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ORIGINAL ARTICLE

Coordination of stomatal control and stem water storage on plant water use in desert riparian trees

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Abstract

Populus euphratica Oliv. is a relatively 'conservative' water user even when growing in favourable water conditions, but the mechanistic understanding of this has received little attention. We undertook an experiment to determine trees water use by measuring stem and root sap flow (F_s), variation in stem diameter (D_s), leaf stomatal gas-exchange (e.g. conductance, g_s and transpiration, T_r) and water potential (ψ_L) during the growing season for *P. euphratica*. There was a hysteretic 'apparent feedforward' of stomatal response to increasing VPD. Mean of g_s was not significantly different among months. ψ_L was negatively related to g_s and T_r, but in contrast, stem F_s was positively associated to T_r but not to g_s. There was no lag in the daily onset and cessation of F_s between the bottom and top of the trunk, possibly due to the short distance between measurement points (about 2 m), however, the lag time in F_s between the bottom of the trunk and roots, approximately 30 min, suggested that stored water was withdrawn first from the trunk and subsequently the roots. Daily contraction of D_s $(-D_s)$ increased with increasing F_s during both day and night, and expansion of D_s $(+D_s)$ showed a logarithmic rise to a maximum with increasing F_s during the day. Day F_s and $-D_s$ were also logarithmic with respect to VPD, with a correlation coefficient equal to 0.51 and 0.50, respectively ($P<0.001$). This suggests that water use of *P. euphratica* was determined by the stomatal control and stem water storage together, which has great significance for the species buffers xylem water deficit, maintaining high leaf production, and water use efficiency.

Keywords Stem water storage · Stomatal control · Stem diameter variations · Sap flow · Riparian forest · *Populus*

Introduction

Under steady-state conditions, i.e. assuming plants are unbranched and lacking internal capacitance, whole tree water use can be determined by the soil-to-atmosphere water potential gradient and hydraulic resistance along the water transport pathway (van den Honert 1948), in which stomatal control plays a significant role in regulating water loss (Jarvis and McNaughton 1986; Meinzer 1993). However, it is well-known that most plants are not unbranched and have internal capacitance or water storage capacity (Goldstein et al. 1998; Köcher et al. 2013; Stratton et al. 2000; Tyree and Yang 1990). This suggests water uptake by roots has at least two ways out: (1) vertical upward movement into the atmosphere via stomata; and (2) radial movement of water to recharge storage tissue in the stem (Donnellan Barraclough et al. 2018). The functional linkage between leaf stomatal control and stem water storage has been the subject of numerous studies in seasonally dry tropical forest trees (Brodribb et al. 2003; Meinzer 2002; Meinzer et al. 2008; Pfautsch et al. 2011), but there has been less focus on riparian trees in arid environments (O'Grady et al. 2009).

The presence of apical stem water storage may allow leaves to maintain a water potential amenable to carbon uptake throughout the day (Goldstein et al. 1998; Stratton

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et al. 2000). Moreover, discharge and recharge of internal capacitances appears to provide a signal for stomatal closure preventing runaway embolism (Nardini and Salleo 2000), and generating dynamic changes in apparent leaf-specifc conductance via the variation of leaf water potential (Meinzer 2002; Meinzer et al. 2008). At the whole-tree level, stem water storage recharge is able to help alleviate unfavourable water potential gradients (Tyree and Yang 1990). Conversely, water storage discharge may buffer the system by reducing the xylem pressure decline when transpiration increases, allowing sufficient time lags for stomatal closure with the onset of drought stress, and potentially preventing xylem embolism during water deficit (Domec and Gartner 2001; Ogasa et al. 2013; Zeppel et al. 2014).

Populus euphratica Oliv. is a typically phreatophyte, mainly distributed across riparian areas or in areas with access to water tables in arid regions of Central Asia and, therefore, it does not typically experience soil drought (Thomas et al. 2008). *Populus euphratica* is considered the only dominant species of the riparian forests in these regions and plays an important role in protecting the basin ecosystem, preventing desertification and conserving biodiversity. However, with the excessive use of water resources by human being, the *P. euphratica* forest has declined in extent in recent decades (Wang 1996). Therefore, knowledge of the water use of *P. euphratica* and its control mechanisms is important to protect and restore this endangered species. Previous studies have shown that it has a relatively 'conservative' water use even when it grows under favourable water conditions (Pan et al. 2016). Little is known about how this species regulates its water loss. Some researchers suggest that down-regulation of stomatal sensitivity to leaf-to-air water–vapor pressure has a significant contribution to its conservative water use (Gries et al. 2003; Overdieck et al. 2013; Thomas et al. 2008), but others found that vapor pressure deficit (VPD) has a limited effect on variation of sap flow (Si et al. 2007; Yu et al. 2016; Zhao et al. 2017), suggesting that tree water use is potentially regulated by other biological processes, such as stem water storage, instead of stomatal control solely.

Recently, we observed substantial nocturnal sap flow in *P. euphratica* (Yu et al. 2016), of which approximately 80% was attributed to stem storage recharge (Yu et al. 2018). Therefore, we expected that water use of *P. euphratica* could be determined by leaf stomatal control and stem water storage together. Specifically, we aimed to demonstrate (1) the occurrence of stem water storage based on the hysteresis in sap flow across different plant path lengths (trunk and roots) and external climate drivers (e.g. VPD); (2) plant water use was determined but not entirely by climate drivers via stomatal control; and (3) leaf stomatal control can be coordinated with stem water storage to determine plant water use.

Materials and methods

Site and plant material

The study area was situated in the lower reaches of Heihe River Basin, NW China, normally referred to as the Ejin Oasis. The climate is extremely arid exhibiting a ratio of mean annual precipitation (37.0 mm) to mean annual pan evaporation (2216.5 mm) of <0.02 mm mm^{-1} (Yu et al. 2019). Mean monthly air temperature at the Ejin meteorological station ranges from − 11.5 °C in January to 27.0 °C in July, 1957–2016. This study was conducted at the Qidaoqiao *P. euphratica* Forest National Natural Refuge, Ejin county, Inner Mongolia, lat 42°59′N, long 100°10′E, 920.5 m AMSL (Si et al. 2007).

The study site is characterized by young *P. euphratica* trees (average 38 year) with a stand density of 350 trees ha^{-1} (Yu et al. 2019). Eighty of the total 350 trees within the 100 m × 100 m quadrat were measured for height (m), diameter at breast height (DBH, cm) and projected crown area (A_c, m^2), and subsequently sapwood area (A_s, cm^2) was estimated from a previously-published relationship between A_s and DBH for the site (Si et al. 2009). Four trees were selected to measure trunk diameter variation and sap flow, and A_s was calculated by increment cores at the end of the experiment. The traits of the four selected trees were not significantly different to the stand means (*t*-test, $P > 0.1$) (Table 1).

Meteorological and hydrologic parameters

Meteorological variables, including net radiation (R_n, W m^{-2}), air temperature (T_a, °C), relative humidity (RH, %), and wind speed (U, m s^{-1}) were recorded at a height of 20 m using a CR3000 datalogger at 0.5 h intervals in 2014

Table 1 Summary of biological parameters for four selected *Populus euphratica* trees and quadrat (Mean ± SE) with the size of 100 m × 100 m for this study area

Number	Height (m)	DBH (cm)	A_s (cm^2)	A_c (m^2)
1	12.6	23.9	225.8	12.6
2	12.4	21.7	189.3	18.2
3	11.7	25.2	248.6	13.1
4	12.3	32.2	388.7	20.7
Mean ± SE	12.3 ± 0.2	25.8 ± 2.3	263.1 ± 43.6	16.2 ± 2.0
Stand (*n* = 80)	11.8 ± 0.2	24.7 ± 0.5	246.1 ± 9.8	16.5 ± 0.8
Sig. (2-tailed)	0.103	0.675	0.723	0.682

Difference was tested by the one-sample *t* test at a significance level of $P = 0.05$

DBH Diameter at breath height, A_s sapwood area, A_c projected area of crown in the *P. euphratica* stand (Yu et al. 2019). Total precipitation was acquired from the nearest meteorological station located in Ejin city, 20 km from the study site. VPD (kPa) was calculated from T_a and RH, and mean daily VPD was not significantly different from that simultaneously measured at the average canopy height (8 m) in 2017 ($P = 0.71$). The depth to the groundwater table (*GWT*, m) was measured automatically by pressure transducers (HOBO-U20, Onset Computer Corporation, Bourne, MA, USA) at 0.5 h intervals. *GWT* decreased gradually until a minimum of 2.22 m on the 18th September, 2014, after which it increased suddenly to 158 mm above ground following a flooding event (Yu et al. 2019).

Stem diameter and sap flow

Four selected *P. euphratica* trees (Table 1) were used to measure stem diameter variation (D_s, *u*m) at breast height (1.3 m) using point dendrometers (DD-L, Ecomatik, Germany) during the growing season from May through 16 October (168 days), 2014. D_s was separated into two phases: a contraction phase ($-D_s$) and an expansion phase ($+D_s$) following Xiao et al. (2014). Owing to the failure of power to the datalogger, D_s data from 26 May through 16 June (12%) were lost.

Owing to limitations of the instruments, three of the four selected trees (No. 1 to 3, Table 1) were used to measure sap flow using the heat ratio method (SFM1, ICT Inc., Armidale, Australia). Sensors were radially inserted into the xylem tissue of the trunk (canopy break and DBH, 3.5 m and 1.3 m height, respectively) and root (0.3 m depth) on the north side of the selected trees. After insertion, the exposed cambium was covered with aluminium foil to reduce the effects of ambient temperature fluctuation and direct solar radiation. Heat pulse velocity (V_h, cm h^{-1}) was recorded and all corrections related to probe wounds and misalignment were made according to Burgess et al. (2001). Sap velocity (V_s, cm h^{-1}) was also calculated following Burgess et al. (2001). Because the sapwood depths (26 ± 1.0 mm) were less than the needle lengths (35 mm), V_s of the inner depth measurement point (7.5 mm from the tip of the needle) was always low and smooth, and even negative (data not shown), suggesting that the probe was inserted in heartwood. Thus, V_s of the outer measurement point (22.5 mm from the tip of the needle) was only selected for analysis. All raw data were continuously recorded at 0.5 h intervals using a microSD card.

Zero flow could not be determined by tree xylem cutting methods because the research site was located in a national nature reserve (Yu et al. 2013). Instead near-zero sap flow was assumed during a night (3 June 2014) with low T_a and extended rainfall (17.2 mm in 3 h), causing VPD to be the lowest (< 0.18 kPa for 3 h) throughout the entire measurement campaign. Recorded V_s ceased quickly with the onset of rainfall and then stabilized at the lowest recorded velocities (1.6 cm h^{-1}). The A_s for each selected tree (Table 1) was calculated using measurements of sapwood depth from four increment cores at the same height but different aspects, extracted from each tree after completion of sap flow measurements. Whole tree sap flow (F_s, L h^{-1}) was calculated as the product of A_s and V_s of the outer measurement point (calculated as the mean of radial variation given the slight difference along the radius of stem section) (Si et al. 2007), and integrated over 24 h to give daily F_s (L d^{-1}).

Leaf gas-exchange and water potential

Three scaffold towers 2 m high were set up to access tree crowns for leaf measurements on selected trees. Once a month on clear sunny days (from June 17th to 19th, July 18th and 24th to 25th, August 24th to 26th, and September 11th to 13th) during the growing season, 2014, field experiments were conducted to determine diurnal variation in leaf gas exchange of the three selected *P. euphratica* trees. Three healthy, fully expanded leaves on each selected tree were marked and measured continuously under ambient conditions using a portable gas-exchange system (LI-6400XT, LI-COR Biosciences Inc., USA) at 1 h intervals during days and at 2 to 3 h intervals during the nights of 18th and19th June. For each measurement period, the leaf level photosynthesis (A_n, mmol H_2O m^{-2} s^{-1}), transpiration (T_r, mmol H_2O m^{-2} s^{-1}), stomatal conductance (g_s, mol H_2O m^{-2} s^{-1}) and environmental factors were calculated. Diurnal variation in leaf water potential (ψ_L, MPa) was measured on three leaves collected from each tree to the west, south, and east of the crown. Samples were wrapped in a sealed plastic bag with moist paper towel before cutting from the petiole with a razor blade, to prevent sudden dehydration under high temperature conditions. ψ_L was measured immediately using a plant pressure chamber (1505D, PMS Instrument Co., Albany OR, USA).

Statistical analysis

The mean and standard error (SE) of all variables were calculated. The difference between biological parameters (height, DBH, A_s and A_c) of the selected trees and population means was tested using a one-sample *t*-test at a significance level of $P = 0.05$. The differences in means of leaf gas exchange variables and ψ_L among the months was examined via repeated-measures ANOVA at significance level of $P = 0.05$ in conjunction with Tukey's post-hoc test for continuously measured data. Pearson's correlation was applied to examine the correlations between paired variables (trait-to-trait or trait-to-climate). Given that the different response of plant physiology to envrionmental factors, a linear modelling was performed to assess the relationship between $-D_s$ and $+D_s$, $-D_s$ and F_s, F_s and VPD in the night; and a sigmoidal model with 3 parameters ($f = a/(1 + \exp(-(x - x_0)/b))$) was fitted to assess the relationship between $+D_s$ and F_s and VPD, F_s and gs, T_r, and ψ_L. All statistical analyses were performed with the software package SPSS Statistics (version 19.0; IBM, Armonk, NY, USA).

Results

Stem radial variation and sap flow

Diurnal increases in V_s preceded VPD increase in the mornings. Variation in D_s was the opposite to both of V_s and VPD (Fig. 1). The time of onset (6:30 am) and cessation (6:00 am, the next day) of V_s was roughly equivalent to D_s, but the pattern of diurnal variation was obviously different, in that V_s increased quickly in the morning hours when VPD was less than 2.0 kPa, and stabilized until VPD had increased to the maximum of 4.0 kPa. After this V_s decreased quickly until around 23:00, and subsequently more slowly, with a significant difference in in the slope of the relationship early and later in the day ($P < 0.001$). In contrast, D_s initially decreased until around 14:00 and then increased gradually during the afternoon and into the evening. There were differences in the time of onset of increasing D_s between two days (14:00 pm v.s. 19:00 pm), but not in when D_s started to decrease (6:00 am).

Seasonal variation of daytime F_s (Fig. 2d) was also consistent with R_n, T_a (Fig. 2a) and VPD (Fig. 2c). It increased rapidly to a maximum in June and decreased gradually with declining R_n, T_a, VPD and the groundwater table especially after 10 days flooding (Fig. 2f). At night F_s was always stable throughout the growing season (Fig. 2d). RH was interrupted by rainfall and was negatively related to U (Fig. 2b, c). Heavy rainfall events had a greater effect on RH and subsequent F_s than light events (abrupt drop in mid-June, Fig. 2d). Contraction of D_s was higher than the expansion of D_s in May to mid-July, after which contraction and expansion were almost consistent with each other (Fig. 2e).

In the hottest period, mid-July, the F_s measured at the bottom of the trunk was generally lower than at the top of the trunk in both day and night, but F_s in the stem was lower than that in roots during the day, and higher at night. Whether in the stem or roots, maximum F_s was always stable during the day especially on days with high VPD, but during the night the trend in F_s was similar to VPD and the opposite of D_s (Fig. 3a-c). There was no hysteresis in F_s between the top and bottom of the trunk and slight hysteresis (0.5 h) between stem and roots with a counterclockwise pattern observed (Fig. 3d), suggesting F_s at both the top and bottom of the trunk was activated earlier than in the roots. However, a clockwise pattern was observed between F_s and D_s at the bottom of the trunk, suggesting F_s was activated earlier than D_s (Fig. 3e). Apparently D_s remained constant with increasing F_s in the morning and then dropped with constant F_s in the afternoon, and increased linearly with decreasing F_s in the evening (Fig. 3e). Hysteresis relationships between stem D_s, F_s either in stem or roots and VPD were consistent, with a clockwise hysteresis observed between VPD and D_s and F_s, suggesting VPD was increased earlier than both of F_s and D_s (Fig. 3e, f).

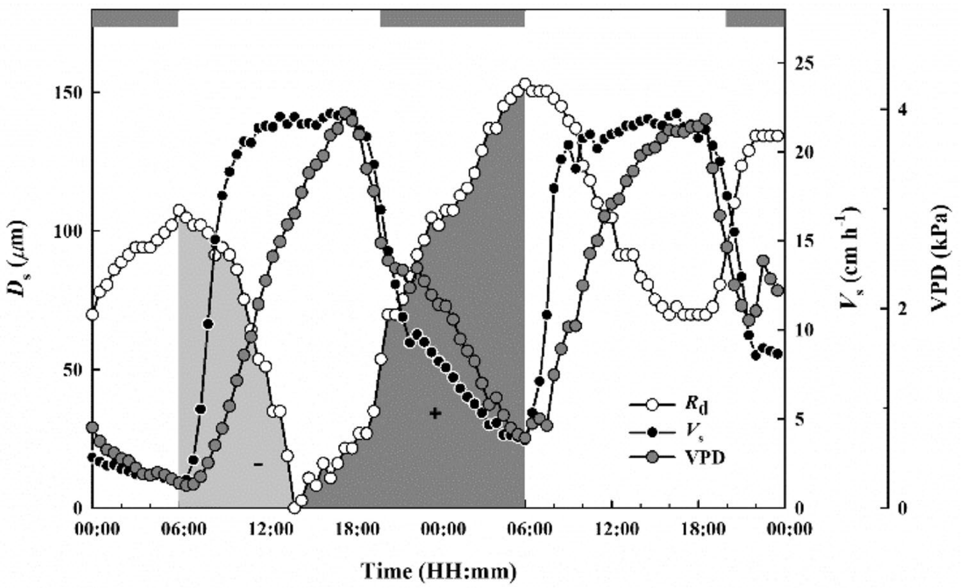


Fig. 1 Diurnal variation of stem diameter (D_s, μm), sap velocity (V_s, cm h^{-1}) and vapor pressure deficit (VPD, kPa) during the typical sunny days (June 19th to 20th, 2014). The D_s was separated to two section: contraction (−, grey) and expansion (+, dark grey) phase. The night was represented by the grey horizontal bar at the top. These data were collected synchronously with the consecutive 2 days measurement of leaf gas exchange and water potential

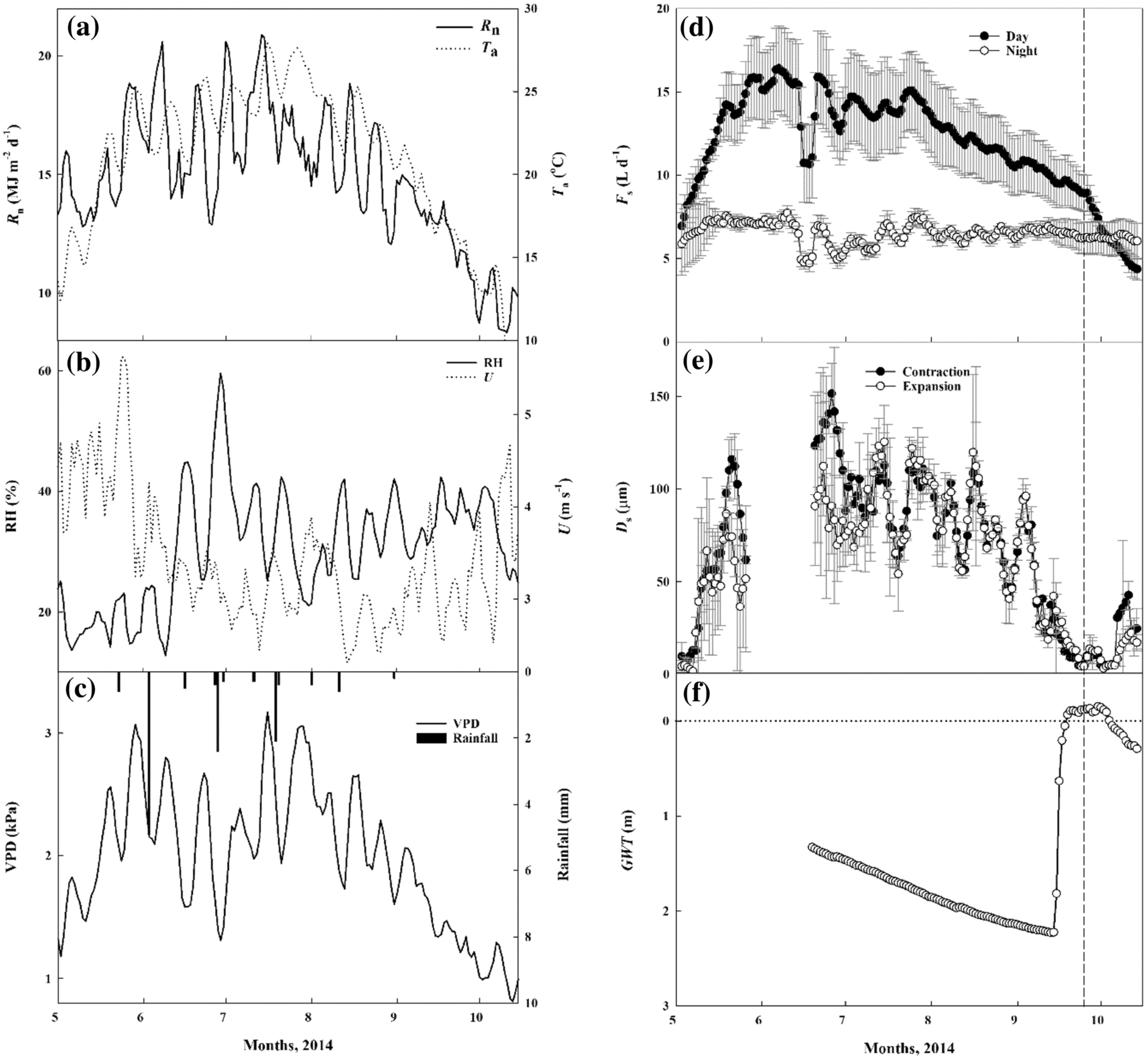


Fig. 2 Seasonal variation of the 5-days mean of **a** net radiation (R_n), air temperature (T_a), **b** relative humidity (RH), wind speed (U), **c** vapor pressure deficit (VPD) and rainfall, **d** stem sap flow (F_s) at day and night, **e** stem diameter variation (D_s) at contraction and expansion phase, and **f** groundwater table (*GWT*) for the *P. euphratica* forest during the growing seasons, 2014

Leaf gas exchange and leaf water potential

Diurnal variation in leaf gas exchange (g_s, A_n and T_r), ψ_L, VPD and F_s was also different among the months (Fig. 4). Conductance, g_s, increased quickly from the onset of daylight until 11:00 and decreased gradually into the night, with a slight increase heading into dawn in June (Fig. 4a). Photosynthesis, A_n, lagged behind g_s with a lower value and midday depression observed in June and July than in the following two months (Fig. 4b). Transpiration, T_r, increased in the morning until the peak at around 14:00, after which it decreased symmetrically in the afternoon and into the evening (Fig. 4c). Mean ψ_L showed the opposite pattern to T_r during the day, with a minimum of − 2.3 MPa in July, which increased to close to − 0.2 MPa in the evening in June (Fig. 4e). Hourly F_s did not change much during day, but quickly decreased into the evening (Fig. 4f). This was consistent with the decreased VPD at night (Fig. 4d). There was a hysteresis and time dependence 'apparent feedforward' (Fig. 5), i.e. the relationship between transpiration (T_r) and water potential (ψ_L) and VPD depended on the time of day, such that the same VPD yielded higher T_r and ψ_L in the

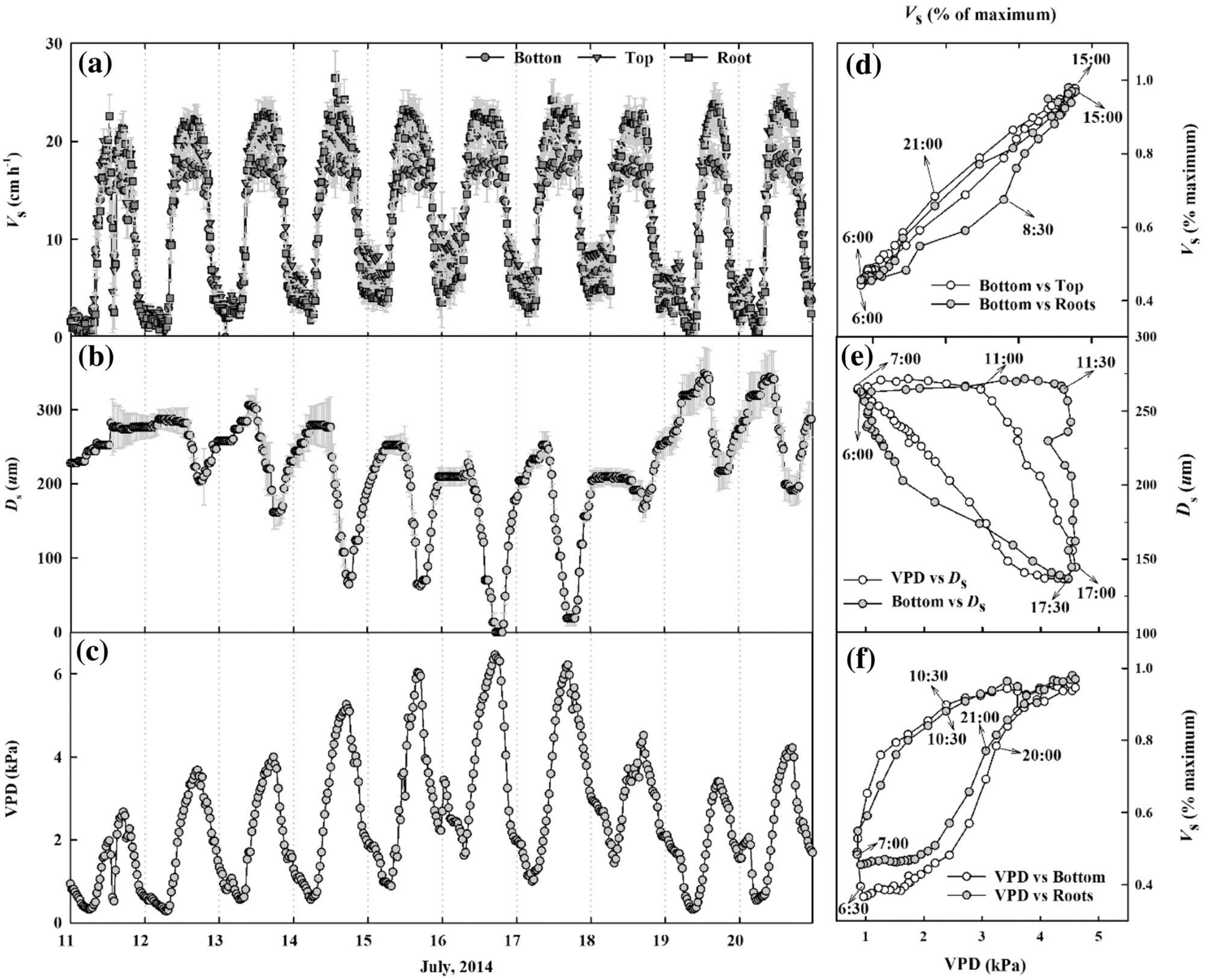


Fig. 3 Diurnal changes in **a** sap velocity (V_s) at the bottom and top of the trunk and the roots, **b** the normalized stem diameter (D_s) by minimum of days, **c** vapor pressure deficit (VPD), and the hysteresis **d** between the ten-days mean of normalized V_s by maximum at the bottom and top of the trunk and the roots, **e** D_s and **f** VPD with during the summer (July 11 to 20), 2014

morning than in the afternoon, and when VPD increased beyond a certain point, there was decreasing T_r and hence reducing ψ_L. With the exception of g_s, daily mean A_n, T_r and ψ_L were significantly different among months during the growing season (Table 2). A_n steadily increased over time although the difference was not significant between August and September. In contrast, T_r increased initially until it reached a maximum in July, after which it decreased, in contrast to the trend observed for ψ_L.

The relationship between stem water storage, water use and environmental variables

Daily stem water storage discharge as represented by $-D_s$ was linear associated with increasing F_s both during the day ($P < 0.001$) and night ($P = 0.0013$) (Fig. 6a). Stem water storage recharge, as represented by $+D_s$, was significantly sigmoidal ($P < 0.001$) in the day but not at night F_s (Fig. 6b). F_s showed an exponential increase with increasing VPD to a maximum during the day ($P < 0.001$) and a linear increase with increasing VPD at night (Fig. 7). Discharge ($-D_s$) was also significantly sigmoidal ($P < 0.001$) associated with increasing VPD (Fig. 8a), and $+D_s$ was significantly linear ($P < 0.001$) associated with -D_s (Fig. 8b).

At the leaf level, A_n and g_s were positively correlated with T_r, and all leaf-level variables were negatively correlated with ψ_L ($P < 0.05$). Stem F_s was also positively correlated with T_r and negatively with ψ_L ($P = 0.001$) (Table 3). Hourly Ψ_L always decreased with increasing g_s or T_r, but the relationships were significantly different among months, of which ψ_L decreased in June and July in a curvilinear relationship with increased g_s, but with a linear relationship in August and September

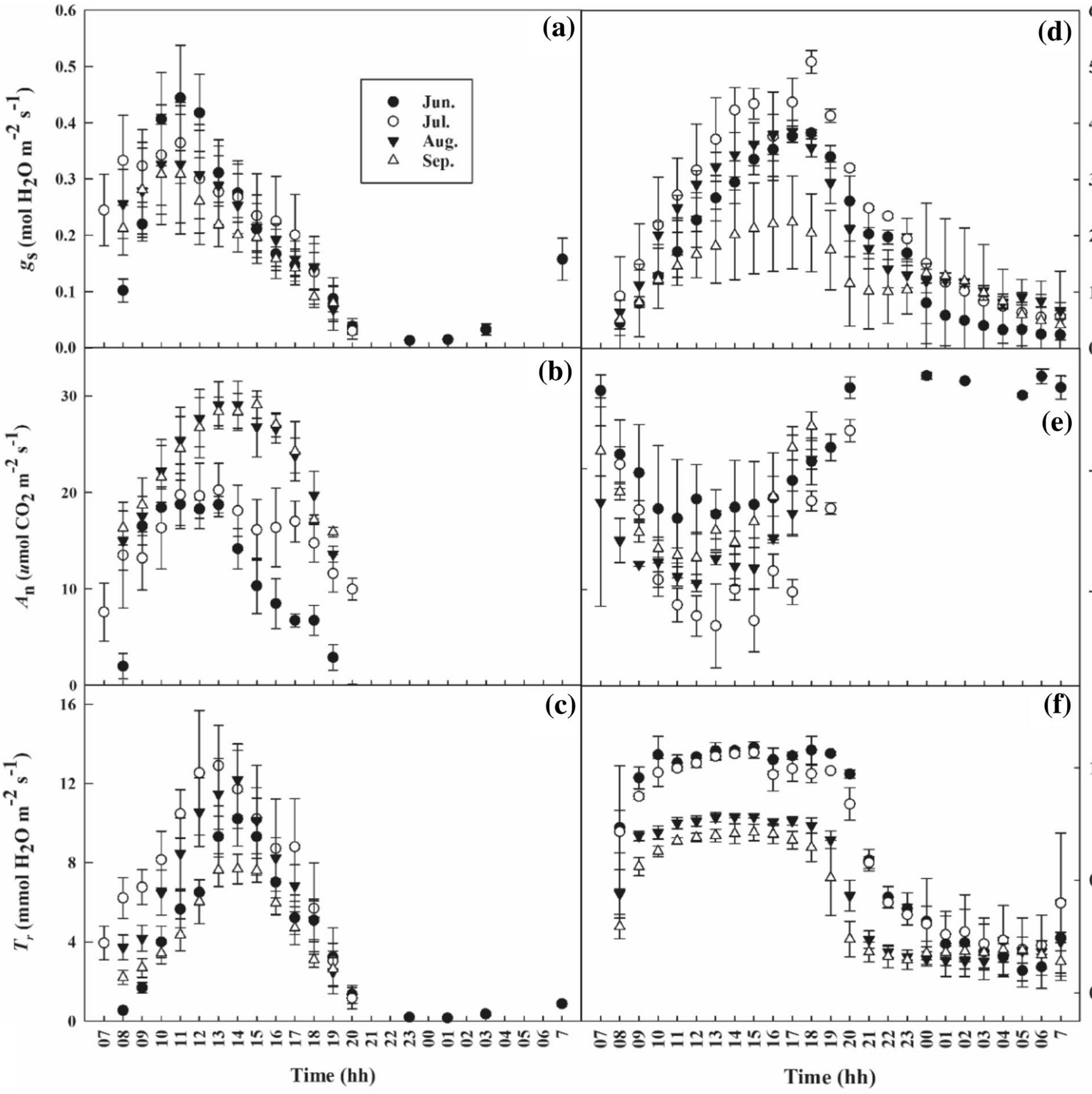


Fig. 4 Hourly change of leaf **a** stomatal conductance (g_s), **b** photosynthesis (A_n), **c** transpiration (T_r) and **d** vapor pressure deficit (VPD), **e** leaf water potential (ψ_L) and **f** stem sap flow (F_s) at different months during the growing season, 2014

(Fig. 9a). ψ_L decreased exponentially with increased T_r in July but the decrease was linear in June (Fig. 9b). There was no significant relationship between stem F_s and leaf g_s (Fig. 9c), that potentially was confounded by stem water storage. Stem F_s was significantly related with T_r except in July (Fig. 9d).

Discussion

Numerous researchers have shown that plant water use is the result of a strong coordination between the systems

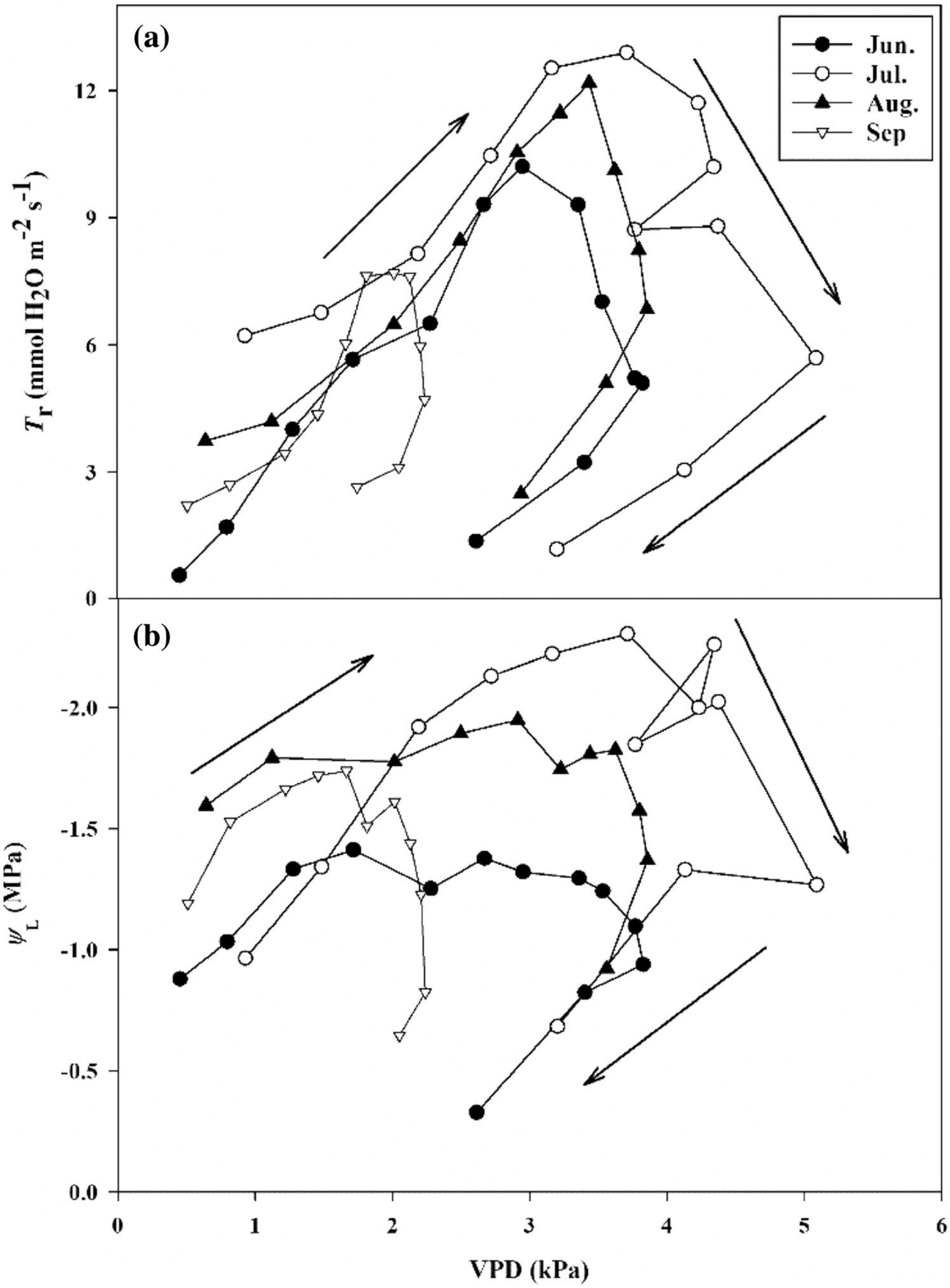


Fig. 5 A hysteretic 'apparent feedforward' relationship between (a) transpiration (T_r) and (b) water potential (ψ_L) and evaporative demand (VPD). Arrows indicate the order in which data points were obtained

Table 2 Seasonal variations of daily mean ± SE ($n = 12$) of leaf gas exchange parameters included photosynthetic (A_n, mmol CO_2 m^{-2} s^{-1}), stomatal conductance (g_s, mol H_2O m^{-2} s^{-1}), transpiration (T_r, mmol H_2O m^{-2} s^{-1}) and water potential (ψ_L, MPa) during the growing season, 2014

Months	Jun.	Jul.	Aug.	Sep.
A_n	7.24 ± 0.77^a	16.38 ± 0.80^b	23.05 ± 1.56^c	23.17 ± 1.45^c
g_s	0.25 ± 0.02^a	0.26 ± 0.03^a	0.23 ± 0.02^a	0.21 ± 0.02^a
T_r	3.65 ± 0.44^a	8.77 ± 0.86^b	7.49 ± 0.92^c	4.84 ± 0.60^d
Ψ_L	-1.17 ± 0.06^a	-1.80 ± 0.13^b	-1.63 ± 0.09^c	-1.33 ± 0.11^d

The different alphabets represent the significant difference among the months (repeated-measures ANOVA, $P = 0.05$)

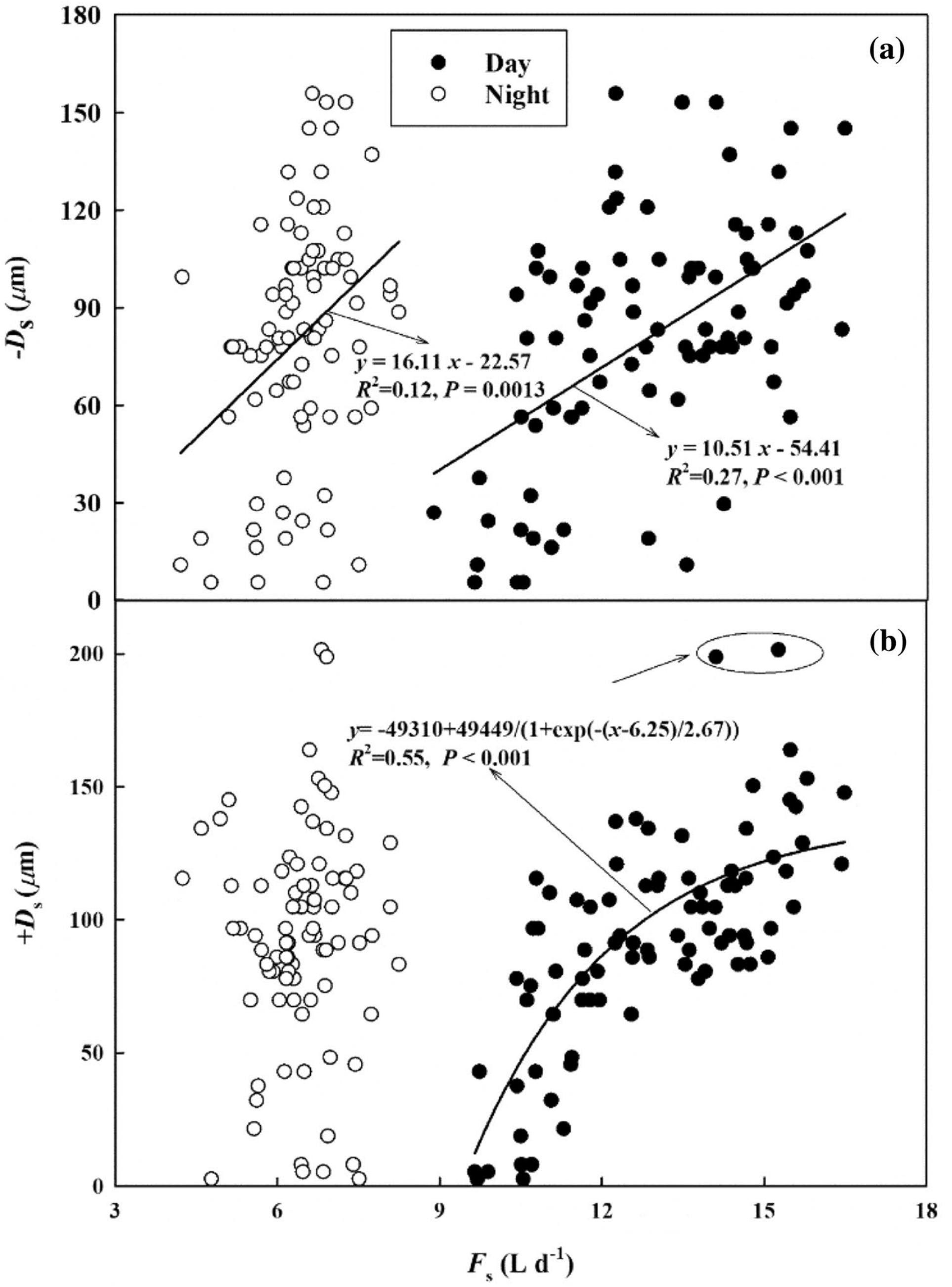


Fig. 6 Daily stem diameter **a** contraction ($-D_s$) and **b** expansion ($+D_s$) as a function of sap flow (F_s) at day and night. The fitting line, determination coefficient (R^2) and significance level (P) were shown. The outlier in **b** was induced by the high U at night

regulating water delivery (xylem) and water loss (stomata) (Brodribb et al. 2003; Meinzer 2002; Meinzer et al. 2009, 2008; Pfautsch et al. 2011). This study supported our hypothesis that (1) stem water storage occurred based on the hysteresis among the sap flow along different water pathways, stem diameter variation and meteorological factors (e.g. VPD) (Figs. 1, 3); (2) stomatal control has great significance but is not the sole driver of leaf and whole-tree water use (Table 3; Figs. 4, 5, 6); and (3) trees can use tissue-stored water preferentially but not immoderately, and this is strongly controlled by stomatal behavior suggesting g_s can be coordinated with stem water storage to determine plant water use (Figs. 7, 8, 9).

Stem water storage

There is some controversy around using branch and basal trunk sap flow measurements alone to estimate whole-plant water storage (Burgess and Dawson 2008; Phillips et al. 2009), because lags between crown transpiration and basal sap flow have been observed in some species (Čermák et al. 2007; Goldstein et al. 1998; Köcher et al. 2013), but not in

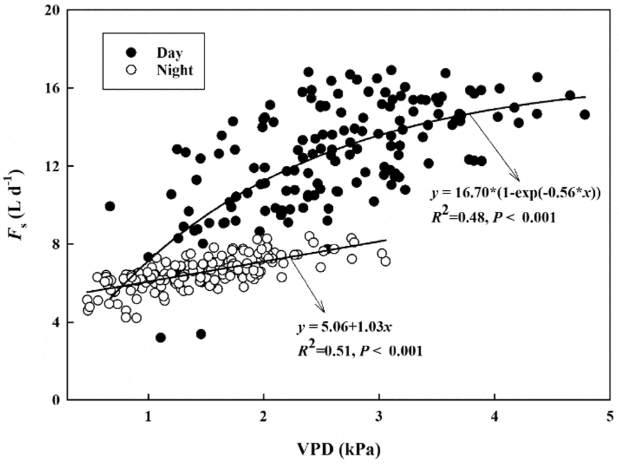


Fig. 7 Daily sap flow (F_s) as a function of vapor pressure deficit (VPD) during day and night

others (Burgess and Dawson 2008; Pfautsch et al. 2011). Other than sap flux, measurements of stem diameter variation are among the most useful plant-based measurements to evaluate plant water consumption, and indicate the discharge and recharge of internal stores (Čermák et al. 2007; Scholz et al. 2008; Zweifel et al. 2001). Observations from other studies suggest that the patterns of water use within a plant can be better understood by combining sap flow and stem diameter variations measurement (Köcher et al. 2013; Sevanto et al. 2008).

For *P. euphratica*, there was no phase shift between the traces at the bottom and top of the trunk, at least within the 30 min resolution period of our data (Fig. 3d). This may be a result of the short distance between measurement sites on the main trunk (about 2 m). Such a height effect on diurnal water storage has been observed in other tree species (Goldstein et al. 1998; Köcher et al. 2013). Even so, we conclude that the discharge and recharge of stored water for the studied species occurred as illustrated by the following:

First, we observed a 'plateau effect' in sap flow (Figs. 1, 3a) just as in many other species (Goldstein et al. 1998; Scholz et al. 2008), especially wet–dry tropical savanna ecosystem (Eamus et al. 2000; O'Grady et al. 2009, 1999; Pfautsch et al. 2011). This suggests that the discharge of stem water, evidenced by quickly declining D_s at the same time in the study (Figs. 1, 3b), can maintain maximum or near maximum transpiration rates for a longer period of time (Eamus et al. 2000; Goldstein et al. 1998; Pfautsch et al. 2011). The time of stable sap flow was about 9–10 h (Figs. 1, 3a), similar to *Eucalyptus victrix* in semi-arid regions (Pfautsch et al. 2011).

Second, there was a slight hysteresis between F_s in the bottom of the trunk and the roots (Fig. 3b). It is well-known that stored water is withdraw firstly from branches, and subsequently stem and roots, although we did not measure this for branches in our study. The apparent lag of approximately 30 min between F_s in stem and roots, was consistent with savanna trees, in which root diameter declined about 40 min after changes were observed at the base of the stem (Scholz et al. 2008).

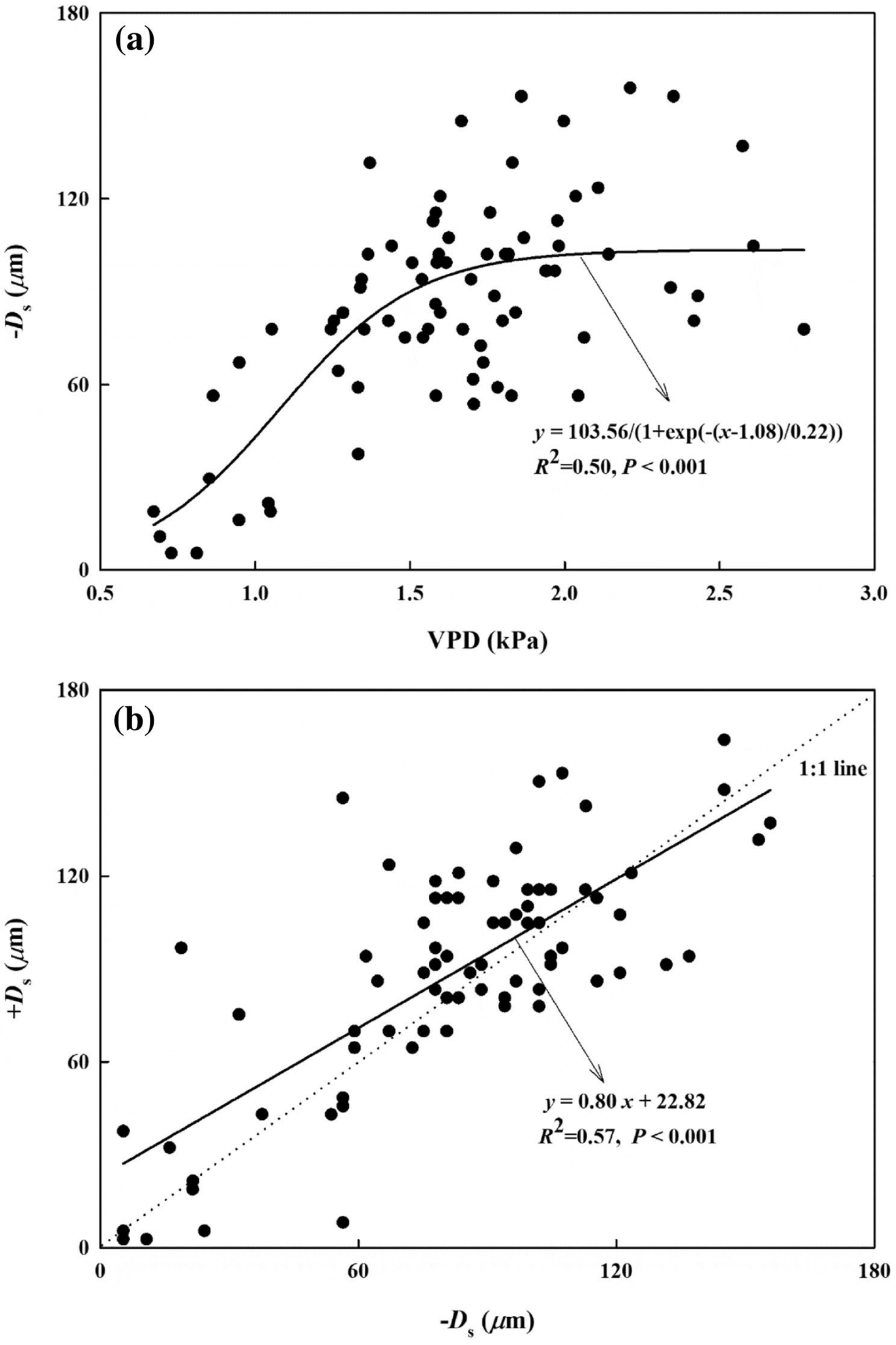
Third, the stem diameter variation (D_s) was large (Fig. 2b) and closely related to F_s (Fig. 5), suggesting that discharge of and recharge to stem stored water occurred (Zeppel et al. 2014; Zweifel et al. 2001). The large daily amplitude of variation in whole-stem diameter (Fig. 2b) in our study was similar to whole-stem diameter variation in Cerrado trees (Scholz et al. 2008) and previous measurements on radius variation for *P. euphratica* (Xiao et al. 2014). The strong relationship between stem diameter variation during the contraction phase ($-D_s$) and VPD (Fig. 7a) and $+D_s$ (Fig. 7b) also suggest the daily discharge and recharge of stored water (Scholz et al. 2008).

Stomatal and stem hydraulic regulation on diurnal water use

It has been shown that components of the tree water transport pathway (roots, trunks, branches and leaves) can also serve as water storage compartments (Scholz et al. 2011). Thus, the amount of water that is withdrawn and used on a daily basis will not only depend on the environmental conditions experienced by the plant, but also on stomatal regulatory behaviour and water storage (Meinzer et al. 2009; O'Grady et al. 2008; Scholz et al. 2011).

Hysteresis in the relationship between diurnal sap flow (or tree water use) and environmental factors (e.g. VPD) has been observed in a number of species (Hogg and Hurdle 1997; Meinzer et al. 1997; O'Grady et al. 1999, 2008; Zeppel et al. 2004), including old-aged *P. euphratica*, in which V_s came in advance of VPD by 0.5 h (Li et al. 2016). The potential reasons for hysteresis can be related to either increased water use in the morning (e.g. water storage capacity, 'stem hydraulic regulation') or reductions in the afternoon (e.g. stomatal response to environmental factor, 'stomatal regulation'). The reason for declining water use in the afternoon have been explained as associated with stomatal sensitivity to VPD (Hogg and Hurdle 1997; Meinzer et al. 1997; O'Grady et al. 1999; Zeppel et al. 2004). Previously, the stomatal sensitivity to VPD was attributed to increased resistance in the soil-plant-atmosphere continuum, and more precisely to increased leaf resistance, given that it accounts for 30%–90% of whole-tree resistance (Brodribb and Holbrook 2006) with declining ψ_L (Brodribb and Holbrook 2006; Buckley 2005; O'Grady et al. 2008). However, this explanation was not consistent with the observation in the current study that g_s and T_r did not decrease significantly with increased VPD and/or decreased ψ_L (Fig. 4; Table 2).

Fig. 8 Relationship between contraction of stem diameter ($-D_s$) and **a** vapor pressure deficit (VPD), and **b** expansion of stem diameter ($+D_s$)



If, following a reduction in VPD, embolism repair lagged behind the recovery of leaf water status, then the trajectory of T_r vs VPD was altered (Buckley 2005).The high T_r during the hottest months was consistent with high F_s (Fig. 4), which perhaps is necessary to avoid overheating, particularly for plants from hot dry habitats (Lin et al. 2017). This suggests that trees must withdraw more water (from soil and/or tissues) to prevent the catastrophic decline in ψ_L (Fig. 4e). Obviously, constant and steady flow (i.e. the 'plateau effect', Figs. 1, 3a) may not be met by root uptake ('steep' pattern of V_s) (Fig. 3a), but by the intermediate sources of water from stem water storage for transpiring leaves (Goldstein et al. 1998; Stratton et al. 2000).

Populus euphratica, has an 'anisohydric' behaviour (Fig. 4e), that seems to use an 'apparent feedforward' mechanism (Buckley 2005) to control its water use under

Table 3 The Person's coefficient between leaf A_n, g_s, T_r, ψ_L and stem sap flow (F_s) with all data pooled

Pearson's coefficient	g_s	T_r	Ψ_L	F_s
A_n	0.09^{ns}	0.62^{**}	-0.63^{**}	-0.01^{ns}
g_s		0.30^{*}	-0.48^{**}	0.19^{ns}
T_r			-0.74^{**}	0.53^{**}
Ψ_L				-0.45^{**}

Definition of variables was same as Table 2

ns $P > 0.05$; * $P = 0.01$; **$P = 0.001$

high evaporative demand in arid environments (Fig. 5). In addition, VPD had not completely determined influence on sap flow or stem diameter variation in this study (Figs. 7, 8a), in line with the previous work on *P. euphratica* (Li et al. 2016; Xiao et al. 2014; Yu et al. 2018, 2016), suggesting that the water use of this tree was partially regulated by the transpirational demand (VPD), and hence stomatal control (Fig. 9). In addition, the positive relationship between F_s and stem diameter variation (D_s) (Fig. 6) suggests increased sap flow was partly used to recharge stem water storage, and subsequent compensates the sap flow under high transpirational demand. This supports the hypothesis that water storage capacity or hydraulic capacitance play an important role in refilling the stem following depletion by transpiration (Ogasa et al. 2013; Scholz et al. 2011).

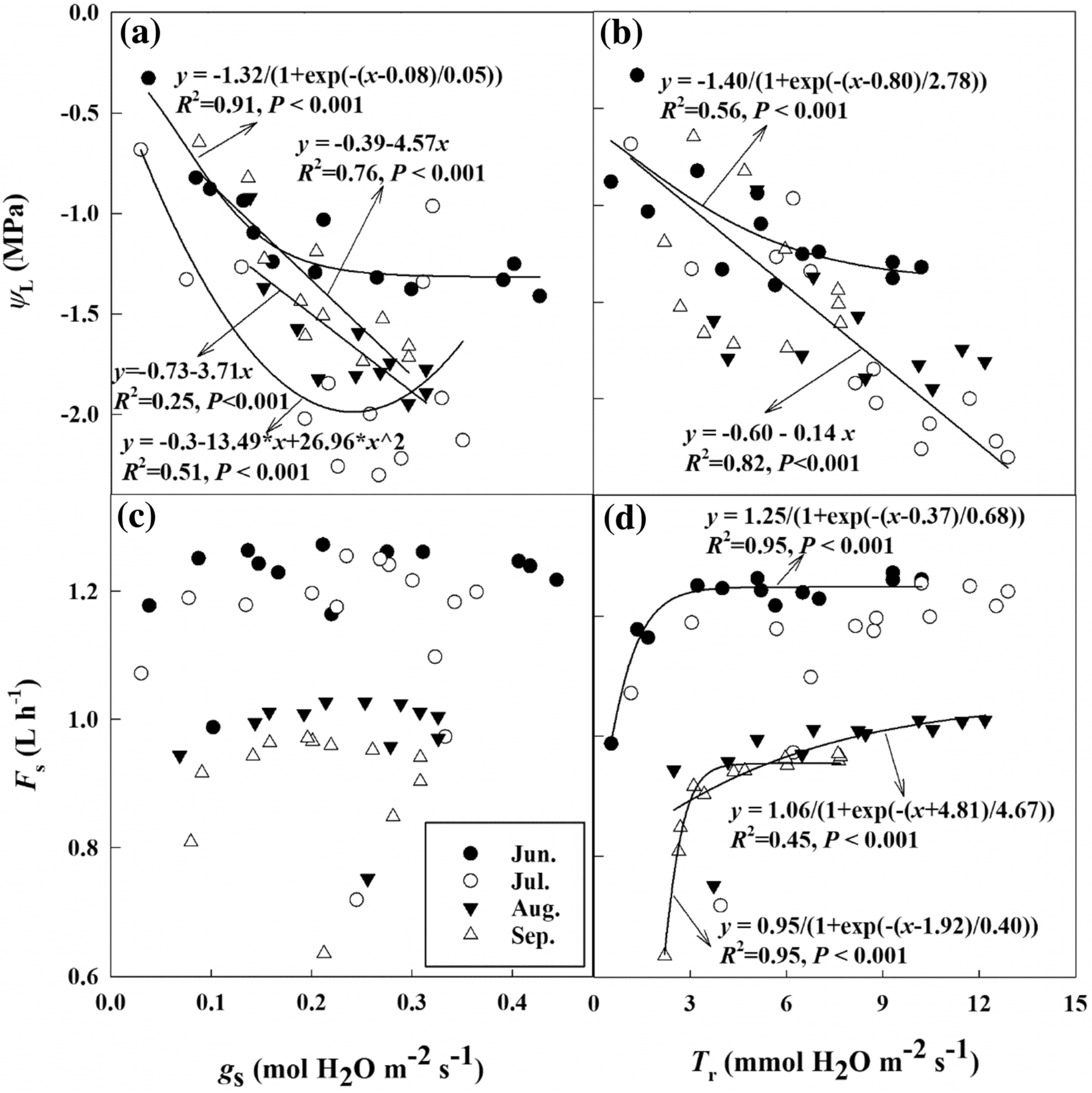


Fig. 9 Relationship between leaf stomatal conductance (g_s), transpiration (T_r) and leaf water potential (ψ_L) and sap flow (F_s). **a** g_s v.s. ψ_L; **b** T_r v.s. ψ_L; **c** g_s v.s. F_s; **d** T_r v.s. F_s; Data were pooled from 2 to 3 days of measurement for each month

The significance for tree growth

Midday minimum ψ_L (-2.3 MPa) in our study was similar to the woody phreatophytes in riparian areas of the arid zone (Gries et al. 2003; Zeng et al. 2006) included *P. euphratica* seedlings under drought (Li et al. 2012), but higher compared to typical desert plants (see review in Thomas et al. 2008). A lower ψ_L that induced 50% loss of hydraulic conductance (P_{50}, ~ -2.7 MPa), was reported for a shallower water table than deeper, suggesting a positive hydraulic safety margin defined as the difference between midday ψ_L and P_{50} (Pan et al. 2016). This suggests that in this study trees did not experience drought stress under the current water table. This may explain why seasonal variation of g_s remained constant during the whole growing season (Table 2) as it is strongly related to soil drought (Garnier and Berger 1987; Giorio et al. 1999). The early peak of g_s and subsequent gradual decline, while VPD continued to increase (Fig. 4), helps plants to minimize the risk of leaf cavitation (Brodribb et al. 2003; Goldstein et al. 1998; Pfautsch et al. 2011). Recently, a multi-layer porous media model predicted that the use of stored water remains constant as a result of water depleted in plant xylem tissues can be completely recovered to its previous state within a single diurnal cycle (Huang et al. 2017). This was supported by the stable nocturnal sap flow in the stem (Fig. 2d), which was substantially attributed to stem water storage (Yu et al. 2018). Because diameter expansion ($+D_s$), which of including the irreversible radial growth except the increases in stored water, was first increased and then declined, Thus, nighttime F_s is not related to $+D_s$ (Fig. 6b). This suggests coordination of stomatal control and stem water storage to buffer xylem water deficit, and subsequent prevention of embolism risk.

The A_n was greater in the late growing season compared with the early for *P. euphratica* (Fig. 4b; Table 2). It was consistent with that observed in the lower Tarim River (Chen et al. 2012), suggesting higher carbon uptake in the late growing season compared with the early (Thomas et al. 2008). However, T_r and g_s did not increase as A_n increased in study (Fig. 4b; Table 2), suggesting enhanced water use efficiency in the late growing season (Chen et al. 2012). Mean g_s (Table 2) was higher compared to the same species growing in the desert environment (Thomas et al. 2008), but similar to that determined in the riparian zones (Chen et al. 2012). High leaf A_n was inconsistent with low stem radial increment in the late growing season (See Fig. 2b for the indistinguishableness between $+D_s$ and $-D_s$). One possible explanation is that the carbohydrates synthesised by photosynthesis were transported downwards into the roots, as evidenced by increased belowground biomass and rooting depth with increasing groundwater table (Li et al. 2012). In all, insignificant difference in stomatal conductance during the growing season suggests the stomatal control has a limited effect on plant water loss. Alternatively, daily stem water storage from groundwater provides sufficient water supply for leaves to maintain high transpiration, thereby high photosynthesis and water use efficiency. In turn, transpiration reduces plant water potential that provides the water potential gradient needed to store the next day's water and limit losses to hydraulic redistribution (Yu et al. 2018).

Conclusions

Populus euphratica, a deciduous broad-leaved tree distributed in the riparian zone in arid regions of Central Asia, has a relatively 'conservative' water use strategy even when growing in the favourable water conditions, which was not solely attributed to stomatal regulation in contrast to the previous conclusion. The lag time in sap flow between the bottom of the trunk and roots and diameter variation suggests that stem water storage discharge and recharge occurred. The relationships between leaf gas exchanges, stem sap flow and/or diameter variation and meteorological factors demonstrate that the pattern of water use of *P. euphratica* was the coordination of leaf stomatal control and stem water storage. This has great significance for buffering xylem water deficit, preventing the risk of embolism, maintaining high leaf production, and water use efficiency.

Author contribution statement TY carried out the experiment, analysed the data, and wrote the first draft. QF and JS help to design the experiment and discuss the results. EAP helped to review and revise the article.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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