Stomatal Sensitivity to Vapor Pressure Deficit and the Loss of Hydraulic Conductivity Are Coordinated in *Populus euphratica*, a Desert Phreatophyte Species

Da-Yong Fan1*, Qing-Lai Dang2, Cheng-Yang Xu1, Chuang-Dao Jiang3, Wang-Feng Zhang4, Xin-Wu Xu4,5, Xiao-Fang Yang3 and Shou-Ren Zhang3*

1 College of Forestry, Beijing Forestry University, Beijing, China, 2 Faculty of Natural Resources Management, Lakehead University, Thunder Bay, ON, Canada, 3 State Key Laboratory of Vegetation and Environmental Change, Institute of Botany, The Chinese Academy of Sciences, Beijing, China, 4 The Key Laboratory of Oasis Eco-agriculture, Xinjiang Production and Construction Corps, Shihai University, Shihai, China, 5 China Meteorological Administration, Beijing, China

There are considerable variations in the percentage loss of hydraulic conductivity (PLC) at midday minimum water potential among and within species, but the underpinning mechanism(s) are poorly understood. This study tested the hypothesis that plants can regulate leaf specific hydraulic conductance (\(K\)) via precise control over PLC under variable \(D_Y\) (water potential differential between soil and leaf) conditions to maintain the \(-m/b\) constant (\(-m\): the sensitivity of stomatal conductance to VPD; \(b\): reference stomatal conductance at 1.0 kPa VPD), where VPD is vapor pressure deficit. We used *Populus euphratica*, a phreatophyte species distributed in the desert of Northwestern China, to test the hypothesis. Field measurements of VPD, stomatal conductance (\(g_s\)), \(g_s\) responses to VPD, mid-day minimum leaf water potential (\(\Psi_{50}\)), and branch hydraulic architecture were taken in late June at four sites along the downstream of Tarim River at the north edge of the Taklamakan desert. We have found that: 1) the \(-m/b\) ratio was almost constant (=0.6) across all the sites; 2) the average \(\Psi_{50}\) (the xylem water potential with 50% loss of hydraulic conductivity) was \(-1.63\) MPa, and mid-day PLC ranged from 62 to 83%; 3) there were tight correlations between \(\Psi_{50}\) and wood density/leaf specific hydraulic conductance (\(k_l\)) and between specific hydraulic conductance sensitivity to water potential \([dk_l/dln(-\Psi)]\) and specific hydraulic conductivity (\(k_l\)). A modified hydraulic model was applied to investigate the relationship between \(g_s\) and VPD under variable \(D_Y\) and \(K\) conditions. It was concluded that *P. euphratica* was able to control PLC in order to maintain a relatively constant \(-m/b\) under different site conditions. This study demonstrated that branchlet hydraulic architecture and stomatal response to VPD were well coordinated in order to maintain relatively water homeostasis of *P. euphratica* in the desert. Model simulations could explain the wide variations of PLC across and within woody species that are often observed in the field.

**Keywords:** hydraulic model, xylem cavitation, leaf specific hydraulic conductance, stomatal conductance, water homeostasis
INTRODUCTION

A global convergence has been demonstrated in the relationship between drought-induced embolism and daily minimum xylem water potential (Choat et al., 2012; Choat et al., 2018). The safety margin of the plant hydraulic system refers to the difference between the daily minimum xylem water potential and the xylem water potential at which 50% of the hydraulic conductance is lost due to the cavitation of xylem vessels. Plants are generally able to maintain the integrity of their hydraulic system within the safety margin by the stomatal regulation of water loss to maximize the carbon gain without the risk of catastrophic hydraulic failure. However, the functional association between minimum xylem water potential and hydraulic safety does not prove that all the plants can control embolisms to the same extent because PLC is a function of water potential, Ψ50, and the slope of the cavitation vulnerability curve. As such, there are considerable inter- and intra-specific variations in PLC at the daily minimum xylem water potential (Pockman and Sperry, 2000; Johnson et al., 2009b; Fan et al., 2018). However, the underpinning mechanism(s) are not fully understood.

The stomatal regulation of xylem pressure is a function of vapor pressure deficit (VPD), leaf specific hydraulic conductance (Ki), soil water potential (Ψ), and leaf water potential (Ψ) (see Table 1 for the definitions of major acronyms/symbols in the present study) according to the following simplified hydraulic model (Oren et al., 1999; Landsberg et al., 2017):

\[ g_L = K_i \cdot (1/VPD) \cdot (\Psi - \Psi_f) \]  

Where \( g_L \) is leaf conductance to water vapor, which is a function of boundary layer conductance to water vapor (gba) and stomatal conductance (gs). It has been demonstrated that the sensitivity of stomatal conductance to VPD (−m) has a close relationship with the stomatal conductance at 1 kPa VPD (b) and the −m/b ratio is found to be 0.6 for various mesic species across a variety of growth forms and habitats (Dang et al., 1997; Oren et al., 1999; Bucci et al., 2005; Landsberg et al., 2017) and the relationship is described as follows:

\[ g_s = m \cdot \ln VPD + b \]  

The above models predict that if \( K_i \) decreases due to xylem cavitation, the −m/b ratio will need to increase because a more sensitive stomatal response is required to keep transpiration and stomatal conductance to water vapor pressure deficit, the response of branch and leaf hydraulic conductance to water potential differential between leaf and soil, and xylem vulnerability to cavitation. We conducted the study on four populations of a desert phreatophyte tree species, *Populus euphratica*, along a gradient of water table depths. We test the hypothesis that if stomata are perfectly efficient in regulating leaf water status as indicated by a constant −m/b both within and between species (Oren et al., 1999; Ewers et al., 2000), plants would fine-tune \( K_i \) via precise control over PLC (control the embolism degree) under variable \( \Delta \Psi \) and \( K_i \) conditions. The results can provide an explanation for the considerable inter- and intra-specific variations in PLC at the daily minimum xylem water potential in the field.

From Equation 1, \( g_s \) can be obtained with the input of \( K_i \), VPD, \( \Psi_f \) and \( \Psi_a \), while \( K_i \) is the product of maximum \( K_i \) and PLC. \( g_s \) can be obtained provided \( g_{ba} \) is known. Then −m/b can be calculated based on Equation 2. Among all parameters required by the model, \( K_i \), VPD, \( \Psi_f \) and PLC can be measured/calculated in the field. In desert environment, \( g_{ba} \) is large and has minor impact on the model simulation (Comstock and Mencuccini, 1998; Oren et al., 1999). As such, the only obstacle to verify the above hypothesis for trees with a deep root system is that it is difficult to know the water availability in the entire rhizosphere because of the difficulty in obtaining a reliable \( \Psi_a \), mainly due to the temporal–spatial soil moisture heterogeneity and nocturnal transpiration (Kavanagh et al., 2007; Landsberg et al., 2017). In this study, we used *Populus euphratica*, an obligate phreatophyte

### Table 1 | List of symbols, abbreviations and their units.

| Symbol/Abbreviations | Definition | Units          |
|----------------------|------------|----------------|
| \( a \)              | vulnerability curve steepness | mmol m⁻² s⁻¹ |
| \( b \)              | reference conductance at VPD = 1 kPa | mmol m⁻² s⁻¹ |
| \( \frac{dK_i}{d\psi_f} \) | sensitivity of \( K_i \), decreasing water potential | kg m⁻¹ MPa⁻² s⁻¹ |
| \( g_{ba} \)          | the boundary layer conductance to water vapor | mmol m⁻² s⁻¹ |
| \( g_s \)            | leaf conductance to water vapor | mmol m⁻² s⁻¹ |
| \( g_{min} \)        | stomatal conductance | mmol m⁻² s⁻¹ |
| \( \Delta \psi \)     | the maximum physiological \( g_s \), mmol m⁻² s⁻¹ |
| Huber value          | the total cross-section sapwood area per unit leaf area | m² |
| \( k_i \)            | leaf specific hydraulic conductivity | kg m⁻¹ MPa⁻¹ s⁻¹ |
| \( k_s \)            | specific conductivity | kg m⁻¹ MPa⁻¹ s⁻¹ |
| \( K_{hi} \)         | the maximum hydraulic conductivity | kg m MPa⁻¹ s⁻¹ |
| \( K_{li} \)         | the hydraulic conductivity measured at pressure i | kg m MPa⁻¹ s⁻¹ |
| \( K_i \)            | leaf specific hydraulic conductivity | mmol m⁻² MPa⁻¹ s⁻¹ |
| \( \Delta \psi \)     | the sensitivity of \( g_s \) to VPD | mmol m⁻² s⁻¹ |
| \( VPD \)            | leaf vapor pressure deficit | kPa |
| \( WD \)             | woody density | g dry mass cm⁻³ |
| \( \psi_f \)         | the negative of the injection pressure for vulnerability curve establishment | MPa |
| \( \psi_{min} \)     | leaf water potential | MPa |
| \( \psi_{bl} \)      | daily minimum branchlet xylem water potential | MPa |
| \( \psi_{min} \)     | daily minimum leaf xylem water potential | MPa |
| \( \psi_s \)         | soil water potential | MPa |
| \( \Delta \psi \)     | water potential differential between soil and leaf | MPa |

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species, to test the hypothesis. Because the root system of phreatophytes can reach and access the groundwater to avoid drought stress (Pockman and Sperry, 2000; Choat et al., 2012; Volaire, 2018), the $\Delta \Psi$ is largely determined by $\Psi_{s}$ because $\Psi_{f}$ is close to zero and the gravitational potential ($\sim 0.01\text{MPa m}^{-1}$) is ignorable for groundwater tables of a few meters (Scholander et al., 1965). $P. \text{euphratica}$ mainly grows along the riverside of Tarim River at the north edge of the Taklimakan Desert, NW China. Previous greenhouse studies have found that stems of $P. \text{euphratica}$ seedlings are highly vulnerable to cavitation (high $\Psi_{s0}$) and considerable PLC occurs at noon (Hukin et al., 2005), but there are no such field studies on this species. Thomas et al. (2008) and Gries et al. (2003) have found associations between $g_{s}$, VPD, $k_{s}$, and $\Psi_{s}$, but the relationship between stomatal sensitivity to VPD and hydraulic traits is still poorly understood. We hypothesize that the stomatal response to VPD and xylem response to water potential are functionally converged to maintain a functional coherence and integrity of the hydraulic system of the tree.

MATERIALS AND METHODS

Study Site

The study was carried out at four sites along the downstream of Tarim River (elevation of 931 m) in the Xinjiang Uighur Autonomous Region, NW China (Figure 1). The four sites are located at least 138 km east of Korla, at the northern fringe of the Taklamakan desert. Korla has a warm temperate continental arid climate; the average length of the frost-free season is 210 days. The annual average temperature is about 11°C, the average maximum temperature and average minimum relative humidity in June are 30.9°C and 9.9% respectively.

The four sites had natural $P. \text{euphratica}$ stands with relatively uniformly distributed trees. The stand density was 100–300 stems per hectare. Four to five trees with diameter at breast height of 30–40 cm were selected from each site and south-facing sunlit branchlets, and leaves at 1.3–1.5 m height from the outermost part of the lower canopy were selected for measuring in situ $g_{s}$ and hydraulic characteristics. Two branches per tree were selected for the branch architecture measurement and one to two leaves per tree were used to measure in situ $g_{s}$ response to VPD. The groundwater tables of the four sites measured at local wells within 1 km from the sites were 2.49, 3.49, 4.46, and 7.92 m, respectively, for site 31 Tuan (site A), 33 Tuan (site B), Yingsu (site C) and Alagan (site D).

Measurements of $g_{s}$ Response to VPD

$g_{s}$ responses to VPD were measured on clear days in the field around noon (12:00 to 14:00 h) in late June under two sets of conditions: (1) controlled VPD and (2) un-controlled natural VPD, using a Li 6400 open gas exchange system (Li-Cor Cooperative, Lincoln, NE, USA). In the controlled-VPD measurements, a range of VPD from 0.8 to 3.5 kPa was achieved by using the apparatus on the equipment to vary the mixing ratio of water-vapor saturated air and dry air (after passing through desiccant). When the relative humidity in the leaf chamber exceeded 80% (VPD was about 0.8 kPa), the instrument displayed a warning sign of “High humidity alert”, $g_{s}$ and intercellular carbon dioxide concentration ($C_{i}$) readings fluctuated (e.g., $C_{i}$ fluctuated from negative to very large values), indicating the $g_{s}$ measurement was not reliable. Therefore, data points with VPD values less than 1 kPa were discarded. Other environmental conditions in the leave cuvette were set as follows: Leaf temperature 31°C, Photosynthetically active radiation (PAR) 1,200 $\mu$mol m$^{-2}$ s$^{-1}$, CO$_{2}$ concentration 390 $\mu$mol mol$^{-1}$. Only steady-state $g_{s}$ readings at each VPD were recorded (Dang et al., 1997; Dang, 2013). Measurements under un-controlled natural VPD were taken in June and again in July. The conditions in the leaf chamber were set the same in the two measurements (Leaf temperature 31°C, PAR 1,200 $\mu$mol m$^{-2}$ s$^{-1}$, CO$_{2}$ concentration 390 $\mu$mol mol$^{-1}$). The $-m$ and $b$ were estimated using Equation 2 and the non-linear regression model with glns () function of the R software (R Development Core, 2017).

Leaf Water Potential and Branchlet Xylem Water Potential Measurements

The daily minimum leaf xylem water potential ($\Psi_{\text{min}}$) was measured in the field between 12:00 and 14:00 using a Scholander pressure chamber (PMS Instrument, Corvallis, Oregon, USA). The measurements were taken on the same trees on which the VPD responses were measured. The daily minimum branchlet xylem water potential ($\Psi_{\text{min}}$) was estimated according to the method of Pockman and Sperry (2000): a branchlet of similar size to that used in subsequent cavitation
vulnerability measurements was selected and sealed in a plastic bag containing a moist paper towel for 30 min in darkness to allow the equilibration of water potential between leaves and the subtending branchlet before a leaf was sampled and the petiole water potential was measured.

**Cavitation Vulnerability Curve Measurement**

A branchlet (50–70 cm long, 2–4 year-old) near that used for the $g_s$–VPD response measurement was cut from each sample tree before sunrise (before 8:00 AM) to measure $k_t$ and the cavitation vulnerability curve. The branchlet was wrapped in moist paper towels immediately after being cut and transported to the laboratory. The maximum vessel length was measured from six samples randomly chosen from all the four sites together, based on the method (pressurized gas bubble under water) of Jacobsen et al. (2007). Since the maximum measured vessel length was less than 21 cm, all the samples (7–10 per site) were re-cut to 22–24 cm under water, and all the measurements were carried out in an air-conditioned laboratory (26°C). The maximum flow rate was measured under 8 kPa hydrostatic pressure after air emboli were collected and conditioned laboratory (26°C). The maximum under water, and all the measurements were carried out in an air-

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The vulnerability of xylem to cavitation was characterized using a vulnerability curve which was measured using a Cavitation pressure chamber (PMS Instrument, Corvallis, Oregon, USA) according to Sperry and Salienatra (1994). A branch segment was inserted into a collar and sealed with both ends protruding. Air was injected into the collar at a set pressure, which was maintained for 15 min and then slowly decreased to 0.1 MPa. The hydraulic conductivity was then re-measured at a higher pressure. This procedure was repeated until at least 85% loss of hydraulic conductivity was reached. The PLC following each pressurization was calculated as $PLC = 100 \times (K_{ai} - K_{bi})/K_{bi}$, where $K_{ai}$ is the hydraulic conductivity measured at pressure $i$. The vulnerability curve for each sample was fitted with an exponential sigmoidal equation (Pammenter and Vander Willigen, 1998):

$$PLC = \frac{100}{1 + e^{(\Psi - \Psi_{so})/\Psi_{50}}}$$

where $\Psi$ is the negative of the injection air pressure and coefficients $a$ and $\Psi_{50}$ are estimated using a non-linear regression model with gnls() function of R software (R Development Core, 2017). $\Psi_{50}$ represents the xylem water potential at which 50% of the hydraulic conductance is lost, $a$ represents the steepness of vulnerability curve. $k_t$ at noon was estimated from $Y_{s_{num}}$, the vulnerability curve, and maximum $k_t$ (Pockman and Sperry, 2000; Johnson et al., 2009b).

**Wood Density and $k_s$ Sensitivity to Water Potential**

Wood density (WD) was measured on stem segments used in the measurement of vulnerability curves after the removal of pith and bark, and the fresh volume was measured by the Archimedes principle of water displacement. The dry mass was determined after drying at 104°C for 24 h. WD is expressed as dry mass per unit fresh volume (g cm$^{-3}$).

Specific hydraulic conductance sensitivity to water potential $[d(k_s)/dln(-\Psi)]$ was calculated based on the method by Ewers et al. (2000): we related maximum $k_s$, obtained at $\Psi = 0$, to the branchlet $k_s$ sensitivity to decreasing $\Psi$ from $-0.5$ to $-3.0$ MPa. The slope of the $-\Psi-k_s$ relationship was linearized by using the natural logarithm of $-\Psi$, and the logarithm transformation resulted in a good fit ($R^2 = 0.91$ to 0.95).

**The Hydraulic Model**

We used Equation 1 and the following equation:

$$g_s = (g_s \cdot g_w)/(g_s + g_w)$$

to model the response of $g_s$ to VPD at noon. We set constraints for $g_{sm}$ (the maximum physiological $g_s$ for *P. euphratica*), $g_{bo}$, $K_t$, and $\Delta\Psi$ according to the corresponding measured physiological range for *P. euphratica*. It is assumed that $g_s$ had an upper limit of $g_{sm}$ which was set as 1,000 mmol m$^{-2}$ s$^{-1}$, based on our field measurements and the reported values for poplars (Haque, 2015). The $g_w$ for desert environment was set as 2,000 mmol m$^{-2}$ s$^{-1}$ (Comstock and Mencuccini, 1998). $K_t$ at noon was set between 0.5 and 4.0 mmol MPa$^{-1}$ m$^{-2}$ s$^{-1}$. $\Delta\Psi$ at noon ($\Psi_s - \Psi_{s_{num}}$) was set at 2.0 to 3.2 MPa according to the measured range of $\Psi_{s_{num}}$ in the field. VPD was allowed to vary between 1 and 4 kPa, similar to the range observed in the field (Gries et al., 2003). Before running the simulation, we calculated $K_t$ at noon from the estimated $k_t$ at noon, assuming hydraulic path length = underground water table + sample height + branch length, and hydraulic conductance was uniformly distributed along the flow path from soil to branchlet (Pockman and Sperry, 2000). Note the unit of $k_t$ is kg m$^{-1}$ MPa$^{-1}$ s$^{-1}$, and the unit of $K_t$ is mmol m$^{-2}$ MPa$^{-1}$ s$^{-1}$. We converted the unit VPD into the unit of mol mol$^{-1}$ as required by the model. We relaxed the assumption of constant $\Delta\Psi$ when exploring the relationship between $K_t$ and $-m/b$. By allowing $K_t$ and $\Delta\Psi$ to vary simultaneously, the $g_s$ responses to VPD ($-m/b$) under all the combinations of $K_t$ and $\Delta\Psi$ were solved. The simulation procedure was as follows (Oren et al., 1999): 1) the $K_t$ and $\Delta\Psi$ were assigned to specific values; 2) $g_s$ as the function of VPD was calculated from Equation 1; 3) $g_s$ was solved from Equation 4; 4) when $g_s > g_{sm}$ (occurred...
RESULTS

$g$, $\Psi_{\text{min}}$, $b$ were significantly lower, and VPD was significant higher at Alagan than other sites (Table 2). Transpiration rate ($T_c$), $-m$, and $-m/b$ (0.57–0.61) were not significantly different among the four sites (Table 2). Differences in all the traits were smallest between 31 Tuan site and Yingsu site than among all the sites.

The branchlet hydraulic architecture of *P. euphratica* also varied with site (Table 3). Yingsu had significantly greater $k_s$, $k_l$, and $d(k_l)/d\ln(-\Psi)$ than the other three sites (Table 3). Huber value was lowest at Alagan and highest at 33 Tuan among the four sites although their differences from 31 Tuan and Yingsu were not statistically significant (Table 3). $WD$ was lowest at 31 Tuan and highest at Alagan, but their differences from 33 Tuan and Yingsu were not statistically significant (Table 3). $\Psi_{\text{min}}$ had the same trend as $\Psi_{\text{lim}}$, i.e., significantly more negative at Alagan than at all other sites, while there was no significant difference among the other sites (Tables 2 and 3). $\Psi_{50}$ was most negative at Alagan ($-2.22$ MPa) and the least negative at Yingsu ($-1.22$ MPa) among the four sites, but the trend for $a$ was the opposite (Table 3).

As there was no significant difference in $-m/b$ among the sites, we pooled all the VPD response data from the four sites and evaluated the general relationship between $g$, VPD for the species. We fit Equation 1 separately for the two sets of VPD response data. The estimated $-m/b$ was 0.607 for the controlled-VPD data set and 0.615 for the natural VPD field measurement (Figures 2A, B). $-m$ was positively correlated with $b$ across the individuals of the four sites (Figure 2C).

The estimated PLC ranged from 62% at Alagan site to 83% at Yingsu site (Figure 3). The corresponding estimated $k_l$ at noon for 31 Tuan, 33 Tuan, Yingsu, and Alagan sites was $1.11 \times 10^{-4}$, $1.09 \times 10^{-4}$, $1.12 \times 10^{-4}$, and $1.16 \times 10^{-4}$ kg m$^{-1}$ MPa$^{-1}$ s$^{-1}$, respectively.

$k_l$ was positively correlated with $k_b$ ($F = 6.637$, $P = 0.014$), negatively correlated with Huber value ($F = 19.407$, $P < 0.001$) (Table 4). However, $k_l$ showed no significant relationship with safety ($\Psi_{50}$) ($F = 1.917$, $P = 0.175$) (Table 4). There was a negative association between $\Psi_{50}$ and $WD$ ($F = 8.566$, $P = 0.006$) across the four sites (Table 4, Figure 4A). There was a positive correlation between $\Psi_{50}$ and $k_l$ ($F = 5.937$, $P = 0.017$) (Table 4, Figure 4B); $k_l$ also showed a positive correlation with the reference stomatal conductance at 1.0 kPa ($F = 37.274$, $P = 0.009$) at the population scale (Figure 4C). $d(k_l)/d\ln(-\Psi)$ was positively correlated with $k_s$ ($F = 680.782$, $P < 0.001$) (Figure 4D) across the individuals, and $b$ at the population scale ($F = 33.249$, $P = 0.01$) (Figure 4F), but had no relationship with $\Psi_{50}$ ($F = 0.438$, $P = 0.51$) (Figure 4E). There was no association between $g$, and $\Psi_{\text{lim}}$ at the population scale ($F = 12.047$, $P = 0.071$) (Figure 4H). There was no significant

### Table 2 | Means and standard error of the mean for $g$, $T_c$, VPD, $\Psi_{\text{lim}}$, $-m$, $b$ and $-m/b$ at the four sites.

| Population     | $g$         | $T_c$      | VPD       | $\Psi_{\text{lim}}$ | $-m$      | $b$       | $-m/b$     |
|----------------|-------------|------------|-----------|---------------------|-----------|-----------|------------|
| 31 Tuan        | 536 ± 68ab  | 7.28 ± 1.48ab | 1.56 ± 0.10b | -2.30 ± 0.03ab | 519.8 ± 130.6ab | 802.5 ± 102.9ab | 0.61 ± 0.10ab |
| 33 Tuan        | 396 ± 39ab  | 7.62 ± 0.63ab | 1.96 ± 0.10b | -2.55 ± 0.05ab | 333.7 ± 54.8ab | 588.1 ± 72.0ab | 0.57 ± 0.07ab |
| Yingsu         | 490 ± 41ab  | 8.73 ± 0.90ab | 1.88 ± 0.22ab | -2.45 ± 0.06ab | 435.2 ± 60.9ab | 769.7 ± 83.5ab | 0.57 ± 0.08ab |
| Alagan         | 328 ± 39ab  | 8.07 ± 0.65ab | 2.46 ± 0.08ab | -3.01 ± 0.09ab | 328.3 ± 33.2ab | 577.1 ± 35.7ab | 0.58 ± 0.08ab |
| P value        | ≤0.05       | >0.05      | ≤0.06     | ≤0.05              | >0.05     | >0.05     | >0.05      |

Symbols, their definition and units are provided in Table 1. Different letters among populations indicate significant difference at $p = 0.05$.

### Table 3 | Means and the standard error of the mean for $k_s$, $k_l$, $WD$, $\Psi_{\text{lim}}$, Huber value, $\Psi_{50}$, $d(k_l)/d\ln(-\Psi)$, and $a$ at the four sites.

| Population     | $k_s$       | $k_l$(×10$^{-4}$) | $WD$    | $\Psi_{\text{lim}}$ | Huber(×10$^{-4}$) | $\Psi_{50}$ | $a$        | $d(k_l)/d\ln(-\Psi)$ |
|----------------|-------------|-------------------|---------|---------------------|-------------------|------------|-----------|----------------------|
| 31 Tuan        | 1.52 ± 0.16ab | 3.51 ± 0.43ab    | 0.405 ± 0.035ab | -2.14 ± 0.06ab | 2.79 ± 0.34ab | -1.39 ± 0.12ab | 1.71 ± 0.18ab | 0.59 ± 0.06ab |
| 33 Tuan        | 1.51 ± 0.34ab | 3.68 ± 0.28ab    | 0.491 ± 0.007ab | -2.27 ± 0.16ab | 3.05 ± 0.35ab | -1.67 ± 0.15ab | 1.35 ± 0.15ab | 0.49 ± 0.15ab |
| Yingsu         | 2.94 ± 0.36ab | 6.63 ± 0.84ab    | 0.474 ± 0.006ab | -2.23 ± 0.08ab | 2.40 ± 0.36ab | -1.22 ± 0.23ab | 1.72 ± 0.19ab | 1.08 ± 0.20ab |
| Alagan         | 2.02 ± 0.49ab | 3.04 ± 0.53ab    | 0.496 ± 0.010ab | -2.73 ± 0.03ab | 31.63 ± 0.22ab | -2.22 ± 0.11ab | 0.94 ± 0.08ab | 0.83 ± 0.17ab |
| P value        | ≤0.01       | ≤0.001           | ≤0.01   | ≤0.001              | ≤0.01           | ≤0.001     | ≤0.01     | ≤0.05               |

Symbols, their definition, and units are given in Table 1. Different letters among populations indicate significant difference at $p = 0.05$. 

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The distribution normality of branchlet xylem hydraulic traits and leaf water status data were tested by calculating the Shapiro-Wilk W statistics for each sample (n = 4–5 for leaf water status variables, n = 7–10 for branchlet xylem hydraulic traits). Differences between sites were tested using Kruskal-Wallis H test if P(W) < 0.05. The Spearman rank correlation analysis was applied to investigate correlations among branchlet xylem hydraulic traits. ANOVA and Pearson correlation analysis were subsequently conducted if P(W) > 0.05. We conducted all the statistical analyses using R version 3.4.0 (R Development Core, 2017).
relationship between $g_s$ and $T_r$ ($F = 0.99$, $P = 0.33$) (Figure 4G).

There was also a marginally positive association ($F = 13.048$, $P = 0.061$) between $Y_{50}$ and $Y_{min}$ across the four sites, and the slope of this relationship is similar to the slope for other angiosperm species in the world (Figure 5). The safety margin ($Y_{min} - Y_{50}$) was negative (i.e., below the 1:1 line in Figure 5) because the actual measured $Y_{min}$ was more negative than $Y_{50}$ and the actual PLC was greater than 50%. $g_s$ increased with increasing (i.e., becoming less negative) $Y_{min}$, and the rate of increase was greater at sites with less negative $Y_{min}$ (Figure 4H).

**DISCUSSION**

The $Y_{50}$ values measured in this study are within the range of values reported for poplar trees around the world, e.g., $-1.30$ MPa for *P. tremula*, $-2.95$ MPa for *P. nigra* (Choat et al., 2012), $-0.69$ MPa for *P. deltoids*, and $-2.75$ MPa for *P. tremuloides* (Fichot et al., 2015). Hukin et al. (2005) have reported that *P. euphratica* seedlings have a $Y_{50}$ for xylem cavitation of only $-0.7$ MPa, while the field-grown *P. euphratica* trees in our study had an average $Y_{50}$ of $-1.63$ MPa across the four sites. These results suggest that the seedlings of *P. euphratica* may be much more vulnerable to xylem cavitation than trees at a later developmental stage. Although the seedlings of *P. euphratica* were measured at a different location in a different study (Hukin et al., 2005) from the larger trees, the response trend is consistent with that of another poplar species, *P. tremuloides*, the field grown trees which have a $Y_{50}$ of $-2.75$ MPa (Sperry and Sullivan, 1992) while its seedlings only $-0.68$ to $-0.84$ MPa (Way et al., 2013).

Furthermore, the value of $Y_{50}$ that we measured on *P. euphratica* in this study ($-1.63$ MPa) is much less negative than the reported values for other drought resistant tree species, e.g., $-2.75$ MPa for *P. tremuloides* (Sperry and Sullivan, 1992), $-8.42$ MPa for *Pistacia terebinthus* (Maherali et al., 2004), suggesting that *P. euphratica* may be more vulnerable to cavitation than other drought tolerant desert species. Our measurement of PLC was in line with the mid-day PLC of 76% reported by Zhou et al. (2013). The results of this study suggest that *P. euphratica* is a mesic-adapted species. In a mesic-adapted species, $g_s$ generally has a much tighter relationship with VPD (Figures 2A, C) than with $k_v$. 

![Figure 2](image-url) | Relationships between $g_s$ and VPD (A, B), and the relationship between $-m$ and $b$ (C) of *Populus euphratica* among the four sites. The measurements were taken by manipulating VPD in late June (A, C), and natural VPD in late June and late July (B). The curves were generated by using the hydraulic model (Equation 1). In (C), red line represents the theoretical line of the expected relationship ($-m = 0.68$), black dash lines represent 95% confidence intervals of linear regression between observed $-m$ and $b$. The safety margin ($Y_{min} - Y_{50}$) was negative (i.e., below the 1:1 line in Figure 5) because the actual measured $Y_{min}$ was more negative than $Y_{50}$ and the actual PLC was greater than 50%. $g_s$ increased with increasing (i.e., becoming less negative) $Y_{min}$, and the rate of increase was greater at sites with less negative $Y_{min}$ (Figure 4H).
conductance controls the leaf water potential and transpiration hydraulic model (Equation 1) that assumes that stomatal
The number under the horizontal dotted line is the PLC at noon. See Table 1 for the definition of symbols.

| k_s | k_t | WD | Huber | \( \Psi_{50} \) |
|-----|-----|-----|-------|------------|
|     |     |     |       | 1.01 MPa  |

Symbols, their definition, and units can be found in Table 1. * * * * and ns denote significance at \( P \leq 0.001 \), \( P \leq 0.01 \), \( P \leq 0.05 \), and no significant difference, respectively.

The nearly isohydric behavior could also be demonstrated by the close association between \(-m\) and \(b\) across the individuals from the four populations (Figure 2C). The high xylem vulnerability and the pattern of \(g_s\), response to VPD found this study provide physiological explanations for some of the ecological phenomena that are often observed in the field, e.g., very little sexual reproduction (Hukin et al., 2005), extensive clonal growth (Bruehlheide and Jandt, 2004). We observed that there were very few seedlings at the four sites of this study. The limited number of seedlings on the sites may have been a result of the inability of seedlings to access the ground water, particularly during the dry season. The groundwater table generally deepens as a result of the management of the river system (Chen et al., 2015). In order to survive a drought spell, the root system of the seedlings must be able to reach and access the groundwater because of the high vulnerability to xylem cavitation and the inability of the species to effectively control water loss when the transpirational demand is high (i.e., mesic \(g_s\), response to VPD). Because the root system of seedlings generally cannot penetrate deep enough to tap the groundwater as the ground table deepens or if they grow far away from the river bank, the mortality rate of tree seedlings is very high (Chen et al., 2015), leading to a lower rate of successful sexual regeneration. Consequently, the proportion of vegetative regeneration from suckering generally increases with increasing distance from the river bank. Similar phenomena on \(P. euphratica\) have been reported by other studies (e.g., Wu et al., 2010). These results suggest that the distribution of this species in the desert primarily depends on its access to groundwater (Gries et al., 2003).

The “safety margin” (\(\Psi_{min} - \Psi_{50}\)) of \(P. euphratica\) ranged from \(-0.5\) to \(-1.01\) MPa across the four sites in this study. While these values are within the general range of values reported for other tree species in the world that grow under comparable environmental conditions to those of our study sites (Choat et al., 2012), \(P. euphratica\) tended to have a more negative \(\Psi_{min}\) than other species with the same \(\Psi_{50}\) (Figure 5). The linear regression line between \(\Psi_{min}\) and \(\Psi_{50}\) (marginally significant) had a similar slope to that of angiosperm species in the literature (Choat et al., 2012), suggesting that the species tended to regulate stomatal aperture to maintain water homeostasis but was less able to do so. However, the negative value of the safety margin suggests that \(P. euphratica\) operated beyond the hydraulic safety margin and thus suffered more than 50% loss of hydraulic conductivity around noon. Indeed, the PLC at noon ranged from 62% at Alagan to 83% at Yingsu site. Since it is generally believed that plants can fine-tune PLC to avoid catastrophic hydraulic dysfunction (Tyree and Sperry, 1988; Macinnis-Ng et al., 2004), it is puzzling why such large differences in PLC occurred in \(P. euphratica\) at different sites. We thus proposed that plants can fine-tune \(K_t\) via precise control over PLC to maintain a constant \(-m/b\) according to the prediction of Equation 1 and Equation 2 (Oren et al., 1999; Ewers et al., 2000), which can provide insight into the mechanism underpinning the large variation of PLC in \(P. euphratica\). The results further suggest that \(P. euphratica\) had a greater ability to restore cavitated xylem vessels daily than most
angiosperm species. However, the factor or factors responsible for such a high ability are not clear and warrant investigations. The results of this study suggest that the hydraulic model (Equation 1) and/or its assumptions may need to be modified when used to examine the relationship between $K_l$ and $-m/b$. The model predicts that if $K_l$ decreases due to xylem cavitation, the $-m/b$ will increase because a greater stomatal response is required to keep transpiration and $D_Y$ (Soil water potential minus leaf water potential) constant (Oren et al., 1999; Landsberg et al., 2017). However, the $-m/b$ in the current study was relatively constant (close to 0.6) across the four sites despite the large declines in $K_l$ at noon. Furthermore, the model assumes that $\Delta Y$ remains constant when $K_l$ varies, which unlikely occurs in nature. In this study, we allowed $K_l$ and $\Delta Y$ to vary concurrently to relax the assumptions and set values for $K_g$, $\Delta Y_g$, $g_{sm}$, and $g_{bl}$ based on the measured physiological ranges for *P. euphratica* in our investigation of the relationship between $K_l$ and $-m/b$.

The output of the hydraulic model with our modifications was supported by our field measurements. The modeled relationship between $K_l$ and $\Delta Y$ at noon for our four sites was within the band of 0.58–0.60 $-m/b$ (Figure 6), and the $-m/b$ range calculated from our field measurements was 0.57–0.61. The *in situ* native midday PLC for *P. euphratica* (76%) measured by Zhou et al. (2013) along the Arim River is also consistent with our modeled value. A 1:1 correspondence between native embolism and the embolism predicted from vulnerability curves for desert plants is also reported by Pockman and Sperry (2000). These results suggest that correctly constructed VC curves (Wheeler et al., 2013) and hydraulic models can reliably predict native embolism in the field. It is also reported that xylem embolism is likely a critical element for the decrease of leaf hydraulic conductance during the daytime (Kikuta et al., 1997; Woodruff et al., 2007; Johnson et al., 2009a; Zhang et al., 2016), particularly for poplar species (Laur and Hacke, 2014; Scoffoni et al., 2017). *P. euphratica* could tolerate more than 50% xylem cavitation around noon and that it regulated PLCs based on the different conditions of the four sites in order to achieve a similar stomatal sensitivity under the condition where water supply and irradiance were not limited. This hydraulic strategy might be critical for *P. euphratica* to maximize its carbon gain and facilitate its growth in an arid environment. It can be inferred that *P. euphratica* trees may have the capacity of

![Figure 4](link-to-figure)
refilling the embolized xylem vessels or producing new vessels to restore the hydraulic capacity quickly (Gleason et al., 2016; Choat et al., 2018). However, the literature indicates that not all the species have the capacity to refill caviated vessels (Charrier et al., 2016; Torres-Ruiz, 2020). Further research in this area is warranted.

There are generally considerable variations in PLC at mid-day minimum xylem water potential among and within species (Pockman and Sperry, 2000; Johnson et al., 2009b; Fan et al., 2018), and based on the PLC at the mid-day water potential, a species can be classified into one of the two strategic groups: the conservative group (PLC < 50%) or the radical group (50% < PLC < 100%). Interestingly, the results of model simulation in the present study indicate that the two strategy groups could have similar stomatal sensitivity (e.g., belt A for the radical strategy and belt B for the conservative strategy in Figure 6 had the same range of stomatal sensitivity), suggesting that maintaining the theoretical threshold stomatal sensitivity (−m/b = 0.6) is probably critical for the fitness of mesic species regardless of which strategy they adopt. A −m/b above 0.62 (Belt C in Figure 6, with smaller PLC than the radical strategy and greater PLC than the conservative strategy) might be detrimental to photosynthesis because a small increase in VPD would induce a large decline in stomatal conductance and thus CO2 supply for photosynthesis even when water supply and irradiance are not limited, possibly reducing the competitiveness of the species. However, the reason why P. euphratica has adopted the radical strategy (belt A in Figure 6) instead of the conservative strategy (belt B in Figure 6) remains unknown. It is possible that xylem cavitation may help plants to survive drought stress by rationing water use (Sperry, 1995) and temporarily releasing the effects of water stress for a portion of the tree (Hölttä et al., 2011). It is also worth noting that P. fremontii (a riparian species in Sonoran desert), a comparable species to P. euphratica, has 16.5–31.97% embolism at noon (Pockman and Sperry, 2000) and is likely located in belt B of Figure 6 and has adopted a conservative strategy.

The result that increased cavitation resistance was linked to increased wood density (Figure 4A) is expected because denser wood tends to be better able to sustain the compressive forces generated by lower negative pressures and to minimize air permeability that might cause xylem cavitation (Pockman and Sperry, 2000; Hacke et al., 2001; Bucci et al., 2013). Further, the positive relationship between kₜ and Ψ₅₀ (Figure 4B) suggests there was a functional trade-off between efficiency and safety at the leaf level. The positive relationship between kₜ and d(ln(−Ψ))/d(ln(VPD)) (Figure 4E) is coherent with the positive relationships between stomatal sensitivity to VPD and stomatal conductance at low VPD (i.e., 1.0 kPa) and between leaf hydraulic conductance and stomatal conductance at low VPD, providing evidence to support the functional convergence between xylem and leaves. Furthermore, faster growing species or populations tend to have lower wood density, higher stomatal and xylem conductance but lower drought resistance. The curvilinear relationship between gₑ and Ψ₅₀ suggests that trees with less negative Ψ₅₀ had higher but more sensitive gₑ, which also coincided with lower wood density and higher hydraulic conductance as well as sites with shallower water tables. The results of this study provide physiological evidence for the mechanisms governing the tradeoff between growth rate, anatomy, physiological functioning, and stress resistance.

Transpiration is controlled by both vapor pressure deficit and leaf conductance. Therefore, it is not surprising that gₑ was not significantly correlated to Tₑ (Figure 4G). The leaf conductance in turn is controlled by VPD and the internal water status as...
demonstrated by Equations 1 and 2. Equation 1 demonstrates that leaf conductance is the linkage between the internal water relations in the tree and the moisture conditions of the ambient air. This conclusion can further enforced the coherent functional relationships discussed in the previous paragraph, such as the significant, linear relationship between $d(k)/d\ln(-\Psi)$ and $k$, (Figure 4D). This relationship could facilitate the fine-tuning of PLC to sustain transpiration (Ewers et al., 2000) across the individuals (Table 2, Figure 2). More importantly, the lack of significant relationship between $g_s$ and $\Delta/\Psi_{\text{min}}$ (Figures 4G, H) indicates that the hydraulic behavior of $P.$ euphratica resembled that of an isohydric species, which is in consistence with the observation on $P.$ euramericana (Tardieu and Simonneau, 1998) and several poplar genotypes (Navarro et al., 2018). The nearly isohydric behavior also indicates higher $b$ (same meaning as $-m$, Oren et al., 1999) is functionally associated with higher $d(k)/d\ln(-\Psi)$ and higher $k_l$ (at the population scale) (Figures 4C, F), consistent with the observation that stomata respond to changes in branchlet hydraulic conductance in a manner of feedback response to leaf water status (Saliendra et al., 1995). The results can be explained solely by hydraulic signaling or by an interaction between hydraulic and chemical signaling in the control of stomatal conductance (Tardieu and Simonneau, 1998; Comstock, 2002; Buckley, 2019; Qu et al., 2019).

In summary, this study demonstrates that the hydraulic architecture of branchlets and stomatal response to VPD were well coordinated with each other so that the water homeostasis of $P.$ euphratica was maintained in the desert environment. The high xylem vulnerability to cavitation and the pattern of $g_s$ response to VPD measured in the field further corroborated previous conclusions that the distribution and growth of $P.$ euphratica in the desert solely depend on its access to groundwater (Gries et al., 2003; Hukin et al., 2005; Thomas et al., 2008). Thus, the populations of this phreatophyte species may decline if and when the groundwater table deepens as a result of reduced precipitation induced by global climate change, river management, or dam constructions (Zhou, 1993; Gries et al., 2003; Chen et al., 2015). We also demonstrated that the observed $-m/b$ of $P.$ euphratica is consistent with the theoretical value derived from a simple hydraulic model when the assumption of constant $\Delta\Psi$ was relaxed. Our results demonstrate that model simulations can potentially explain the wide range of variations in PLC across and within woody species that is often observed in the field but further research efforts in this area is warranted.

**DATA AVAILABILITY STATEMENT**

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

**AUTHOR CONTRIBUTIONS**

D-YF and S-RZ designed the experiment. D-YF, C-DJ, X-WX, and X-FY carried out the experiment. D-YF, S-RZ, C-YX, and Q-LD performed the statistical analyses and drafted the manuscript. W-FZ assisted in the experiment. All authors commented on the submitted version.

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Fan et al. Hydraulic Architecture of Populus euphratica

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Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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