different species within same DBH class. For instance, water transpired by E. bungeanus (0.195 mm. d\(^{-1}\) was nearly 3-fold than that by Z. schneideriana (0.03 mm d\(^{-1}\) as measured for 14 cm DBH trees of these two species. When considering the statistical relationship between DBH and \( E_{\theta} \), the biggest M. glyptostroboidea triggered an exponential rise (\( R^2 = 0.72 \)).

| Species          | DBH(cm) | Projected Crown area (m\(^2\)) | Tree Height (m) | Sapwood area (cm\(^2\)) |
|------------------|---------|--------------------------------|----------------|-------------------------|
|                  | Mean    | SE    | Mean    | SE    | Mean    | SE    | Mean    | SE    |
| C. deodara       | 17.27   | 3.02  | 16.56   | 5.19  | 7.03    | 0.93  | 33.99   | 8.19  |
| Z. schneideriana | 13.93   | 3.11  | 18.77   | 4.32  | 5.30    | 0.49  | 18.99   | 5.84  |
| M. glyptostroboide | 19.33  | 4.10  | 4.80    | 2.10  | 11.60   | 1.06  | 36.63   | 14.46 |
| E. bungeanus     | 13.50   | 2.53  | 34.96   | 10.17 | 5.63    | 0.48  | 51.44   | 12.31 |

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

doi:10.1371/journal.pone.0047882.t001
EC response to environmental drivers

Daily EC was closely related to Rs and VPD (P<0.05) and the introduction of other variables did not further normalize the residual distribution. Curve fitting results showed that EC saturated at higher VPD and total radiation (Rs) (Fig. 3, 4A). It was also observed that higher Rs would significantly enhance EC under same VPD condition (Fig. 3). However, EC under same Rs condition failed to show significant differences among VPD ranks (P>0.05). REW ranks neither affected the relationship between daily EC and Rs nor EC and VPD (P>0.05).

Daily water transpired by trees did not show a significant correlation with REW (P>0.40) for plants did not react to concurrent soil water status. However, cumulative daily transpiration was significantly related to the cumulative soil water status.

Figure 1. Water supply and transpiration. A: Rainfall and soil water condition during the studied period. B: Comparison of average daily EC among different months and species. Significant differences among months within the same species are indicated by upper different lower case letters. Vertical bars stand for S.E.. C: Progression of sap flux density (J) under different soil water conditions (REW>0.4 and REW<0.2) in comparison with contemporary VPD and Rs. doi:10.1371/journal.pone.0047882.g001
depletion during each drying cycle (Fig. 4B). When compared according to different REW ranks under similar VPD conditions (P = 0.024), diurnal course of transpiration exhibited contrasting patterns (Fig. 1C). The Jm decline of *E. bungeanu*s in afternoon was steeper under soil water stress and the Jm of *Z. schneideriana* was suppressed during the whole day. By contrast, no significant reduction of Jm was observed for *C. deodara* and *M. glyptostroboide*s.

**Gc sensitivity**

Logarithmic decrease of midday canopy conductance against VPD suggested progressive stomata closure to prevent excessive cavitation as the air turned drier across species [31]. There were significant species difference in the Gc sensitivity to VPD (−dGc/dlnVPD or −d) and the Gcmax value within each REW and R rank (Table 3). No significant difference was observed for parameters of the same species under contrasting soil water and R ranges, and paired −dGc/dVPD and Gcmax of different species still followed a strong linear relationship of ~0.6 slope (Fig. 5). Similar results were also obtained by boundary line analysis of the relationship between Gcmax andREW (data not shown). The lack of significant deviation from a 0.6 slope indicates that all species were isohydric under all environmental conditions.

**Model simulation**

Average $E_{c,48}$ of all three trees within the same species from 30 days was included for model calibration and 6 days were randomly chosen for validation. Model performances were satisfactory for both calibration (see $R^2_{adj}$>0.89 in Table 4) and validation as the simulated half-hourly $E_{c,48}$ agreed well with observed values (Fig. 6). Model parameters showed significant differences in maximum transpiration (parameter a, P<0.001, one-way ANOVA) and in light saturation level (parameter b, P=0.004) among species. For species response to VPD, significant differences were found for VPD corresponding to the level at half maximum transpiration (parameter c, P=0.024, one-way ANOVA) and the slope between $E_{c,48}$ and VPD (parameter d, P=0.035, one-way ANOVA) across species. Moreover, the level of response to VPD remained stable across days as $c$ and $d$ did not show significant differences among the replicate days (P=0.552 for $c$ and 0.621 for $d$) for each species.

**Discussion**

**Influences from tree size and Species on Transpiration**

Comparable to general conclusion drawn from previous studies that tree size plays an overwhelming role in influencing stand water use [9,25,26,45,46], our study observed a positive relationship between transpiration and DBH independent of species (Fig. 2). The significant relationship between transpiration and DBH is attributable to the positive relationship between DBH and sapwood area which directly transports sap flow [47]. A sigmoidal increase portrayed the relation between water use and DBH among 18 angiosperm species in tropical forest [45]. Similarly, tree size has been found in some studies to be more important than species in determining transpiration [28] which is explained by pipe model theory [48]. It is a robust non-destructive method to estimate biomass [49–52]. According to the theory, the amount of leaves on a tree is supported by a proportionate cross sectional area of a bundle of pipes with equal hydraulic conductance. Therefore, the greater the living biomass the tree has the more sapwood area it has. However, the theory also indicates that the relationship between leaf area and sapwood cross area is species-specific. Consequently, the species effects on transpiration also can be strong even with changing tree size. In our study, the variation of average daily transpiration by four species ranged from 0.07 to 0.20 mm. d$^{-1}$. This can also be ascribed to species specific canopy conductance, such as *E. bungeanu*s in comparison with other species within ~14 cm DBH class. Such appreciable species-specific differences in transpiration suggested potential large influence of species composition at scales larger than stands [22].

Tree size can be a determinant factor on transpiration of highly structured stands [53], but the relationship may be more depend on the stand DBH composition. For example, Pataki et al. did not observe significant relationship between tree size and transpiration in urban areas and the author attributed it to limited range of DBH distribution which was common in the urban green spaces [8]. In our study the exponential increase between $E_{c}$ and DBH

**Table 2.** Statistics of atmosphere variables.

| Month      | Averaged daily VPD (kPa, Mean(S.E.) | Daily total Solar radiation (MJ.m$^{-2}$, Mean(S.E.) | Averaged daily Temperature (°C, Mean(S.E.) | Monthly Rainfall(mm, Sum) |
|------------|-------------------------------------|----------------------------------------------------|------------------------------------------|--------------------------|
| July       | 0.85*(0.07)                         | 13.54*(0.99)                                      | 23.94*(0.25)                             | 265.25                   |
| August     | 1.33*(0.1)                          | 14.59*(0.77)                                      | 25.47*(0.44)                             | 106.75                   |
| September  | 1.05*(0.08)                         | 9.67*(0.67)                                       | 20.85*(0.29)                             | 60.5                     |

Significant differences (P<0.05) among months are indicated by different upper lower case letters.

**Figure 2.** Tree size and transpiration. Relationship between daily canopy transpiration and DBH of individual trees of all investigated species.

doi:10.1371/journal.pone.0047882.g002
was triggered by one big *M. glyptostroboides* without which the relationship changed to linear and the $R^2$ decreased significantly (Fig. 2). It shows the influence of DBH composition, especially the large ones, on the relationship with transpiration. In urban green space, the tree size is usually unbalanced to represent a continuous DBH range, so it is not reliable to predict water use of urban trees using its relationship with tree size.

Response to Environmental variables and Seasonal Transpiration Patterns

All four species showed saturation of tree transpiration to high VPD and $R_s$ and this phenomenon has been widely reported [54–57]. When the canopy is well-coupled with the atmosphere [31], plants exert effective stomatal control over transpiration to regulate the minimum water potential according to VPD and it was also predictable from the 0.6 relationship between $G_{sref}$ and $-dG_s/dlnVPD$. Therefore, $E_c$ plateaus with increasing VPD as exhibited in this study. The $E_c$ saturation to increasing $R_s$ can be ascribed to the fact that stomata are fully opened at certain level of irradiance [58] and energy is not limiting to transpiration for these trees, and therefore do not react to higher radiation levels.

The influence of soil moisture on transpiration has not been consistent among studies [59–62]. In this study, daily $E_c$ did not show significant correlation with soil moisture content. At the sub-daily time scales, mesic tree species show a greater response to light and VPD with soil moisture playing a limited role except under conditions where root to soil moisture resistance is high [63]. However, soil moisture content is an important environmental driver for tree transpiration for longer time scales (Fig. 4B) [64,65].

Varied pattern of species transpiration in response to seasonal weather progression (Fig. 1B) was also observed. Due to $J_s$ sensitivity to soil water stress (Fig. 1C), the transpiration of *Z. schneideriana* decreased along the progression of rain fall reduction through the months. However, the declining trend of transpiration of *M. glyptostroboides* should be ascribed to variation of VPD because of the sensitive $G_s$ response to VPD by this species and high $G_{sref}$ (Fig. 5A). Therefore, transpiration by this species declined as VPD increased in August and recovered in September as VPD declined. In addition to the low rainfall, the high transpiration of *C. deodara* and *E. bungeanus* in August may contribute to the build up cavitation in the xylem and subsequently reduce transpiration thereafter [30].

Sensitivity to VPD

On a plot basis, trees of different species observed same hydraulic control (Fig. 5) and species differences in $G_{sref}$ led to varied magnitude of canopy transpiration across species (Fig. 1B, 3). In our study, even though $-dG_s/dlnVPD$ and $G_{sref}$ showed significant difference among species, their ratios for all these four species converged to ~0.6 as reported [27,66]. The changes of $G_{sref}$ and $-dG_s/dlnVPD$ were along the 0.6 slope under varying REW and solar radiation conditions and no significant bias existed in relation to tree size similar to what was found by Ewers et al [43] for one tree species exposed to manipulated soil moisture and nutrients. The interpretation is that isohydric regulation of water loss through $G_s$ response to VPD [27,67] is the same among the four species regardless of varying tree sizes and environmental conditions, while the $G_{sref}$ is species-specific. This relationship also means that $G_s$ sensitivity to VPD [67] and the transpiration of urban trees can be reliably predicted from $G_{sref}$ [68,69].

Since environmental conditions did not influence the relationship between $-dG_s/dlnVPD$ and $G_{sref}$, $G_{sref}$ can serve as an efficient indicator of species differences. The constant relationship between $-dG_s/dlnVPD$ and $G_{sref}$ reflects an isohydric stomatal control which protects the xylem from developing runaway cavitation by guaranteeing safe water potential [63]. Species difference in $G_{sref}$ may be related to xylem characteristics which tolerate cavitation. In addition to the partitioning of xylem

Figure 3. VPD and transpiration. Relationship between daily canopy transpiration in relation to VPD under different solar radiation ($R_s$) ranks with data on rainy days removed. Black dots represent average $E_c$ values within every 0.2 kPa rank. If a rank has less than 3 data, this rank is not considered to reduce potential bias from lack of representativeness.

doi:10.1371/journal.pone.0047882.g003
resistance as well as aquaporin activity [70,71], xylem anatomic differences were most commonly related to species' cavitation tolerances [30,72–74]. Species difference in xylem tolerance to cavitation was explicitly revealed through the daily $J_s$ rate under contrastingREW conditions (Fig. 1C). With larger diameter xylem vessels, ring-porous trees were less tolerant to negative water potential and xylem cavitation than diffuse-porous species due to intrinsic vulnerability of large diameter conduits to cavitation [30,75], such as $Z$. schneideriana versus $E$. bungeanus in our case. This is further reflected by the decreased $J_s$ of $Z$. schneideriana under water stress (Fig. 1C). However $E$. bungeanus could afford the same magnitude of transpiration under water stress as under no water stress during first half of the day. By contrast, $C$. deodara and $M$. glyptostroboides were able to maintain normal transpiration rate. That is probably because as gymnosperm species, they have tracheids of small diameter and strong cell wall, features that are resistant to cavitation.

Sensitivity of canopy conductance to VPD has great implications for the survival of trees in urban landscape. Trees of high canopy conductance at low VPD shows higher sensitivity to VPD [27,76], such as trees with higher $G_{c_{ref}}$ in this study. Active control over $G_c$ enables isohydric species to maximize carbon assimilation under low VPD and avoid the risk of runaway cavitation under atmospheric or soil drought [77]. Therefore, these species are suitable for urban environment where unpredictable local change is widespread [78]. Artificial activity produces extra thermal energy, which could be complicated temporally and spatially due to air turbulence caused by building arrangement [79]. Another factor comes from irrigation scope and intensity. Without irrigation, soil water condition is more likely to be stressed because of prevented rainfall percolation from pavements and enhanced soil evaporation in unpaved area. Although effective in $G_c$ control that guarantees tree survival, species with low maximum canopy conductance through the entire VPD range have less advantage in competitive situation, such as multi-species urban forest in summer, because lower $G_c$ does not favor carbon assimilation for growth in competition with high $G_c$ species. Low carbon assimilation might be potentially harmful to tree survival through a major drought event from the perspective of water safety [80]. As a result, species with different water use strategies will be differently affected by shifts of the frequency, duration, and intensity of drought [81].

Figure 4. Influences of solar radiation and soil water over transpiration. Daily $E_c$ in response to $R_s$ (A) and the relationship between sums of daily transpiration and cumulative soil water depletion for each drying cycle between two consecutive rainfall events (B). The lines are the fitting curves for different species. (A) and (B) share the same legends. $R^2$ for each species is denoted with subscripted first letter of the Latin name. doi:10.1371/journal.pone.0047882.g004

Figure 5. The sensitivity of canopy conductance. Relationship between sensitivity of canopy conductance to VPD ($-dG_c/d\ln\text{VPD}$) and canopy conductance at VPD = 1 kPa ($G_{c_{ref}}$) under (A) all environmental conditions, (B) contrasting Rew levels and (C) different solar radiation ($R_s$) levels. Data dots were from data in Table 3. doi:10.1371/journal.pone.0047882.g005
Implication of Species Differences on Urban Transpiration

Species differences tended to be revealed through the relationship between transpiration and environmental drivers. In our study, the modified Jarvis-type model described the environmental control over plants transpiration well (Fig. 6) and model parameters captured species differences in responding to the environment influences (Table 4). Parameter differences, i.e. species differences in responding to environmental factors, were also found among species by studies in tropical forest [42] and in Philippines [53]. Our study also showed increased expression of species differences under water stress (Fig. 1C).

Under urban environment, species differences in transpiration and response to the environment may cause spatial difference in hydraulic redistribution among green space even within small scope of area. Also, it may influence the effect of micro-meteorology modulation by vegetation. Even with such appreciable species differences, it is possible to predict urban canopy transpiration using their shared hydraulic control character. Unlike natural setting where transpiration can be assessed using the relationship with DBH, the influence of DBH on canopy transpiration is undermined because of the limited DBH distribution in the city. Our results recommend using the relationship between \( G_c \) and VPD under 1 kPa can be accurately tested via proper measurements including tree-based or remote sensed techniques, \( G_c \), and thus canopy transpiration, can be assessed at any scale through concurrent VPD.

Conclusion

Species differences were found in an urban environment in the response of transpiration to environmental drivers including light, soil moisture and vapor pressure deficit and in the control of tree size on transpiration. Despite significant species differences, all species showed declining \( G_c \) against increasing VPD, and the theoretical \( -\frac{dG_c}{dnVPD} \) to \( G_{cref} \) ratio of \( -0.6 \) was observed across studied species and under contrasting soil water and \( R_s \) conditions in the urban area. We, therefore, concluded that urban trees show isohydric regulation of minimum leaf water potential as

### Table 3. Parameters and significance for \( G_c = -m \times \ln VPD + G_{cref} \), under different soil moisture and radiation conditions.

| Species             | General condition | REW<0.4 | REW>0.4 | \( R_s <1.8 \) MJ m\(^{-2} \) | \( R_s >1.8 \) MJ m\(^{-2} \) |
|---------------------|-------------------|---------|---------|----------------------------|----------------------------|
|                     | \(-m\)            | \( G_{cref}\) | \(-m\)  | \( G_{cref}\)  | \(-m\)   | \( G_{cref}\)  | \(-m\)   | \( G_{cref}\) |
| C. deodara          | 0.26(0.06)        | 0.43(0.12) | 0.27(0.03) | 0.51(0.05) | 0.26(0.06) | 0.49(0.18) | 0.17(0.07) | 0.40(0.11) | 0.31(0.11) | 0.57(0.19) |
| Z. schneideriana    | 0.12(0.02)        | 0.10(0.02) | 0.07(0.02) | 0.11(0.03) | 0.09(0.04) | 0.14(0.02) | 0.12(0.01) | 0.10(0.02) | 0.23(0.03) | 0.16(0.03) |
| E. bungeanus        | 0.22(0.07)        | 0.42(0.13) | 0.21(0.11) | 0.44(0.13) | 0.19(0.02) | 0.36(0.02) | 0.24(0.10) | 0.44(0.17) | 0.25(0.22) | 0.51(0.35) |
| M. glyptostroboides | 0.28(0.06)        | 0.50(0.09) | 0.27(0.06) | 0.46(0.07) | 0.25(0.05) | 0.43(0.07) | 0.32(0.17) | 0.49(0.21) | 0.21(0.08) | 0.38(0.18) |

Data were given as mean of all sampled trees of the same species and S.E. in parenthesis.

\( R_s \): Solar radiation.

a,b,c,d: Significant difference of the parameter among species.

doi:10.1371/journal.pone.0047882.t003

Figure 6. Model simulation. Simulated and observed hourly canopy conductance (\( E_{c-H} \)) for model \( E_{c-H} = a \times \frac{R_s}{R_s + b} \times \frac{1}{1 + e^{(-\ln VPD)}} \), validation using six sampled days in August and September. Observed data were presented as mean of the trees within the same species ± SD.

doi:10.1371/journal.pone.0047882.g006
reflected in their response to VPD and that transpiration can be predicted with appropriate assessment of $G$, at VPD = 1 kPa.

### Acknowledgments

The authors would like to extend our sincere gratitude to Mr. Xiaofang Zhang and Mr. Keyun Dong for their help to collect data and providing logistic support during the study. We also thank the Dalian Forestry Administration and Dalian Landscape Architecture Administration, Liaoning Province, China for their valuable assistance on our field experiment and permitting our access to the park.

### Author Contributions

Conceived and designed the experiments: ZZ LC. Performed the experiments: LC ZZ. Contributed reagents/materials/analysis tools: ZZ. Wrote the paper: LC ZZ BEE.

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### Table 4.

Calibrated parameters for $E_{H1} = a \times \frac{R_{p/c}}{1 + c \times \frac{1}{\text{VPD} - 1}}$ for species.

| Species                  | a (mm.h$^{-1}$) Mean SE | b (MJ.m$^{-2}$h$^{-1}$) Mean SE | c (kPa) Mean SE | d (kPa) Mean SE | $R_{adj}^2$ Mean SE |
|--------------------------|-------------------------|---------------------------------|-----------------|----------------|-------------------|
| Cedrus deodora           | 0.035b 0.001            | 1.00b 0.20                      | 0.26b 0.06      | 1.65b 0.1      | 0.96 0            |
| Zeikova schneideriana    | 0.009b 0.004            | 1.88b 0.02                      | 0.41b 0.11      | 1.14b 0.7      | 0.92 0.03         |
| Euonymus bungeanus       | 0.065b 0.001            | 3.09b 0.03                      | 1.41b 0.12      | 1.57b 0.9      | 0.88 0.11         |
| Metasequoia glyptostroboides | 0.050b 0.001        | 1.76b 0.03                      | 1.72b 0.32      | 1.78b 0.16     | 0.92 0.04         |

Significant differences across species ($P<0.05$) are indicated with upper lower case letters. doi:10.1371/journal.pone.0047882.t004
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