

Nighttime sap flow and its driving forces for *Populus euphratica* in a desert riparian forest, Northwest China

SI Jianhua^{1,2*}, FENG Qi^{1,2}, YU Tengfei^{1,2}, ZHAO Chunyan¹

¹ Alxa Desert Eco-hydrology Experimental Research Station, Cold and Arid Regions Environmental and Engineering Research Institute, Chinese Academy of Sciences, Lanzhou 730000, China;

² Gansu Hydrology and Water Resources Engineering Center, Lanzhou 730000, China

Abstract: Nighttime sap flow is a potentially important factor that affects whole-plant water balance and water-use efficiency (WUE). Its functions include predawn disequilibrium between plant and soil water potentials as well as between the increments of oxygen supply and nutrient uptake. However, main factors that drive nighttime sap flow remain unclear, and researches related to the relationship between nighttime sap flow velocity and environmental factors are limited. Accordingly, we investigated the variations in the nighttime sap flow of *Populus euphratica* in a desert riparian forest of an extremely arid region, Northwest China. Results indicated that *P. euphratica* sap flow occurred throughout the night during the growing season because of the partial stomata opening. Nighttime sap flow for the *P. euphratica* forest accounted for 31%–47% of its daily sap flow during the growing season. The high value of nighttime sap flow could be the result of high stomatal conductance and could have significant implications for water budgets. Throughout the whole growing season, nighttime sap flow velocity of *P. euphratica* was positively correlated with the vapor pressure deficit (VPD), air temperature and soil water content. We found that VPD and soil water content were the main driving factors for nighttime sap flow of *P. euphratica*.

Keywords: nighttime sap flow; stomatal conductance; vapor pressure deficit; driving factors; desert riparian forest

Citation: SI Jianhua, FENG Qi, YU Tengfei, ZHAO Chunyan. 2015. Nighttime sap flow and its driving forces for *Populus euphratica* in a desert riparian forest, Northwest China. Journal of Arid Land, 7(5): 665–674. doi: 10.1007/s40333-015-0009-0

It is generally assumed that sap flow only occurs during the day because leaf stomata close at night (Meidner and Mansfield, 1965; Ritchie, 1974). According to this assumption, both photosynthesis and transpiration cease as solar radiation ceases. Nevertheless, there is increasing evidence that stomata opening occurs at night for many species and in a range of habitats (Snyder et al., 2003; Bucci et al., 2004; Caird et al., 2007a; Dawson et al., 2007; Bruno et al., 2012; José et al., 2013), which would promote nighttime sap flow under sufficient environmental driving factors (Daley and Phillips, 2006). This phenomenon has become a hot topic due to a recent study (Phillips et al., 2010). However, we do not yet have a thorough understanding of abiotic and biotic controls for this phenomenon

(Bruno et al., 2012), which raises the question of why plants behave in this manner (Musselman and Minnick, 2000; Daley and Phillips, 2006).

Researchers observed a close relationship between nighttime sap flow and nighttime stomatal conductance in some plant species. Caird et al. (2007b) reviewed previous studies related to nighttime transpiration and found that nighttime transpiration accounted for 5%–15% of daytime transpiration across a diverse range of species. The high nighttime transpiration could reach 30%–60% in arid desert environments (Snyder et al., 2003), although it is commonly around 7%–10% in most other ecosystems. These potentially high values may have significant implications for water budgets and need to be accurately quantified.

*Corresponding author: SI Jianhua (E-mail: jianhuas@lzb.ac.cn)

Received 2014-12-22; revised 2015-03-20; accepted 2015-04-17

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Despite that nighttime sap flow is a potentially important factor that affects water balances and water use efficiency (WUE) of whole plants (José et al., 2013), for which functional consequences include predawn disequilibrium as well as the increments of oxygen supply (Daley and Phillips, 2006) and nutrient uptake (Donovan et al., 2001; Snyder et al., 2003), limited researches related to such nighttime fluxes in *Populus euphratica* riparian desert forests have been conducted.

Although little is known concerning nighttime sap flow controls, a strong linear positive relationship between nighttime sap flow and the vapor pressure deficit (VPD) has been documented in several ecosystems, suggesting that VPD is the most important environmental driving factor related to nocturnal water loss (Dawson et al., 2007; Fisher et al., 2007). In addition, wind speed is another important determinant for the velocity of nighttime sap flow. A previous report indicated that up to 30% of total daily water use of kiwifruit can occur during the windy night (Green et al., 1989).

P. euphratica is a typical desert riparian forest species. This species, common in the lower reaches Heihe River of Northwest China, is strongly drought-resistant. Previous studies have shown that *P. euphratica* sap flow was observed only during daytime, and nighttime sap flow was almost nonexistent (Xiao et al., 2012). *P. euphratica* sap flow velocity is influenced by multiple environmental factors such as relative humidity, VPD, air temperature and soil moisture (Zhang et al., 2003). Most studies reported that *P. euphratica* sap flow velocity continually declined along with a decrease in VPD, air temperature and soil moisture, but the reverse was true for relative humidity for which sap flow velocity continually decreased with increasing relative humidity (Yu et al., 2012). Also, certain researchers assumed that VPD is a primary driving factor for significant decreases in water potential as well as being a significant factor on the differences in water potentials between plant leaves and the atmosphere, contributing to the acceleration of sap flow velocity (Cao et al., 2012). However, studies related to nighttime sap flow and its relationship to environmental factors throughout the whole growing seasons remain unclear and limited. Therefore, it is

important to study *P. euphratica* nighttime sap flow to understand regional forest water balances and ecological environmental stability. Thus, we examined variations in *P. euphratica* nighttime sap flow behavior in a desert riparian forest using whole-tree sap flux sensors as well as leaf-level stomatal conductance measurements to answer the following questions: Does *P. euphratica* nighttime sap flow take place in desert riparian forests? If so, are there higher rates of nighttime sap flow relative to daily maximum values? Lastly, what factors are potential environmental driving forces behind nighttime sap flow? Answering such questions will increase our understanding of the structural and functional complexity of these valuable forests, which are currently facing threats related to fragmentation and shifting environmental conditions.

1 Materials and methods

1.1 Study area

The data were collected from the Alxa Desert Eco-hydrology Experimental Research Station, Chinese Academy of Sciences (42°01'N, 100°21'E; 883.5 m asl) in the lower reaches of Heihe River, Northwest China in 2012. The climate in this region is typical of a continental arid zone. Mean annual precipitation is 37.4 mm, 75% of which occurs between June and August. Pan evaporation (3,390 mm) is much greater than precipitation. Mean temperatures of 27.0°C in July and -11.7°C in January were recorded at the Ejina Weather Station during 1959–2011 (Yu et al., 2013). Apart from precipitation, groundwater from the Heihe River provides the main sources of water that sustains both local residents and regional ecosystems. The average groundwater level in this region is 2.15±0.35 m throughout the whole growing season. *P. euphratica* is the dominant plant species. Its density is 148 stems/hm², contributing approximately 75% of the total basal area in the region. Soils are derived from fluvial sediments mixed with gray-brown desert deposits.

1.2 Tree-level sap flow measurements

We used the heat ratio method (HRM) to carry out continuous sap flow measurements in the trunks of three individual species situated within the study site. HRM measurements increase in temperature follow-

ing a heat pulse at two symmetrical points, 5 mm above and below a heater inserted 30 mm into the active sapwood. This technique allows for bidirectional measurements of sap flow, while also measures very slow flow rates, which would be expected during the night. We inserted sap flow sensors (HRM30 ICT International Pty Ltd., Armidale, NSW, Australia) into the xylem tissue of trunks at breast height of the three individual species. The heater was programmed to send a pulse every 30 min, and temperature ratios were recorded continuously with a data logger (SL5 Smart Logger ICT International Pty Ltd, Armidale, NSW, Australia). Heat pulse velocity (cm/h) was calculated according to Burgess et al. (2001) as follows:

$$F_v = \frac{k}{x} \ln\left(\frac{v_1}{v_2}\right) \times 3600. \quad (1)$$

Where k is the thermal diffusivity of fresh (green) wood; x is the distance (cm) between the heater and the thermocouples; and v_1 and v_2 are the differences between the initial temperature ($^{\circ}\text{C}$) at the two thermocouples (downstream and upstream of the flow in relation to the position of the heater, respectively) and the temperature measured after a heat pulse was initiated. To estimate k , we measured the density of sapwoods and the water content on wood cores taken from stems (Burgess et al., 2001) in September 2012. Since the xylem could not be cut to establish zero flow, we selected a series of overcast days at daybreak after a rainfall event where VPD was close to zero to establish the baseline.

1.3 Leaf-level conductance and transpiration measurements

We measured gas exchange parameters (leaf stomatal conductance, transpiration, leaf temperature and VPD) at night (between 20:00 pm and 6:00 am), starting 1 h after sunset and finishing 1 h before sunrise from mature and fully-expanded leaves from three branches in the upper canopy of each species. They were sampled each subsequent 2 h using LI-6400, an infrared open gas exchange system (LI-COR Biosciences Inc., Lincoln, NE, USA) equipped with a 6 cm² chamber. Nighttime measurements were made using a green safe-lite that was not detectable by the LI-190 sensor (PPFD, LI-COR, Nebraska, USA) to avoid promoting stomatal opening. A mobile canopy aerial access vehicle was fitted to the upper canopy of each species.

For daytime measurements, a red-blue light source maintained photosynthetically active radiation (PAR) inside the LI-6400 cuvette at 1,800 $\mu\text{mol}/(\text{m}^2\cdot\text{s})$ photosynthetic photon flux density (ambient light conditions at the time of measurement). Measurements were recorded after a 5 to 15 min stabilization period, depending on ambient humidity, where nighttime stomatal conductance (g_{night}) and nighttime transpiration (E_{night}) values were almost constant.

1.4 Environmental condition measurements

Meteorological data, including photosynthetically active radiation (PAR, $\text{mmol}/(\text{m}^2\cdot\text{s})$), nighttime temperature (T_a , $^{\circ}\text{C}$), relative humidity (RH, %), wind speed (u_z , m/s) and rainfall (mm) were recorded by a data logger as mean values of 0.5 h intervals. PAR was measured in an open field using a pyranometer (CM5, Kipp & Zonen, Netherlands), whereas T_a , RH and u_z were measured at a 2-m height using a Rotronic Sensor (RS2, Rotronic, Switzerland). VPD (kPa) was calculated from RH and T_a . The groundwater table (GW, m) was measured at 0.5-h intervals by a self-recording limnimeter (HOBO U20, Onset Cor., USA) in conjunction with the sap flow measurement period.

2 Results

Estimates of *P. euphratica* nighttime sap flow and leaf conductance *in situ* were in agreement. By applying HRM and the LI-6400 system, we found that stomata remained partially opened throughout the night and subsequently substantial amounts of water were lost. Compared to daytime values, nighttime values were much lower (Fig. 1). From day 95 to day 116, nighttime sap flow was greater than daytime sap flow (Fig. 2). Thereafter, daytime sap flow values were greater than nighttime flow values. For *P. euphratica*, it was found that averages of daytime and nighttime sap flow increased as summer progressed and decreased as autumn progressed, and that both daytime and nighttime sap flows peaked during the summer (from day 200 to day 210). Daytime and nighttime sap flows differed, and no negative sap flow occurred during the growing season (Fig. 2).

Nighttime sap flow throughout the growing season is shown in Fig. 2. This figure showed that nighttime

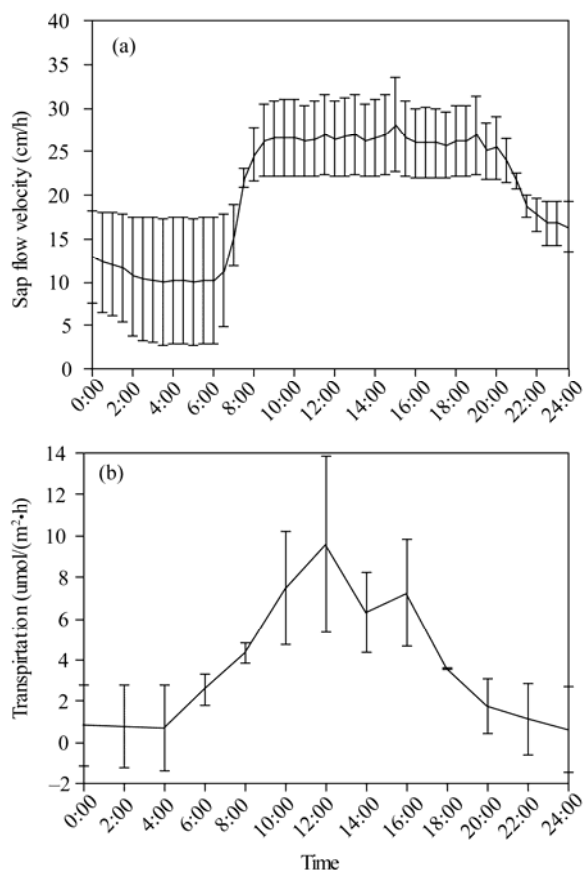


Fig. 1 Daily variations in average stem sap flow velocity (a) and transpiration (b) of *P. euphratica* on 15 June, 2012

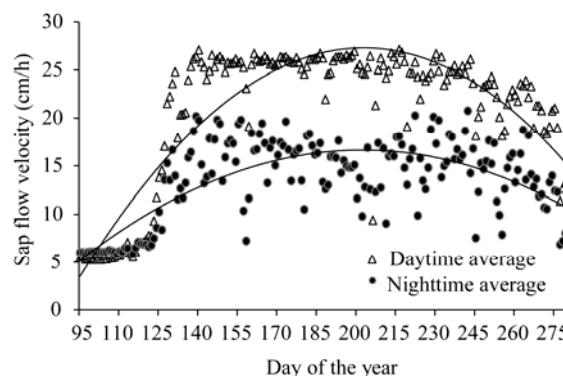


Fig. 2 Daytime and nighttime mean *P. euphratica* sap flow rates of 2012. Polynomial fits were overlaid to visualize general patterns.

sap flow prior to midnight was generally much higher, and it experienced greater change than after midnight. From seasonal changes in nighttime sap flow, it was determined that sap flow variation was highest in June, July and August. It was moderately high in May and September, and it was lowest in April and October. Descriptive statistics of *P. euphratica* daytime and nighttime sap flow velocity from April to September are shown in Table 1.

Daily and nighttime water consumption was low between day 95 and day 125 and after day 265. These values were relatively high for all other days with the

Table 1 Average variations of nighttime sap flow velocity of *P. euphratica* throughout the growing season in 2012

Time	April	May	June	July	August	September
	(cm/h)					
20:00	4.74±0.34	26.12±0.32	32.02±0.28	32.19±0.15	33.43±0.24	23.83±0.52
20:30	4.71±0.43	22.83±0.16	28.81±0.36	28.04±0.57	29.02±0.33	21.64±0.49
21:00	4.70±0.18	19.72±0.39	24.40±0.28	22.60±0.52	25.25±0.54	20.25±0.23
21:30	4.69±0.22	17.92±0.62	21.29±0.53	19.21±0.41	23.00±0.66	19.22±0.18
22:00	4.61±0.42	16.62±0.34	19.50±0.16	17.32±0.23	21.69±0.37	18.34±0.64
22:30	4.54±0.44	15.95±0.33	18.44±0.56	16.37±0.72	20.68±0.69	17.62±0.73
23:00	4.55±0.38	15.28±0.25	17.71±0.73	15.68±0.11	19.77±0.23	17.10±0.29
23:30	4.51±0.24	15.22±0.63	17.03±0.44	14.81±0.32	19.17±0.55	16.42±0.48
0:00	4.41±0.47	15.16±0.34	16.42±0.62	14.20±0.27	18.38±0.38	15.84±0.63
0:30	4.43±0.53	15.03±0.16	15.69±0.23	13.69±0.56	18.01±0.56	15.40±0.28
1:00	4.41±0.43	14.63±0.31	15.63±0.42	13.17±0.24	17.46±0.48	15.22±0.74
1:30	4.36±0.32	14.52±0.54	15.40±0.26	13.01±0.18	16.98±0.95	14.90±0.29
2:00	4.32±0.19	14.42±0.27	15.05±0.53	12.73±0.85	16.39±1.32	14.45±1.63
2:30	4.34±0.35	14.36±0.44	14.92±0.22	12.69±0.79	16.33±1.53	14.49±1.27
3:00	4.40±0.27	14.43±0.67	14.99±0.26	12.64±0.28	16.05±0.98	14.76±1.55
3:30	4.30±0.34	14.56±1.13	15.07±0.35	12.68±0.67	15.97±0.47	14.57±0.84
4:00	4.19±0.41	14.71±0.52	15.27±0.27	12.98±0.88	16.26±1.23	14.19±0.35
4:30	4.32±0.31	14.45±0.36	15.52±0.62	13.16±0.14	16.48±1.56	13.67±1.37
5:00	4.29±0.32	14.36±0.18	15.50±1.32	13.49±0.46	16.29±1.64	13.61±1.55
5:30	4.29±0.25	14.33±0.73	15.77±1.11	13.51±0.77	16.61±1.47	13.47±1.29
6:00	4.29±0.37	14.13±0.25	16.16±0.91	13.60±0.52	16.42±1.88	13.08±3.65

Note: Nighttime sap flow velocity calculation was taken between 20:00 pm and 6:00 each day. Monthly nighttime sap flow velocity was the average value of each night.

exception of days in which precipitation occurred. Mean daily water consumption was 3.66 mm, and mean nighttime water consumption was 1.30 mm (Fig. 3a). From seasonal variation in daily and nighttime water consumption, it was found that daily and nighttime water consumption was low in April and October, and both values were high during other months. The contribution of nighttime water consumption to total daily water consumption in April was clearly higher than other months. The amount of *P. euphratica* nighttime water consumption accounted for 31%–47% of total daily water consumption (Fig. 3b).

Stomatal conductance during the growing season was measured simultaneously with sap flow velocity (Fig. 4a). Our results for *P. euphratica* stomatal conductance throughout the whole growing season showed a positive correlation to sap flow velocity (Fig. 4b). Moreover, we found a significant and consistent

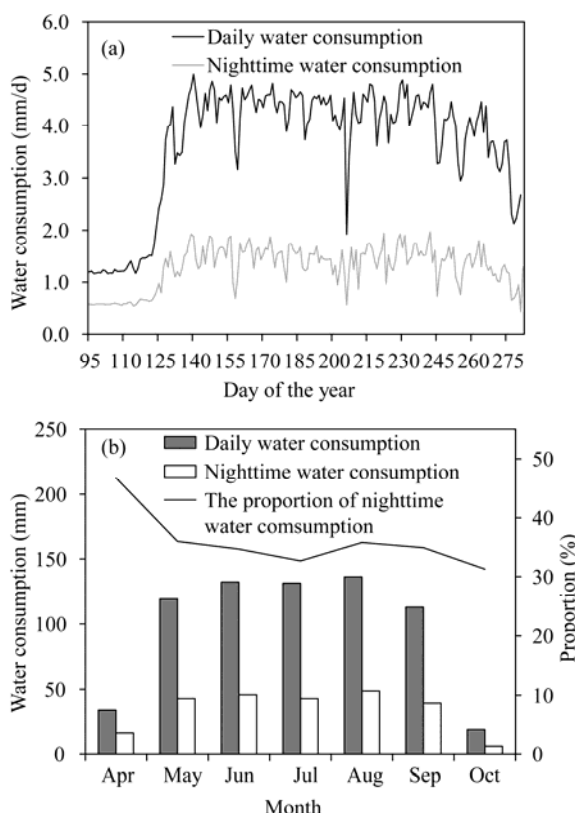


Fig. 3 Daily and nighttime water consumptions per day of *P. euphratica* (a) and seasonal variations of daily and nighttime water consumptions and the corresponding proportion of nighttime water consumption to total water consumption (b).

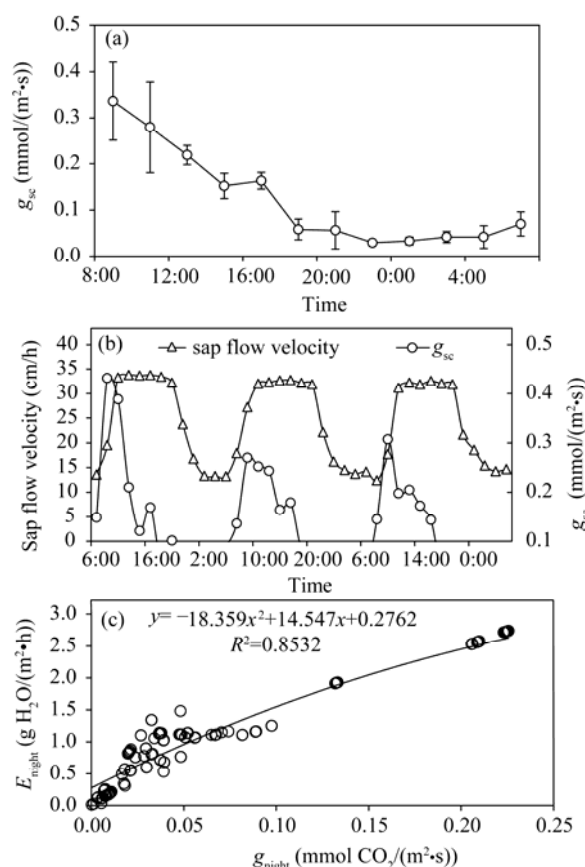


Fig. 4 Mean stomatal conductance (g_{sc}) throughout the growing season (a); the nighttime sap flow velocity and stomatal conductance (b); and the relationship between nighttime leaf conductance (g_{night}) and nighttime transpiration (E_{night}) (c). Measurements were taken between 20:00 pm and 6:00 am. Data were fitted by a polynomial function ($P < 0.01$).

correlation between nighttime stomatal conductance and nighttime transpiration when all experiments were combined and analyzed (Fig. 4c). Changes in nighttime stomatal conductance were also clearly correlated to variations in VPD (Fig. 5a). A similar correlation was observed between nighttime stomatal conductance and internal CO_2 concentrations (Fig. 5b).

VPD is a primary driving factor behind nighttime transpiration of plant species (Benyon, 1999; Oren et al., 2001), and this conclusion is consistent with theoretical considerations (Monteith, 1965). However, VPD will not influence transpiration if it reaches zero each night (Fisher et al., 2007). The site selected by this study is extremely dry with the exception of days of precipitation during the growing season. Thus, VPD

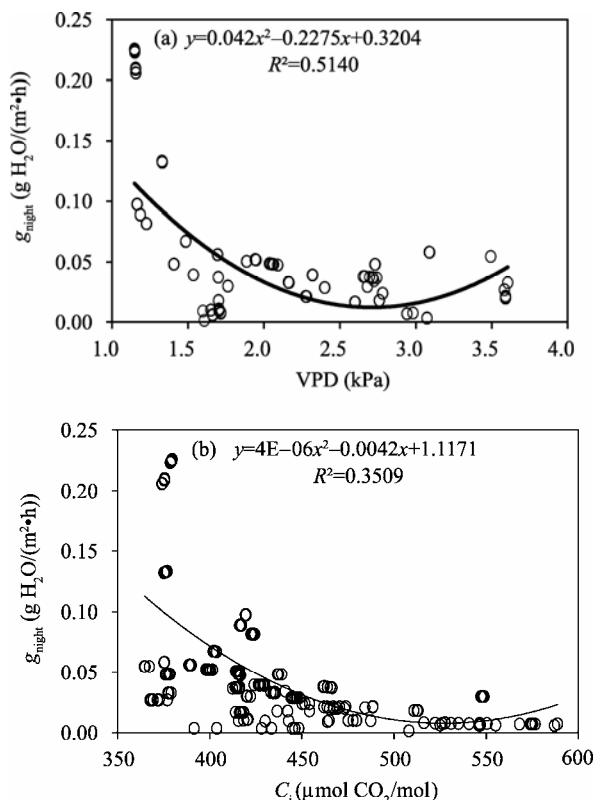


Fig. 5 Correlations between nighttime leaf conductance (g_{night}) and VPD (a) and internal CO_2 concentrations (C_i) (b) of *P. euphratica*

remained positive throughout the night, particularly during summer. We found strong positive relationships between nighttime sap flow and VPD during all periods (Fig. 6a), indicating that the atmospheric demand for water was driving nighttime sap flow. Linear regression fits (Fig. 6d) were in good agreement for *P. euphratica* ($R^2=0.42$, $P<0.0001$). As nighttime temperatures increased during the summer, nighttime sap flow increased more rapidly (Fig. 6b). The linear regression fit ($R^2=0.43$, $P<0.0001$) was similar to VPD for *P. euphratica* (Fig. 6e). Given that soil water content was maintained between 26% and 40% throughout the growing season, there was a good positive correlation between soil water content and nighttime sap flow (Fig. 6c). Linear regression fits (Fig. 6f) also showed good agreement for *P. euphratica* ($R^2=0.41$, $P<0.0001$).

Groundwater depth is an important factor that influences nighttime sap flow. Our results indicated that groundwater depth had a significant effect on *P. euphratica* nighttime sap flow velocity and nighttime water consumption (Fig. 7).

3 Discussion

It is commonly assumed that transpiration does not occur at night because leaf stomata close after sunset. Contrary to previous results, however, we found, using HRM and the LI-6400 system, that *P. euphratica* lost a substantial amount of water throughout the night. This clearly indicates that stomata remained partially opened at night (Fig. 1). Nighttime sap flow of *P. euphratica* accounted for at least 31%–47% of daily water use throughout the growing season (Fig. 3). Implications of nighttime stomatal conductance and transpiration beyond additional water loss may be important when considering how the magnitude of water loss relates to an environment. This finding is consistent with a study that reported that the contribution of nighttime sap flow to total daily sap flow was high in some extreme cases (Field et al., 2000). Previous studies have also shown that nighttime sap flow accounted for up to 15%–30% of total daily sap flow (Dawson et al., 2007; Scholz et al., 2007), and that nighttime sap flow could represent a significant fraction of total sap flow. The above results, however, are in opposition to a previous study that reported that nighttime sap flow was almost nonexistent (Tateishi et al., 2008). Although our study specifically measured *P. euphratica*, our measurements of nighttime leaf conductance or sap flow using different methods suggest that significant nighttime sap flow is in fact a general phenomenon related to increasing plant water usage. Implications of water loss through partially opened stomata during non-photosynthetic periods are significant, especially when considering the importance of water as a resource for plant and that drought is a major plant stress factor throughout the world. For example, such water loss can decrease the predawn water status of plants (Donovan et al., 2003), which may shorten the period during which photosynthetic carbon gains can effectively occur during the day (Rawson and Clarke, 1988). This effect would lead to the loss of a limited resource without any carbon gain benefit, therefore reducing overall plant WUE, particularly in hot and arid environments.

Nighttime sap flow is correlated to daytime sap flow. Both increased in summer and decreased in autumn, the peak period being in summer (Fig. 2).

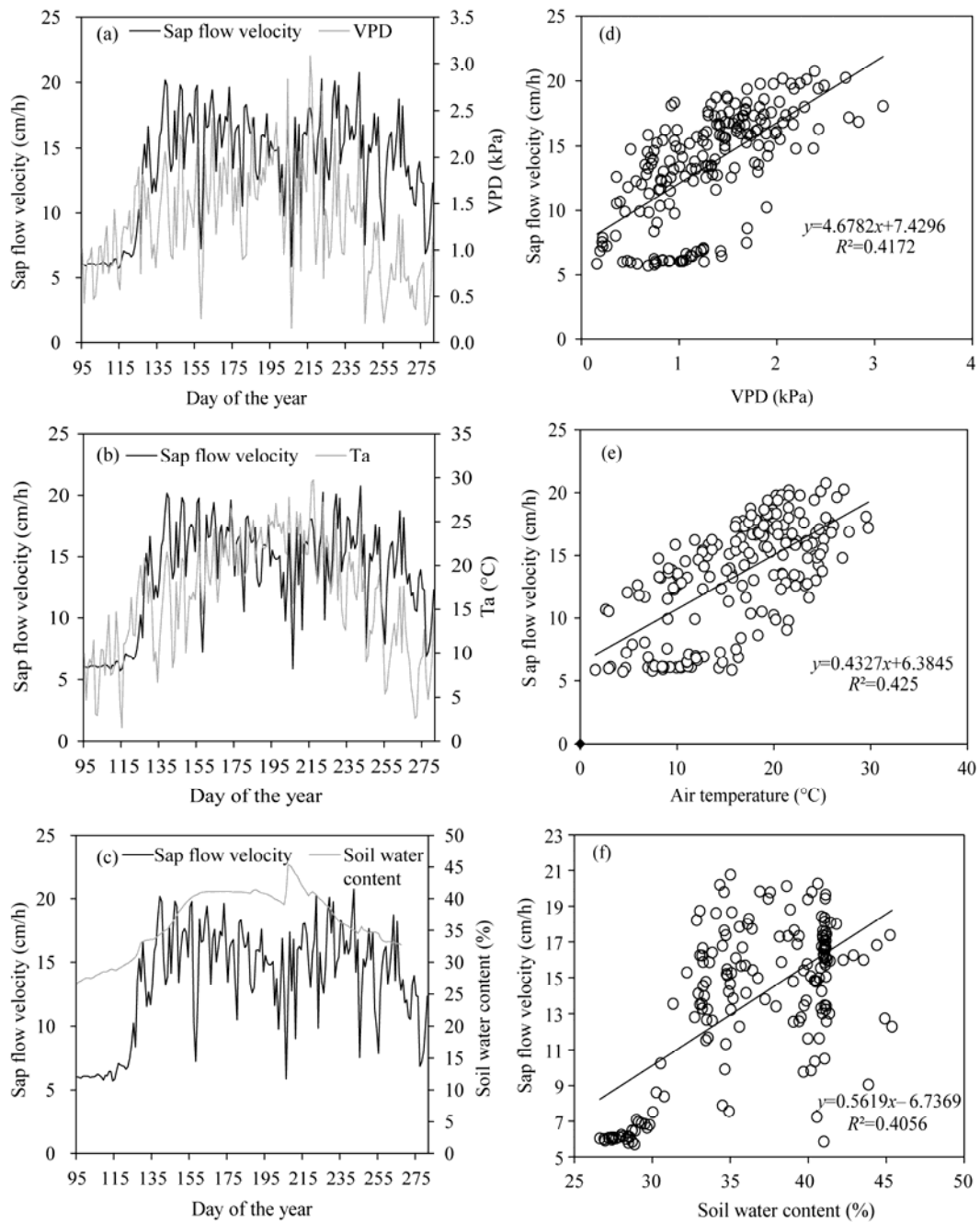


Fig. 6 Mean nighttime VPD and sap flow velocity of *P. euphratica* (a); mean nighttime temperature and sap flow velocity of *P. euphratica* (b); and mean nighttime soil water content and sap flow velocity of *P. euphratica* (c). The corresponding linear regression results were shown in Figs. d–f, respectively.

Snyder et al. (2003) found a similar result, showing higher nighttime stomatal conductance and transpiration associated with higher daytime values across species and habitats, implying that a significant amount of nighttime sap flow was used to refill stem water deficits as a result of high water loss during the preceding day. Although nighttime water loss appears

intuitively wasteful when taking into account carbon gains, it may in fact be beneficial by increasing nutrient mass flow supply to roots or by affecting daytime gas exchanges the following day, thus increasing overall plant productivity (Caird et al., 2007). To date, nighttime transpiration under ambient conditions has been found in many species in the field. Measurement

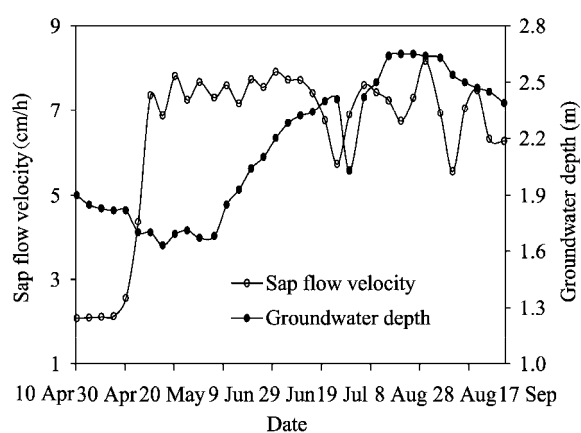


Fig. 7 Changes in *P. euphratica* sap flow velocity and groundwater depth throughout the whole growing season of 2012

are commonly around 5%–15% of daytime rates (Caird et al., 2007), and proportions can reach 30%–60% in arid desert environments (Snyder et al., 2003). Our study site was located in the extremely arid region of Northwest China, an ecological system belonging to arid desert riparian forests. Thus, nighttime sap flow was inherently higher. These potentially high values may have significant implications for water budgets and must therefore be accurately quantified.

Conversely, Fisher et al. (2007) reported a different finding while investigating *Quercus douglasii* and *Pinus ponderosa* in the field. The results showed that nighttime sap flow peaked later than daytime sap flow during the summer, implying that transpiration would be “down-regulated” when soil water became limited.

Sap flow became steadier and experienced less change after midnight, implying that the trunk had been refilled and the water storage compartments were saturated. As nighttime sap flow stabilized, stems gradually refilled. Nighttime sap flow behavior after midnight may be due to mature leaf lenticel and cutin transpiration.

Nighttime stomatal conductance values resulted in high values of nighttime sap flow (Fig. 4b). Moreover, nighttime stomatal conductance from the early evening hours to sunrise was negatively correlated to changes in VPD during the night (Fig. 5). Similar results were reported for *Ricinus communis* (Barbour and Buckley, 2007) and *Vitis vinifera* L. (José et al., 2013). Different ambient CO₂ concentrations and

temperatures can stimulate changes between nighttime stomatal conductance and VPD (Zeppel et al., 2012), but variations in nighttime stomatal conductance were mostly attributable to VPD induced changes in the stomatal aperture. CO₂ concentrations can even be internally regulated in nighttime stomatal conductance (Fig. 5).

VPD is a well-known driver of transpiration owing to the water potential gradient and the ability of dry air to pull in water from a source of higher water potential (Monteith, 1965). Numerous studies have found much stronger correlations between VPD and nighttime sap flow under field conditions (Green et al., 1989; Herzog et al., 1998; Fisher et al., 2007). Benyon (1999) found that 54% of variation in mean nighttime sap flow velocity in a *Eucalyptus grandis* plantation was associated with VPD. Richard (1999) found that nearly 70% of variation in nighttime sap velocity was explained by nighttime mean VPD and nighttime mean wind speed. Several studies have suggested that the predawn water potential gradient between plants and soil and high nighttime VPD drives nighttime sap flow (Burgess et al., 2004; Bucci et al., 2005; Kavanagh et al., 2007). Vilagrosa et al. (2003) suggested that the greater the daytime transpiration is, the greater the water demand at night will be, which would in itself drive nighttime sap flow. We believe that multiple environment factors such as high temperatures and strong evaporation demands are drivers in arid desert environments during the night.

Air temperature is an important driver that influences nighttime sap flow. The relationship between air temperature and nighttime sap flow is similar to VPD for *P. euphratica* (Fig. 6e), although air temperature and VPD showed a strong exponential correlation because the hottest period of the year is in the summer (data not shown). Fisher et al. (2007) found similar results for *P. ponderosa* and *Q. douglasii*.

For our study site, soil water and groundwater table depth were perhaps the most important inputs, without which water loss cannot occur. Nighttime sap flow minimized when soil water content was at its lowest (26%–29%) at approximately day 95 to day 116. Soil water content was maintained above 30% during the summer (Fig. 6f). Fisher et al. (2007) argued that soil water is perhaps the most important factor, and with-

out soil water sap flow cannot occur regardless of values related to VPD, temperature or other drivers, and sap flow was minimized when soil water content was at its lowest. Ma et al. (2007) and Kohler et al. (2010) also suggested that sap flow has a linear relationship to soil water content (Ma et al., 2007; Kohler et al., 2010).

In general, conditions of soil water and groundwater table depth determine the overall level of nighttime sap flow while meteorological factors determine instantaneous variations in nighttime sap flow.

4 Conclusions

Maintaining nighttime sap flow through the soil-plant-atmosphere continuum can promote nutrient uptake and supply oxygen to xylem parenchyma cells throughout the night. Results from this study showed that significant stomatal opening persists during the night in *P. euphratica* forests, leading to the occurrence of substantial water losses. Moreover, variations in nighttime stomatal conductance along the course of the night confirmed that nighttime stomatal conductance responds to changes in VPD during the day. Nighttime sap flow of *P. euphratica* was observed during the whole growing season. Mean nighttime sap flow velocity as a percentage of daytime sap flow velocity ranged 31%–47%. Nighttime sap flow velocity was affected by multiple environmental factors. Throughout the whole growing season, VPD, air temperature, soil water content and the groundwater table depth were important driving factors that influenced nighttime water loss, in which soil water conditions determine the overall level of nighttime water loss.

Acknowledgements

This work was supported by the Major Research Plan of the National Natural Science Foundation of China (91025024), the Key Project of the Chinese Academy of Sciences (KZZD-EW-04-05) and the West Light Foundation of the Chinese Academy of Sciences.

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