

ORIGINAL RESEARCH

Depressed hydraulic redistribution of roots more by stem refilling than by nocturnal transpiration for *Populus euphratica* Oliv. in situ measurement

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Funding information

Youth Foundation of the National Natural Science Foundation of China, Grant/Award Number: 41401033; the Chinese Postdoctoral Science Foundation, Grant/Award Number: 2014M560819; Key Research Program of Frontier Sciences; CAS, Grant/Award Number: QYZDJ-SSW-DQC031; National Key R&D Program of China, Grant/Award Number: 2017YFC0404305

Abstract

During the night, plant water loss can occur either through the roots, as hydraulic redistribution (HR), or through the leaves via the stoma, as nocturnal transpiration (E_n), which was methodologically difficult to separate from stem refilling (R_e). While HR and E_n have been reported across a range of species, ecosystem, and climate zone, there is little understanding on the interactions between E_n and/or R_e and HR. As water movement at night occurs via gradients of water potential, it is expected that during periods of high atmospheric vapor pressure deficit (VPD), water loss via E_n will override water loss via HR. To test this hypothesis, sap flow in stems and roots of *Populus euphratica* Oliv. trees, growing in a riparian zone in a hyperarid climate, was measured once in a year. Nocturnal stem sap flow was separated into E_n and R_e using the “forecasted refilling” method. Substantial nocturnal sap flow (38% of 24-hr flux on average) was observed and positively correlated with VPD; however, the strength of the correlation was lower ($R^2 = .55$) than diurnal sap flow (E_d) ($R^2 = .72$), suggesting that nocturnal stem sap flow was attributed to both water loss through the canopy and replenishment of water in stem tissues. Partitioning of nocturnal sap flow shows that R_e constituted approximately 80%, and $E_n \sim 20\%$, of nocturnal sap flow. The amount of root sap flow attributed to redistribution was negatively related to E_d ($R^2 = .69$) and the amount of acropetally sap flow in stems, R_e ($R^2 = .41$) and E_n ($R^2 = .14$). It was suggested that the magnitude of HR is more strongly depressed by R_e that was recharge to the water loss via E_d than by E_n . It was consistent with whole-tree water balance theory, that the nighttime upward sap flow to xylem, stem refilling and transpiration, may depress hydraulic redistribution of roots.

KEYWORDS

desert riparian trees, hydraulic redistribution, nocturnal transpiration, sap flow, stem refilling

1 | INTRODUCTION

During the night, plant water movement can occur via two major pathways: (1) the roots, where the movement of water is from different parts of the root zone with large gradients in water status [hydraulic redistribution (HR)] (Burgess, Adams, Turner, & Ong, 1998; Nadezhdina et al., 2010) or (2) the leaves, nocturnal transpiration (E_n) from the canopy via the stoma (Dawson et al., 2007; Howard, van Iersel, Richards, & Donovan, 2009). While HR and E_n have been reported across a range of species, ecosystem, and climatic conditions, the relationship between both of them remains poorly understood (Bauerle, Richards, Smart, & Eissenstat, 2008; Dawson et al., 2007; Howard et al., 2009). Thus, determining the patterns of HR and E_n and their interaction is important to better understand plant water relations and ecosystem water balance.

It has been widely documented that HR can occur between the roots and soil environment in upward, downward, and lateral directions (Burgess et al., 1998; Hultine, Scott, Cable, Goodrich, & Williams, 2004; Nadezhdina et al., 2010; Prieto, Armas, & Pugnaire, 2012; Richard & Caldwell, 1987; Smith, Jacson, Roberts, & Ong, 1999) across a broad range of species and ecosystem, but it is particularly prevalent in arid and semiarid ecosystems (Caldwell & Richard, 1989; Hultine, Cable, Burgess, & Williams, 2003; Hultine et al., 2004; Yoder & Nowak, 1999; Yu & D'Odorico, 2015; Yu et al., 2013). HR most often occurs at night when the soil water potential of layers is larger than the canopy water potential while transpiration is low (Burgess et al., 1998; Prieto et al., 2012). However, where stem sap flow is significant, the predominant flow of water may be toward the leaves and thus override the driving force of water flow between root compartments (Burgess & Bleby, 2006; Howard et al., 2009; Neumann et al., 2014).

Owing to the water potential gradient between leaves and atmosphere at night, E_n has also been reported across a range of taxa and biomes under various climatic conditions (Forster, 2014), certainly including the desert settings (Ludwig, Jewitt, & Donovan, 2006; Ogle et al., 2012; Snyder, Richards, & Donovan, 2003; Yu et al., 2016). E_n is often positively correlated with the nighttime leaf-to-air vapor pressure deficit (VPD) (Christman, Donovan, & Richards, 2009; Hogg & Hurdle, 1997; Pfautsch et al., 2011; Zeppel, Tissue, Taylor, Macinnis-Ng, & Eamus, 2010; Zeppel et al., 2012) although some data indicate inverse relationship [see the review by Caird, Richards, and Donovan (2007)], or the combination of VPD and wind speed (Benyon, 1999; Phillips, Lewis, Logan, & Tissue, 2010), or the soil water availability (Cavender-Bares, Sack, & Savage, 2007; Zeppel et al., 2012) and further regulated by the circadian clock (Resco de Dios et al., 2013). E_n may therefore result from increased stomatal conductance caused by a combination of high temperature, low humidity, and high soil water availability. These conditions are often typical to riparian forests in the hyperarid climate where soil water availability remains high because of trees' access to shallow groundwater throughout the summer (Yu et al., 2016).

Nocturnal sap flow is commonly estimated using sap flow techniques (Burgess et al., 2001; Dawson et al., 2007; Zeppel et al., 2010); however, partitioning of nocturnal sap flow into E_n and stem refilling (R_e) components is methodologically difficult (Dawson et al., 2007). While

E_n can potentially be observed directly via measurements of leaf-level transpiration with canopy or leaf chambers (Caird et al., 2007; Cirelli, Equiza, Lieffers, & Tyree, 2016; Ogle et al., 2012), a precise determination of R_e is more difficult. Several methods have been suggested to determine the R_e component of nocturnal sap flow. For example, Phillips et al. (2010) suggested an empirical method that is related to patterns of VPD across various days. Zeppel et al. (2010) estimated the contribution of nocturnal sap flow to R_e by subtracting the sap flow at the height of crown from that at the ground level. The "forecasted refilling" involves extrapolating forward the declining portion of the diurnal curve of sap flow until it approaches to zero flow as stomatal closure completely. The area above the extrapolated curve is identified as E_n and that below the curve is R_e (Fisher, Baldocchi, Misson, Dawson, & Goldstein, 2007). The "forecasted refilling" method has previously been applied to cloudless, rain-free days and nights with low VPD (Alvarado-Barrientos et al., 2014; Buckley, Turnbull, Pfautsch, & Adams, 2011).

The study site was located at a riparian forest dominated by *Populus euphratica* Oliv. trees (Euphrates poplar) and *Tamarix ramosissima* Ledeb. shrubs growing in a hyperarid climate in northwestern China. It provides an ideal system to observe HR and E_n , given the relatively stable soil water availability due to the shallow water table and high evaporative conditions at night. Previously, HR was observed from *P. euphratica* and *T. ramosissima* roots (Yu et al., 2013), but the magnitude of HR in the *P. euphratica* trees was lower (Yu, Feng, Si, & Zhang, 2014) than that previously reported (Neumann & Cardon, 2012) and for which no immediate causal explanation was evident. Furthermore, we previously observed a significant nocturnal sap flow at the site (Si, Feng, Yu, & Zhao, 2015) of which 34% was attributed to E_n roughly estimated as the sum of sap flow from midnight to predawn (Yu et al., 2016).

Given that, this study focused on the relationship between HR and E_n and/or R_e based on the hypothesis that the magnitude of HR was limited by E_n and/or R_e (Bauerle et al., 2008; Caird et al., 2007; Dawson et al., 2007; Howard et al., 2009). Specifically, we evaluate the contributions of these different sources of sap flow in this species by (1) separating nocturnal sap flow into E_n and R_e and (2) determining the relationship between HR and E_n and/or R_e of *P. euphratica* through in situ measurement in a hyperarid climate in NW China.

2 | MATERIALS AND METHODS

2.1 | Research area and field site

The research area is situated at the northwest of the Badain Jaran Desert and is dissected by the Heihe River, the second inland river of China. The climate of the region is extremely arid with the average annual rainfall of 37.5 mm, of which greater than 75% falls between June and August. Pan evaporation measured by E-601B pan is 2,226 mm p.a. (2002–2015) (Yu, Feng, Si, Zhang, & Zhao, 2017a). The field site located at the lower Heihe river basin (lat 42°01'N, long 100°21'E, 934 m AMSL) is composed of remnant populations of broad-leaved *P. euphratica* tree (Yu et al., 2017a), with the stand density of 146

TABLE 1 Summary of biological parameters for three selected *Populus euphratica* trees and quadrat with the size of 100 m × 100 m for this study area

Trees	Height (m)	DBH (cm)	A_s (cm ²)	A_c (10 ³ cm ²)
Stem	11.1	43.35	268.68	220.51
	11.4	49.47	324.35	301.75
	12.1	41.38	251.49	255.05
Mean ± SD	11.53 ± 0.51	44.73 ± 4.22	281.51 ± 38.09	259.10 ± 40.77
Stand (N = 146)	11.17 ± 2.35	45.90 ± 14.38	304.48 ± 143.74	292.46 ± 142.92
Sig. (2-tailed)	0.343	0.679	0.406	0.292

DBH, diameter at breast height; A_s , sapwood area; A_c , projected area of crown.

individuals ha⁻¹, an average height of 11.17 m, and diameter at breast height (DBH) of 45.9 cm (Table 1). *P. euphratica* contributes the majority (~75%) of total basal area in the study site. Sapwood area (A_s) of the stand was estimated from the allometric model between A_s and DBH, $y = 1.2828 x^{1.4223}$ ($R^2 = .87$, $p < .01$, $N = 59$) in the whole study area according to Keyimu, Halik, and Kurban (2017), in which sapwood width was firstly measured by caliper rule by taking 5-mm-diameter cores (Haglof, Sweden), and then, A_s was estimated by combining it with DBH. Soils at the site are sandy loam and silt loam above 82 cm and below 124 cm, respectively, with a distinct sand layer between them. The soil moisture content was obtained gravimetrically from soil pits during the growing season of 2012 and then multiplied by soil bulk density to obtain soil volumetric moisture content (θ). Soil, c. 2 m west of the selected trees, was sampled monthly using an auger from 0 to 160 cm depth at 20-cm intervals (three sets of samples were obtained). Vertical profile of θ showed a distinctly higher value at 20–60 cm with an average of 16.7% in stand, and it was in consistent with the fine root (<2 mm) length density that suggests potentially HR (Yu et al., 2013).

2.2 | Meteorological data

Meteorological parameters were measured at a height of 3 m in a nearby clear space and included the following: net radiation (R_n , W/m²), air temperature (T_a , °C), relative humidity (RH, %), and wind speed (U , m/s). These data were recorded at 0.5-hr intervals in 2012 (CR3000, Campbell Inc., USA) (Yu, Qi, Si, Zhang, & Zhao, 2017b). Daily rainfall (mm) was acquired from the nearest meteorological station belonging to the China Meteorological Administration and located in Ejn, which is 8 km from the study site. VPD was calculated from T_a and RH.

2.3 | Sap flow measurements

Three mature trees were randomly selected to measure the sap flow of stems and roots using the heat ratio method (Burgess et al., 2001) during the growing season of 2012, from first foliation stage to leaf coloration stage (roughly from April 4th to October 28th) and after that until the foliation stage of the next year was classified as the dormancy period. The selected trees were representative of the surrounding stand and had similar height, DBH, and A_s with stand (one-sample t -test, $p = .05$) (Table 1). The sap flow probe sets used in this

study (SFM1, ICT Inc., Armidale, Australia) contain one heater and two temperature probes, positioned upstream and downstream of the heater (35 mm long). Each temperature probe measures sap velocity at 7.5 and 22.5 mm distance from the tip of the probe. Probes were radially inserted into the xylem tissue of the stem (i.e., northern side, 130 cm in height) and two lateral roots (i.e., northern and southern sides, respectively, 30 cm in depth distance to trunk) for the selected trees. The diameter and A_s of lateral roots were 6.90 ± 1.27 cm and 152.04 ± 55.15 cm², respectively (Yu et al., 2013). Heat pulse velocity was measured at 0.5-hr intervals. All corrections related to the probe wounds and misalignments and calculation of sap velocity (V_s , cm/hr) on a sapwood area basis were made according to Burgess et al. (2001).

Zero flow adjustment was of vital importance to determine E_n (Alvarado-Barrientos et al., 2014; Zeppel et al., 2010). It can be determined using two methods: (1) severing the tree xylem to reduce the flow to zero and (2) estimating nocturnal V_s at night when atmospheric demand is low, that is, low VPD. Previous studies have shown that both methods have no significant differences ($p < .05$) (Zeppel et al., 2010). In this study, the cutting of the tree xylem was not possible because research sites were located in a natural forest national reserve. Instead, near-zero sap flow was assumed during night (25 July 2012) with substantial rainfall (12.4 mm in 3 hr, Figure 1), causing VPD to be the lowest recorded throughout the entire measurement campaign (<0.18 kPa). Recorded V_s ceased quickly with the onset of rainfall and then stabilized at the lowest recorded sap velocities (1.6 cm/hr). To compare with dimension of HR, the sapwood-related sap flow (Q_s , kg/hr) was calculated by multiplying V_s by A_s and water density.

2.4 | Separation of transpiration and refilling

Whole-tree crown-related sap flow (Q_c , equal to transpiration E , mm/hr) was calculated by dividing the product V_s and A_s by the projected area of crown (A_c , cm²). A_c was calculated as the circular area via measurement of diameter of crown at four directions. Q_c was separated into daytime (equal to E_d , mm/hr), and nighttime Q_c according to R_n is greater than or less than 5 W/m² (Daley & Phillips, 2006). Previously, Fisher et al. (2007) suggested that the early sloped phase of nighttime Q_c represents mostly R_e and the later, nonzero linear phase represents E_n . Thus, we separated the E_n and R_e components of nighttime Q_c using an exponential decay model ($y = a e^{bx}$). The relationship between nighttime Q_c and VPD for the first 3 to 5 hr after dusk was determined with R^2 consistently >.97 (Figure S1), since nighttime Q_c

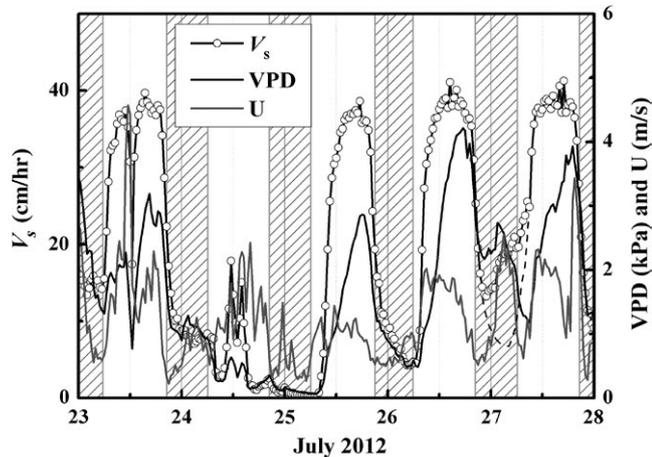


FIGURE 1 Hourly variation in stem sap velocity (V_s , cm/hr) of *Populus euphratica*, vapor pressure deficit (VPD, kPa), and wind speed (U, m/s) that, in combination, drive nocturnal sap flow after a rainfall event (12.4 mm, 24th July). The shaded area represents the nighttime

from sunset to sunrise did not exponentially decreased (Alvarado-Barrientos et al., 2014) but first decreased from sunset to midnight with decreased VPD and then stabilized and increased until sunrise of the next day, thus the above of the extrapolated curve is identified as E_n and below of the curve is R_e . The last fitted Q_c data point was before an inflexion point was reached (i.e., when nighttime Q_c was not continuing to decline). Daily E (mm/day) was the 24-hr sum of E from sunrise to sunrise of the next day, and then, the contribution of E_n to E ($E_n:E$) was computed.

2.5 | Hydraulic redistribution

HR was quantified as the total volume water estimated from negative sap flow (i.e., flow directionally away from the trunk) measured on roots. HR was presented as nighttime sap flow (kg/day), by summing the product of sap velocity by the cross-sectional area of similar lateral roots and water density, instead of volumetric flow velocities (mm/day) owing to the latter it is difficult to scale up with the size of each individual lateral root monitored. Because it was difficult to measure sap flow on all roots, only large lateral roots with a west-to-east orientation were instrumented with sap flow sensors.

2.6 | Statistical analysis

Mean and standard error (SE) of all variables were calculated. Difference between the mean of samples and population of stand ($N = 146$) was tested by the one-sample t -test at a significance level of $\alpha = 0.05$. The differences in means of sap flow fluxes (E , E_d , E_n , R_e) were examined via one-way ANOVA at a significance level of $\alpha = 0.05$ in conjunction with Tukey's post hoc test for the continuously measured data. The exponential decay modeling ($y = a e^{bx}$) was applied in the "forecasted refilling" method and to determine the relationship between sap flow fluxes (E_n , R_e , and E_d) and HR. The sigmoidal function with three parameters ($f = a/(1 + \exp(-(x - x_0)/b))$) was used

to determine the relationship between E_n , R_e , and E_d . To determine the relationship between HR and E_n , and R_e , the stepwise regression analysis was used, which only considered the inclusion of additional parameters if an improvement of $R^2 > 5\%$ was shown and if parameter estimates were significant. Those statistical analyses and plotting were performed with the software package of SPSS Statistics (version 19.0; IBM, Armonk, NY, USA) and SigmaPlot (version 13.0; Systat Software, Erkrath, Germany), respectively.

3 | RESULTS

3.1 | Sap velocity and meteorological factors

Peak hourly V_s generally occurred in the early afternoon, whereas zero-to-low V_s occurred on nights of low VPD and high V_s occurred on nights of higher VPD and U. V_s reached a maximum velocity of ~ 40 cm/hr during the daytime. V_s was close to zero on the night of 24th/25th July when VPD was ~ 0 kPa following a 12.4-mm rainfall event. On the night of 26th/27th July, when VPD was greater than 2 kPa and U greater than 1 m/s, nighttime V_s was relatively high (Figure 1).

Compared to the daytime V_s with an average of 32 cm/hr, nighttime V_s averaged 16 cm/hr. When devoid of rainfall days, there was a significant ($p < .01$) logarithmic relationship between V_s and VPD for both daytime and nighttime periods during the growing season. However, the goodness of fit was higher in the daytime ($R^2 = .72$) than in the nighttime ($R^2 = .55$) (Figure 2).

3.2 | Partitioning of nocturnal transpiration and xylem refilling

Daytime Q_c increased suddenly during early May and slightly raised from May to mid-July, and after that, it sharply decreased to October and maintained the lowest from mid-October to the dormant period (Figure 3a). Substantial nighttime Q_c (38% of 24-hr flux on average) was observed and is higher than daytime Q_c in defoliation period, but it is less than and opposite during daytime Q_c at the whole-leaf stage (Figure 3a). Overall, the forecasted refilling method found that R_e and E_n on average accounted for approximately 80% and 20% of nighttime Q_c , respectively. E_n was increased during early May and stabilized at the whole-leaf stage and decreased after defoliation. R_e , however, showed peaks in spring and autumn and a relative decline in mid-summer, which is obviously higher than E_n (Figure 3b).

The monthly totals of E , E_d , E_n , and R_e and the contribution of E_n and R_e to E are presented in Table 2, in which R_e increased proportionally with E_d , but not the case for E_n . Compared to E_n with a mean of 7.5% of daily E , R_e was substantial, accounting for an average of 29.7% of daily, which suggests that high nighttime Q_c was mainly attributed to R_e . E_n was consistent throughout the year with the $E_n:E$ ratio approximately 5% to 10%.

A significant logarithmic relationship was observed between E_d versus E_n and versus R_e , but the goodness of fit was better for the

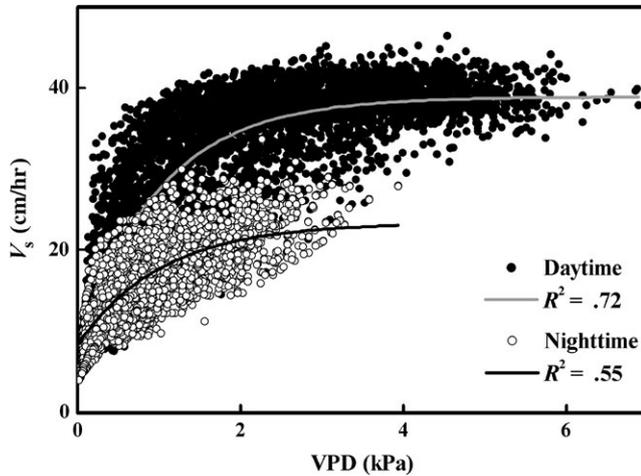


FIGURE 2 Relationship between sap velocity (V_s , cm/hr) and vapor pressure deficit (VPD, kPa) throughout the growing season (from May 4th to October 15th) devoid of rain days in 2012 for *Populus euphratica*. Logarithmic relationships are shown for both daytime and nighttime

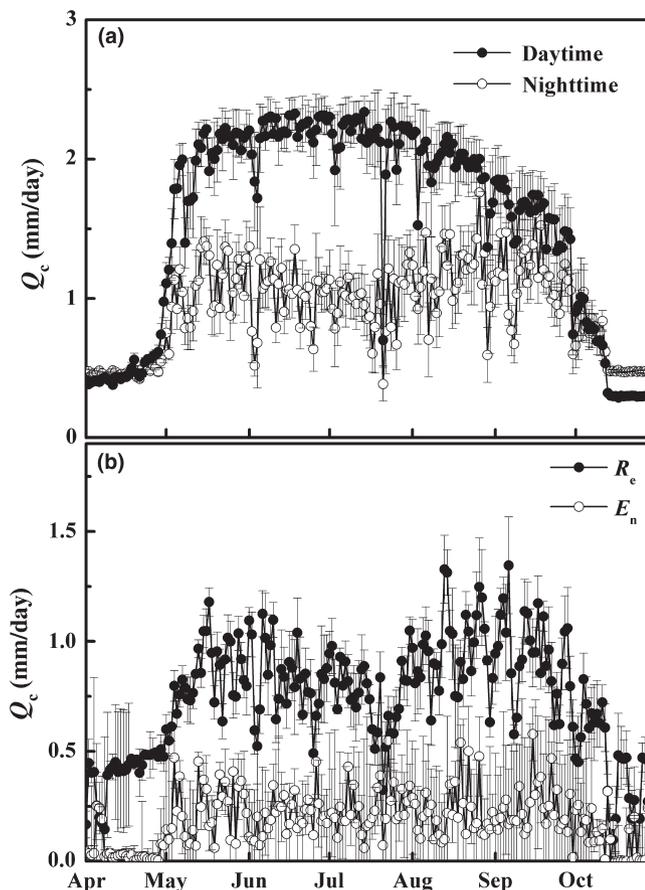


FIGURE 3 The daily variation (mean \pm SE) in (a) sap flow (Q_c , mm/day) at daytime and nighttime and (b) partitioned nocturnal transpiration (E_n , mm/day) and stem refilling (R_e , mm/day) during the growing season of 2012

latter ($R^2 = .18$) than for the former ($R^2 = .12$) (Figure 4) throughout the growing season (when days of rainfall were removed from the analysis).

3.3 | Relationship between hydraulic redistribution and nocturnal transpiration and stem refilling

Devoid of the rainfall days, V_s of stem was always positive; conversely, V_s in lateral roots was positive at daytime but negative at nighttime, that is, moving away from the base of the stem toward the root tips, which strongly suggests HR. Comparisons between V_s (as a percentage of maximum daytime rate, %) of stem and lateral roots show variation (Figure 5), whereby reverse nighttime V_s increased in lateral roots after rain (25th and 26th July) and rapidly decreased with rising daytime V_s later in the second day (27th July), which suggests that HR was possibly limited by sap flow of stem, R_e and/or E_n . Daily HR of roots (Figure 6) was reverse to the variation of Q_c , in particular to the daytime Q_c (Figure 3).

A significantly exponential decay relationship was found between HR and E_n (Figure 7a) and R_e (Figure 7b) at daily scale during the growing season, and the goodness of fit was better for R_e ($R^2 = .41$) than for E_n ($R^2 = .14$), which suggests that HR was mainly inhibited by R_e and E_n . A negative coefficient of multiple linear regression model ($HR = -0.533R_e - 1.522E_n + 3.563$, $R^2 = .41$, $p < .001$) and mixed exponential model ($HR = 2.051\exp(-21.682R_e) + 7.719\exp(-2.559E_n)$, $R^2 = .47$, $p < .001$) also demonstrated the decreased HR with the increasing R_e and E_n . A stepwise regression analysis showed that the proportion of the variance in the model explained by R_e and E_n ($R^2 = .40$) was 4% higher than that explained by R_e alone ($R^2 = .36$, $p < .001$). And, it is interesting that HR was significantly decreased with the increasing E_d ($R^2 = .69$) (Figure 7c).

4 | DISCUSSION

4.1 | Substantial nocturnal sap flow: transpiration or stem refilling?

Nocturnal water loss was once thought to be zero, or negligible; however, over the last two decades, a growing body of researchers have observed that it can contribute significantly to total daily water use across a range of natural ecosystems (see the review by Forster, 2014). The significance of nighttime Q_c to daily sap flux has been defined in a number of ways and one of which as a proportion of whole-day flow has been reported as high as 38% and 39% in *Phillyrea latifolia* and *Quercus ilex*, respectively (Barbeta, Ogaya, & Peñuelas, 2012). Particularly, the ratio of nighttime sap flow in the C_3 -CAM species, *Clusia minor*, can be up to 70% with the increase in nocturnal acid accumulation (Herrera, Ballestrini, & Tezara, 2008). For *P. euphratica*, the ratio of nighttime Q_c to total daily flow (38%) was significantly higher than the average of 12% across seasons, biomes, and phylogenetic groups (Forster, 2014). Nocturnal Q_c ratio in other poplar species has an average of 7.71% and 9.33% with a maximum record of 29.07% and 23.93% for *Populus grandidentata* and *Populus deltoides*, respectively (Marks & Lechowicz, 2007), and continental (i.e., arid) biomes have an average of 13.88% with a maximum record of 24.37% using the sap flow measurement (Forster, 2014), all of those less than

Months	4	5	6	7	8	9	10	Sum or mean
E	24.2	87.5	96.7	96.6	99.7	83.3	36.2	524.3
E_d	12.4	56.0	65.5	66.3	62.5	48.2	18.1	329.0
E_n	1.2	6.6	6.5	7.2	7.3	7.2	3.5	39.4
R_e	10.6	24.9	24.7	23.2	29.9	27.8	14.7	155.9
$E_n:E$	5.0	7.6	6.7	7.4	7.3	8.7	9.6	7.5
$R_e:E$	43.9	28.4	25.6	24.0	30.0	33.4	40.6	29.7

TABLE 2 Seasonal variation in daily transpiration (E , mm), daytime transpiration (E_d , mm), nighttime transpiration (E_n , mm), tissue refilling (R_e , mm), and the contribution of E_n and R_e to E ($E_n:E$ and $R_e:E$, %) during the growing season from April to October of 2012 for *Populus euphratica* trees

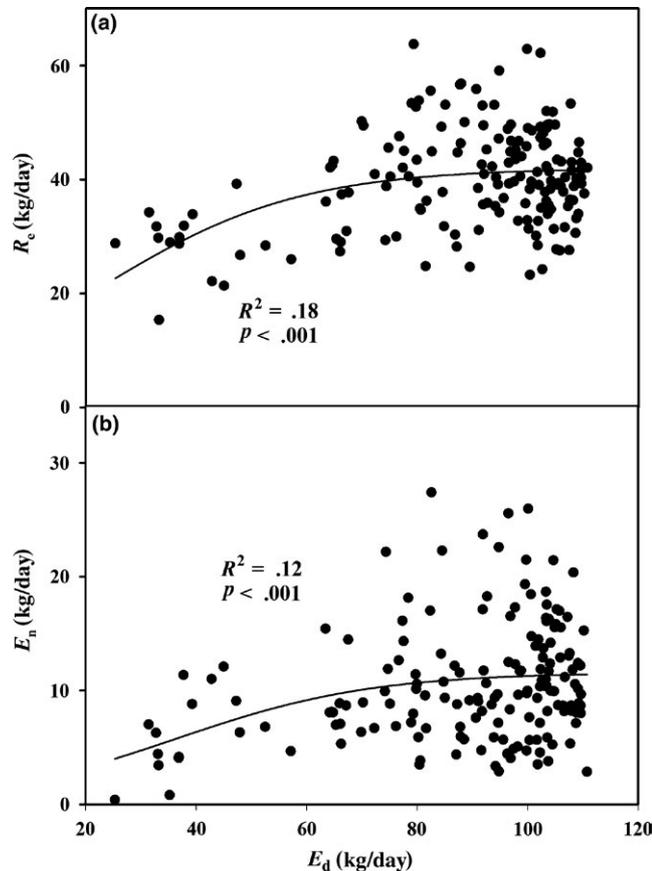


FIGURE 4 Relationships between daytime transpiration (E_d , kg/day) and (a) stem refilling (R_e , kg/day) and (b) nighttime transpiration (E_n , kg/day) during the growing season of 2012. Sigmoidal function with three parameters ($f = a/(1 + \exp(-(x - x_0)/b))$) is used to fit the relationships

those reported in this study. However, Rohula, Kupper, Räm, Sellin, and Söber (2014) using weighed method of excised shoots growing in the flasks of greenhouse found high nighttime water loss (i.e., >50%) for *Populus balsamifera* L. and *Populus × wettsteinii* Hamet-Ahti just at predawn. Therefore, our studied species growing in a natural environment with a hyperarid climate had an exceptional rate of nighttime Q_c , which is a significant proportion of total daily Q_c with observed values on some nights over 50%.

However, the relative contribution to nighttime Q_c via either E_n or R_e is unknown largely due to methodological difficulties in accurately assigning nighttime Q_c to E_n or R_e (Zeppel, Lewis, Phillips, & Tissue, 2014). Just as Fisher et al. (2007) stated, Resco de Dios et al.

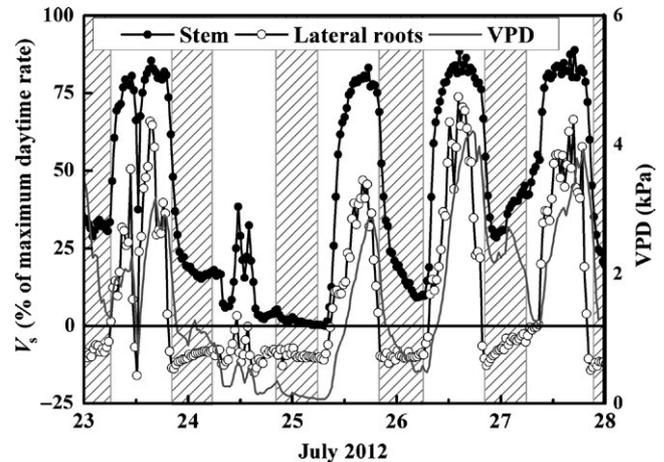


FIGURE 5 Hourly variation in sap velocity (V_s , as a percentage of maximum daytime rate, %) of stem and lateral roots of *Populus euphratica* and vapor pressure deficit (VPD, kPa) over five successive days surrounding a rainfall event (12.4 mm, 24th July) of 2012. The shaded area represents the nighttime

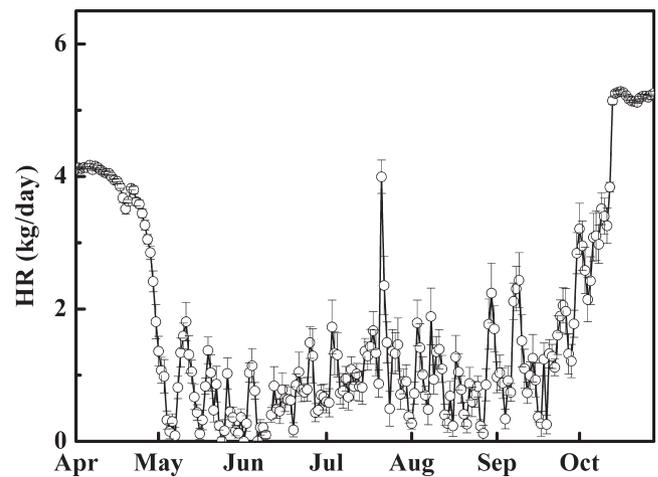


FIGURE 6 The daily variation (mean \pm SE) in hydraulic redistribution (HR, kg/day) of roots of *Populus euphratica* during the growing season of 2012

(2013) also attributed the initial decrease in Q_c early in the night (the first c. 3 hr after dusk) to a sluggish stomatal response and/or stem water refilling. Similarly, the initial decrease time owing to stem refilling is up to 5 hr after dusk in *Eucalyptus saligna* growing in whole-tree chambers (Zeppel et al., 2011). Consistent with these

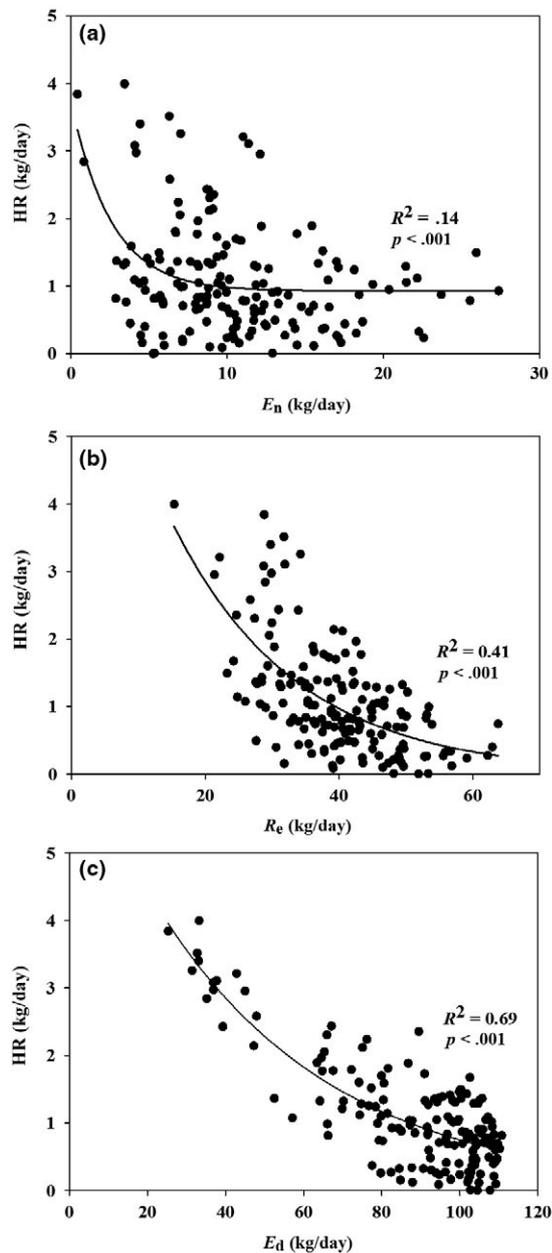


FIGURE 7 Relationships between hydraulic redistribution (HR, kg/day) and (a) nighttime transpiration (E_n , kg/day), (b) stem refilling (R_e , kg/day), and (c) daytime transpiration (E_d , kg/day) during the growing season of 2012. Exponential decay function ($y = a \exp(-bx)$) is used to fit the relationships

studies, we also thought that the initial decrease in Q_c after dusk was primarily induced by the stem refilling for the daytime water loss (Figure S1).

While E_n has been observed across a range of species, plant function types, and environments (Benyon, 1999; Caird et al., 2007; Dawson et al., 2007; Ogle et al., 2012; Snyder et al., 2003), its regulating mechanisms remain poorly understood (Zeppel et al., 2014). With the exception of the exogenous environmental regulation, for example, soil moisture content, VPD, and U (Zeppel et al., 2014), recent studies demonstrated that circadian clock also plays an important role in regulating nighttime water use (Resco de Dios et al.,

2013), in which the contribution of circadian regulation to nocturnal Q_c variation (23%–56%) was comparable to that of VPD (25%–58%). This study shows that VPD can account for 55% of variation in nighttime V_s (Figure 2), indicating the potentially combined effect of exogenous and endogenous regulation on nighttime Q_c , which was also supported by the rising Q_c with the decreased VPD at predawn (Figure S1. e). Therefore, we concluded that the substantial nighttime Q_c was constituted by water loss from leaves via stoma (i.e., E_n) and water refilling of tree capacitance to replace water lost via daytime transpiration (i.e., R_e).

It is notable that proportions of E_n/E were lower with an average of 7.5% for *P. euphratica* (Table 2) than those of 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), and a Mediterranean holm oak forest (10%–30%) (Barbeta et al., 2012). However, R_e was significantly higher, accounting for 80% of nighttime Q_s , than that of two evergreen temperate woodland species (30%–50%, Zeppel et al., 2010), but was comparable to that of Mediterranean trees and shrubs (Fisher et al., 2007) and a mixed New England deciduous forest (Daley & Phillips, 2006). In addition to the uncertainty of “forecasted refilling” method (Alvarado-Barrientos et al., 2014; Buckley et al., 2011), the high R_e potentially resulted from large stem water capacitance of studied species (observed the spouting sap out hole after drilling the tree-cores), that enables the trees to maintain maximum or near maximum transpiration rates for a longer period of time (Figure 3), just as in the tropical forest canopy trees, *Anacardium excelsum* and *Ficus insipida* (Goldstein et al., 1998). That R_e can contribute one-third of total E (29.7%) is a unique result, and then, the high internal water storage capacity may provide insights into tree species’ water relations and water use strategies in extremely dry desert riparian ecosystems.

4.2 | Limited hydraulic redistribution: nocturnal transpiration or stem refilling

Based on the whole-tree water balance theory, the nighttime root water uptake was the sum of HR, E_n , and the refilling of internal water reservoirs (roots, stem, and leaves, i.e., R_e) (Dawson et al., 2007), which indicated that HR may be depressed by the large fluxes of water moving toward the canopy in the stem (R_e and E_n). Consistent with this theory, greenhouse studies have shown that HR is experimentally reduced when E_n is increased by lighting at night (Bauerle et al., 2008; Caldwell, 1990; Caldwell & Richard, 1989). Howard et al. (2009) demonstrated that HR can also increase by artificially suppressing E_n via canopy bagging of *Artemisia tridentata* and *Helianthus anomalous* subjects, which is similar to Scholz et al. (2008).

Although the “forecasted refilling” method (Fisher et al., 2007) was previously applied to cloudless, rain-free days and nights with low VPD (Alvarado-Barrientos et al., 2014; Buckley et al., 2011), we suggest that the method could be applicable to fit the decreased Q_c owing to R_e under moderate VPD in night with potentially overestimated but less effect on the relationship between R_e and HR. Indeed, we observed that the leaf stomatal conductance and transpiration rate were

close or equal to zero from sunset to midnight across different seasons (Yu et al., 2016). The negative logarithmic relationship between HR and R_e was better than E_n (Figure 7), which suggested that HR is predominantly controlled by R_e and subsequently by E_n . It is demonstrated that the more water loss in daytime, the more water recharge in nighttime (Figure 4) and then less water redistribution to the soil layer via roots (Figure 6), which could explain the stronger relationship between HR versus E_g and R_e than between HR versus E_n (Figure 7). Under the stable resistance of sapwood, the root water uptake was preferentially transferred to the stem and then canopy to recharge water lost (Figure 5) rather than roots (Figure 6). Therefore, HR was depressed by the upward sap flow draw via refilling of unsaturated tissue and then transpiration, both of which acted as competing water sink.

The magnitude of R_e indicates the higher capacitance of stem, which is a measurement of the store water of plants (McCulloh, Johnson, Meinzer, & Woodruff, 2014) that could buffer the system by reducing the xylem pressure drop when transpiration increases (Meinzer, Domec, Johnson, McCulloh, & Woodruff, 2013). Studies found that stem water storage was negatively associated with wood density in five coexisting temperate broad-leaved tree species (Köcher, Horna, & Leuschner, 2013), suggesting the higher water storage as lower wood density. Many studies suggest that most *Populus* species are highly vulnerable to cavitation causing 50% loss of hydraulic conductivity (P_{50}) occurring between -1 and -2.5 MPa (Hacke, 2015; Hukin, Cochard, Dreyer, Le Thiec, & Borgeat-Triboulot, 2005; Pan, Chen, Chen, Wang, & Ren, 2016). For *P. euphratica*, the basic wood density of stem was less than that of the co-occurring species, *T. ramosissima*, 0.41 versus 0.73 g/cm³ (Yu et al., 2013), suggesting that *P. euphratica* can store more water than *T. ramosissima*. Although the nocturnal water fluxes may be a key process driving refilling of storage of sapwood (Daley & Phillips, 2006) and HR (Bleby, McElrone, & Jackson, 2010), this remains generally untested for *Populus* species. Stem refilling is crucial for trees to avoid xylem cavitation and water deficit (Daley & Phillips, 2006; Zeppel et al., 2014) and need further investigation particularly for the riparian trees growing in the hyperarid area.

Our study also demonstrated that E_n can reduce the magnitude of HR, a finding that may have further implications for arid riparian trees under the future climate where nighttime temperatures are projected to rise at higher rates than daytime temperatures (Peng et al., 2013). This relationship may have important disadvantageous consequences for plant survival in arid area. Experimental evidence and the use of novel modeling approaches suggest that HR may affect tree water use and productivity at the community scale (Domec et al., 2010; Prieto et al., 2012). Models that incorporate HR but not consider E_n into an atmospheric general circulation model may overestimate the impact of HR on ecosystem water use (Jackson, Sperry, & Dawson, 2000) and seasonal climate cycles (Lee, Oliveira, Dawson, & Fung, 2005), and it therefore should be considered based on the negative effect of E_n on HR in the future climate change scenarios.

5 | CONCLUSION

Substantial nighttime V_s was observed and increased with VPD but with low determination coefficient ($R^2 = .55$), which suggests that the nocturnal V_s should be attributed to both of E_n and R_e . We estimated that E_n accounted for approximately 7.5% of 24-hr sap flow, compared to R_e of 29.7%. Here, we showed that the magnitude of HR can partially reduce by naturally occurring E_n , which would increase under further climate change scenarios. Surprisingly, the negative exponential decay relationship between HR and R_e was better than E_n , which demonstrated that HR of roots was depressed more by stem refilling than by nocturnal transpiration for *P. euphratica* Oliv. through in situ measurement in a hyperarid climate in NW China.

ACKNOWLEDGMENTS

This study was funded by the Youth Foundation of the National Natural Science Foundation of China (41401033), the Chinese Postdoctoral Science Foundation (2014M560819), Key Research Program of Frontier Sciences, CAS (QYZDJ-SSW-DQC031), and National Key R&D Program of China (2017YFC0404305).

CONFLICT OF INTEREST

We declare that we have no conflict of interest.

AUTHOR CONTRIBUTION

T. Y. and C. Z. carried out the experiment and analyzed the data and wrote the first draft. Q. F., J. S., and X. Z. obtained the funds to support the project and reviewed the article. P. M. and M. F. reviewed the article and helped to revise the language.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

How to cite this article: Yu T, Feng Q, Si J, et al. Depressed hydraulic redistribution of roots more by stem refilling than by nocturnal transpiration for *Populus euphratica* Oliv. in situ measurement. *Ecol Evol*. 2018;8:2607–2616. <https://doi.org/10.1002/ece3.3875>