

# Responses of nighttime sap flow to atmospheric and soil dryness and its potential roles for shrubs on the Loess Plateau of China

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## Abstract

### Aims

Nocturnal sap flow ( $E_{night}$ ) has been observed in a variety of plant species and environmental conditions. In water-limited environments,  $E_{night}$  is important in the regulation of plant water's physiology. This study was designed to evaluate the way in which  $E_{night}$  (defined as sap flow from 20:30 to 06:00) responded to changes in the atmospheric vapor pressure deficit (VPD) and the soil water content (SWC), and explored its potential physiological significance for different plant species in a semi-arid area.

### Methods

We selected three shrub species: *Vitex negundo* L. (VN), *Hippophae rhamnoides* L. (HR) and *Spiraea pubescens* Turcz (SP) in the semi-arid Loess Plateau of China. The plots of the three communities dominated by each of three species were on the same hill slope. Half-hourly sap flow density was measured in six to seven sample stems for each species during the main growing season (June to August 2015). VPD, SWC, leaf water potential ( $\Psi_{leaf}$ ) and stomatal conductance ( $G_s$ ) were measured at the same time. Regression analyses were conducted to determine the relationships between  $E_{night}$ ,  $E_{day}$ ,  $E_{night}/E_{daily}$ , VPD and SWC at half-hourly and daily time scales, as well as between  $E_{night}$ ,  $E_{day}$  and  $\Psi_{leaf}$ .

### Important Findings

The mean values of  $E_{night}$  and  $E_{day}$  were higher, but  $E_{night}/E_{daily}$  values were lower for VN compared to HR and SP. The responses

of sap flow density to VPD and SWC varied at different temporal scales. VPD was the dominant factor that affected  $E_{night}$  and  $E_{day}$  at the half-hourly scale for all three species. In contrast, SWC was the key factor that influenced  $E_{day}$  at the daily time scale. The values of  $E_{day}$  and  $E_{night}/E_{daily}$  correlated negatively with SWC because the effect of SWC was stronger on  $E_{day}$  than on  $E_{night}$ . Although the low fraction of  $E_{night}/E_{daily}$  (4%–7%) may indicate a minor short-term effect of  $E_{night}$  on the standing water balance,  $E_{night}$  had eco-physiologically significance to the plants. The discrepancy in  $\Psi_{leaf}$  between sunset and the following day's predawn ( $\Delta\Psi$ ) indicated that stem refilling occurred during this period. SP had the higher fraction of recharge water among the three species, as it had the relatively higher value of  $\Delta\Psi/E_{night}$ .  $E_{night}$  had positive relationship with predawn  $G_s$ . The increased  $G_s$  facilitated rapid onset of photosynthesis in the early morning. In addition, the positive correlation between  $E_{night}$  and  $E_{day}$  from 06:00 to 10:30 suggested that  $E_{night}$  was beneficial for transpiration in the following morning. The responses of  $E_{night}$  to VPD and SWC indicated differences in plant adaptation to drought stress, which provides important information for our understanding of the reactions to climate changes among species in semi-arid areas.

**Keywords:** nocturnal sap flow, stem refilling, stomatal conductance, leaf water potential, Loess Plateau

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## INTRODUCTION

Nocturnal sap flow ( $E_{night}$ ) has been observed in a wide range of plant species from diverse ecosystems (Dawson *et al.* 2007; Kupper *et al.* 2012; Marks and Lechowicz 2007). Recently,  $E_{night}$  variation and its mechanisms have attracted increasing interest from the scientific community (Moore *et al.* 2008; Phillips *et al.* 2010; Yu *et al.* 2016). Across a range of different habitats, the contribution of  $E_{night}$  to total daily sap flow ( $E_{daily}$ ) ( $E_{night}/E_{daily}$ ) is typically 1%–28% (Zeppel *et al.* 2014), though tending to be higher in arid areas (Snyder *et al.* 2003). The finding of  $E_{night}$  also challenged the assumption that plant leaf water potential ( $\Psi_{leaf}$ , MPa) is in equilibrium with soil water potential at predawn (Donovan *et al.* 1999, 2001).

$E_{night}$  is simultaneously affected by multiple environmental variables. In water-limited environments, vapor pressure deficit (VPD) and soil water content (SWC) are key factors affecting the variations of plant water use (Cavender-Bares *et al.* 2007; Zeppel *et al.* 2012), as values of the two variables represent atmospheric and soil dryness, respectively. Their influences on  $E_{night}$  may vary at different time scales from half-hourly to daily, seasonally and annually. It is therefore essential to examine the responses of  $E_{night}$  across varied time scales in order to get a clearer picture about the temporal patterns of plant water use. Generally,  $E_{night}$  is often positively correlated with nighttime VPD in a linear or nonlinear fashion (Fisher *et al.* 2007; Snyder *et al.* 2003; Zeppel *et al.* 2010). However, there are still no consistent findings in terms of the relationship between  $E_{night}$  and SWC. Earlier studies have reported positive correlations (Rawson and Clarke 1988; Snyder *et al.* 2003; Zeppel *et al.* 2010) or no relationships between  $E_{night}$  and SWC (Donovan *et al.* 1999), no matter under wet or dry conditions (Wang *et al.* 2012).

The magnitude of  $E_{night}$  and its response to environmental conditions also vary among species (Zeppel *et al.* 2010). Some studies have shown large inter-specific variations in  $E_{night}$  among sympatric species (Caird *et al.* 2007a, b; Marks and Lechowicz 2007). For example, in a mixed deciduous forest in the north-eastern region of the USA, the  $E_{night}/E_{daily}$  value was 13% for paper birch (*Betula papyrifera* Marsh), but only 2–7% for red oak (*Quercus rubra* L.) and red maple (*Acer rubrum* L.; Daley and Phillips 2006). Co-occurring species usually have different survival patterns to minimize water loss while maximizing carbon gain. Differences in leaf area, wood density and water uptake patterns are reported as possible reasons for species co-occurrence (Zeppel *et al.* 2010). The physiological attributes of species would lead to difference in  $E_{night}$  (Daley and Phillips 2006; Phillips *et al.* 2010). However, one key unknown is the degree to which inter-specific variations in  $E_{night}$  are within the same microclimate (Phillips *et al.* 2010; Zeppel *et al.* 2010).

The ecological significance of  $E_{night}$  in water-limited environments is still poorly understood, despite this question being put forth decades ago (Cavender-Bares *et al.* 2007).

Basically, we do not know if  $E_{night}$  variations are an adaptation mechanism of the plants and represent a response to changing atmospheric and soil water conditions. In some circumstances,  $E_{night}$  may represent a large proportion of daily water use ( $E_{daily}$ ) of plants, with significant consequences on local and regional water balances (Cirelli *et al.* 2016; Pfautsch *et al.* 2011). Some studies suggest that nighttime transpiration is a main component of  $E_{night}$  when  $E_{night}$  and VPD showed a significant positive correlation (Hogg and Hurdle 1997). However, that is not the case all the time, and measurements of  $E_{night}$  do not necessarily indicate nighttime transpiration as stem refilling may also occur at the same time (Huang *et al.* 2017). Daytime water use causes a deficit in the internal water storage of plants, which could primarily be recharged through nighttime stem refilling. The refilling of depleted water storage in the stems could contribute as much as 15%–25% to daily sap flow (Daley and Phillips 2006; Wang *et al.* 2012). Along with the occurrences of nighttime stem refilling and transpiration,  $E_{night}$  can potentially enhance nutrient supply to distal parts of a plant's crown (Scholz *et al.* 2007), prevent excess leaf turgor at night (Donovan *et al.* 2001) and promote carbon fixation early in the daylight hours as the stomata is open (Daley and Phillips 2006). If plants do not completely close their stomata at night, photosynthesis can begin without delay at sunrise when VPD is low (Cavender-Bares *et al.* 2007; Dawson *et al.* 2007), avoiding time lags between assimilation and increased stomatal conductance ( $G_s$ , mol H<sub>2</sub>O m<sup>-2</sup> s<sup>-1</sup>; Oren *et al.* 2001). In addition, due to the water refilling processes during the night,  $E_{night}$  may increase predawn leaf water potential ( $\Psi_{pd}$ , MPa) and minimize the risks of xylem embolism, especially during dry seasons (Maherali *et al.* 2004; Mitchell *et al.* 2008). This would help plants to survive under drought stress conditions.

The Loess Plateau in China is a transitional zone between the south-eastern humid monsoon climate and the north-western continental dry climate. Since 1990s, a series of large-scale re-vegetation projects have been initiated in this region. The eco-hydrological effects of the plantations and their adaptability to local environments are among the major research questions. Many studies have examined sap flow dynamics and transpiration rates and their relationships with climate and soil water variables for the some main restoration species (Jian *et al.* 2014; Jiao *et al.* 2015; Zhang *et al.* 2015). However, the occurrence and importance of  $E_{night}$  for species adaptation in this region have not been well studied. Therefore, the magnitude of  $E_{night}$  and its potential roles for plants in this area are still not clear.

The objectives of this study were to (i) investigate the magnitudes and temporal variations in  $E_{night}$  in the main growing season (i.e., June to August) for three shrubs that were widely planted in the re-vegetation campaigns in the Loess Plateau, (ii) examine the effects of VPD and SWC on  $E_{night}$  at half-hourly and daily time scales, and (iii) explore the potential roles of  $E_{night}$  in adapting to drought.

## MATERIALS AND METHODS

### Study site

This study was carried out in the Yangjuangou catchment in Yan'an City, Shaanxi Province, China (36°42'N, 109°31'E), at an elevation of 1050 m to 1298 m above sea level. The area is characterized by a semi-arid continental climate with a mean annual temperature of 10.6°C and a mean annual precipitation of 530 mm. Rainfall in this area has large intra-annual variations, with 79% of the annual precipitation occurring between May and September, which also coincides with the growing season for most species. The study area is gully and hilly; the soil type is Calcaris Cambisol of a uniform texture (Liu et al. 2012).

We selected three shrub species—*Vitex negundo* L. (VN), *Hippophae rhamnoides* L. (HR) and *Spiraea pubescens* Turcz (SP)—as they are among the most frequently planted shrubs on the Loess Plateau for controlling soil erosion and water loss. The shrubs were planted on abandoned croplands in the 1990s with little subsequent disturbances by human activities. Three 5 × 5 m plots, in which the communities were dominated by each of the three species, were selected for this study. In all three plots, the understory vegetation was scarce. The three plots were located on the same hill slope characterized by a western aspect and a medium slope position. Micro-environmental conditions were assumed to be similar for the plots.

### Sap flow measurements

Because  $E_{night}$  rates are typically low, accurate quantification is difficult for instantaneous gas exchange measurements on sample leaves (Barbour et al. 2005). So, we used the heat balance method to continually measure diurnal stem sap flow density. The theory and methodology of this method

**Table 1:** characteristics of the sampling plots and basal area of individual stems for measurement of sap flow density ( $\text{g h}^{-1} \text{cm}^{-2}$ ) of three species *Vitex negundo* L. (VN), *Hippophae rhamnoides* L. (HR) and *Spiraea pubescens* Turcz (SP)

	Species		
	VN	HR	SP
Average height (m)	1.54 ( $\pm 0.13$ )	1.65 ( $\pm 0.20$ )	1.50 ( $\pm 0.12$ )
Average stem diameter (mm)	11.32 ( $\pm 0.28$ )	19.58 ( $\pm 0.94$ )	10.43 ( $\pm 0.13$ )
LAI ( $\text{m}^2 \text{m}^{-2}$ )	3.24 ( $\pm 0.22$ )	2.33 ( $\pm 0.31$ )	4.54 ( $\pm 0.16$ )
Basal area of sampled trees ( $\text{cm}^2$ )	1.87	4.98	1.96
	1.95	4.10	1.82
	2.31	3.55	2.00
	1.56	4.38	2.08
	2.16	8.03	1.48
	3.27	7.53	1.52
	4.24	7.34	

Values in parentheses are standard deviations.

have been described by previous studies (Yue et al. 2008). Nighttime was defined as the period from 1 h after sunset to 1 h before sunrise. For a conservative estimate, we defined  $E_{night}$  as the average sap flow from 20:30 to 06:00, and  $E_{day}$  is the average sap flow from 06:00 to 20:30. The proportional contribution of nighttime sap flow to total daily sap flow, i.e.,  $E_{night}/E_{daily}$ , was calculated as the ratio between the sum of sap flow from 20:30 to 06:00 to that of the 24-h sap flow for that day.

Six to seven stems in each of the plots were selected to install the sap flow sensors and the basal diameter was measured for each of them. Different types of sensors were used according to the basal diameter of the stems (Dynamax Inc., Houston, TX, USA; Model SGA 13, SGB 19, and SGB 25; Table 1). The stems selected for measurements were in good condition and sufficiently developed to support the weight of the sensors. The measurements were taken from 8 June to 31 August 2015. Because this method requires a steady state and a constant energy input, the sample stems must be protected from changes in the surroundings. The sensors were fixed at least 30 cm above the ground to minimize the influence of thermal gradients induced by the environment (Yue et al. 2008). The signals from the gauges were recorded every 10 s and stored as 30-min averages with CR1000 data loggers (Campbell Scientific Inc., Logan, UT, USA). All sensors and data loggers were solar-powered. Some data were lost during the measurements due to dysfunction of the power system, especially in the SP stand (~20% data loss).

### Meteorology and SWC

Meteorological variables, including solar radiation ( $R_s$ ,  $\text{W m}^{-2}$ ), air temperature ( $T_a$ , °C) and relative humidity (RH, %), were measured by an automated weather station that was located 50 m away from our study plots.  $R_s$  was measured using a pyranometer (Li-200, Li-Cor, Lincoln, NE, USA), which was installed about 2 m above ground in the open field. The parameters  $T_a$  and RH were monitored by a HMP35C probe (Vaisala Co., Helsinki, Finland), which was installed at the same height with the pyranometer. Rainfall was recorded using a ground-level, tipping-bucket rain gauge (TE 525). These meteorological variables were sampled every 30 s and recorded the average of 30 min by the data logger (Campbell Scientific). VPD (kPa) was calculated based on  $T_a$  and RH using following equation:

$$\text{VPD} = a \times \exp\left(\frac{bT_a}{T_a + c}\right) \times (1 - \text{RH})$$

where a, b and c are constant parameters that are 0.611 kPa, 17.502 (unitless) and 240.97°C (Campbell and Norman 1998).

The data SWC (%) was measured at depths of 5, 10, 20, 40, 80, 120, 160, and 200 cm, respectively, using EC-5 sensors (Decagon Devices Inc., Pullman, WA, USA) and recorded with HOBO loggers (H21, Onset Computer Corp., Bourne, MA, USA) at 30-min intervals.



## Measurements of leaf ecophysiological indicators

$\Psi_{\text{leaf}}$  illustrates the hydraulic state of the vegetation and is usually regarded as an indicator of water stress (O'Toole and Cruz 1980). In our study, we measured  $\Psi_{\text{leaf}}$  from June to August once a month in three to five fully expanded leaves of each sample tree in all three plots by using a pressure chamber (PMS Instrument Co., Corvallis, OR, USA). Measurements were taken every two hours from 06:00 to 18:00, where the value taken at 06:00 (before sunrise) was regarded as  $\Psi_{\text{pd}}$ , and the value from 18:00 as sunset leaf water potential ( $\Psi_{\text{sunset}}$ , MPa). Xylem water potential ( $\Psi_{\text{xylem}}$ , MPa) was automatically measured for species of HR and SP using thermocouple stem psychrometers (PSY, ICT International Pty., Australia) and recorded at 10-min intervals.

At the same time, leaf-level gas exchange and  $G_s$  were measured under natural conditions on sunny and calm days by using the Li-6400 gas exchange system (Li-Cor Inc.) with a flow velocity set at 500  $\mu\text{mol s}^{-1}$  for measurements. Most measurements were logged multiple times within 1–2 min for a given leaf and the values were averaged to obtain a single observation for this leaf. Measurements were taken every 2 hours from 06:00 to 18:00 for selected young and fully expanded leaves. Measurements of stand leaf area index (LAI) using a plant canopy analyzer (LAI-2000, Li-Cor.) were undertaken under diffuse light conditions at dusk once a month from June to August in 2015.

## Statistical analyses

In order to account for differences of stem size among species (Hu *et al.* 2017), we normalized sap flow velocity by stem area (i.e., sap flow density,  $\text{g h}^{-1} \text{cm}^{-2}$ ). In the rainy period, plants may present upward or downward sap flow in stem tissues at night; therefore, we only included rainless periods in the statistical analyses (Burgess and Bleby 2006; Dawson *et al.* 2007). It is critical to calculate and distinguish the amount of  $E_{\text{night}}$  used for stem refilling or transpiration during the night in studying the significance of  $E_{\text{night}}$ . From the whole-plant water balance framework (Williams *et al.* 2001), when the capacitor (i.e., the amount of water that a stem can store) is constant, the change in  $\Psi_{\text{leaf}}$  is positively correlated with the change in stem water storage (Dawson *et al.* 2007; Williams *et al.* 2001). Therefore, the ratio of the discrepancy of  $\Psi_{\text{leaf}}$  between sunset and predawn ( $\Delta\Psi$ ) to  $E_{\text{night}}$  ( $\Delta\Psi/E_{\text{night}}$ ) could be used to represent the proportion stem refilling out of  $E_{\text{night}}$ . In our study, the mean height of the three shrubs had no significant differences ( $P > 0.05$ ), and sap flow was normalized by stem area. Hence, we used the ratio of  $\Delta\Psi$  to  $E_{\text{night}}$  ( $\Delta\Psi/E_{\text{night}}$ ) to compare the fraction of stem refilling out of total  $E_{\text{night}}$  among the three species.

Simple correlation analyses were used to examine the responses of sap flow density ( $E_{\text{night}}$ ,  $E_{\text{day}}$ ) and  $E_{\text{night}}/E_{\text{daily}}$  to VPD and SWC at half-hourly and daily scale. The relationship between sap flow density and VPD was described using the exponential saturation function:

$$E = a(1 - e^{-bVPD})$$

where  $a$  and  $b$  are fitting parameters (Jiao *et al.* 2015; Phillips *et al.* 2010).

Descriptive statistics were used to calculate average and standard deviation. For  $E_{\text{night}}$ ,  $E_{\text{day}}$  and  $E_{\text{night}}/E_{\text{daily}}$  data, and the Kolmogorov–Smirnov test was used to verify normality. One-way analysis of variance was applied to test whether there were significant differences in  $E_{\text{night}}$ ,  $E_{\text{day}}$  and  $E_{\text{night}}/E_{\text{daily}}$ , and the variations of  $\Psi_{\text{leaf}}$  among three species data. Independent  $t$ -tests were conducted to determine whether there were significant differences of  $E_{\text{night}}$  and  $E_{\text{night}}/E_{\text{daily}}$  between HR and SP. We used stepwise regression analysis to analyze the relative contributions of  $\ln(\text{VPD})$  and SWC on  $E_{\text{night}}$  and  $E_{\text{day}}$ . In addition, we analyzed the relationship between  $E_{\text{night}}$  and total sap flow density from 06:00 to 10:30 in the following day ( $E_{\text{d-ar}}$ ,  $\text{g h}^{-1} \text{cm}^{-2}$ ) using linear correlation analysis. All statistical analysis and charting was performed using Origin (version 9.0, OriginLab Corp., USA). Significance was defined at  $P < 0.05$  for all tests.

## RESULTS

### Meteorology and soil moisture conditions

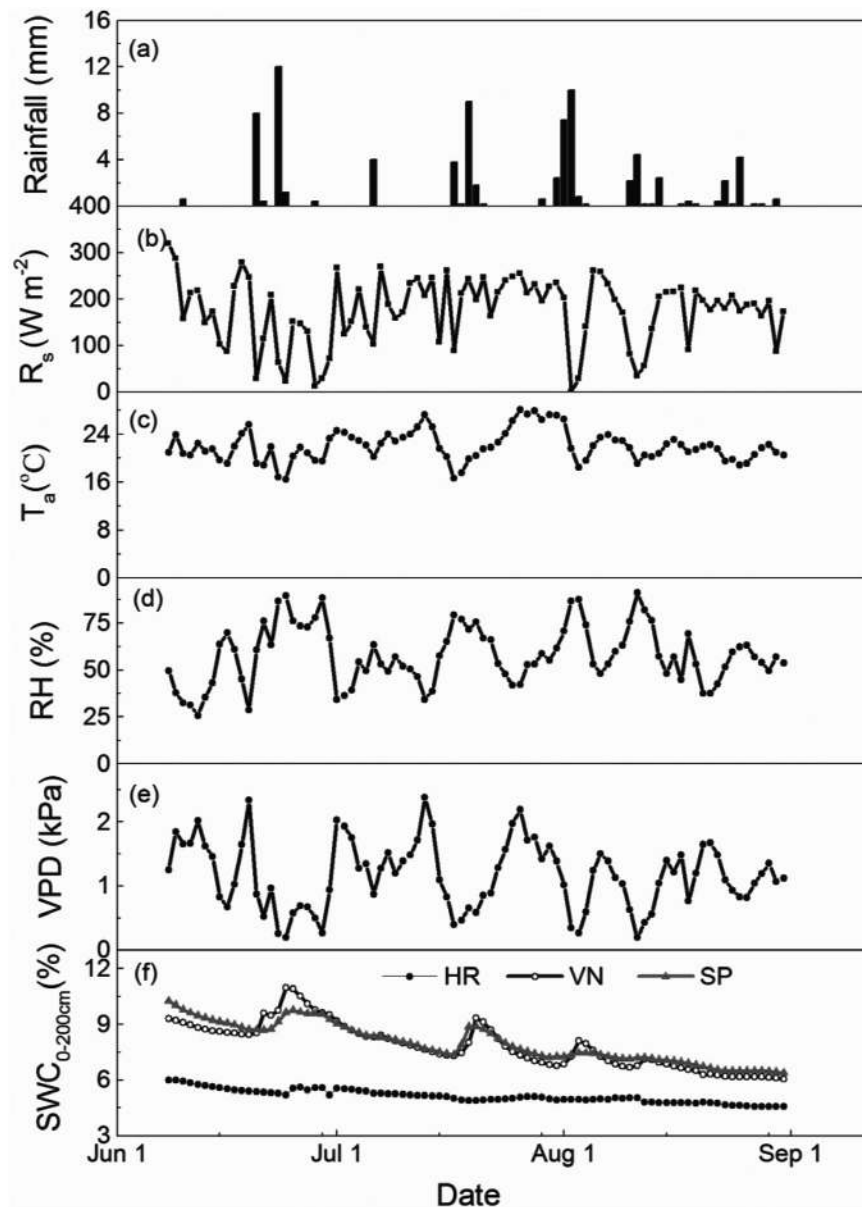
Annual precipitation was 350 mm in the year of study (2015), representing a dry year compared to the long-term mean precipitation (530 mm, 1950–2010). From June to August, a total precipitation of 123.6 mm was recorded, and all rainfall events were  $<12 \text{ mm day}^{-1}$ . Daily mean air temperature ranged from 14.0 to 28.1°C and VPD from 0.19 to 2.38 kPa. The frequency was 56% for the days with VPD  $>1 \text{ kPa}$ . SWC was consistently low and generally decreased over the study period, despite some rainfall events that increased the SWC at surface soils. The mean SWC values of the 0–200 cm soil depth varied from 6.07% to 10.98% for VN, 4.56% to 6.10% for HR, and 6.37% to 10.24% for SP (Fig. 1).

### Magnitudes and temporal variations of $E_{\text{night}}$ , $E_{\text{day}}$ and $E_{\text{night}}/E_{\text{daily}}$

$E_{\text{night}}$ ,  $E_{\text{day}}$  and  $E_{\text{night}}/E_{\text{daily}}$  showed high temporal variations in the growing season (Fig. 2). Averaged across species,  $E_{\text{day}}$  was highest in June for three species and decreased with decreasing SWC from June to August. The mean values of  $E_{\text{night}}$  and  $E_{\text{night}}/E_{\text{daily}}$  were 1.36, 0.77 and 0.96  $\text{g h}^{-1} \text{cm}^{-2}$  and 4.40, 5.76 and 6.94% for VN, HR and SP, respectively (Table 2), with significant differences among them ( $P < 0.05$ ). The values of  $E_{\text{night}}/E_{\text{daily}}$  were highest in August for three of them, ranging from 0.76 to 12.35% for VN, 0.56 to 12.40% for HR and 0.33 to 19.60% for SP, respectively, during the growing season. Generally, both mean values of  $E_{\text{day}}$  and  $E_{\text{night}}$  of VN were significantly higher than HR and SP ( $P < 0.001$ ; Table 2). The values of  $E_{\text{night}}/E_{\text{daily}}$  had no significant difference in HR and SP ( $P > 0.05$ ), but they were higher than VN ( $P = 0.02$ ).

### The effects of VPD and SWC on $E_{\text{night}}$ , $E_{\text{day}}$ and $E_{\text{night}}/E_{\text{daily}}$

At half-hourly and daily time scales, variation trends between sap flow density and VPD corresponded in both daytime and nighttime periods throughout the growing season for all species. However, the correlation coefficient ( $R^2$ ) differed among species (Fig. 3). Furthermore, at daily time scale, goodness of fit between sap flow density and VPD was weak in the nighttime



**Figure 1:** temporal variations in the meteorological variables and SWC during the mean growing season. Rainfall (P) (a), solar radiation ( $R_s$ ) (b), air temperature ( $T_a$ ) (c), relative humidity (RH) (d), vapor pressure deficit (VPD) (e) and soil water content (SWC) <200 cm soil depth (f). The data represented daily sum for P and daily average for the other variables.

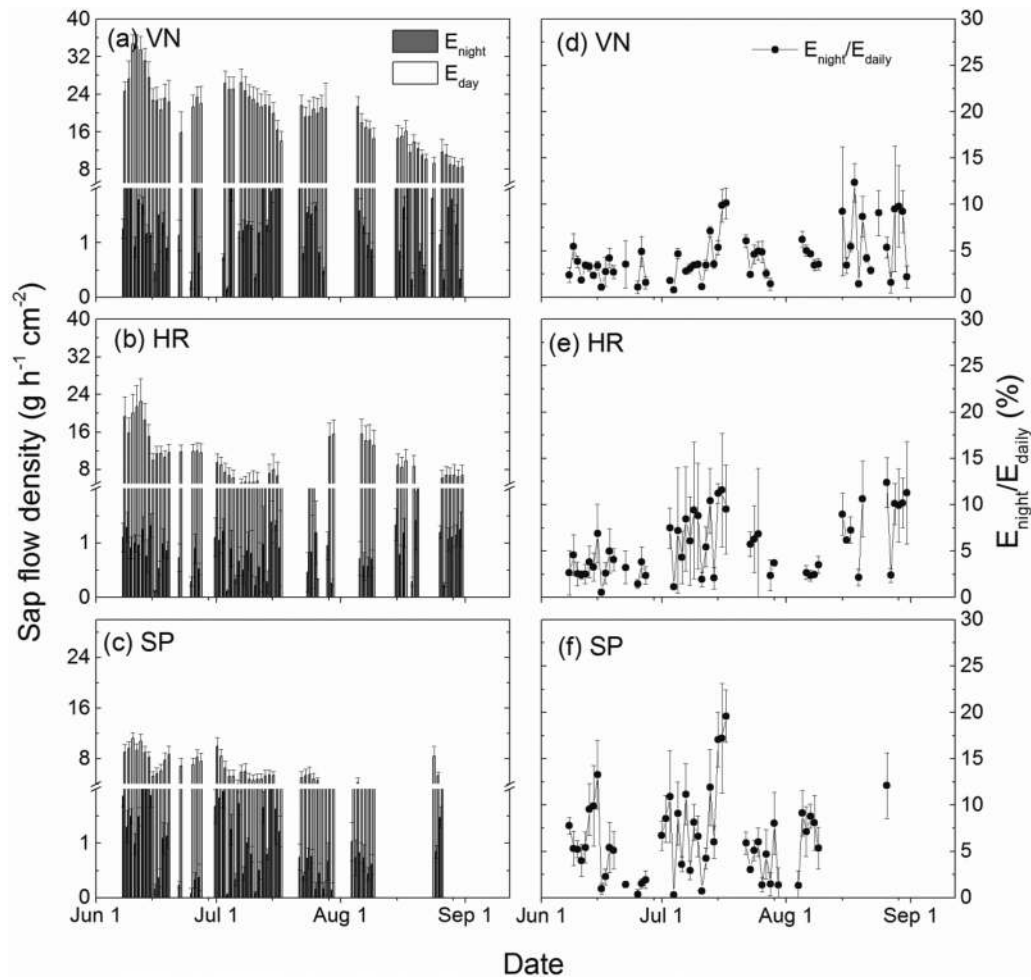
than daytime.  $E_{day}$  and  $E_{night}$  were extremely low or even zero when VPD values were close to zero (or RH close to 100%).  $T_a$  and wind speed had minor effect on  $E_{night}$  (data not shown).

SWC decreased from June to August in all of the three communities, indicating the increase of soil dryness (Fig. 1f). Significant correlations between  $E_{day}$  and averaged SWC >200cm of soil depth for three species were found at both half-hourly and daily time scales. The steepest slope and the strongest correlation between SWC and  $E_{day}$  were found in SP. There was no clear correlation between  $E_{night}$  and SWC, except for HR (Fig. 4). Stepwise regression analyses showed that, at half-hourly time scale, both VPD and SWC affected  $E_{night}$  and  $E_{day}$

and VPD had stronger explanatory power on the temporal variations of  $E_{day}$  and  $E_{night}$  than SWC. At daily time scale, VPD was still the controlling factor for  $E_{night}$ , whereas SWC was the main factor for the temporal variation of  $E_{day}$  (Table 3).

### The potential roles of $E_{night}$ for plants

During three typical sunny days, the daytime variations of  $\Psi_{leaf}$  and  $E_{daily}$  showed contrasting patterns, indicating that  $\Psi_{leaf}$  and plant water use co-evolved during the daytime (Fig. 5). In addition,  $\Psi_{xylem}$  gradually increased after sunset with the occurrence of  $E_{night}$  with the maximum  $\Psi_{xylem}$  value occurring at approximately during 00:00 to 02:00 (Fig. 5a,

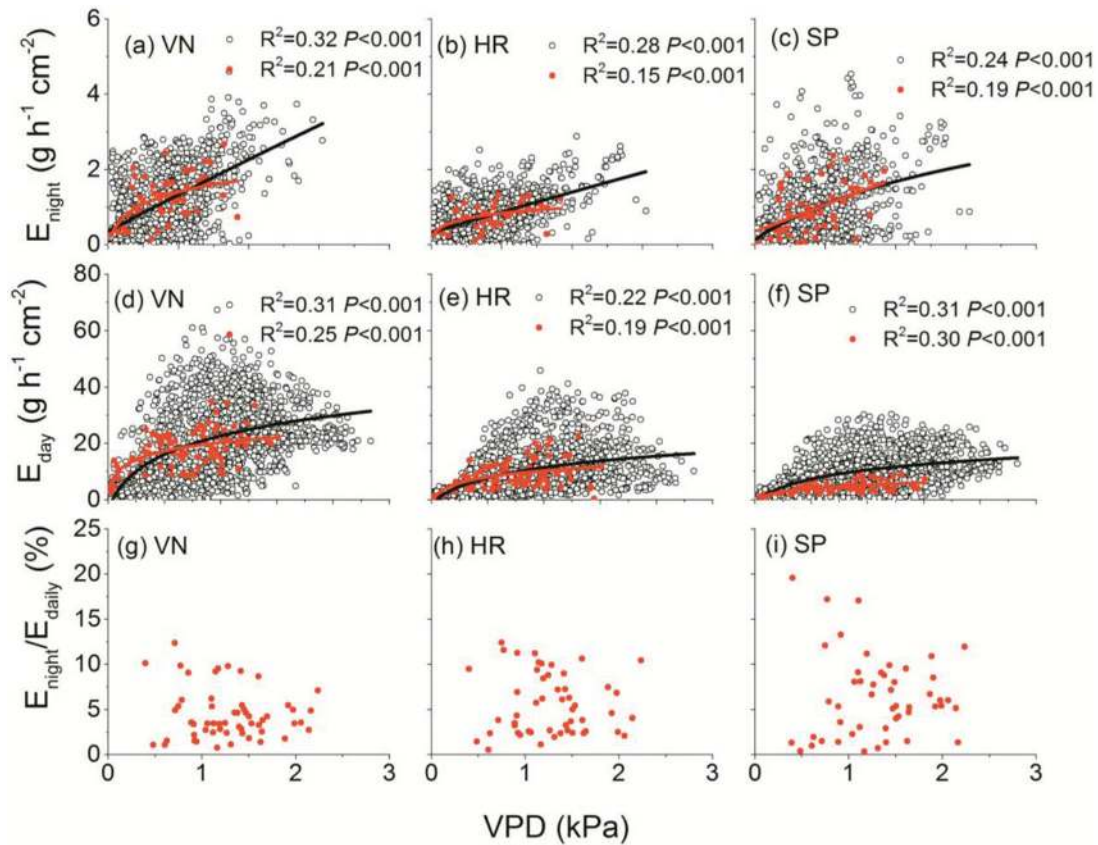


**Figure 2:** the average sap flow density (left panel) for daytime ( $E_{day}$ , white bars, 6:00–20:30) and nighttime ( $E_{night}$ , grey bars, 20:30–06:00) and  $E_{night}/E_{daily}$  (%) (right panel, black line) for species HR, VN and SP. Note different scale of y-axis in the figure of SP in the left panel. And for clear, only the error bar above line was identified in the left panel.

**Table 2:** mean values of sap flow density ( $E_{night}$  and  $E_{day}$ ,  $\text{g h}^{-1} \text{cm}^{-2}$ ) and contribution of  $E_{night}$  to total average 24-h sap flow density ( $E_{daily}$ ,  $\text{g h}^{-1} \text{cm}^{-2}$ ) ( $E_{night}/E_{daily}$ , %) for VN, HR and SP at daily time scale

Species	Month	$E_{night}$			$E_{day}$			$E_{night}/E_{daily}$		
		Max	Min	Average	Max	Min	Average	Max	Min	Average
VN	Jun	2.22	0.3	1.31 ( $\pm 0.14$ )	34.74	15.81	25.42 ( $\pm 1.36$ )	5.45	1.07	2.99 ( $\pm 0.32$ )
	Jul	2.87	0.15	1.42 ( $\pm 0.16$ )	26.41	14.06	21.60 ( $\pm 0.67$ )	10.13	0.76	4.08 ( $\pm 0.57$ )
	Aug	2.81	0.33	1.35 ( $\pm 0.17$ )	21.40	8.48	12.94 ( $\pm 0.81$ )	12.35	1.44	5.86 ( $\pm 0.72$ )
	Jun–Aug	2.87	0.15	1.36 ( $\pm 0.09$ )	34.74	8.48	19.63 ( $\pm 0.87$ )	12.35	0.76	4.40 ( $\pm 0.37$ )
HR	Jun	1.32	0.29	0.87 ( $\pm 0.07$ )	22.54	9.96	14.70 ( $\pm 1.07$ )	6.91	0.56	3.24 ( $\pm 0.37$ )
	Jul	1.22	0.11	0.72 ( $\pm 0.07$ )	15.56	0.34	6.61 ( $\pm 0.73$ )	11.58	1.15	6.46 ( $\pm 0.65$ )
	Aug	1.24	0.24	0.70 ( $\pm 0.11$ )	15.54	3.65	9.14 ( $\pm 0.92$ )	12.40	2.17	6.50 ( $\pm 1.30$ )
	Jun–Aug	1.32	0.11	0.77 ( $\pm 0.05$ )	22.54	0.34	9.77 ( $\pm 0.69$ )	12.40	0.56	5.76 ( $\pm 0.52$ )
SP	Jun	2.26	0.09	1.07 ( $\pm 0.19$ )	9.53	4.69	6.94 ( $\pm 0.37$ )	13.28	0.39	4.97 ( $\pm 0.92$ )
	Jul	2.36	0.05	0.91 ( $\pm 0.13$ )	8.51	2.27	4.35 ( $\pm 0.27$ )	19.60	0.33	8.06 ( $\pm 1.12$ )
	Aug	1.48	0.44	0.87 ( $\pm 0.11$ )	3.89	2.43	3.21 ( $\pm 0.20$ )	12.09	5.35	8.43 ( $\pm 0.92$ )
	Jun–Aug	2.36	0.05	0.96 ( $\pm 0.09$ )	9.53	2.27	5.03 ( $\pm 0.27$ )	19.60	0.33	6.94 ( $\pm 0.71$ )

Values in parentheses are standard deviations.



**Figure 3:** responses of nighttime sap flow density ( $E_{night}$ ,  $g\ h^{-1}\ cm^{-2}$ , **a**, **b** and **c**), daytime sap flow density ( $E_{day}$ ,  $g\ h^{-1}\ cm^{-2}$ , **d**, **e** and **f**) and  $E_{night}/E_{daily}$  (%), **g**, **h** and **i**) to VPD of corresponding time periods ( $VPD_{night}$ ,  $VPD_{day}$  and  $VPD_{daily}$ ) at half-hourly and daily time scales, respectively, in the three species. The symbols were the averaged values across 6–7 sample stems for each three species from June to August. Red and solid symbols represented daily time scale; black and open symbols were half-hourly time scale. Exponential saturation curves were well fitted to  $E_{night}$ -VPD and  $E_{day}$ -VPD data sets at half-hourly and daily time scales.

**c** and **e**). This indicated that the stem water refilling process mainly occurred in the plants from sunset to midnight, although the absolute magnitudes were unknown. The species of SP recharged the highest fraction of water to increase  $\Psi_{leaf}$  because its  $\Delta\Psi/E_{night}$  value was the highest among the three species (SP = 0.76 in July and 2.38 in August; VN = 0.35 in August; HR = 0.28 in July and 0.31 in August).

$E_{night}$  was positively correlated to predawn  $G_s$  and  $\Psi_{pd}$  (Fig. 6). This indicated that nighttime stem refilling may facilitate the stomatal opening and the  $\Psi_{pd}$  increasing, reducing leaf water stress in the early morning. In addition, average  $E_{night}$  was positively correlated with  $E_{d-a}$  (Fig. 7), indicating that stem refilling during the night benefited leaf transpiration in the following morning.

## DISCUSSION

### Magnitude of $E_{night}$

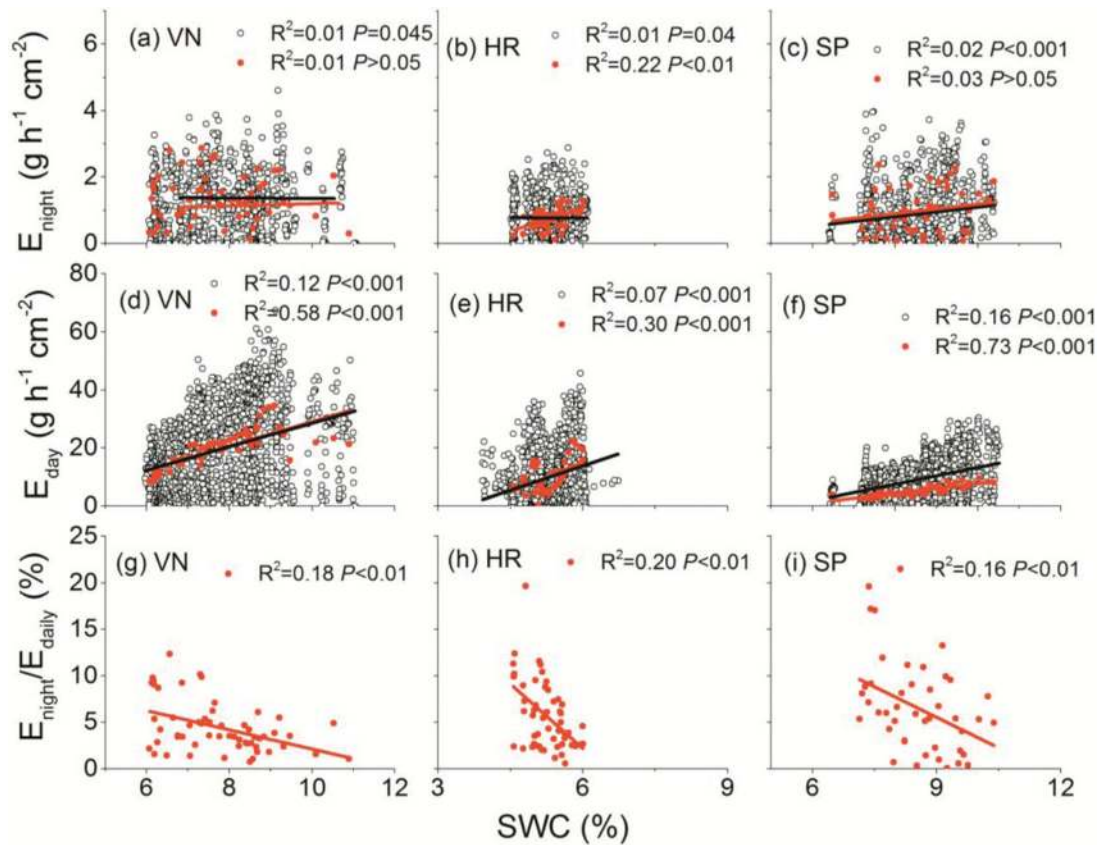
This study compared  $E_{night}$  in three shrub species under similar edaphic and climatic conditions. In general,  $E_{night}/E_{daily}$  ranges from 1% to 28% (Bucci et al. 2004; Green et al. 1989; Novick et al. 2009; Zeppel et al. 2010). It was higher at dry conditions

compared to well-watered soils (Forster 2014), reaching as high as 60% in the desert area in western USA (Snyder et al. 2003). Consistently, high  $E_{night}/E_{daily}$  may reflect high  $E_{night}$  or low daytime water use (low  $E_{day}$ ). In our study, the mean value of  $E_{night}/E_{daily}$  was 5.6% for the three species, and it had a maximum of 19.60% when drought occurred. The change of  $E_{night}/E_{daily}$  in our study is in the range of the variations reported in other studies. The possible reason for the relative low value of  $E_{night}/E_{daily}$  may be partly because the study area was relatively humid compared to the arid or desert environments. Under climate change scenarios where nighttime temperatures are predicted to increase at higher rates than daytime temperatures (Peng et al. 2013),  $E_{night}$  would increase because of high temperature and low humidity.

### Effects of VPD and SWC

Understanding how VPD and SWC regulate sap flow is critical for evaluating plant water use in water-limited areas.  $E_{night}$  positively correlates with VPD at both hourly and daily scales, which is in agreement with previous studies (Forster 2014; Moore et al. 2008; Zeppel et al. 2010). It is worth noting that the responses of  $E_{night}$  and  $E_{day}$  to VPD were similar between half-hourly and





**Figure 4:** response of averaged values of  $E$  (a, b and c),  $E$  (d, e and f) and  $E/E$  (g, h and i) to average soil water content (SWC, %) in 0–200 cm soil depth of corresponding time periods at half-hourly and daily time scales for VN, HR and SP, respectively. The symbols were the averaged values across 6–7 sample stems for each three species from June to August. Red and solid symbols represented daily time scale; black and open symbols were half-hourly time scale. Linear relationships were fitted to  $E_{\text{night}}$ -SWC,  $E_{\text{day}}$ -SWC and  $E_{\text{night}}/E_{\text{daily}}$ -SWC data sets at half-hourly and daily time scales.

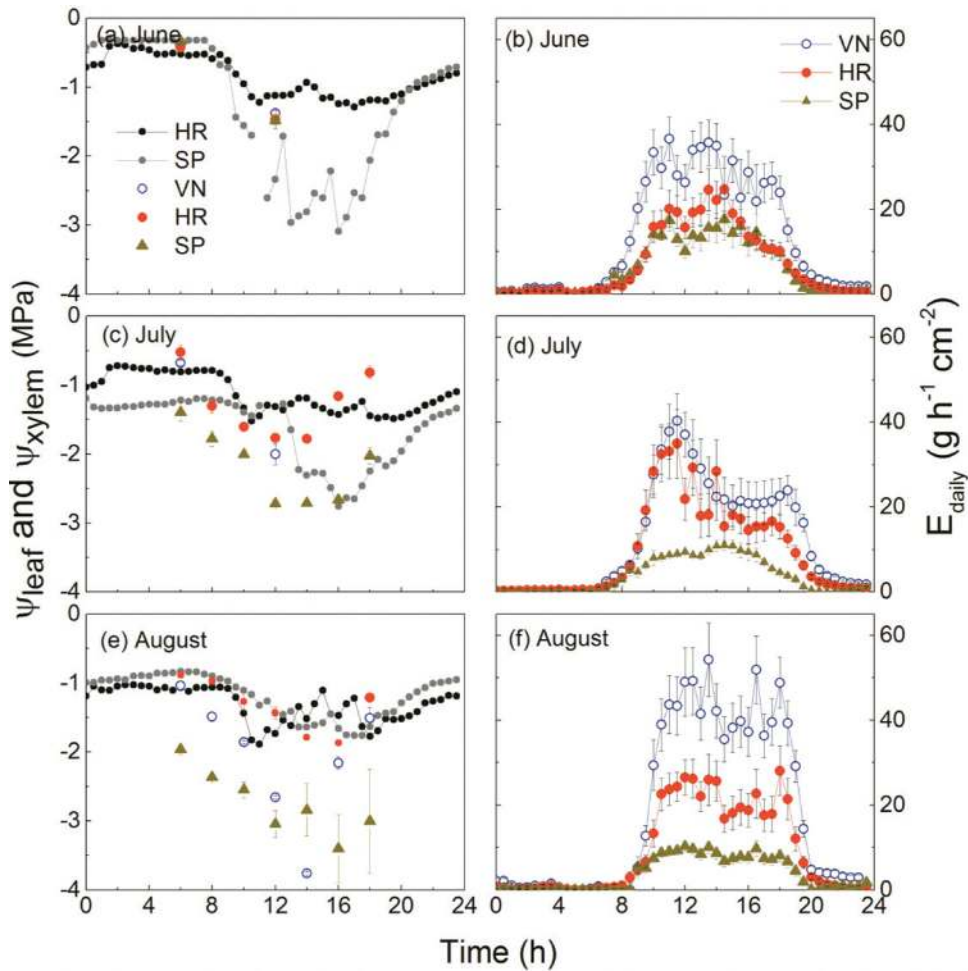
**Table 3:** equations from regressions between sap flow density ( $\text{g h}^{-1} \text{cm}^{-2}$ ) and environmental factors (VPD and SWC) for the three shrub species

Species	Scales	Regression equation	Degree of explanation		
			Total	VPD	SWC
VN	Hourly	$E_{\text{night}} = 0.92 + 0.46 \times \ln(\text{VPD}) + 0.06 \times \text{SWC}$	24.90%	24.30%	0.60%
	Hourly	$E_{\text{day}} = -16.1 + 7.67 \times \ln(\text{VPD}) + 4.32 \times \text{SWC}$	42.70%	29%	23.70%
HR	Hourly	$E_{\text{night}} = 1.72 + 2.61 \times \ln(\text{VPD}) + 0.15 \times \text{SWC}$	18.80%	18%	0.80%
	Hourly	$E_{\text{day}} = -13.95 + 3.95 \times \ln(\text{VPD}) + 4.36 \times \text{SWC}$	25.40%	21.50%	3.90%
SP	Hourly	$E_{\text{night}} = -0.44 + 0.38 \times \ln(\text{VPD}) + 0.18 \times \text{SWC}$	24.40%	20.90%	3.60%
	Hourly	$E_{\text{day}} = -21.36 + 3.52 \times \ln(\text{VPD}) + 3.45 \times \text{SWC}$	49.90%	28.70%	21.20%
VN	Daily	$E_{\text{night}} = 1.48 + 0.88 \times \ln(\text{VPD})$	13.50%	13.50%	—
	Daily	$E_{\text{day}} = -22.38 + 4.93 \times \ln(\text{VPD}) + 4.66 \times \text{SWC}$	77.60%	7.10%	70.50%
HR	Daily	$E_{\text{night}} = 0.83 + 0.18 \times \ln(\text{VPD}) + 0.05 \times \text{SWC}$	18.80%	18.30%	0.50%
	Daily	$E_{\text{day}} = -27.13 + 8.3 \times \ln(\text{VPD}) + 7.06 \times \text{SWC}$	34.60%	5%	29.60%
SP	Daily	$E_{\text{night}} = -0.32 + 0.12 \times \ln(\text{VPD})$	28.30%	28.30%	—
	Daily	$E_{\text{day}} = -9.27 + 1.07 \times \ln(\text{VPD}) + 146 \times \text{SWC}$	79.50%	4.70%	75.70%

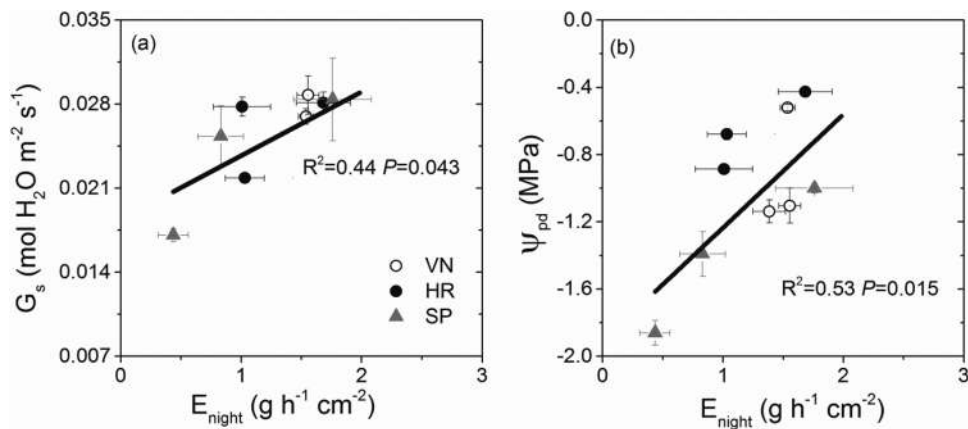
daily time scales. The fitted exponential curve between  $E_{\text{day}}$ ,  $E_{\text{night}}$  and VPD tended to be flattening when VPD was high (>1 kPa), indicating the stomatal limitation of water loss with aggregating atmospheric dryness (Pfautsch *et al.* 2011).

SWC was positively correlated with  $E_{\text{night}}$  at half-hourly time scale, although it explained a relatively small portion of variance in  $E_{\text{night}}$  for all three species. Because the temporal variations in the VPD occurred at a faster scale than SWC, VPD had





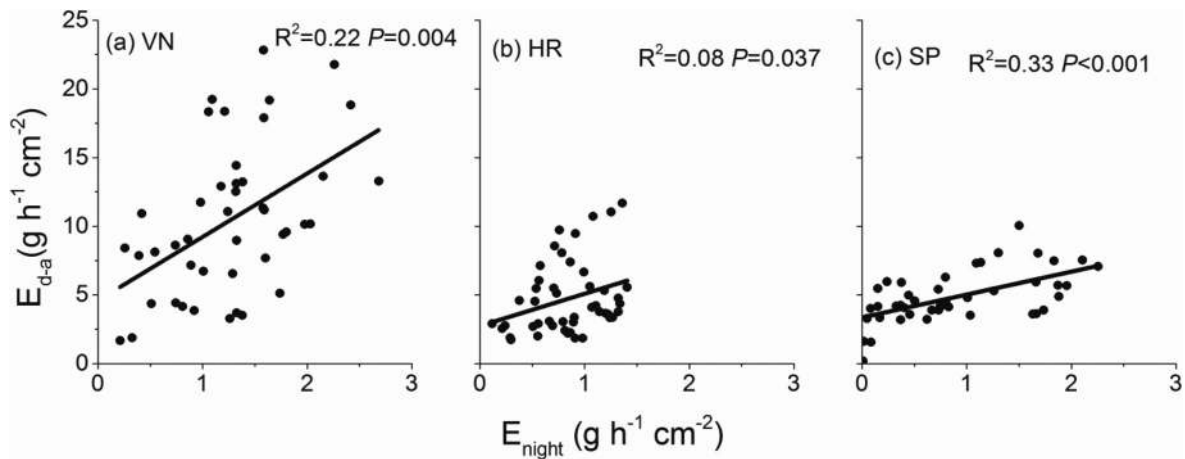
**Figure 5:** comparison of diurnal dynamics in leaf water potential ( $\Psi_{\text{leaf}}$ ) and xylem water potential ( $\Psi_{\text{xylem}}$ ) (a, c and e), averaged half-hourly diurnal patterns of sap flow density ( $E_{\text{daily}}$ ) (b, d and f) during three representative sunny and clear days from June to August (30 June, 28 July and 15 August) for the three species. The blue, red and dark yellow dots were leaf water potential for VN, HR and SP; black, grey dot and line symbols were xylem water potential for HR and SP (a, c and e).



**Figure 6:** relationships between  $E_{\text{night}}$  and stomatal conductance ( $G_s$ ) (a),  $E_{\text{night}}$  and predawn leaf water potential ( $\Psi_{\text{pd}}$ ) (b) in three represented days from June to August (30 June, 28 July and 15 August) for the three species.

stronger explaining power on the variations of  $E_{\text{night}}$  and  $E_{\text{day}}$  in comparison to SWC. Here, we also demonstrated that both SWC and VPD influenced  $E_{\text{day}}$ , and SWC had a much stronger

influence on  $E_{\text{day}}$  than VPD at daily time scale. Previous studies showed that root water uptake is reduced if the majority of root system is concentrated within the upper dry soil layers,



**Figure 7:** correlations between average nighttime sap flow density ( $E_{night}$ ,  $\text{g h}^{-1} \text{cm}^{-2}$ ) and average daytime sap flow density from 06:00 to 10:30 AM ( $E_{d-a}$ ,  $\text{g h}^{-1} \text{cm}^{-2}$ ) for VN, HR and SP on calm and sunny days.

resulting in the  $E_{day}$  decreasing as well (Huang *et al.* 2017). In our study, the roots were found to be mainly distributed in the upper layer with 79% for VN, 62% for HR and 83% for SP within 0–100cm (data not published), although the roots of shrubs could reach a maximum >200 cm for all of them. However, SWC had a minor effect on  $E_{night}$  at daily time scale. It is likely that the shrubs are well adapted to drought and do not lose water at night unless the soil water is freely available (Fisher *et al.* 2007; Grossiord *et al.* 2014). During periods of higher water stress and relatively low daily transpiration, as in some typical deserts,  $E_{night}$  may represent a greater percentage of daily transpiration, although absolute values of  $E_{day}$  and  $E_{night}$  may be lower under these conditions (Cavender-Bares *et al.* 2007). In our study, the values of  $E_{night}/E_{daily}$  were negative correlated with SWC, largely due to low  $E_{day}$  rather than  $E_{night}$  with decreasing SWC.

### Ecophysiological significance of $E_{night}$

In this study, the low fraction of  $E_{night}/E_{daily}$  of the three shrubs indicates that  $E_{night}$  may have a low impact on the stand water balance in the short term in this study. However,  $E_{night}$  may play a significant role in the ecophysiological processes of the plants. First of all, the occurrence of  $\Delta\Psi$  indicated occurrence stem refilling during the night. Stem refilling process (mainly occurred during from sunset till midnight) enhanced  $\Psi_{leaf}$  and  $\Psi_{xylem}$ , although a certain amount of water was lost by transpiration after midnight. The measurement of nighttime  $G_s$  indicated that the stomata were partially open in the night (according to a measurement taken on 18 August 2016). The results showed that  $G_s$  ranged from 0.018 to 0.026  $\text{mol m}^{-2} \text{s}^{-1}$  and transpiration ranged from 0.22 to 0.37  $\text{mmol H}_2\text{O m}^{-2} \text{s}^{-1}$  during night for the three species. Other studies also showed that nighttime  $G_s$  of shrubs was in the range of 0.01–0.02  $\text{mol m}^{-2} \text{s}^{-1}$  (Rogiers *et al.* 2009). Under water-limited conditions, the occurrence of stem refilling may be beneficial for plants in repairing embolized xylem conduits and decreasing the risk of xylem cavitation (Buckley 2005; Sperry 2000). Plants could

also avoid limitation of leaf water deficit when proceeding carbon fixation in the morning (Oren *et al.* 1999; Pearcy 1988).

Furthermore, the correlation between  $E_{night}$  and  $E_{d-a}$  indicated that  $E_{night}$  facilitated transpiration in the following day. Yu *et al.* (2016) also reported a positive relationship between  $E_{night}$  and  $E_{day}$ , indicating that  $E_{night}$  may facilitate early onset of photosynthesis via quickly open stomata due to higher  $\Psi_{pd}$  (Dawson *et al.* 2007; Maherali and DeLucia 2001; Oren *et al.* 2001). Daley *et al.* (2006) reported that the sap flux at the location of upper stem are greater than breast height in the early morning, indicating that the plants can utilize water stored in the bole for transpiration (Daley and Phillips 2006). The leaf-level gas exchange could be affected by SWC through the water potential gradient from the leaf to the soil. So using the plant-stored water might be especially advantageous in water-limited habitats because  $G_s$  could be out control of SWC limitation (Huang *et al.* 2017). It is worth noting that the interactions between nighttime stem refilling and nighttime transpiration are complex and their individual roles are hard to separate and evaluate. As reported by Huang *et al.* (2017), nighttime transpiration may even prompt plant water storage. More studies are needed to quantify the nocturnal stem refilling and transpiration process, indentifying them importance for plant growth and survival.

### Differences among species

Even under the same environmental conditions,  $E_{night}$  can largely differ between species due to their different ecophysiological attributes (Caird *et al.* 2007a; Phillips *et al.* 2010). In our study, HR experienced the lowest SWC condition in the growing seasons, but it had a narrow range of  $\Psi_{leaf}$  (–0.8––1.9 MPa), which was less than those of VN (–0.3––3.8 MPa) and SP (–0.3––3.4 MPa; Fig. 5). In terms of the characteristic of  $\Psi_{leaf}$ , the species of the HR tended to be isohydric, which is generally attributed to the strong stomatal control of transpiration, resulting in  $\Psi_{leaf}$  values remaining relatively constant during periods of minor-to-moderate water stress conditions, regardless of the soil water

status (Rogiers et al. 2009). In contrast, SP and VN showed the characteristics of anisohydric, which allowed  $\Psi_{\text{leaf}}$  values to decrease under drought conditions, reaching a lower  $\Psi_{\text{leaf}}$  value that maintained the driving force for water flow to the leaves (Attia et al. 2015). The water status regulation of the two categories (isohydric and anisohydric) may be an important factor in the regulation of plant survival during drought periods (McDowell et al. 2008).

The two categories of species may affect the response of sap flow to environmental factors. The process of sap flow is associated with stomatal behavior (Ogle et al. 2012). Different responses of  $G_s$  to environmental factors may be related to the relative control of photosynthesis feedbacks during the daytime (Huxman and Monson 2003). Carbon gain is not directly relevant at nighttime, and nighttime stomatal regulation is expected to affect water balance (Ogle et al. 2012). Although the  $R^2$  was low at daily time scale,  $E_{\text{night}}$  increased with increasing SWC for HR, while the others did not show such relationships. This suggested a comparatively greater importance of controlling water balance for HR than the other two species during the night. The species of VN and SP were more responsive to VPD during the day, suggesting that the optimization of carbon uptake is important. Furthermore, anisohydric behavior is considered to allow carbon uptake and maintain high growth rates, although it subjects the plant to a greater risk of drought-induced mortality if the drought persists (Attia et al. 2015). The lower sensitivity of  $E_{\text{day}}$  to SWC in HR at daily time scale, compared to that of the two other species, was also influenced by  $G_s$ , which declines in order to maintain  $\Psi_{\text{leaf}}$  (Jones and Tardieu 1998). Drought tolerance is a characteristic usually associated with isohydric species, which are expected to survive under prolonged severe drought (West et al. 2008).

### Implications for reality

In the context of climate change, nighttime temperature is expected to increase at higher rates than daytime temperatures (Easterling et al. 1997). With warmer and drier conditions at night, values of  $E_{\text{night}}/E_{\text{daily}}$  are likely to increase and the subsequent higher evaporation demand during night may alter the diurnal balance of plant water use and change the competitive abilities of species with different water use strategies (Snyder et al. 2003). In addition, stem refilling and continued transpiration water loss cause a disequilibrium between soil and leaf, with implications for some of the commonly used models in plant–soil–water relation research and some long-standing theories in plant science, which assumed  $E_{\text{night}}$  to be zero (Bucci et al. 2004). Therefore, in-depth knowledge about  $E_{\text{night}}$  may provide more detailed information for species adaptation and selection in re-vegetation programs in arid and semi-arid Loess Plateau.

### CONCLUSIONS

The mean contribution of  $E_{\text{night}}$  to  $E_{\text{daily}}$  was relatively small (4%–7%), suggesting that water transport at night is a minor

component of the standing water budget for the three shrub plantations. VPD had significant effects on  $E_{\text{night}}$  and  $E_{\text{day}}$  at both half-hourly and daily time scales; SWC, instead of VPD, was the key factor impacting  $E_{\text{day}}$  at the daily time scale, which was consistent for the three species. The stem refilling process occurred during the night evidenced by the decreased  $\Psi_{\text{xylem}}$  and  $\Psi_{\text{leaf}}$  during night. The occurrence of  $E_{\text{night}}$  increased  $\Psi_{\text{pd}}$  and  $G_s$ , which would be beneficial for effective photosynthesis and daytime transpiration in the morning. The species of SP had a higher fraction of refilling water because it had relatively higher  $\Delta\Psi/E_{\text{night}}$  value than the other two species. The three species showed different ecophysiological attributes on the basis of  $\Psi_{\text{leaf}}$  variation, which led to different responses of  $E_{\text{night}}$  to environmental factors. We suggest that  $E_{\text{night}}$  is an adaptive response to water stress in water-limited conditions. Our findings contribute to a better understanding of nighttime plant water use and its ecophysiological response and adaptation to the environment in a changing climate.

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