

Biophysical controls on nocturnal sap flow in plantation forests in a semi-arid region of northern China

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ARTICLE INFO

Keywords:

Nocturnal sap flow
Tree species
Tree age
Biophysical control
Semi-arid region
Nighttime sap flow partitioning

ABSTRACT

Recent studies have recognized the importance of nocturnal sap flow (Q_n) in affecting forest carbon and water budgets and responses to climate change at stand, regional, and global scales. However, biophysical controls on Q_n are not fully understood, and their implications for land surface and vegetation models are unclear. We measured growing season sap flow of two widely distributed afforestation species, *Pinus tabulaeformis* and *Acer truncatum*, in a middle-aged and a young monoculture forest stand, respectively, in a semi-arid mountainous area of northern China. We found a convergence in Q_n between the two species and in the proportion of Q_n to the total sap flow (12.2–15.0%) across species and ages. Total growing season Q_n was higher for middle-aged stands than for young stands because of larger diameters at breast height of older stands. Nighttime vapor pressure deficit (VPD_n) influence on Q_n of young stands was soil moisture dependent. Nighttime wind speed indirectly controlled Q_n through enhancing VPD_n in young stands and directly promoted Q_n in middle-aged stands with relatively low tree densities. For each species, both increased and decreased soil water content were able to promote Q_n in stands with relatively dry soils, which might be due to enhanced nighttime water recharge for capacitance refilling and for avoiding hydraulic failure under prolonged water stress, respectively. Total effects of these three environmental factors explained less than 55% of the Q_n variations. This study highlights uncertain physiological influences of VPD_n on nighttime stomatal water loss, the nighttime water loss induced by wind, region-specific patterns of nighttime water recharge, and the importance of biotic controls on Q_n . Our findings help to improve the existing VPD -based method for partitioning nighttime transpiration and water recharge at tree and stand levels, and suggest the importance of incorporating nocturnal sap flow into large-scale models.

1. Introduction

During the past two decades, nocturnal sap flow (Q_n) has been widely observed for a range of tree species and forest ecosystems (Dawson et al., 2007; Forster, 2014; Zeppel et al., 2014). It can reach up to 69% of total water uptake from trees and forest stands with an average of 12% (Forster, 2014). Nocturnal sap flow can affect not only the carbon and water budget of forest ecosystems but also their response to water and nutrient stress (i.e., resistance and resilience) (e.g., Zeppel et al., 2014) as it involves two ecophysiological and ecohydrological significant components: nighttime capacitance refilling (Daley and Phillips, 2006; Pfautsch et al., 2011; Wang et al., 2012a; Zeppel et al., 2010) and transpiration (Caird et al., 2007; Pfautsch et al., 2011; Phillips et al., 2010; Zeppel et al., 2012). For example, nighttime

plant water movement facilitates nutrient (Goldstein et al., 2013) and O_2 (Gansert, 2003) transport for tree growth (Caird et al., 2007), which is important for nutrient-limited regions (Rohula et al., 2014; Scholz et al., 2007). Competition for water between Q_n (e.g., refilling and/or transpiration) and hydraulic lifting/redistribution within dry rhizosphere soils reduces the forest productivity in water-limited regions (Caird et al., 2007; Domec et al., 2012; Howard et al., 2009; Yu et al., 2018). Nighttime stomatal opening can increase plant growth rate through increased carbon gains in early morning hours of the following day in one way (Fricke, 2019; Resco de Dios et al., 2019) and decrease plant growth rate through exacerbated O_3 concentrations in the other (Matyssek et al., 1995). Moreover, to avoid the hydraulic failure and drought induced mortality that frequently occurs in arid regions, both nighttime capacitance refilling and transpiration

Abbreviations: Q_n , nocturnal sap flow; VPD_n , nighttime vapor pressure deficit; v_n , nighttime wind speed; SWC, soil water content; Q , daily total sap flow; Q_d , daytime sap flow; E_n , nighttime transpiration; R_n , nighttime water recharge; ρ , standardized path coefficients

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<https://doi.org/10.1016/j.agrformet.2020.107904>

Received 25 September 2019; Received in revised form 10 January 2020; Accepted 10 January 2020

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contribute to removing embolism and repairing cavitation (Dawson et al., 2007; Klein et al., 2018; Zeppel et al., 2019). Despite underlying advantages for competition and evolution (Fricke, 2019; Yu et al., 2019), nighttime stomatal opening and water loss have been projected globally to increase transpiration, depress carbon gain, and aggravate soil hydrologic droughts (Lombardozzi et al., 2017); therefore, it is necessary to take Q_n into account in global land surface and vegetation models. However, the governing mechanisms of Q_n are not fully understood, particularly for semi-arid regions (Lombardozzi et al., 2017). Plants grown in, or biogeographically originating from, arid regions generally have higher nighttime water loss than those from other regions (Yu et al., 2019; Zeppel et al., 2019), and nighttime plant water loss may accordingly be a more important process than in humid regions. To evaluate and predict how forest ecosystems respond and adapt to climate change, further understanding of the biophysical controls on Q_n is therefore essential, especially for semi-arid regions.

Due to worldwide afforestation and reforestation, global forest cover increased with more young plantations during the past decades (Chen et al., 2019; Song et al., 2018), particularly in China where one-third of the forest consists of plantations with an average age less than 40 years (Zhang et al., 2017). It is therefore critical to elucidate biotic controls of tree species and age on Q_n , especially for widely distributed afforestation species. So far, Q_n variations across biometrics of tree and forest have been partially elucidated (e.g., see reviews by Zeppel et al., 2014). While proportions of Q_n to total water uptake are variable across genera and biomes globally (Forster, 2014), two case studies have reported no species difference for plants grown on the same site, although individual variation was pronounced (Phillips et al., 2010; Zeppel et al., 2010). Given that functional convergence in water use tends to occur more in water-limited regions and is important for large-scale modeling (Zeppel, 2013), we hypothesize that both the Q_n proportion in the total sap flow and Q_n itself are similar between tree species in semi-arid regions. In addition, it is unclear whether young trees or forests take up more water from the soil during the nighttime than mature ones (Alvarado-Barrientos et al., 2013; Yu et al., 2016). Here, we further hypothesize that Q_n and its proportion in the total sap flow are not affected by tree age.

Reported crucial environmental drivers of Q_n include vapor pressure deficit (VPD) (Burgess and Dawson, 2004; Fuentes et al., 2013; Pfautsch et al., 2011; Siddiq and Cao, 2018; Zeppel et al., 2014), wind speed (Chu et al., 2009), and soil water content (Fuentes et al., 2013; Zeppel et al., 2014). However, the environmental mechanism of Q_n is still uncertain and further complicated by interactions among all the above factors, particularly in the context of global climate change characterized by increasing nighttime temperature (IPCC, 2007), stilling wind (McVicar et al., 2012), and expanding drought areas (Huang et al., 2016). For example, VPD influences on Q_n can be as low as nearly negligible (Dawson et al., 2007; Wang et al., 2012a), and its influences on nighttime stomatal conductance can be negative (Bakker, 1991; Bucci et al., 2004; Cavender-Bares et al., 2007; Oren et al., 2001), positive (Dawson et al., 2007; Zeppel et al., 2012), or irrelevant (Barbour et al., 2005; Cavender-Bares et al., 2007). Phillips et al. (2010) have found that it is the product of VPD and wind speed, rather than the VPD or the wind speed alone, that significantly triggers Q_n . While Q_n is generally reduced by hydrological drought (i.e., low soil water content) and increased by atmosphere drought (e.g., high VPD), the compound effect of these two concurrent water stresses increases Q_n and its proportion to total daily sap flow (Pfautsch and Adams, 2013). Accordingly, advanced understanding of the total effect of concurrent environmental controls on Q_n is needed, especially among the three widely concerned drivers, i.e., VPD , wind speed, and soil water content.

Furthermore, it would be a large step forward in our understanding of Q_n if nighttime water loss, which is normally quantified through the discretely measured nighttime stomatal conductance (Caird et al., 2007; Pfautsch et al., 2011; Phillips et al., 2010; Zeppel et al., 2012),

could be estimated from the widely and continuously measured sap flow (Poyatos et al., 2016). Because Q_n is mainly considered as water recharge when stomata tend to be closed (Caspary et al., 1993; Pfautsch and Adams, 2013; Zeppel et al., 2010), and nighttime transpiration is thought to be promoted by VPD (Alvarado-Barrientos et al., 2015; Daley and Phillips, 2006; Gotsch et al., 2014; Pfautsch et al., 2011; Zeppel et al., 2010), a VPD -based method has been developed to differentiate nighttime transpiration and water recharge (Fisher et al., 2007; Phillips et al., 2010). It essentially treats Q_n as water recharge in nights with low VPD , and as the combination of this recharge and additional transpiration in nights with high VPD . Such a method offers an opportunity for estimating the two components of Q_n (Alvarado-Barrientos et al., 2015; Di et al., 2019; Karpul and West, 2016; Pfautsch and Adams, 2013; Siddiq and Cao, 2018). However, given the increasing knowledge of Q_n mechanisms, the VPD -based partitioning method needs further improvements.

To better understand how a 'greener' world with younger plantation forests copes with climate change through altering forest diurnal water uptake patterns, this study examined biophysical controls of Q_n in plantation forests with different ages in a semi-arid region. We measured sap flow of *Pinus tabulaeformis* and *Acer truncatum*, two widely distributed afforestation species in semi-arid regions of northern China, in a middle-aged and a young monoculture stand each, in a mountainous area of Badaling Forest Park, Beijing, China during the growing season of 2013. Climatic variables and soil water content in the four study stands were also measured synchronously. The objectives of the study were to: (1) test the hypotheses that Q_n and its proportion to daily total sap flow are not dependent on tree species and age in a semi-arid region, (2) explore total effects of concurrent environmental controls on Q_n , and (3) discuss implications for the VPD -based partitioning method of Q_n .

2. Material and methods

2.1. Site description and stand selection

The study was conducted in Badaling Forest Park (40°20' N, 116°01'E), a mountainous area in Beijing, northern China with an elevation of ca. 780 m a.s.l. According to the long-term meteorological records (1981–2010) at the closest weather station (Yanqing Weather Station, 40°27' N, 115°58'E), the region has a temperate semi-arid climate (Peel et al., 2007). The mean annual and growing season (from June to September) air temperature is 9.7 °C and 21.8 °C, respectively. The mean precipitation during the growing season is 321 mm, or 75% of the mean annual of 430 mm. About 64% of this Park is covered by plantation forests dominated by *Pinus tabulaeformis* and *Acer truncatum*. Other species include *Larix principis-rupprechtii*, *Platycladus orientalis*, *Pinus armandii*, *Picea asperata*, *Populus davidiana*, *Armeniaca sibirica*, *Cotinus coggygria*, and *Robinia pseudoacacia*. Understory species are mainly *Ziziphus jujuba* var. *spinosa* and *Vitex negundo*. Most of the forests were planted dating back to the 1950s–1970s, and some young plantations were planted in early 2000s. Covered with a ca. 3-cm humus horizon, the 30–50 cm cinnamon soils derive from limestone, marble, conglomerate, granite, and syenite-aplite. Measurements were made in four monoculture stands: a 45-year-old *P. tabulaeformis*, a 10-year-old *P. tabulaeformis*, a 34-year-old *A. truncatum*, and a 6-year-old *A. truncatum* stand, hereafter referred as the MP, YP, MA, and YA, respectively (Table 1). All of these stands are on a similar slope (21–24°) and elevation (ca. 650 m a.s.l.). Soils are dominated by cinnamon soil with a 50-cm depth and are covered by *Vitex negundo* understories. This study was performed from the day of year (DOY) 152 to 282 (1st June to 9th October) representing the growing season in 2013. A forest stand survey was made at the beginning of the growing season.

Table 1
Biometric characteristics of stands and sap flow sampled trees.

Biometric characteristics	MP	YP	MA	YA
Species	<i>P. tabuliformis</i>	<i>P. tabuliformis</i>	<i>A. truncatum</i>	<i>A. truncatum</i>
Age class	Middle-aged	Young	Middle-aged	Young
Age ^a	45	10	34	6
DBH ^{b,c} (cm)	20.3 ¹ ± 4.4	9.3 ² ± 1.8	14.8 ³ ± 3.0	5.0 ⁴ ± 0.7
Tree height ^b (m)	9.7 ± 2.3	3.6 ± 0.8	8.0 ± 3.0	3.5 ± 0.4
Stand density (stem ha ⁻¹)	983	2333	1125	1714
Trees for sap flow measurements				
Sample size	6	6	8	5
DBH ^b (cm)	20.4 ± 5.8	9.2 ± 1.7	15.5 ± 3.3	5.4 ± 0.9
Tree height ^b (m)	9.2 ± 2.5	3.7 ± 1.0	8.6 ± 2.6	3.6 ± 0.3

^a Age in 2013.

^b Standard deviations followed the mean values with a ' ± '.

^c Superscript number of diameter at breast height (DBH) represent statistical differences between stands.

2.2. Micrometeorology and soil water content

Precipitation (P , mm), air temperature ($^{\circ}\text{C}$), relative humidity (%), wind speed (v , m s^{-1}), and solar radiation (W m^{-2}) were measured continuously with an Onset HOBO U30 automatic weather station (Onset Computer Corp., Bourne, MA, USA) located in an open field about 200–400 m away from the experimental plots. These variables were scanned every 30 s and recorded as the mean or the total values at 30-min intervals. To represent atmospheric water demand, VPD was calculated by using air temperature and relative humidity (Campbell and Norman, 1998). Daily total solar radiation (R_s) was expressed as a unit of $\text{MJ m}^{-2} \text{d}^{-1}$.

Soil volumetric water content was measured half-hourly at depths of 20 cm and 40 cm in each plot using the Hydra Probe II (Stevens Water Monitoring System, Inc., Portland, OR, USA). The sensors were inserted horizontally into the soil. Measurements were taken every 10 s and the 30-minute averages were recorded by CR1000 data loggers (Campbell Scientific Inc., Logan, UT, USA). The soil water content values used in the present study (SWC , $\text{m}^3 \text{m}^{-3}$) were the averages of measurements at the depths of 20 cm and 40 cm for each plot.

2.3. Sapwood area estimates

Sapwood area (A_s) was determined by its relation with diameter at breast height (DBH), since their close relationships (Bai et al., 2017; Jonard et al., 2011) are species-specific (Wullschlegel et al., 2001) and are influenced by age (Alzheimer et al., 1998). In each stand, 8–15 trees were sampled to cover the whole range of DBH classes (Oren et al., 2001). Wood samples from each sampled tree were taken at breast height using a 5-mm increment corer. The sapwood area was identified as the area turning red after treating the increment cores with a safranin-O solution (Spicer and Gartner, 2001). No heartwood was observed for trees in young stands, since transformations from sapwood to heartwood had not occurred yet (Chang et al., 2009).

2.4. Sap flow measurements

With comparable sample sizes and a methodology similar to previous studies, five to eight sap flow sampled trees were chosen to be representative of DBH class distributions for each plot (Ghimire et al., 2014; Jonard et al., 2011; Reyes-Acosta and Lubczynski, 2014; Zeppel et al., 2010). This sampling strategy was satisfactory in representing the individual variability of each studied stand, as indicated by the closely matched biometric characteristics of sap flow sampled trees and the stands (Table 1). Specifically, trees were only selected when they had symmetrical stems and no branch or bark deformities within 15 cm above or below breast height (1.3 m).

Sap flux densities were measured by Granier-type thermal dissipation sensors at breast height. All sensors were selected with relatively

short probes to minimize estimation errors caused by possible sap flux density gradients along the length of probe (Clearwater et al., 1999); 10 mm probes were used for trees with $\text{DBH} < 20$ cm and 20 mm probes for trees with $\text{DBH} > 20$ cm. Moreover, sensors were installed on the north aspect of the stem, since circumferential variations in sap flux density have been shown not to generate significant errors in the whole tree sap flow measurement for *Pinus tabuliformis* and *Acer truncatum* in the mountainous area of Beijing (Wang, 2006). The sensor units were wrapped with aluminum foil to shield from solar radiation and rainwater. For our homogeneous and dense plantation stands with no exposed roots, the influences of natural thermal gradients on sap flow measurements were assumed to be negligible (Do and Rocheteau, 2002a, Do and Rocheteau, 2002b; Lu et al., 2004; Lubczynski et al., 2012).

Measurements were taken every 10 s, and the averaged values for each 30 min were recorded by CR1000 data loggers (Campbell Scientific Inc., Logan, UT, USA). According to energy conservation principles, sap flux density (J , $\text{g cm}^{-2} \text{s}^{-1}$) can be calculated based on the temperature difference (ΔT , $^{\circ}\text{C}$) between the heated and reference probes following a commonly-used equation (Granier, 1987):

$$J = 0.0119 \cdot \left(\frac{\Delta T_m - \Delta T}{\Delta T} \right)^{1.231} \quad (1)$$

where ΔT_m represents the ΔT when sap flux density is zero. Considering the sap flux density may not reach zero every night, the daily maximum values of ΔT are not appropriate to represent ΔT_m . Accordingly, a physically-based approach was applied to determine the ΔT_m (Oishi et al., 2016; Rabbel et al., 2016). Specifically, principles for selecting the points of ΔT_m are: (1) solar radiation $< 5 \text{ W m}^{-2}$, (2) VPD $< 0.05 \text{ kPa}$ for at least 2 h (i.e., nighttime water loss is negligible), and (3) during each period that meets the above two conditions, the variable coefficient of the four highest ΔT values is less than 0.5% (i.e., nighttime water recharge above the sensor is negligible). Afterwards, a ΔT_m baseline is interpolated between two adjacent selected points, where ΔT exceeds the ΔT_m baseline is integrated into this line. The calculation of sap flux density was performed using Baseline Software (version 3.0.7; Ram Oren, Duke University, Durham, NC, USA) (Oishi et al., 2016).

To incorporate radial variations, we applied two generalized Gaussian functions in describing the radial profiles of gymnosperm and angiosperm sap flux density (Pataki et al., 2011). The mean sap flux density (J_{tree} , $\text{g cm}^{-2} \text{s}^{-1}$) was calculated using the measured sap flux density (J) and the corresponding relative sapwood depth (i.e., the ratio of the measuring depth to the sapwood depth) (see details in Litvak et al., 2012 and Wang et al., 2012b). The estimation uncertainty produced by generalized functions was assumed minor. Daily sap flow (Q_{tree} , kg d^{-1}) for each sampled tree was calculated as follows:

$$Q_{\text{tree}} = \frac{1}{1000} \sum_{j=1}^{48} J_{\text{tree},j} \cdot 1800 \cdot A_s \quad (2)$$

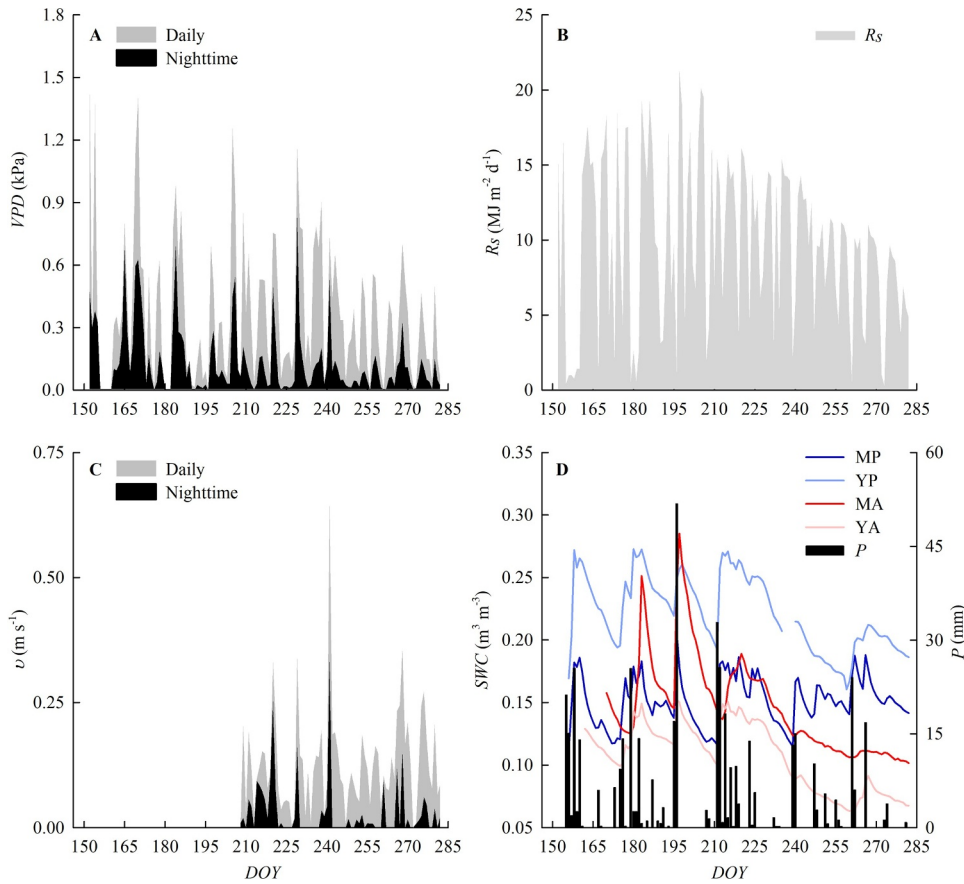


Fig. 1. Daily variations of (A) vapor pressure deficit (VPD, kPa), (B) solar radiation (R_s , $\text{MJ m}^{-2} \text{d}^{-1}$), (C) wind speed (v , m s^{-1}), (D) precipitation (P , mm), and soil water content (SWC, $\text{m}^3 \text{m}^{-3}$) of each stand. Wind speed was recorded from DOY = 208 on. The soil water content values are the averages of measurements at the depths of 20 cm and 40 cm for each plot. MP, YP, MA, and YA refer to stands of 45-year-old *P. tabuliformis*, 10-year-old *P. tabuliformis*, 34-year-old *A. truncatum*, and 6-year-old *A. truncatum*, respectively.

where $J_{tree,j}$ represents the j th J_{tree} value over a one-day period, and A_s represents the sapwood area of the tree. There were 48 values for each day because of the 30-min recording intervals.

Furthermore, we scaled up the tree-level sap flow to the stand level by sapwood area. Stand daily sap flow (Q , kg d^{-1}) was calculated as follows (Bai et al., 2017; Jonard et al., 2011):

$$Q = \frac{1}{1000} \sum_{i=1}^n \sum_{j=1}^{48} J_{tree,i,j} \cdot 1800 \cdot A_{si} \quad (3)$$

where $J_{tree,i,j}$ represents the j th value over a one-day period of the averaged J_{tree} of the i th DBH class, and A_{si} represents the total sapwood area of the i th DBH class. The stand daily sap flow is also expressed as a unit of mm d^{-1} through dividing by the density of water and the horizontal projected area of slope stands (Bai et al., 2017; Ghimire et al., 2014; Jonard et al., 2011).

In the present study, we assumed that sap flow measured at breast height corresponds to plant water use, which is the water absorbed from the soil. At daily or larger temporal scales, sap flow could also be considered equal to plant water loss to the atmosphere, i.e., canopy transpiration. At smaller temporal scales, e.g., during daytime or nighttime, sap flow only represented the plant water use rather than the synchronous plant water loss because of their hysteresis caused by the regulation of tree capacitance. The nighttime period was defined when R_s was less than 5 W m^{-2} (Daley and Phillips, 2006). Nevertheless, variations of daytime transpiration or capacitance utilization can be reflected by daytime sap flow (Q_d), since Q_d is the combination of these two highly positively related fluxes (Sun et al., 2011).

2.5. Data analysis

Student's t -test was used to examine whether nighttime climatic variables were significant or were significantly different from daily or

daytime values. Given the noisy sap flow data on rainy days, all statistical analysis of sap flow was conducted for non-rainy days (Pfautsch and Adams, 2013). Differences in sap flow between species and ages were obtained based on the two-way repeated measures ANOVA, with treating sap flow sampled trees as statistical samples. Subsequently, the source of any differences was further explored by ANCOVA. Although ANOVA is a better option when data does not follow the normal distribution, corresponding non-parametric test was still applied, and the results were similar to ANOVA (data not shown). Moreover, functional relationships between two significantly correlated variables were built using regression analysis. All statistical analyses were carried out with SPSS (version 19; Chicago, IL, USA), and significance was reported at the 0.05 level. Curve fittings were run through Sigmaplot (version 12.5; Systat Software, San Jose, CA, USA).

We developed a path coefficient model for each stand to identify and quantify direct and indirect effects of environmental factors on nocturnal sap flow (Q_n). Even though path analysis cannot establish the direction of causality (Jeon, 2015), the initial model includes all potential paths according to current knowledge and specific conditions in the present study. First of all, nighttime VPD (VPD_n), nighttime wind speed (v_n), and SWC were considered to directly affect Q_n . Daily SWC was used since it did not vary significantly between daytime and nighttime ($p > 0.05$) in this region. Second, v_n may affect Q_n by altering VPD_n since v could mitigate nighttime temperature inversion (Green et al., 1989). Third, considering that daytime transpiration can be partially promoted by SWC, the highly related capacitance utilization (Sun et al., 2011) could also be enhanced by SWC. Accordingly, SWC may affect Q_n through nighttime water recharge demand, which can be reflected by the variations of Q_d . Using standardized data, the standardized path coefficients (ρ) and the discrepancy were calculated through the maximum likelihood method. To simplified the model structure, insignificant ($p > 0.05$) paths and paths with ρ within a range

of $[-0.1, 0.1]$ were excluded recursively by removing the path with the largest p -value each time (Shao et al., 2016). Final adopted models met the following conditions: normed chi-squares were within the range of $[1, 3]$, the root mean square residuals were < 0.05 , and the good fit index values were greater than 0.9 (Markus, 2012). The path analysis was applied within AMOS (version 24.0, IBM SPSS, Chicago, IL, USA).

3. Results

3.1. Climatic and soil water dynamics

During the growing season of 2013, mean daily R_s was 9.80 ± 5.58 (SD) $\text{MJ m}^{-2} \text{d}^{-1}$. Mean daily VPD and wind speed were 0.35 ± 0.33 kPa and 0.13 ± 0.10 m s^{-1} , respectively, and the

corresponding nighttime values were 0.13 ± 0.17 kPa and 0.03 ± 0.06 m s^{-1} , respectively (Fig. 1). The nighttime VPD and wind speed values were significantly greater than zero ($p < 0.05$). SWC increased similarly in response to rainfall events across four stands and quickly reduced afterwards (Fig. 1). Mean daily SWC, averaged from the measured values at the depths of 20 cm and 40 cm, was 0.15 ± 0.02 $\text{m}^3 \text{m}^{-3}$, 0.22 ± 0.03 $\text{m}^3 \text{m}^{-3}$, 0.15 ± 0.04 $\text{m}^3 \text{m}^{-3}$, and 0.11 ± 0.03 $\text{m}^3 \text{m}^{-3}$ for MP, YP, MA, and YA, respectively.

3.2. Q_n and Q_n/Q for different species and ages

Daily variations in Q and Q_n for middle-aged and young *P. tabuliformis* and *A. truncatum* stands were similar (Fig. 2). Total Q for the MP, YP, MA, and YA during the growing season was 127.0 mm, 56.9 mm,

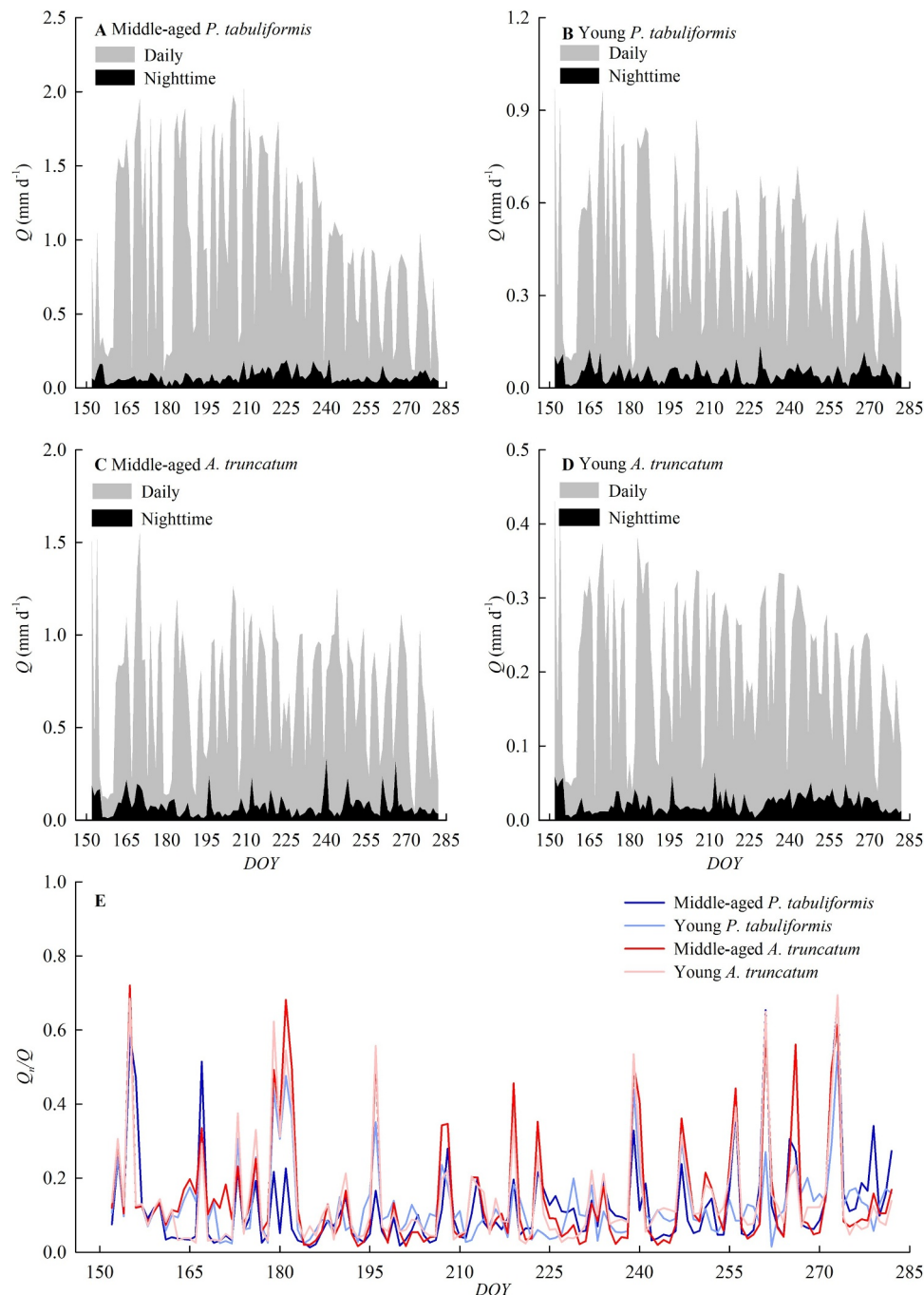


Fig. 2. Daily variations of stand sap flow (Q) and nocturnal sap flow (Q_n) for (A) middle-aged and (B) young *P. tabuliformis* stands, (C) middle-aged and (D) young *A. truncatum* stands, and (E) proportions of Q_n to total sap flow (Q_n/Q) for each stand.

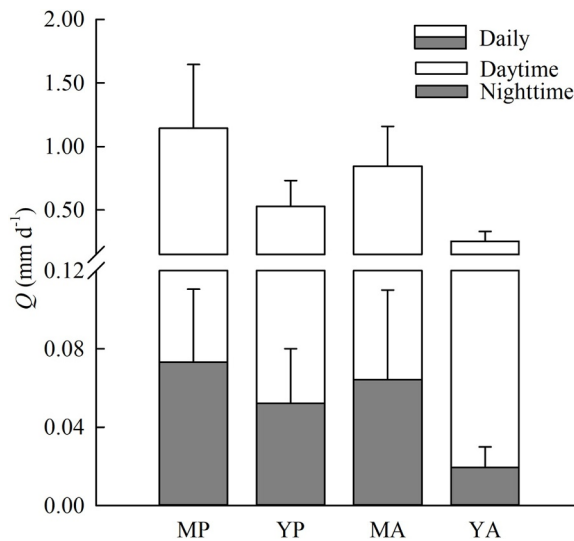


Fig. 3. Daily stand sap flow (Q) and nocturnal sap flow (Q_n) for non-rainy days. Tops of white bars equal to daily total sap flow, and gray bars represent nocturnal sap flow. Distances between the tops of the gray and the white bars represent daytime values. Error bars represent standard deviations. MP, YP, MA, and YA refer to stands of 45-year-old *P. tabuliformis*, 10-year-old *P. tabuliformis*, 34-year-old *A. truncatum*, and 6-year-old *A. truncatum*, respectively.

90.3 mm, and 27.9 mm, respectively, and the concurrent Q_n was 9.9 mm, 5.9 mm, 9.8 mm, and 2.9 mm, respectively. While the proportion of Q_n to Q (Q_n/Q) was similar for each stand, at $12.3 \pm 12.3\%$, $13.1 \pm 10.7\%$, $15.0 \pm 15.4\%$, and $14.5 \pm 14.2\%$ for the MP, YP, MA, and YA, respectively (Fig. 2e), Q_n for *P. tabuliformis* was larger than for *A. truncatum*, and values for middle-aged stands were larger than for young stands.

3.3. Variations and differences between species and ages

For non-rainy days, mean daily stand Q_n for MP, YP, MA, and YA was 0.07 ± 0.04 mm d⁻¹, 0.05 ± 0.03 mm d⁻¹, 0.06 ± 0.05 mm d⁻¹ and 0.02 ± 0.01 mm d⁻¹, respectively (Fig. 3). Variation of Q_n within species and age was remarkably large ($> 65\%$). In particular, Q_n variation within species of 75% and 85% was much greater than the variation between species of 44% and 2% for middle and young aged stands, respectively (Table 2). The larger Q_n values were not significant for *P. tabuliformis* compared with *A. truncatum* ($p = 0.258$), but were significant for middle-aged compared with young stands ($p = 0.014$). The significant effect of age on Q_n diminished after the effect of DBH was considered ($p = 0.397$) (Table 2). This finding suggests that the significant power-function relations between Q_n and DBH were independent of species and age (Fig. 4), and the significantly larger Q_n for middle-aged than for young stands derived from their significantly larger DBH (Table 1).

Meanwhile, mean daily stand Q_n/Q was $8.7 \pm 7.9\%$, $10.5 \pm 5.2\%$, $8.6 \pm 7.3\%$ and $8.6 \pm 6.2\%$ for the MP, YP, MA, and YA, respectively (Fig. 3). With more pronounced Q_n/Q variations within species or age (31–59%) than variations between species or age (8–20%) (Table 2), Q_n/Q values were not significantly different despite species and age ($p > 0.05$) (Table 2).

Table 2

Variations and differences for nocturnal sap flow (Q_n) and its proportion to total sap flow (Q_n/Q) with different species and ages.

Stands	Variations ^a	Q_n (kg d ⁻¹)		Q_n/Q (%)	
		SD	CV	SD	CV
For middle-aged	Within species	0.56	75%	3.0%	31%
	Between species	0.30	44%	1.0%	11%
For young	Within species	0.16	85%	6.4%	59%
	Between species	0.00	2%	1.9%	18%
For <i>P. tabuliformis</i>	Within age	0.52	95%	3.6%	37%
	Between age	0.50	92%	0.8%	8%
For <i>A. truncatum</i>	Within age	0.20	65%	5.8%	53%
	Between age	0.20	61%	2.1%	20%
Statistical analysis ^b Without considering covariant ^c	Factors	<i>F</i> values	<i>p</i>	<i>F</i> values	<i>p</i>
	Species	1.353	0.258	0.091	0.766
	Age	7.114	0.014	0.239	0.630
	Age*Species	1.303	0.267	1.070	0.313
Considering covariant ^d	Species	2.089	0.134		
	Age	0.750	0.397		
	Age*Species	2.148	0.158		
	DBH	11.405	0.003		

^a Variations within and between groups were calculated according to Phillips et al. (2010).

^b Effects of within-subjects (repeated measures) were all insignificant ($p > 0.05$).

^c Results of the two-way repeated measures ANOVA.

^d Results of the two-way repeated measures ANCOVA with the covariant of DBH. Since the relationship between Q_n and diameter at breast height (DBH) followed a power function for each stand (data not shown), linearized data were used. Given the non-significant effect of age*species*DBH ($F = 1.482$, $p = 0.255$), the covariant effect of DBH could be evaluated.

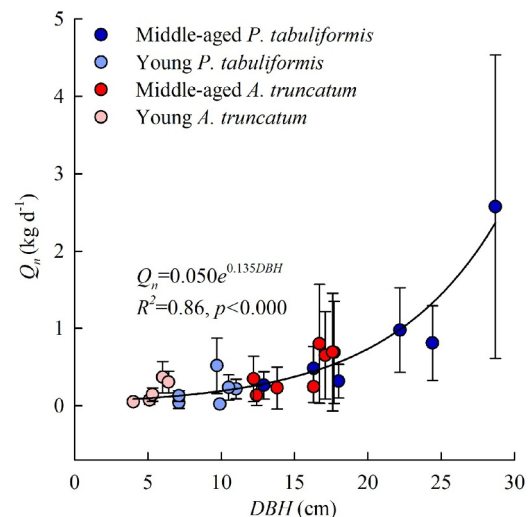


Fig. 4. The relation between nocturnal sap flow (Q_n) and diameter at breast height (DBH). Each symbol represents the mean value of each sampled tree in each stand during the non-rain period. Error bars represent standard deviations. The line is the fitted curve across all sampled trees.

3.4. Total effects of environmental factors on Q_n

Nighttime vapor pressure deficit affected Q_n of young stands (Fig. 5) in a positive way in the wettest (highest SWC) young *P. tabuliformis*

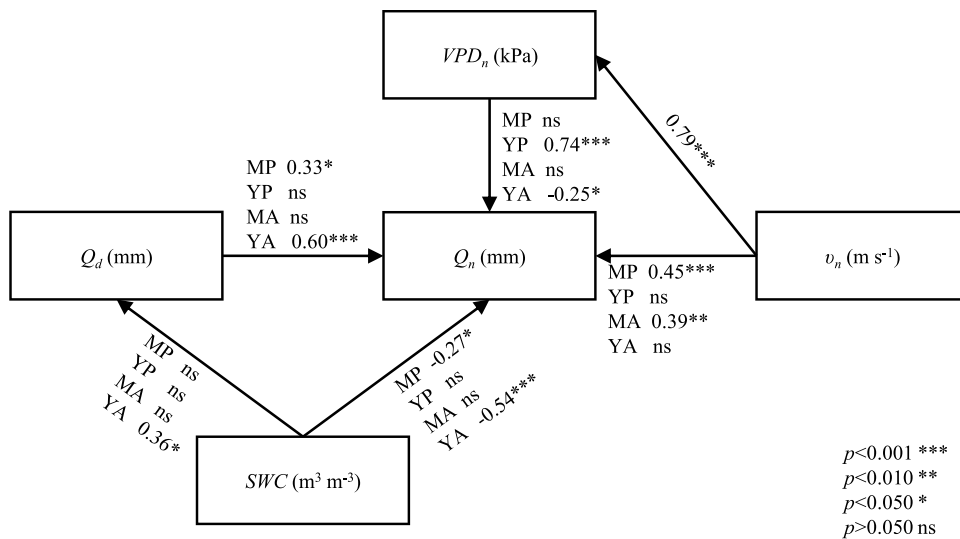


Fig. 5. Direct and indirect effects of nighttime vapor pressure deficit (VPD_n), nighttime wind speed (v_n), and soil water content (SWC) on nocturnal sap flow (Q_n) for each stand during the non-rain period. Q_d represents daytime sap flow. Standardized path coefficients (ρ : -1 to 1) are indicated along path arrows, where positive and negative values represent positive and negative effects, respectively. Asterisks represent significance levels. MP, YP, MA, and YA refer to stands of 45-year-old *P. tabuliformis*, 10-year-old *P. tabuliformis*, 34-year-old *A. truncatum*, and 6-year-old *A. truncatum*, respectively.

stand ($\rho = 0.74$) and in a negative way in the driest (lowest SWC) young *A. truncatum* stand ($\rho = -0.25$). Other than increasing VPD_n significantly ($\rho = 0.79$), v_n directly enhanced the Q_n of middle-aged *P. tabuliformis* ($\rho = 0.45$) and *A. truncatum* stands ($\rho = 0.39$), where their stand densities were relatively low comparing to the other two (Table 1). Combined with the direct and indirect effects, the total standardized effect of v_n on Q_n was positive for MP, YP, and MA, which was 0.45, 0.59, and 0.39, respectively, and was negative (-0.20) for YA (Table 3).

Table 3

Standardized total effects of nighttime vapor pressure deficit (VPD_n), nighttime wind speed (v_n), and soil water content (SWC) on nocturnal sap flow (Q_n) and the squared multiple correlation (R^2) for each stand.^a

Effects of environmental factors	MP	YP	MA	YA
Standardized total effects ^b				
VPD_n	ns	0.74	ns	-0.25
v_n	0.45	0.59	0.39	-0.20
SWC	-0.27	ns	ns	-0.33
R^2	0.38	0.55	0.15	0.48

^a MP, YP, MA, and YA refer to stands of 45-year-old *P. tabuliformis*, 10-year-old *P. tabuliformis*, 34-year-old *A. truncatum*, and 6-year-old *A. truncatum*, respectively.

^b The 'ns' indicates the standardized total effect was insignificant.

Increases in SWC in the young *A. truncatum* stand that had the lowest SWC indirectly increased Q_n ($\rho = 0.22$) through the enhanced Q_d (Fig. 5). Meanwhile, declined SWC could also directly induce higher Q_n in the stands with lower SWC for each species, i.e., the middle-aged *P. tabuliformis* stand ($|\rho| = 0.27$) and the young *A. truncatum* stand ($|\rho| = 0.54$). For the young *A. truncatum* stand, the promoted effect of the drier soil on Q_n exceeded the promoted effect of wetter soil; overall, the declined SWC increased the Q_n ($\rho = -0.33$) in this driest stand (Table 3).

When VPD_n , v_n , and SWC directly and/or indirectly affected Q_n for each stand through different ways, the total effect of these three environmental factors explained 38%, 55%, 15%, and 48% of the Q_n variations for MP, YP, MA, and YA, respectively.

4. Discussion

4.1. Effects of tree species and age on Q_n and Q_n/Q

We confirmed the hypothesis that Q_n are similar between tree species in a semi-arid region, but rejected the hypothesis that Q_n is not affected by tree age. The much greater intraspecific variation compared with the interspecific variation explained the insignificant Q_n difference between *P. tabuliformis* and *A. truncatum* (Table 2). This is essentially consistent with that the larger DBH for middle-aged stands (Table 1) was the source of the significantly larger Q_n for middle-aged stands compared with young stands (Table 2). Inter-species Q_n differences are associated with species-specific stem cuticular photosynthesis (Chen et al., 2018), leaf nitrogen concentration, extension growth, and shade tolerance (Marks and Lechowicz, 2007). Intra-species Q_n differences can be detected by biometric characteristics of tree size (e.g., DBH or/and canopy height) (Table 2) (Chen et al., 2010; Zhao et al., 2013), since nighttime water recharge is related with tree size (Phillips et al., 2003; Wang et al., 2008). Moreover, given the large explanatory power of DBH regarding variation of Q_n between individuals (Fig. 4), DBH could be considered as a potential metric for modeling large-scale Q_n across species and ages.

We confirmed the hypothesis that Q_n/Q is not dependent on tree species in a semi-arid region. With more pronounced intra-species variations than inter-species variations, Q_n/Q ratios in the present semi-arid region were similar between species of two distinct plant functional types (i.e., evergreen needle-leaved and deciduous broad-leaved tree species) (Table 2). Comparable results have also been found for two co-occurring evergreen species (*Eucalyptus parramattensis* and *Angophora bakeri*) in a temperate woodland (Zeppel et al., 2010), and for eight species that belong to the subgenus *Symphyomyrtus* in a forest plantation (Phillips et al., 2010). Furthermore, Q_n/Q differs significantly among sites rather than species (*Eucalyptus delegatensis* and *Eucalyptus pauciflora*) (Buckley et al., 2011). Together with the similar Q_n in *P. tabuliformis* and *A. truncatum*, these phenomena indicate a convergence in nighttime water uptake magnitude and in nighttime proportion to the total water use for species grown on the same site.

Moreover, our observations also confirmed the hypothesis that Q_n/Q is not dependent on tree age, which is different from previous observations. Yu et al. (2016) found lower Q_n/Q for sapling *Populus euphratica* than for mature individuals, whereas Alvarado-Barrientos et al. (2013) found higher Q_n/Q for younger *Pinus patula*. Clearly, further studies are needed to mechanistically explore forest age effects on Q_n/Q for understanding dynamics of water fluxes and the

associated carbon fluxes of forest ecosystems, and for further addressing large scale questions, such as climate adaptation (Allen et al., 2010) under a 'greening' world (Chen et al., 2019).

4.2. Environmental effects on Q_n

4.2.1. Influences of VPD_n

We only found significant effects of VPD_n on Q_n in young stands (Fig. 5). This observation agreed with responses of Q_n to VPD_n observed for young *Pinus patula* (Alvarado-Barrientos et al., 2013). VPD -influenced nighttime stomatal conductance is larger for pole-size trees than for mature trees (Grulke et al., 2004). As a main transpiration driver, VPD can increase transpiration even when light is absent (Alvarado-Barrientos et al., 2015; Daley and Phillips, 2006; Gotsch et al., 2014; Pfautsch et al., 2011; Zeppel et al., 2010), facilitating Q_n in previous studies (Burgess and Dawson, 2004; Fuentes et al., 2013; Pfautsch et al., 2011; Pfautsch and Adams, 2013; Zeppel et al., 2014, 2011) as well as in the wettest young *P. tabuliformis* stand in the present study (Fig. 5). Nevertheless, associated with decreased hydraulic conductance within plant tissues (Cavender-Bares et al., 2007), stomatal closure can also be triggered by low soil moisture (Cavender-Bares et al., 2007; Cirelli et al., 2015; Dawson et al., 2007; Howard and Donovan, 2007; Zeppel et al., 2010, 2012) and atmospheric drought (Bakker, 1991; Barbour and Buckley, 2007; Bucci et al., 2004; Cirelli et al., 2015; Oren et al., 2001) during the nighttime when no light is able to induce stomatal opening with rising VPD_n . Therefore, in the driest young *A. truncatum* stand, it was possible that the physiological restraint of VPD_n on stomatal opening overwhelmed the physical promotion of VPD_n on stomatal water loss. As a result, nighttime transpiration (Yu et al., 2016) and the Q_n (Fig. 5) was depressed by VPD_n . These contrary relations imply that influences of VPD_n on Q_n was soil water content dependent.

4.2.2. Impacts of v_n

An increase in wind speed can lower aerodynamic resistance, accelerate water vapor diffusion from moist canopy air to dry aloft air (Kim et al., 2014) through cuticles and opened leaf stomata (Fricke, 2019), and physically increase water loss at night. However, these direct positive effects of v_n on Q_n were only significant in the middle-aged stands with relatively low tree densities rather than the young stands where wind speed within/under their canopies would be weakened by their relatively high tree density (Fig. 5). Overall, as indicated by the total effects (Table 3), v_n promoted Q_n for MP, YP, and MA stands. This finding was consistent with previous studies (Chu et al., 2009; Phillips et al., 2010). Whereas the total effect for the young *A. truncatum* stand was -0.20 , which was attributed to the depressed Q_n by the increased VPD_n that can be enhanced by wind (Fig. 5) through mitigating the nighttime temperature inversion (Green et al., 1989). Nevertheless, all the positive or negative, direct or indirect pathways highlight the considerable impacts of v_n on Q_n (Table 3).

4.2.3. Responses to SWC

As the limiting factor of transpiration in this semi-arid mountain was soil water availability (reflected by SWC) rather than atmospheric water demand (reflected by VPD) (according to our unpublished results), increasing SWC in the driest young *A. truncatum* stand promoted daytime transpiration. Reflected by variations of Q_d , the following capacitance utilization/refilling (Sun et al., 2011) can account for Q_n from less than 25% to nearly 100% (Daley and Phillips, 2006; Pfautsch et al., 2011; Zeppel et al., 2010). Accordingly, Q_n indirectly increased by the relief of soil water stress through promoted Q_d in the young *A. truncatum* stand with dry soils (Fig. 5) might be due to enhanced nighttime water recharge for capacitance refilling.

On the contrary, decreasing SWC also directly induced Q_n in the middle-aged *P. tabuliformis* stand and the young *A. truncatum* stand (Fig. 5), where soils were relatively dry within each species (Fig. 1).

These induced Q_n were more likely to be related to nighttime water recharge rather than to suppressed nighttime transpiration by low SWC. Similar to what we found, following depressed daytime sap flow, Q_n of *Eucalyptus regnans* gradually increased as well as nighttime water recharge and its proportion in Q_n when soil drought and heatwave were sustained (Pfautsch and Adams, 2013). Furthermore, considering the direct pathway was irrelevant to the variation in daytime water use (Fig. 5) and the corresponding capacitance utilization/refilling, increasing Q_n under prolonged water stress might represent nighttime water recharge for embolism removal, cavitation repairing, and tissues rehydration (Pfautsch et al., 2011) for avoiding hydraulic failure. Such processes could be facilitated by sufficient root pressure (Yang et al., 2012) since the precipitation received during the study period was 48% higher than the long-term average.

Overall, both increased and decreased SWC in the stands with relatively dry soils within each species had abilities to increase Q_n , which might be due to enhanced nighttime water recharge for two distinct purposes. Accordingly, positive total effects of decreasing water availability on Q_n were observed (Table 3). This suggests the existence of a comparable mechanism of drought adaption of *Pinus tabuliformis* and *Acer truncatum* in semi-arid regions and is worth further ecophysiological study.

4.3. Implications for the VPD -based partitioning method of Q_n

Considering Q_n was not always significantly and positively related with VPD_n and could also be affected by v_n , SWC, and their interactions (Fig. 5), some concerns emerged regarding the existing VPD -based partitioning method of Q_n (Fig. 6a).

4.3.1. Uncertain physiological influences of VPD_n on nighttime stomatal water loss

Observed contrasting relations between VPD_n and Q_n (Fig. 5) lead to gradual realizations of complex influences of VPD_n on nighttime stomatal conductance (e.g., Cavender-Bares et al., 2007 and Zeppel et al., 2012). Thus, the estimation of nighttime transpiration would be inaccurate if it were treated as simply increasing with rising VPD_n (Fig. 6b). Moreover, stomatal water loss can also be physiologically regulated by plant endogenous processes, such as underlying circadian rhythms (Cirelli et al., 2015; Resco de Dios et al., 2015, 2013), starch metabolism (Lascève et al., 1997), and stomatal obstructions (Dawson et al., 2007). So far, whether and how these processes would be influenced by environmental conditions, e.g., VPD_n , remains uncertain (Fig. 6b), therefore, is worth for further investigations.

4.3.2. Overlooked nighttime water loss induced by wind

Given the considerable impacts of v_n on Q_n (Table 3) (Chu et al., 2009; Phillips et al., 2010) and on nighttime transpiration (Chu et al., 2009; Daley and Phillips, 2006; Karpul and West, 2016), variations of v_n should be included in the partitioning methods. In addition, nighttime water loss through cuticles can account for 5–18% of the total (Cavender-Bares et al., 2007; Phillips et al., 2010; Zeppel et al., 2010). This process is affected by wind speed (Baig and Tranquillini, 1980; Grace, 1974) rather than by VPD_n . Physically, wind speed can accelerate moisture movement around plant layers (Fricke, 2019; Kim et al., 2014), i.e., physical water diffusion through both cuticles and the 'leaky' stomata. Therefore, nighttime water loss would be underestimated as a result of the overlooked v_n (Fig. 6b) under the conditions of high VPD_n .

4.3.3. Region-specific nighttime water recharge responses to VPD

While enhanced water recharge for avoiding hydraulic failure seems to only occur in semi-arid regions with sustained droughts of soil and atmosphere (Pfautsch et al., 2011), nighttime water recharge for capacitance refilling responses to VPD_n depends on whether the limitation of daytime transpiration is soil water availability (SWC) or atmospheric

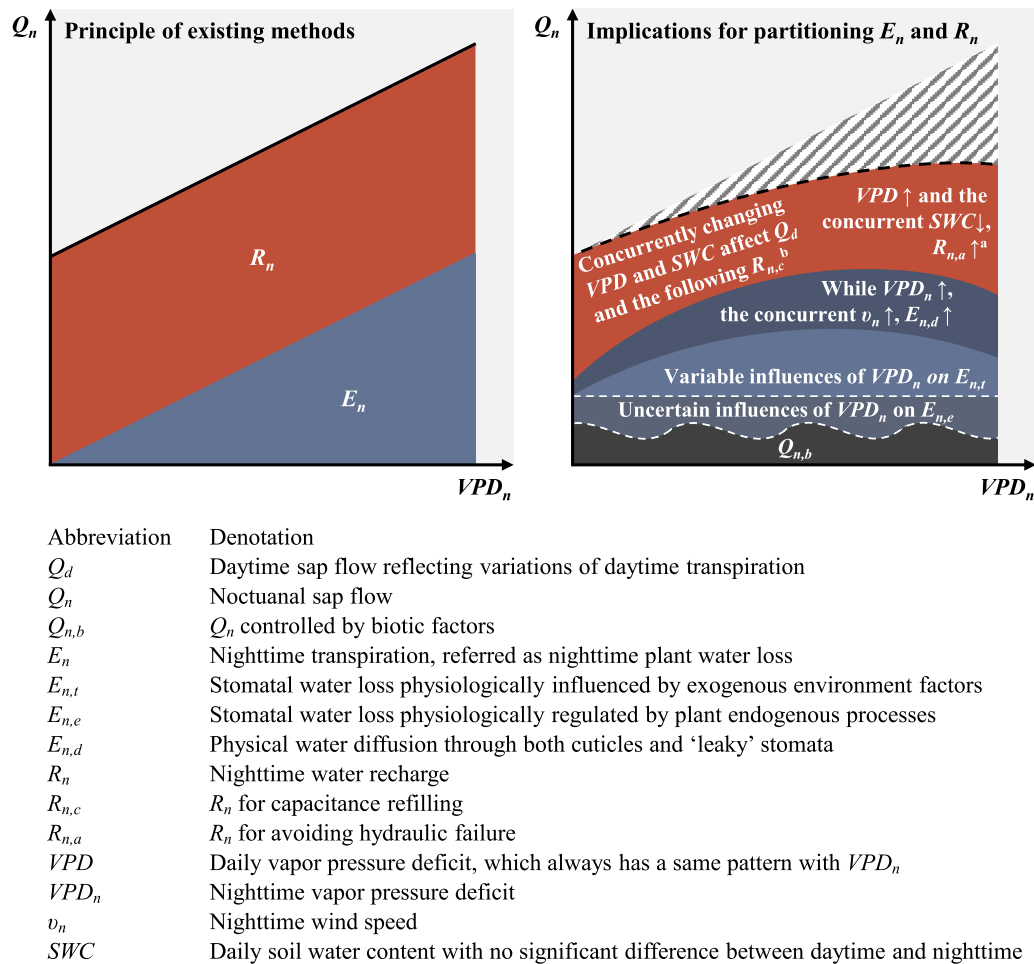


Fig. 6. A conceptual model for describing responses of nocturnal sap flow and its breakdown to nighttime vapor pressure deficit. While the dashed lines indicate uncertain response patterns, the area proportions and the slopes of each component do not represent precise estimates. Constraints: (a) nighttime water recharge for avoiding hydraulic failure seems to only occur in semi-arid regions where plants suffer from prolonged water stress but still have enough root pressure to absorb water from the soil, and (b) nighttime water recharge for capacitance refilling responses to vapor pressure deficit depends on whether the limitation of daytime transpiration is soil water availability (soil water content) or atmospheric water demand (vapor pressure deficit).

water demand (VPD) (Fig. 6b). Overall, in regions where atmospheric water demand is the limitation (e.g., humid regions), nighttime water recharge would increase with higher VPD_n due to enhanced capacitance utilization/refilling led by increasing daytime VPD . In the regions where soil water availability is the limitation (e.g., semi-arid regions), it would be promoted by concurrently changing VPD and SWC through two distinct ways (described in Section 4.2.3). Accordingly, when we differentiate nighttime water recharge from Q_n based on variations of VPD_n , habitat-specific patterns should be considered.

4.3.4. Importance of biotic controls on Q_n

For the three environmental factors that have been considered most in previous studies (VPD_n , v_n , and SWC), their total effect explained less than 55% of the Q_n variations (Table 3). This finding highlights there exist other factors, for instance, biotic characteristics, that affect variation of Q_n and its components (Fig. 6b). It has been reported that nighttime stomatal conductance is generally lower for evergreen needle-leaved trees than for deciduous broad-leaved trees (Caird et al., 2007; Hoshika et al., 2018; Zeppel et al., 2014). While nighttime stomatal conductance is similar for closely related species, it tends to be higher for species native to regions having lower annual precipitation than for those native to humid regions (Yu et al., 2019; Zeppel et al., 2019). Ratios of nighttime stomatal conductance to the daytime values

(Snyder et al., 2003) are dependent on species rather than local temperature or precipitation (Daley and Phillips, 2006; Hoshika et al., 2018). In addition, young leaves generally have larger nighttime stomatal conductance (Phillips et al., 2010) and cuticular conductance (Zeppel et al., 2010) than mature leaves. The magnitude of nighttime water recharge is associated with tree size (Phillips et al., 2003; Wang et al., 2012a, 2008). Clearly, partitioning Q_n should take biotic controls on Q_n components into account.

5. Conclusions

We confirmed the hypothesis that nocturnal sap flow is similar between two tree species in a semi-arid region, while its proportion to daily total was also not dependent on tree species and age. However, the hypothesis that nocturnal sap flow is not affected by tree age was rejected. Nocturnal sap flow of middle-aged stands was significantly higher than that of young stands, with diameter at breast height explaining their major variations. Vapor pressure deficit significantly influenced nocturnal sap flow of young stands, and this process was soil water content dependent. Wind speed had a considerable impact on nocturnal sap flow. It indirectly controlled nocturnal sap flow through enhancing nighttime vapor pressure deficit in young stands and directly promoted nocturnal sap flow in middle-aged stands, which had

relatively low tree densities. Meanwhile, both increased and decreased soil water content had abilities to promote nocturnal sap flow in the stands with relatively dry soils. The two distinct mechanisms might be related to enhanced nighttime water recharge for capacitance refilling following high daytime transpiration in the previous day and for avoiding hydraulic failures under prolonged water stress, respectively. Overall, total effects of the three widely concerned environmental factors (i.e., vapor pressure deficit, wind speed, and soil water content) on nocturnal sap flow were limited.

This study highlights uncertain physiological influences of vapor pressure deficit on nighttime stomatal water loss, the nighttime water loss induced by wind, region-specific nighttime water recharge responses to vapor pressure deficit, and the importance of biotic controls on nocturnal sap flow. Therefore, the existing vapor pressure deficit based method for partitioning nighttime transpiration and water recharge at tree and stand levels requires improvements. Our research suggests the importance for future studies to incorporate nocturnal sap flow and the associated ecophysiological and ecohydrological processes into large-scale models. Such effort could then be used to more accurately project vegetation feedbacks as well as changes in carbon and water cycles, especially in the context of climate change, with rising nighttime temperature and more frequent droughts.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgments

This research was supported by the National Natural Science Foundation of China [grant number 31872711]. We also gratefully acknowledge the Beijing Municipal Education Commission for their financial support through Innovative Transdisciplinary Program of Ecological Restoration Engineering. Beijing Badaling Forest Park assisted the field experiment. The funding agencies had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript. We thank two anonymous reviewers for their insightful comments and helpful suggestions.

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