J. Plant Biol. (2016) 59:648-657
DOI 10.1007/s12374-015-0536-4

ORIGINAL ARTICLE

Evidences and Magnitude of Nighttime Transpiration Derived from *Populus euphratica* in the Extreme Arid Region of China

Tengfei Yu[1,2], Qi Feng[1,2*], Jianhua Si[1,2], Xiaoyou Zhang[1,2], Downey Alec[3] and Chunyan Zhao[1]

[1] *Key Laboratory of Ecohydrology of Inland River Basin, Chinese Academy of Sciences, Lanzhou 730000, China*
[2] *Alax Desert Eco-hydrology Experimental Research Station, Northwest Institute of Eco-Environment and Resources, Chinese Academy of Sciences, Lanzhou 730000, China*
[3] *ICT International Pty Ltd, Armidale NSW 2350, Austrilia*

Received: November 16, 2015 / Accepted: October 11, 2016

Abstract Extensive research has found that nighttime transpiration (E_n) is positively correlated to the vapour pressure deficit (VPD), that suggested E_n was highest during the night under high temperatures and low humidity along with high soil water availability, typically for the riparian forest in the extreme arid region of China. This study used the heat ratio method to measure sap velocity (V_s) for mature and saplings *Populus euphratica* Oliv., and then E_n was conservatively calculated as total nocturnal sap flow (F_s, the product of V_s and sapwood area A_s) between 01:00 to 06:00. A gas exchange system was used to measure the leaf transpiration rate (T_r) and stomatal conductance (g_s) of saplings. For mature trees, nighttime V_s was extensive and logarithmic correlated to VPD (similar to daytime). For saplings, g_s and T_r was extensive in different months, and also a strong logarithmic relationship was found between V_s and VPD for both daytime and nighttime periods. Both of stem sap flow and leaf gas exchange sugqusted the occurrence of E_n, whether mature or sapling trees. E_n contribution to daily transpiration (E_d) was high just as expected for *P. euphratica*, which was confirmed by proportional E_n to E_d (E_n/E_d) means taken in 2012 (24.99%) and 2013 (34.08%). Compared to mature trees, E_n/E_d of saplings in 2013 was lower with means of 12.06%, that supported further by the shorter duration times and less $T_{r,n}$ (16.64%) and $g_{s,n}$ (26.45%) of leaf, suggesting that E_n magnitude is associated to individual the tree size, that effect to stored water of individual trees, although this hypothesis requires further research.

Keywords: Nighttime transpiration, *Populus euphratica*, Sap flow, Stomatal conductance

Introduction

Nighttime transpiration (E_n) as a consequence of incomplete stomatal closure has been observed in a range of species and ecosystems under various microclimatic conditions (Zeppel et al. 2013), particularly in arid environments (Donovan et al. 2003; Snyder et al. 2003; le et al. 2012). Despite the extensive research conducted on E_n, no conclusive mechanism for E_n has been agreed upon at present. Indeed, E_n is often positively correlated to the nighttime leaf-to-air vapour pressure deficit (VPD) (Hogg and Hurdle 1997; Christman et al. 2009; Zeppel et al. 2010; Pfautsch et al. 2011; Zeppel et al. 2012), the product of VPD and wind speed (u) (Benyon 1999; Phillips et al. 2010), or to soil water content (θ) (Cavender-Bares et al. 2007; Zeppel et al. 2012), suggesting that very high E_n may result from high temperatures and low humidity along with high soil water availability and may even increase further under climate change scenarios where nighttime temperatures are predicted to increase at higher rates than daytime temperatures (Peng et al. 2013).

A number of studies have shown that desert plant species can in fact maintain proportionally higher E_n to daily transpiration (E_d) (E_n/E_d, 30%–60%) and/or nighttime stomatal conductance ($g_{s,n}$) to daytime ($g_{s,d}$) ($g_{s,n}/g_{s,d}$, 40%–75%) (Donovan et al. 2003; Snyder et al. 2003; Pfautsch et al. 2011; Ogle et al. 2012) than typical plant species found in wetter environments (Benyon 1999; Bucci et al. 2004; Barbour et al. 2005; Daley and Phillips 2006; Dawson et al. 2007; Novick et al. 2009; Zeppel et al. 2010). The variation in E_n is not only due to environmental differences, but also to intra- and inter-specific variation in physiological traits (Daley and Phillips 2006; Phillips et al. 2010; Zeppel et al. 2010). However, studies related to the E_n and $g_{s,n}$ of desert riparian species is remain less, especially in the extreme arid region of China. Therefore, the accurate quantification of E_n and improved understanding of processes and conditions that facilitate E_n are essential to

---

*Corresponding author; Qi Feng
Tel : +86-931-4967162
E-mail : qifeng@lzb.ac.cn

desert riparian species.

The study site was located in the extreme arid region of northwest China, dominated by riparian phreatophytes consisting of *Populus euphratica* Oliv. trees and *Tamarix ramosissima* Ledeb. shrubs. The climate of study site is extremely arid with high temperatures and low relative humidity, i.e. high VPD, together with high soil water availability due to close to river suggested E_n was expected high for those species. Previous studies reported that nocturnal sap flow was observed in stems of *P. euphratica*, that was attribute to tissue reconstitution resulting from daytime water losses (Si et al. 2015). We also observed a hydraulic lift (HL) from *P. euphratica* roots, but its magnitude was lower (0.16–0.26 mm d^{-1}) than previous reports (0.04–1.3 mm d^{-1}) (Neumann and Cardon, 2012), for which no reasonable explanation was provided. The research suggests that plants can move water through two major pathways at night, i.e. E_n from the canopy and HL from roots (Howard et al. 2009; Domec et al. 2012). Thus, we speculated that E_n could in fact decrease HL magnitude as suggested by Howard et al. (2009). The objectives of this study were therefore to determine the occurrence and magnitude of E_n for *P. euphratica* based on the measurements of stem sap flow, leaf gas exchanges and relevant environmental factors.

Results

Mature Trees: Meteorological Factors and Sap Flow

Variation trends between VPD and V_s was corresponded except midday and nighttime hours. During typical sunny days between July 25 and 28, 2012, 0.5 h mean VPD ranged from 0.59 kPa at 7:00 to 3.79 kPa at 17:30. There was an obvious daily sectional division where VPD increased from a minimum of 0.59 kPa to a maximum of 3.79 kPa during the day and decreased at night with a slight fluctuation at 1:00 (Fig. 1A). Accordingly, V_s increased from sunrise to midday and stabilized with a mean of 40 cm h^{-1} until one hour before sunset, after which V_s decreased from sunset to 0:00, but steadily decreased between 1:00 and 6:00 with a mean of 10 cm h^{-1} (Fig. 1B).

During the two year growing season, 2012 daytime R_n (300.40 ± 66.75 W m^{-2} mean) was lower than 2013 daytime R_n (360.20 ± 77.41 W m^{-2} mean) ($P < 0.01$), that was resulted from the increased upward radiation (104 W m^{-2} v.s. 47 W m^{-2}, $P < 0.01$), that may be induced by the different vegetation coverage for R_n measured, whereas interannual variation in rainfall was less throughout the two year period (32.7 mm v.s. 34.2 mm, $P > 0.1$) (Fig. 2A). Mean daily VPD was less than

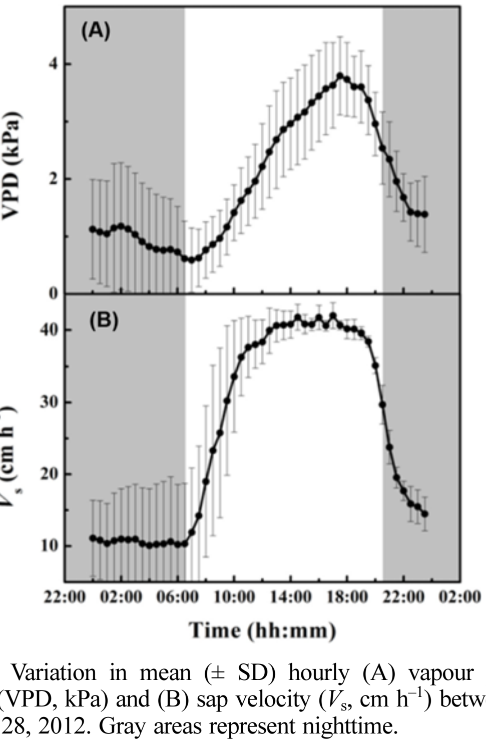

Fig. 1. Variation in mean (± SD) hourly (A) vapour pressure deficit (VPD, kPa) and (B) sap velocity (V_s, cm h^{-1}) between July 25 and 28, 2012. Gray areas represent nighttime.

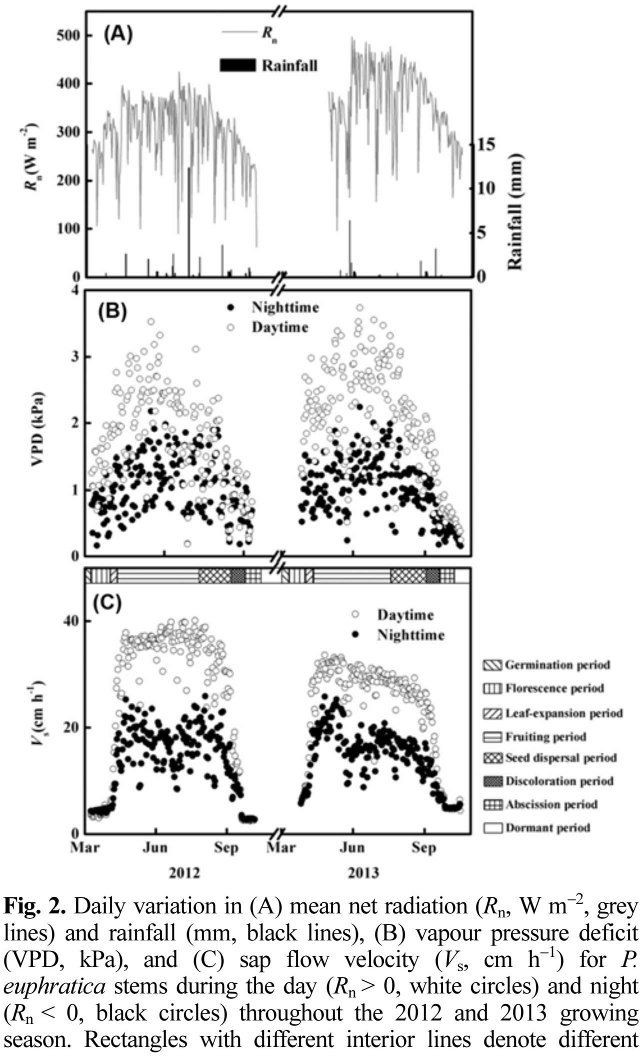

Fig. 2. Daily variation in (A) mean net radiation (R_n, W m^{-2}, grey lines) and rainfall (mm, black lines), (B) vapour pressure deficit (VPD, kPa), and (C) sap flow velocity (V_s, cm h^{-1}) for *P. euphratica* stems during the day ($R_n > 0$, white circles) and night ($R_n < 0$, black circles) throughout the 2012 and 2013 growing season. Rectangles with different interior lines denote different growing periods. Labels are provided at the right of (C).

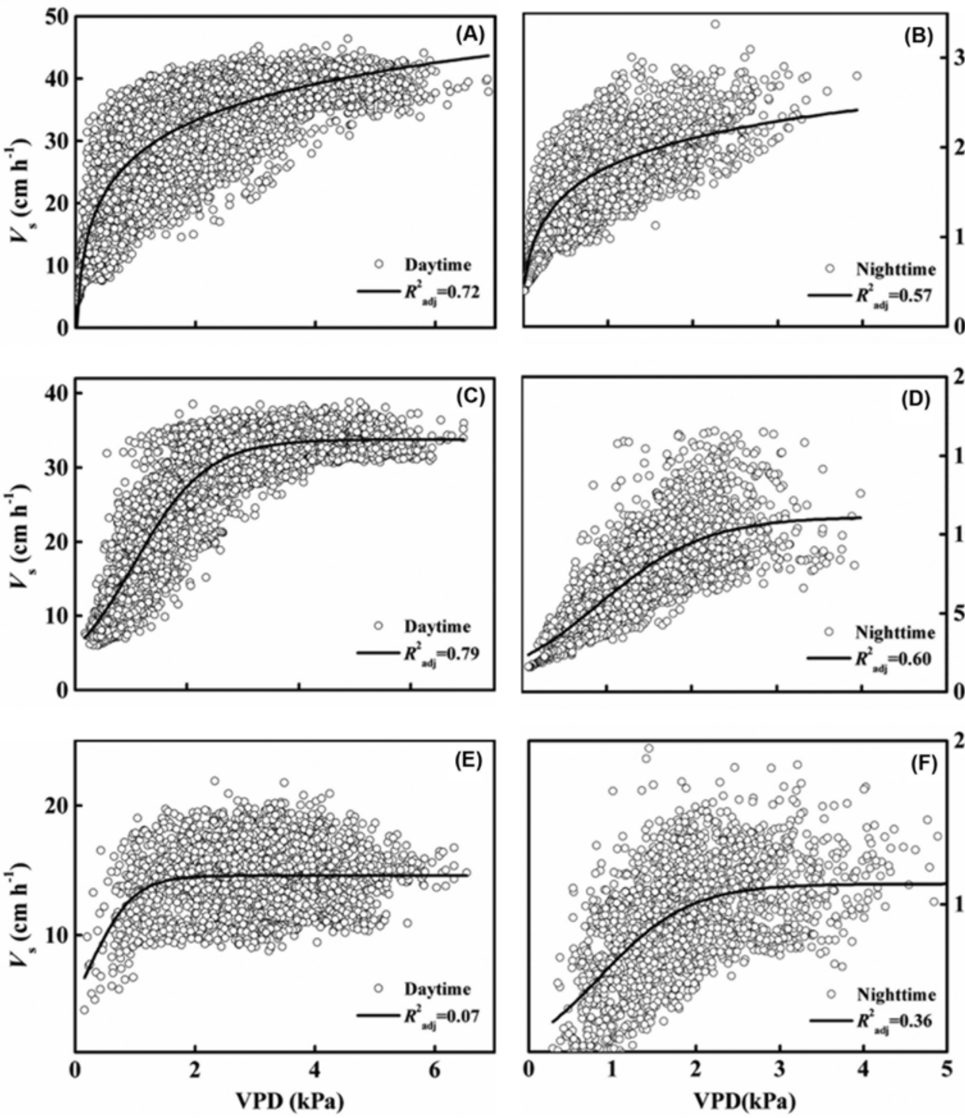

Fig. 3. Sensitivity of sap flow velocity (V_s, cm h^{-1}) to the vapour pressure deficit (VPD, kPa) during the day (A, C and E) and night (B, D and F) throughout the growing season (from May 4th to October 15th) devoid of rain days in 2012 (A, B) and 2013 (C, D) for mature and 2013 (E, F) for sapling *P. euphratica*. Logarithmic relationships are shown for both daytime and nighttime.

4.0 kPa during daytime but higher than nighttime VPD ($P <$ 0.001). Interannual variation in daily VPD was significant during daytime ($P < 0.01$) but not at nighttime ($P = 0.33$) (Fig. 2B). Obviously, daytime VPD variation was consistent with R_n and was interrupted by rainfall (Fig. 2A). From germination to the fruit bearing period, daytime V_s sharply increased and then stabilized from the fruiting to seed dispersal period and after sharply decreased into the dormant period (Fig. 2C). However, mid-summer nighttime V_s was lower (Fig. 2C), which is consistent with high rainfall (Fig. 2A) and low VPD (Fig. 2B). Mean daytime V_s was higher than nighttime V_s throughout the two year study period ($P < 0.001$ and $P <$ 0.001 for 2012 and 2013, respectively), and daytime interannual variation of V_s was significant ($P < 0.01$) but not at nighttime ($P = 0.15$).

A strong logarithmic relationship was found between V_s and VPD for both daytime (Fig. 3A, C) and nighttime periods (Fig. 3B, D) for mature trees through the growing season (when devoid of rainfall). The saturated V_s under same VPD is lower in 2013 than 2012 (Fig. 3A vs. Fig. 3C, Fig. 3b vs. Fig. 3D), that mainly due to the decreased V_s induced from xylem embolism by installed persistently probe at one point from 2012 to 2013 (Fig. 2C). Goodness of fit was better in the daytime than nighttime and differed across years (Fig. 3). u and u×VPD was a poor predictor ($P > 0.1$) of V_s for both years (data not shown). Similarly, the positive relationship was observed between daytime and nighttime daily mean V_s (Fig. 4). Because the lower daytime V_s in 2013, the proportion of E_n to E_d (E_n/E_d) was higher in 2013 with means of 34.08% than in 2012 with means of 24.99% ($P < 0.001$) (Table 2).

Table 1. Summary of biological parameters for three selected mature and sapling *P. euphratica* trees for this study.

Trees	Height m	DBH cm	A_s cm^2	m_c %	ρ_b g cm^{-3}	k 10^{-3} cm^2 s^{-1}
Mature trees	11.1	43.35	268.68	16.90	0.40	3.12
	11.4	49.47	324.35	24.00	0.42	2.83
	12.1	41.38	251.49	22.36	0.42	2.90
Mean±SD	11.53±0.51	44.73±4.22	281.51±38.09	21.09±3.72	0.41±0.01	2.95±0.15
Sapling trees	3.01	5.42	13.89	40.67	0.49	2.55
	2.97	4.18	9.59	44.33	0.53	2.61
	2.91	3.68	7.99	42.26	0.52	2.58
Mean±SD	2.96±0.05	4.43±0.90	10.49±3.05	42.42±1.84	0.51±0.02	2.58±0.03

Abbreviation: DBH, diameter at breast height; A_s, sapwood area; m_c,water content of sapwood; ρ_b, basic density of wood; *k*, thermal diffusivity of green (fresh) wood

Table 2. Seasonal variation in E_n to E_d contribution (E_n/E_d, %) during the growing season from May 4th to October 15th, 2012 and 2013 for mature and June 6th to October 15th, 2013 for sapling *P. euphratica* trees.

Age	Month	5	6	7	8	9	10	Mean
Mature	2012	24.00	25.17	26.63	24.15	27.38	22.63	24.99
	2013	34.94	32.85	30.38	34.39	33.82	38.12	34.08
Sapling	2013		13.98	16.16	16.74	9.97	3.44	12.06

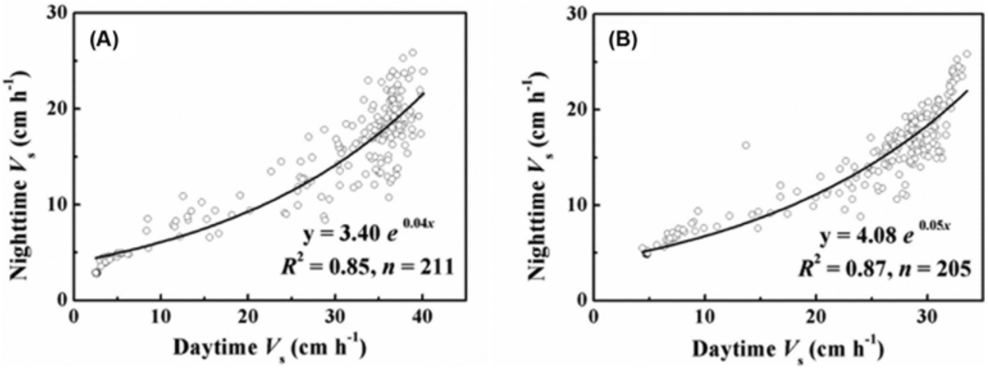

Fig. 4. Relationships between daily mean daytime and nighttime V_s ($cm\ h^{-1}$) throughout the 2012 (A) and 2013 (B) growing season. Exponential relationships are shown.

Sapling Trees: Sap Flow and Leaf Gas Exchange

A strong logarithmic relationship was also found between V_s and VPD for both daytime (Fig. 3E) and nighttime periods (Fig. 3F) for sapling trees through the growing season, 2013. Goodness of fit was weak in the daytime than nighttime. E_n /E_d was low in 2013 with means of 12.06%, especially lowest in October (Table 2). Compared to mature trees, E_n/ E_d of sapling was lower ($P < 0.001$).

P. euphratica saplings experienced extensive g_s and T_r in different months (Fig. 5). For example, leaf g_s peaked at 431.48 and 288.34 mmol H_2O m^{-2} s^{-1} at 08:00 on July 17th and July 31st, respectively, whereas g_s peaked at 307.86 mmol H_2O m^{-2} s^{-1} at 12:00 on September 2nd. After sunset (21:00), g_s decreased to its minimum value (23.78~32.17 mmol H_2O m^{-2} s^{-1} at 22:00) but remained elevated throughout the night between July 17th and 18th and July 31st and August 1st whereas the minimum value throughout the night from September 2nd to 3rd was ~ 9.47 mmol H_2O m^{-2} s^{-1}, which was less and later than previous days. Corresponding to this pattern, T_r varied in synchronization with g_s; however, it lagged four hours behind, reaching its maximum during the day on July 17th and July 31st. Daily trends in Ψ_L and θ_L varied in reverse to g_s and T_r, particularly during the day. It appeared that the higher g_s were, the lower Ψ_L (Pearson's = -0.80, $P < 0.01$) and θ_L (Pearson's = -0.55, $P < 0.05$) were during the day except after rain days (September 2nd to 3rd). However, no significant correlation was observed between Ψ_L and θ_L and g_s and T_r variation during the night (Fig. 6).

Mean nighttime g_s ($g_{s,n}$) and T_r ($T_{r,n}$) was greater than 30

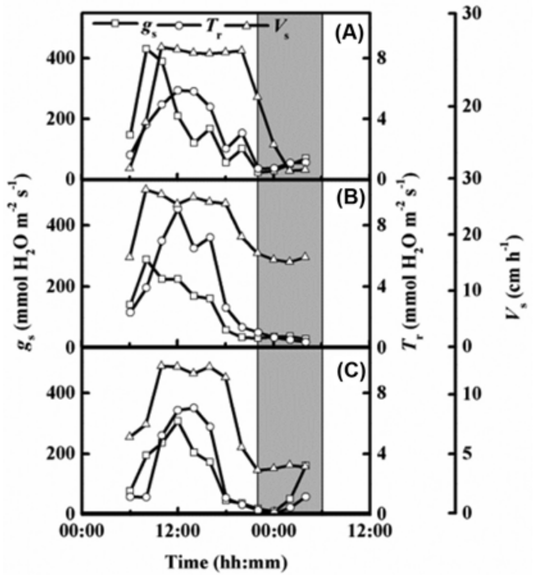

Fig. 5. Daily trends in mean g_s (lines with circles), T_r (lines with squares) and V_s (lines with triangle) during different months: (A) July 17th to 18th, (B) July 31st to August 1st, and (C) September 2nd to 3rd. The grey column indicates nighttime hours.

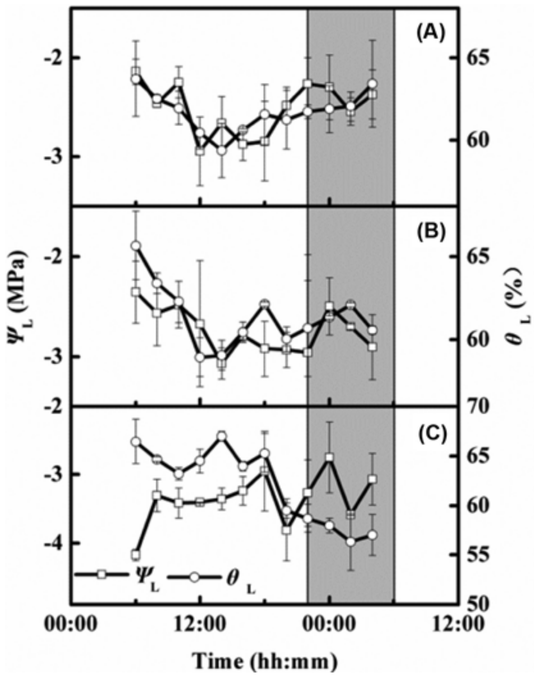

Fig. 6. Daily trends in Ψ_L (mean ± SD, lines with circles) and θ_L (lines with squares) for different months: (A) July 17th to 18th, (B) July 31st to August 1st, and (C) September 2nd to 3rd. The grey column indicates nighttime hours.

mmol H_2O m^{-2} s^{-1} and 0.49 mmol H_2O m^{-2} s^{-1}, respectively, and their contribution to daytime g_s ($g_{s,d}$) and T_r ($T_{r,d}$) was 26.45% and 16.64%, respectively, throughout the measurement period (Table 3). Correlation analysis showed that g_s was positively correlated to T_r and negatively correlated to c_i for both day and night, but negatively correlated to VPD_L and T_L only at night. Similarly, T_r was negatively correlated to VPD_L, c_i and T_L during the day but positively correlated to g_s at night. Both of g_s and T_r were not correlated to Ψ_L, θ_L, Ψ_s, and θ_s for both day and night (Table 4). In summary, nighttime g_s was mainly affected by the atmospheric conditions, but not soil moisture regime.

Mean leaf g_s and T_r were logarithmic correlated to stem V_s throughout the sapling measurement period (Fig. 7). Over time, increased daytime leaf g_s resulted in a linear increase in stem V_s (from 06:00 to 08:00), after which g_s decreased, but V_s only decreased after 18:00. Subsequently, g_s remained unchanged

Table 3. Summary of mean ± SD of nighttime (22:00–4:00) and daytime (6:00–20:00) stomatal conductance (g_s, mmol H_2O m^{-2} s^{-1}) and transpiration (T_r, mmol H_2O m^{-2} s^{-1}), and nighttime and daytime ratios of g_s and T_r throughout the measurement period.

Date	Night		Day		Night/Day (%)	
	$g_{s,n}$	$T_{r,n}$	$g_{s,d}$	$T_{r,d}$	g_s	Tr
July 17–18	42.95±21.45	0.93±0.22	203.16±135.96	3.98±1.64	21.14	23.43
July 31–Aug.1	33.11±4.28	0.65±0.27	162.30±85.64	5.01±2.80	20.40	12.91
Sept. 3–4	60.11±69.62	0.49±0.47	158.94±97.56	3.62±2.85	37.82	13.58

Table 4. Pearson's coefficient of nighttime (22:00–4:00) and daytime (6:00–20:00) g_s and T_r to environmental parameters throughout the sapling measurement period. Superscript letters *a*, *b*, and *n* indicate significance levels at 0.01, 0.05, and no significance found, respectively

Pearson's coefficient		Dependent Variable								
		n	T_r or g_s	VPD_L	c_i	T_L	Ψ_L	θ_L	Ψ_s	θ_s
g_s	*Nighttime*	12	0.64^{b}	-0.39^{b}	-0.62^{b}	-0.41^{b}	-0.18^{n}	-0.35^{n}	-0.32^{n}	-0.36^{n}
	Daytime	27	0.55^{a}	-0.24^{n}	-0.38^{b}	-0.09^{n}	0.26^{n}	0.32^{n}	-0.00^{n}	-0.21^{n}
T_r	*Nighttime*	12	0.64^{b}	-0.34^{n}	-0.28^{n}	-0.37^{n}	0.24^{n}	0.25^{n}	0.17^{n}	0.20^{n}
	Daytime	27	0.55^{a}	-0.58^{a}	-0.79^{a}	-0.77^{a}	0.11^{n}	0.04^{n}	0.31^{n}	0.00^{n}

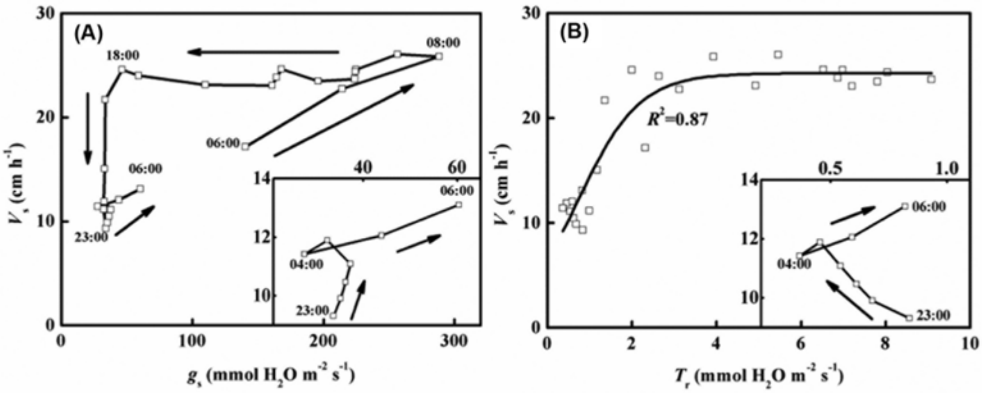

Fig. 7. Leaf mean correlations between (A) g_s and (B) T_r and stem V_s throughout the sapling measurement period. Labels and arrows denote time and direction of varied g_s and T_r. The inlets represent the period between 23:00 and 06:00 (night). The fitted curve is provided in (B) and R^2 is shown ($P < 0.05$).

whereas V_s sharply decreased at 23:00 (Fig. 7A). However, stem V_s increased with leaf g_s, with an apparent nighttime growth rate difference occurring between 23:00 and 03:00 and between 04:00 and 06:00 (Fig. 7A, inlet). Stem V_s also logarithmic increased with T_r with the apparent nighttime growth rate difference mentioned above (Fig. 7B). V_s had a higher goodness of fit with T_r (R^2=0.87) than g_s (R^2=0.62) during the day, but this was not the case at night.

Discussion

Drivers of E_n

As with other species studied (Hogg and Hurdle 1997; Barbour et al. 2005; Daley and Phillips 2006; Barbour and Buckley 2007; Fisher et al. 2007; Moore et al. 2008), *P. euphratica* stem V_s rose logarithmic across the observed VPD range for both daytime and nighttime, indicating that nighttime V_s was not solely due to tissue rehydration (Si et al. 2015), which was demonstrated by the non-zero intercept obtained (Fig. 3). The flattening of the fitted daytime V_s–VPD curve with a high VPD (> 2 kPa), similar to *Eucalyptus victrix* in semi-arid regions (Pfautsch et al. 2011), likely reflected the stomatal limitation of water loss after the midday point (Zhu et al. 2010) as tissue dehydration to prevent runaway embolism under dry season conditions. However, V_s was insignificantly correlated to u and u×VPD (data not shown), which was similarly observed in Californian shrubs and trees (Fisher et al. 2007) as well as in evergreen temperate woodland species (Zeppel et al. 2010). This is in opposition to Phillips et al. (2010) who reported that E_n was more strongly correlated to u×VPD. One possible reason for the insignificant correlations found between u or u×VPD and E_n is the study site used by Phillips et al. (2010), which was a small stand of trees planted in rows and surrounded by low-lying vegetation, and as such was exposed to higher wind speeds than our or other relevant studies (Fisher et al. 2007; Zeppel et al. 2010) that employed larger scale woodland sites with tree species spaced irregularly, which may have produced a better buffering effect against such conditions.

At a leaf level, relationships between g_s and T_r and VPD$_L$ or T_L differed significantly during daytime and nighttime, but both were negatively correlated to VPD$_L$ or T_L(Table 4), which was similar to stomatal limitations observed at high VPD (Fig. 3). Additionally, the positive relationship observed between nighttime g_s and T_r demonstrated that environmental was the main controlling factor. It was, rather, the active biological control (Zeppel et al. 2011). Apparently, both g_s and T_r were negatively correlated to c_i with the exception of nighttime T_r. Surprisingly, however, both of g_s and T_r were not correlated to Ψ_L, θ_L, Ψ_s, and θ_s (Table 4), and this is an obvious difference from eucalypts observations reported by Zeppel et al. (2010); Zeppel et al. (2011), suggesting that E_n increase further under climate change scenarios even though the unlimited water supply with the shallower groundwater table. Another possible interpretation of this inconsistency is that *P. euphratica* is a phreatophyte that can maintain a sufficient water supply through HL (Yu et al. 2013). Although this sapling study covered only three 24-h periods, results are consistent with longer term trends on mature trees where E_n was observed to be lowest between rainfall events (Fig. 2). Along with results from earlier studies (Zeppel et al. 2010; Zeppel et al. 2011; Ogle et al. 2012), our study supports the opinion that E_n is greatest during periods of high transpiration demand and low water stress.

Magnitude of E_n

Mean values of E_n/E_d were 24.99% in 2012 and 34.08% in 2013, and varied between months for mature trees. Compared to mature, E_n/E_d was low with means of 12.06%, and similarly the contribution of $T_{r,n}$ to $T_{r,d}$ was 16.64% in 2013 for saplings.

It is notable that proportions of E_n/E_d or $T_{r,n}/T_{r,d}$ were highest in an arid desert ecosystem, similar to conditions in the semiarid region of the western United States (10%–32%) (Snyder et al. 2003), northwestern Australia (reached a maximum of 50%) (Pfautsch et al. 2011), North American desert ecosystems (17%–26%, with the exception of *Dasylirion leiophyllum*) (Ogle et al. 2012), and a Mediterranean holm oak forest (10%–30%) (Barbeta et al. 2012). One possible reason for this was the higher overall VPD and higher transpiration demand resulting in greater water loss through nighttime transpiration. It should be noted, however, that transpiration did not increased in synchronization with daytime VPD. For plants, consistently high E_n/E_d may reflect high nighttime water loss due to weak stomatal control (high E_n) or, conversely, low daytime water use (low E_d). However, a positive relationship between nighttime and daytime V_s was found. Snyder et al. (2003) reported a similar finding in which higher nighttime conductance and transpiration were positively correlated to higher daytime values, indicating that E_n may facilitate early onset of photosynthesis via quickly open stomata (Daley and Phillips 2006; Dawson et al. 2007; Goldstein et al. 2008; Oren et al. 2001) similar to our data show (Fig. 5).

For this study, the daily ratio of $g_{s,n}$ to $g_{s,d}$ ranged between 21%–37% in summer and autumn, and $g_{s,n}$ magnitude was much higher than reported cuticular conductance (g_c, 4–20 mmol m^{-2} s^{-1}) (Caird et al. 2007), suggesting that extensive nighttime stomatal opening may be important in desert ecosystems. Extensive $g_{s,n}$ has also been reported for 15 species native to North American desert ecosystems (Ogle et al. 2012), such as annual *Helianthus anomalus* in the Great Basin Desert of the United States (Ludwig et al. 2006) as well as seven riparian and warm climate desert species (Snyder et al. 2003) and other species from a variety of environments. Given that g_s was positively correlated to both daytime and nighttime T_r (Table 4), $T_{r,n}$ also largely contributed to $T_{r,d}$ (Table 3). Consequently, $T_{r,d}$ accounted for 87% of mean V_s during the experimental period, having a better goodness of fit of mean V_s to $g_{s,d}$ (Fig. 7).

It is interesting to note that even though there was a decrease in both $g_{s,n}$ and $T_{r,n}$, an increased in V_s was observed between 23:00 and 03:00.This indicated that increased V_s does not promote enhanced $g_{s,n}$ and $T_{r,n}$, which suggests that sap flow was mainly the result of recharging depleted water stores or partial canopy transpiration during this periodin time. Subsequent to that, a linear increase in V_s was observed alongside $g_{s,n}$ and $T_{r,n}$ between 04:00 and 06:00, which more likely was related to transpiration via leaf stomata than stem tissue recharge (Fig. 7, insert).This suggested that no matter the growth stage (whether mature or sapling), storage recharge and E_n occurrences were either synchronous or alternate. The only difference was that saplings had shorter duration times and less E_n compared to mature trees. This suggests that E_n magnitude was associated with the tree size, that effect to stored water of individual trees (Phillips et al. 2003), although this hypothesis requires further research.

Conclusion

Findings from this study add a new species (*P. euphratica*) to the extensive list of existing species for which E_n plays a part as well as those with high E_n to E_d ratios (25%~34%). V_s was logarithmic correlated to VPD during both daytime and nighttime, but this correlation was insignificant for u and $u\times$VPD. It is noteworthy that nighttime V_s was positively correlated to daytime V_s, suggesting that the contribution of E_n to E_d (E_n/E_d) was high for *P. euphratica*. Compared to mature trees, E_n/E_d in 2013 was low with means of 12.06%, that supported further by the shorter duration times and less $T_{r,n}$ (16.64%, 2013) and $g_{s,n}$ (26.45%, 2013) for saplings, which suggests that E_n magnitude was associated with the tree size, that effect to stored water of individual trees, although this hypothesis requires further research.

Materials and Methods

Study Site and Species

This study was conducted between April 2012 and October 2013 at the Alxa Desert Eco-hydrology Experimental Research Station (Alxa Station) operated by the Chinese Academy of Sciences (lat 42°01′N, long 100°21′E, 934 m AMSL). The climate is extremely arid with a mean annual precipitation of 37.4 mm, for which greater than 75% falls between June and August. Pan evaporation (3390.3 mm) in order of magnitude is greater than precipitation by an approximate factor of 90. Mean temperatures in July (27.0°C) and January (-11.7°C) have been calculated from measurements recorded at the Ejin weather station between 1959 and 2011. For details on soil physical and chemical properties related to this study area, see Yu et al. (2013).

The particular riparian forest selected for study is composed of remnant populations of broad-leaved *P. euphratica* and extensive thickets of *T. ramosissima* that typically occur in monocultures or mixtures (Si et al. 2007). The former species is found in higher densities (148 stems ha^{-1}) than the latter (42 stem ha^{-1}) and subsequently contributes the ~75% of total tree basal area in the study site. This is because the average diameter of *P. euphratica* is much larger than *T. ramosissima*. The understory is dominated by grasses, predominantly *Sophora alopecuroides* L., *Karelinia caspica* (Pall.) Less., and *Achnatherum splendens* (Trin.) Nevski (Yu et al. 2013).

Environmental Data

Meteorological factors, 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 3 m using CR3000 at 0.5 h intervals in 2012 at *T. ramosissima* stand (coverage of 52%) and elevated to 10 m at adjacent *P. euphratica* stand (coverage of 68%). R_n was measured using a four-component net radiometer (CNR4, Kipp & Zonen, Delft, The Netherlands); T_a and RH were measured using a temperature and relative humidity sensor (HMP45C, Campbell

Scientific, Inc, USA); and u was measured using a three-dimensional sonic anemometer (CSAT3, Campbell Scientific, Inc., North Logan, UT, USA). Rainfall (mm) was measured using a rain gauge (RG3, HOBO, USA) at 0.7 m height above the surface. VPD was calculated from T_a and RH following the FAO (Campbell and Norman, 1998).

Sap Flow Measurements

Three mature and sapling *P. euphratica* trees were selected to measure sap flow using the heat ratio method (Burgess et al. 2001) (SFM1, ICT Inc., Australia) (Table 1). Sap flow of mature trees was continuously measured throughout the 2012–2013 growing season while saplings were measured throughout the 2013 growing season simultaneously with leaf gas exchangesee below. A single SFM1 sensor contains two temperature probes. Each is composed of two thermocouple junctions and one heater probe that are all integrated to a microprocessor controlled smart interface. Needles are 35 mm long and have two thermocouples located 7.5 mm and 22.5 mm from the tip of the needle. Sensors were radially inserted into the xylem tissue of the stem (i.e., northern side, 130 cm and 30 cm in height for mature and sapling trees, respectively) for the selected trees. Detailed information regarding instrument installation was taken from reference material (Yu et al. 2013).

Heat pulse velocity (V_h, cm h^{-1}) was calculated following Burgess et al. (2001):

$$V_h=\frac{k}{x}ln\left(\frac{v_1}{v_2}\right)\times 3600$$

where k is the thermal diffusivity of fresh wood; x is the distance between heater and thermocouples (with a fixed value of 0.6 cm); and v_1 and v_2 are differences between initial temperatures at two thermocouples (downstream and upstream of flow in relation to the heater, respectively) and temperature measured after a heat pulse. A fixed value of $2.5\cdot10^{-3}$ cm^{2}s^{-1} for k was initially used, but this was corrected after determining the thermal properties of wood (Table 1). The water content of sapwood (m_c, %), basic density of wood (ρ_b, g cm^{-3}), and thermal diffusivity of freshwood (k, 10^{-3} cm^2 s^{-1}) was measured following the SFM1 Sap Flow Meter Manual Version 4.0. All corrections related to probe wounds and misalignments 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 thickness of sapwood was less than the length of probe, the outer (22.5 mm depth) V_s was selected to analysis. The inner (7.5 mm depth) always low and smooth, and even nagative (data not shown), suggested that was inserted in heartwood. Whole tree sap flow (F_s, kg h^{-1}) was calculated as the product of outer V_s and sapwood area (A_s, cm^2) and the density of water (1000 kg m^{-3}) of the selected trees. All data were continuously recorded at 0.5 h intervals using a microSD card.

Daily sap flow was subdivided into daytime and nighttime flow, which was defined as hours during which R_n was less than 5 W m^{-2} (Daley and Phillips 2006). Total daily transpiration (E_d) was the 24-h cumulative sum of F_s of a calendar day. E_n was conservatively calculated as total nighttime F_s between 01:00 and 06:00 according to mean daily V_s variation during typical sunny days between July 25 and 28, 2012 (Fig. 1), for which nighttime (20:30 ~ 6:30) V_s did not exponentially decay (Alvarado-Barrientos et al. 2014) but first decreased (20:30 ~ 00:30) and then stabilized (01:00 ~ 06:00) until sunrise (for which the latter period can be attributable to E_n). The ratio of E_n to E_d (E_n/E_d) was then computed using only days with complete 24-h F_s series.

Leaf Gas Exchange and Water Potential Measurements

Three 24-h field experiments (from July 17th to 18th, from July 31th to August 1st, and from September 3rd to 4th, 2013) were conducted to directly evaluate daytime and nighttime leaf gas exchange of *P. euphratica* sapling samples. Each of the three healthy, fully expanded tree leaves was measured using a portable open-flow gas-exchange system (LI-6400XT, LI-COR Biosciences Inc., USA) every 2 h commencing at 06:00 and concluding at 04:00 the following day. For each measurement period, the leaf level transpiration rate (T_r, mmol H$_2$O m^{-2} s^{-1}), stomatal conductance (g_s, mol H$_2$O m^{-2} s^{-1}), leaf temperature (T_L, °C), ambient leaf-to-air vapour pressure difference (VPD$_L$, kPa) and intercellular and ambient CO$_2$ concentration (c_i and c_a, μmol CO$_2$ mol^{-1} m^{-2} s^{-1}) were measured.

At the same time, leaf and soil samples were collected at 2 h intervals. This is consistent with gas-exchanges measured to monitor daytime variation in leaf and soil water potential (ψ_L and ψ_s, respectively) as well as the mass moisture content (θ_L and θ_s, respectively). Nine leaf samples were collected for each tree: three each from the upper, middle, and lower crown. Similarly, nine soil samples were taken: three each at depths of 20 cm, 40 cm, and 60 cm. Samples were immediately taken to the laboratory and ψ_s and ψ_L were determined using a dew-point water potential meter (WP4C, Decagon Devices, Inc., USA). At the same time, θ_L and θ_s were gravimetrically measured. The means of different highs (leaves) and depths (soil) were used for analysis.

Statistical Analysis

Descriptive statistics were used to calculate average and standard deviation (SD). For ψ_L, θ_L, ψ_s, and θ_s data, the Kolmogorov–Smirnov test was used to verify normality. Data were logarithmically transformed prior to analysis if testing failed. Homogeneity of variance was verified using Levene's test. Repeated measurements of one-way ANOVA were conducted using Mauchly's sphericity test and Tukey'spost-hoc test ($P < 0.05$) to examine variations in ψ_L, θ_L, ψ_s, and θ_s data. One-way ANOVA in conjunction with Tukey'spost-hoc test was also applied to examine differences in means between the continuously measured data. Correlations among variables were examined by correlation analysis. All statistical analyses and chartings was processed using Origin ver. 8 (Origin Lab Corp., USA).

Acknowledgements

We would like to thank the Youth Foundation of the National Natural Science Foundation of China (41401033), the Chinese Postdoctoral Science Foundation (2014M560819), the Foundation for Excellent Youth Scholars of CAREERI, CAS (51Y451071), the General Program of the National Natural Science Fund of China (No. 31370466, 41271037) and the Natural Science Foundation of Gansu Province (No. 145RJZA141) for their financial support. The authors would also like to thank two anonymous reviewers for their constructive and valuable reviews and comments, which helped to improve this article.

Author's Contributions

TY, QF and JS conceived and designed the study, data processing by Origin ver. 8, wrote and revised the manuscript; XZ reviewed and edited the manuscript; DA provided the technical directing of instruments installation of SFM1; CZ performed the experiments of measurement. All the authors agreed on the contents of the paper and post no conflicting interest.

References

Alvarado-Barrientos MS, Holwerda F, Geissert DR, Muñoz-Villers LE, Gotsch SG, Asbjornsen H, Dawson TE (2014) Nighttime transpiration in a seasonally dry tropical montane cloud forest environment. Trees 29:259–274

Barbeta A, Ogaya R, Peñuelas J (2012) Comparative study of diurnal and nocturnal sap flow of Quercus ilex and Phillyrea latifolia in a Mediterranean holm oak forest in Prades (Catalonia, NE Spain). Trees 26:1651–1659

Barbour MM, Buckley TN (2007) The stomatal response to evaporative demand persists at night in Ricinus communis plants with high nocturnal conductance. Plant Cell Environ 30:711–721

Barbour MM, Cernusak LA, Whitehead D, Griffin KL, Turnbull MH, Tissue DT, Farquhar GD (2005) Nocturnal stomatal conductance and implications for modelling delta ^{18}O of leaf-respired CO_2 in temperate tree species. Funct Plant Biol 32:1107–1121

Benyon RG (1999) Nighttime water use in an irrigated Eucalyptus grandis plantation. Tree Physiol 19:853–859

Bucci SJ, Scholz FG, Goldstein G, Meinzer FC, Hinojosa JA, Hoffmann WA, Franco AC (2004) Processes preventing nocturnal equilibration between leaf and soil water potential in tropical savanna woody species. Tree Physiol 24:1119–1127

Burgess SSO, Adams MA, Turner NC, Beverly CR, Ong CK, Khan AAH, Bleby TM (2001) An improved heat pulse method to measure low and reverse rates of sap flow in woody plants. Tree Physiol 21:589–598

Campbell GS, Norman JM (1998). An Introduction to Environmental Biophysics. Springer, Verlag New York, Inc.

Caird MA, Richards JH, Donovan LA (2007) Nighttime stomatal conductance and transpiration in C_3 and C_4 plants. Plant Physiol 143:4–10

Cavender-Bares J, Sack L, Savage J (2007) Atmospheric and soil drought reduce nocturnal conductance in live oaks. Tree physiol 27:611–620

Christman MA, Donovan LA, Richards JH (2009) Magnitude of nighttime transpiration does not affect plant growth or nutrition in well-watered Arabidopsis. Physiol Plantarum 136:264–273

Daley MJ, Phillips NG (2006) Interspecific variation in nighttime transpiration and stomatal conductance in a mixed New England deciduous forest. Tree Physiol 26:411–419

Dawson TE, Burgess SSO, Tu KP, Oliveira RS, Santiago LS, Fisher JB, Simonin KA, Ambrose AR (2007) Nighttime transpiration in woody plants from contrasting ecosystems. Tree Physiol 27: 561–575

Domec JC, Ogee J, Noormets A, Jouangy J, Gavazzi M, Treasure E, Sun G, McNulty SG, King JS (2012) Interactive effects of nocturnal transpiration and climate change on the root hydraulic redistribution and carbon and water budgets of southern United States pine plantations. Tree Physiol 32:707–723

Donovan LA, Richards JH, Linton MJ (2003) Magnitude and mechanisms of disequilibrium between predawn plant and soil water potentials. Ecology 84:463–470

Fisher JB, Baldocchi DD, Misson L, Dawson TE, Goldstein AH (2007) What the towers don't see at night: nocturnal sap flow in trees and shrubs at two AmeriFlux sites in California. Tree Physiol 27:597–610

Goldstein G, Meinzer FC, Bucci SJ, Scholz FG, Franco AC, Hoffmann WA (2008) Water economy of Neotropical savanna trees: six paradigms revisited. Tree Physiol 28:395–404

Hogg EH, Hurdle PA (1997) Sap flow in trembling aspen implications for stomatal responses to vapor pressure deficit. Tree Physiol 17: 501–509

Howard AR, van Iersel MW, Richards JH, Donovan LA (2009) Night-time transpiration can decrease hydraulic redistribution. Plant Cell Environ 32:1060–1070

Ludwig F, Jewitt RA, Donovan LA (2006) Nutrient and water addition effects on day- and night-time conductance and transpiration in a C_3 desert annual. Oecologia 148:219–225

Moore GW, Cleverly JR, Owens M, K. (2008) Nocturnal transpiration in riparian Tamarix thickets authenticated by sap flux, eddy covariance and leaf gas exchange measurements. Tree Physiol 28:521–528

Neumann RB, Cardon ZG (2012) The magnitude of hydraulic redistribution by plant roots: a review and synthesis of empirical and modeling studies. New Phytol 194:337–352

Novick KA, Oren R, Stoy PC, Siqueira MBS, Katul GG (2009) Nocturnal evapotranspiration in eddy-covariance records from three co-located ecosystems in the Southeastern U.S.: Implications for annual fluxes. Agr Forest Meteorol 149:1491–1504

Ogle K, Lucas RW, Bentley LP, Cable JM, Barron-Gafford GA, Griffith A, Ignace D, Jenerette GD, Tyler A, Huxman TE, Loik ME, Smith SD, Tissue DT (2012) Differential daytime and night-time stomatal behavior in plants from North American deserts. New Phytol 194:464–476

Oren R, Sperry JS, Ewers BE, Pataki DE, Phillips N, Megonigal JP (2001) Sensitivity of mean canopy stomatal conductance to vapor pressure deficit in a flooded Taxodium distichum L. forest: hydraulic and non-hydraulic effects. Oecologia 126:21–29

Peng S, Piao S, Ciais P, Myneni RB, Chen A, Chevallier F, Dolman AJ, Janssens IA, Penuelas J, Zhang G, Vicca S, Wan S, Wang S, Zeng H (2013) Asymmetric effects of daytime and night-time warming on Northern Hemisphere vegetation. Nature 501:88–92

Pfautsch S, Keitel C, Turnbull TL, Braimbridge MJ, Wright TE, Simpson RR, O'Brien JA, Adams MA (2011) Diurnal patterns of water use in *Eucalyptus victrix* indicate pronounced desiccation-rehydration cycles despite unlimited water supply. Tree Physiol 31:1041–1051

Phillips NG, Lewis JD, Logan BA, Tissue DT (2010) Inter- and intra-specific variation in nocturnal water transport in *Eucalyptus*. Tree Physiol 30:586–596

Phillips NG, Ryan MG, Bond BJ, McDowell NG, Hinckley TM, ČERMÁK J (2003) Reliance on stored water increases with tree size in three species in the Pacific Northwest. Tree Physiol 23: 237–245

Rosado BHP, Oliveira RS, Joly CA, Aidar MPM, Burgess SSO (2012) Diversity in nighttime transpiration behavior of woody species of the Atlantic Rain Forest, Brazil. Agr Forest Meteorol 58:13–20

Si JH, Feng Q, Yu TF, Zhao CY (2015)Nighttime sap flow and its driving forces for *Populuseuphratica* in a desert riparian forest, Northwest, China. J Arid Land 7: 665–674

Snyder KA, Richards JH, Donovan LA (2003) Night-time conductance in C3 and C4 species: do plants lose water at night? J Exp Bot 54:861–865

Yu T, Feng Q, Si J, Xi H, Li Z, Chen A (2013) Hydraulic redistribution of soil water by roots of two desert riparian phreatophytes in northwest China's extremely arid region. Plant Soil 372:297–308

Zeppel M, Logan BA, Lewis JD, Phillips NG, Tissue DT (2013) Why lose water at night ? Disentangling the mystery of nocturnal sap flow, transpiration and stomatal conductance – When, Where, Who? In IX International Workshop on Sap Flow 991:307–312

Zeppel M, Tissue D, Taylor D, Macinnis-Ng C, Eamus D (2010) Rates of nocturnal transpiration in two evergreen temperate woodland species with differing water-use strategies. Tree Physiol 30:988–1000

Zeppel MJ, Lewis JD, Chaszar B, Smith RA, Medlyn BE, Huxman TE, Tissue DT (2012) Nocturnal stomatal conductance responses to rising [CO_2], temperature and drought. New Phytol 193:929–938

Zeppel MJ, Lewis JD, Medlyn B, Barton CV, Duursma RA, Eamus D, Adams MA, Phillips N, Ellsworth DS, Forster MA, Tissue DT (2011) Interactive effects of elevated CO_2 and drought on nocturnal water fluxes in Eucalyptus saligna. Tree Physiol 31: 932–944

Zhu GF, Li X, Su YH, Huang CL (2010) Parameterization of a coupled CO_2 and H_2O gas exchange model at the leaf scale of *Populus euphratica*. Hydrol Earth Syst Sc 14:419–431