

Quantification of nocturnal water use and its composition in a *Eucalyptus urophylla* × *E. grandis* plantation on the Leizhou Peninsula, South China

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Key Points:

- The nocturnal water use of *E.urophylla* × *E.grandis* accounts for about 12.35% of the daily water use and therefore cannot be ignored.
- Nocturnal transpiration is driven by a combination of vapor pressure deficit, temperature and humidity, with the former being predominant.
- Nocturnal water use in *E.urophylla* × *E.grandis* is mainly for nocturnal transpiration.

Abstract Nocturnal water use (Q_{night}) is an important component of the eucalyptus water budget, but it has always been under-appreciated and poorly understood. To improve the accuracy of water balance estimates and understanding of the nocturnal water use process in eucalypts plantations, we conducted a 3-year study to investigate the characteristics of Q_{night} and its components in a *Eucalyptus urophylla* \times *E. grandis* plantation in southern China. The results showed that the Q_{night} of *E. urophylla* \times *E. grandis* was substantial and its contribution (R_{night}) to daily water use (Q_{daily}) was on average 12.35%, with higher R_{night} (14.97%) in the dry season than in the wet season (9.50%). However, the Q_{night} was used not only for nocturnal transpiration (Tn), but also for stem refilling (Re). Tn was influenced by a combination of vapor pressure deficit (VPD), air temperature (T_a) and relative humidity (RH), with VPD being the dominant driver. Based on this, combined with the fact that Re was closely related to diurnal variations in diameter, we have developed a novel method to distinguish Tn from Re. We found that the compositional ratios of Tn and Re differed between weather conditions and months. However, on a 3-year average, Q_{night} of *E. urophylla* \times *E. grandis* was still mainly used for Tn (58.63%). Our results highlight the non-ignorability of Q_{night} and the high variability of the compositional ratios of Re and Tn, and suggest that Q_{night} and its components should be accurately quantified and taken into account when studying the water balance in eucalyptus stands.

Plain Language Summary Eucalyptus is one of the world's most important fast-growing tree species. Its nocturnal water use plays an important role in many physiological activities. However, it has been neglected and poorly understood due to its relatively low abundance and the difficulty in distinguishing its composition. We analyzed the nocturnal water use of *E. urophylla* \times *E. grandis* on the Leizhou Peninsula, South China, by using accurate monitoring data collected between 2019 and 2021, and developed a novel method to distinguish the components of nocturnal water use - nocturnal transpiration and stem refilling. We found that nocturnal water use by *E. urophylla* \times *E. grandis* was substantial, and although the proportions of its two components varied greatly between weather and months, on average it was still predominantly used for nocturnal transpiration, which was mainly driven by vapor pressure deficit. Our results highlight the non-neglectability of nocturnal water use in eucalypt hydrological budgets and the importance of accurately quantifying its components, and provide a

new quantification method, which can help us improve the accuracy of water budgets and our understanding of nocturnal water use processes.

1 Introduction

Sap flow is the movement of fluid within the sapwood of the plant root, stem, or branch (Forster, 2014). Monitoring plant sap flow is currently recognized as an important method for understanding the status of forest water use (Jonard et al., 2011; Kropp et al., 2017; Peters et al., 2010). However, most of the previous sap flow research ignored night-time patterns (Hasholt, 1997; Jarvis, 1976). Moreover, based on the assumption that leaf stomata are completely closed in the dark (Daley & Phillips, 2006; Meidner & Mansfield, 1965; Priestley & Taylor, 1972; Ritchie, 1974), the multi-scale water balance estimation model assumes no sap flow at night. However, numerous studies have shown that this assumption is not true in many plant species (Escalona et al., 2013; Fisher et al., 2007; Rosado et al., 2012; Siddiq & Cao, 2018; Yu et al., 2018). Stomata in many plant species remain partially open at night (Chowdhury et al., 2022; Wu et al., 2020), which undoubtedly results in nocturnal transpiration (Daley & Phillips, 2006; Wang et al., 2012). Recently, with the development of the thermal dissipation method, considerable nocturnal sap flow has been reported (Barbeta et al., 2012; Forster, 2014; Han et al., 2019; Rosado et al., 2012; Wu et al., 2020; Zeppel et al., 2011), and has been recognized as an important factor affecting different physiological processes in trees, including nocturnal nutrient transport (McDonald et al., 2002), oxygen transfer for nocturnal respiration (Fang et al., 2018; Siddiq & Cao, 2018), and next-day photosynthesis, transpiration, and drought stress resistance (Daley & Phillips, 2006). However, nocturnal sap flow and its composition are not well understood, which hinders accurate estimation of the stand water balance and a proper understanding of crown nocturnal water use processes.

In many tree species, the measured nocturnal sap flow does not necessarily indicate nocturnal transpiration; rather, it often integrates concurrent nocturnal transpiration and the amount of water required to recover from the stem water deficit caused by transpiration that occurred during the previous day (Chen et al., 2020; Di et al., 2019; Liu et al., 2021; Siddiq & Cao, 2018; Snyder et al., 2003; Wang et al., 2007). These two components usually overlap in time and space (Di et al., 2019; Liu et al., 2021), but represent opposite directions of water use: water storage in the stem and water loss to the atmosphere. Distinguishing nocturnal stem refilling (Re) and

nocturnal transpiration (T_n) is a key step to improve the accuracy of stand water consumption estimation and to reveal mechanistic control over crown nocturnal water use. However, this has always been an extremely difficult and challenging task.

Stem diameter of trees fluctuates periodically throughout the day, and follows a diurnal pattern, with the lowest values in the afternoon and highest values in the early morning (Dietrich et al., 2018; Paul et al., 2012; Vilas et al., 2019; Zweifel, 2016). This short-term diurnal variation in stem size is closely related to changes in the water content of stem cells (i.e., live phloem, fibrous phloem, and the live and dead cells of the phellem) caused by an imbalance between transpiration and root water uptake (Chan et al., 2016; Claudia et al., 2015; Zweifel et al., 2000; Zweifel et al., 2005). When transpiration is greater than the root water uptake, the tree stem loses water and shrinks. On the contrary, when transpiration is lower than the root water uptake, the tree stem refills and swells (Claudia et al., 2015; Zweifel et al., 2005). Thus, daily fluctuations in stem diameter can reflect the diurnal rhythms of stem water storage depletion and replenishment (Dietrich et al., 2018; Jiménez et al., 2019). Investigating the dynamic changes in nocturnal forest diameter provides a feasible method to screen out time periods without R_e . This provides a way to exclude the confounding effect of R_e and thus establish a highly explanatory model for estimating T_n using its drivers. This model could be used to separate T_n from R_e at any given time.

Understanding the factors that influence T_n will provide a strong foundation for developing a T_n prediction model. The drivers of T_n can be determined by analyzing the relationship between nocturnal sap flow and potential influencing factors (Doronila & Forster, 2015; Zeppel et al., 2010). Previous studies have investigated the drivers of T_n in trees. However, they have come to different conclusions (Chen et al., 2020; Chowdhury et al., 2022; Di et al., 2019, 2022; Rosado et al., 2012; Sellin & Lubenets, 2010). For example, Siddiq & Cao (2018) found that VPD was the driver of T_n in 18 broadleaf species in a tropical seasonal climate and was independent of wind speed (WS). In contrast, a study by Wu et al. (2020) on T_n of *Acer truncatum* in Beijing concluded that a combination of VPD and wind speed better explained T_n , and this finding has also been observed in many studies (Benyon, 1999; Daley & Phillips, 2006; Phillips et al., 2010). In a study of T_n in two temperate evergreen tree species, Zeppel et al. (2010) concluded that in addition to VPD and WS, soil moisture content (SWC) had a significant positive effect on T_n .

However, in a study of two tree species in semi-arid regions, Chen et al. (2020) found that nocturnal sap flow in the middle-aged *Pinus tabuliformis* stand and the young *Acer truncatum* stand was significantly negatively correlated with SWC, whereas the young *Pinus tabuliformis* stand and the middle-aged *Acer truncatum* stand was not correlated with SWC. Furthermore, numerous studies have also observed strong correlations between atmospheric temperature (Ta) and relative humidity (RH) and nocturnal sap flow (Fisher et al., 2007; Sellin & Lubenets, 2010; Wang et al., 2012). Different findings suggest that the drivers of Tn may vary considerably among plant species, site conditions, ecosystem types and climates (Chen et al., 2020; Chowdhury et al., 2022; Wu et al., 2020). To date, the drivers of Tn in eucalyptus under the marine monsoon climatic conditions in China are still unclear, which hinders further understanding of the mechanistic controls on nocturnal water use by eucalyptus in China.

Eucalyptus is an exotic, fast-growing and high-yielding tree species planted in southern China. The planted area has reached 5,467,400 ha (Arnold et al., 2020). However, the rapid expansion of its plantation area in southern China has raised concerns about the impacts on regional water resource security (Engel et al., 2005; Liu et al., 2017). In order to properly assess and predict the ecological and hydrological impacts of eucalyptus plantations in the context of global climate change, an accurate understanding of their diurnal water use patterns and control mechanisms is required. However, nocturnal water use in eucalyptus plantations has often been overlooked due to its low proportion. Although some studies have been conducted in Australia, the country of origin (Benyon, 1999), the patterns of nocturnal water use are bound to be quite different, as the eucalyptus species and the climatic conditions of the eucalyptus growing areas in China are quite different. Therefore, an in-depth study of the nocturnal sap flow and its components in eucalyptus plantations in China is crucial. *E. urophylla* × *E. grandis* is the most representative eucalyptus species in China, accounting for approximately one-third of the total eucalyptus plantation area. Therefore, this study aimed to: (1) investigate the seasonal dynamics of Q_{daily} , Q_{night} and R_{night} of *E. urophylla* × *E. grandis*; (2) determine the main drivers of Tn in the *E. urophylla* × *E. grandis* plantation and distinguish Tn and Re from nocturnal sap flow; and (3) examine the daily and seasonal variation in the distribution ratios of Tn and Re.

2 Materials and Methods

2.1 Experimental site and plantation

This study was conducted at the Zhanjiang Eucalyptus Plantation Ecosystem Research Station (21°16'N, 110°05'E) in Leizhou Peninsula, Guangdong, China (Figure 1). The terrain is flat with low hills, with elevations ranging from 80–220.8 m above sea level. According to the long-term meteorological records (1980–2020) of the weather station in this area, the region experiences a maritime monsoon climate, with an average annual precipitation of approximately 1,760.9 mm, 77–85% of which occurs in the wet season (May–October). The mean annual temperature is 23.1°C (minimum 1.4°C in January, and maximum 38.1°C in July), and the annual RH is 80.4% (Xu et al., 2020). The soil is classified as Rhodi-Udic Ferralosols, according to World Reference Base for Soil Resources (IUSS Working Group WRB, 2006), which developed from weathered sediments of basalt. The soil is acidic, with a mean pH of 5.7 at 0–100 cm depth.

In 2019, we selected an *E. urophylla* × *E. grandis* plantation, which was established in July 2012 with clone DH32-29 for long term experiment. Trees were planted by digging holes at a density of 1,666 trees·ha⁻¹. At the beginning of the experiment (2019), the mean diameter at breast height (DBH; 1.3 m) was 14.9 cm and mean height was 16.6 m. The mean leaf area index (LAI) of the stand was 1.78. The physico-chemical properties of the soils at the test site are shown in Table 1. The understorey shrub vegetation in the selected experimental plots consisted mainly of *Schefflera octophylla*, *Mallotus apelta*, *Common lantana* and *Melastoma candidum*. The herbaceous layer is relatively rich and consists mainly of *Bidens pilosa*, *Euphorbia hirta*, *Chromolaena odorata* and *Digitaria sanguinalis*.

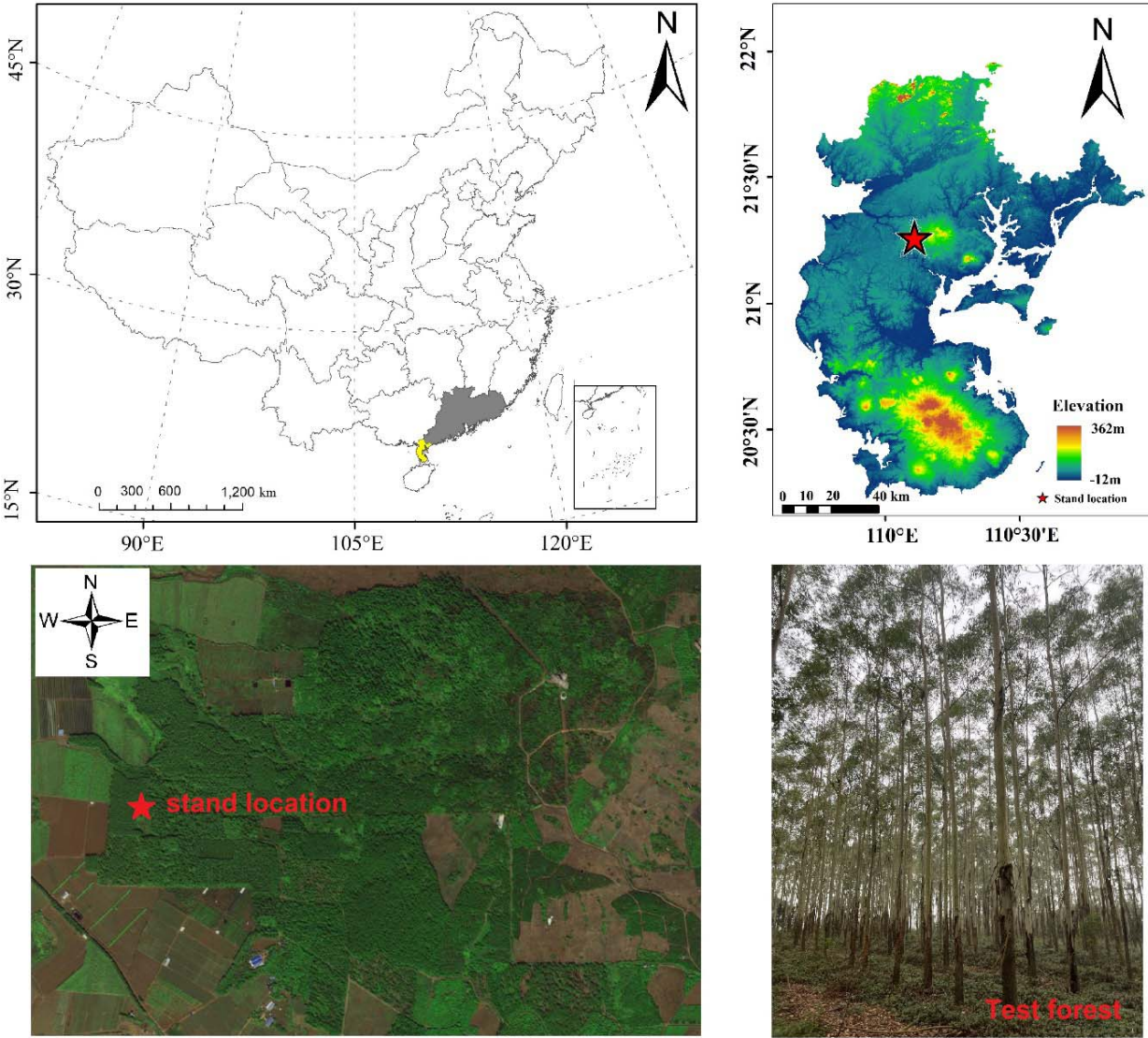


Figure 1. Location of study area and the *Eucalyptus urophylla* \times *E. grandis* plantation planted in 2012 in Leizhou Peninsula, Guangdong, China.

Table 1

Basic Physical and Chemical Properties of the Soils at the Test Site.

Indicator	Soil depth(cm)				
	0-20	20-40	40-60	60-80	80-100
pH	5.44(0.14)	5.89(0.09)	5.82(0.06)	5.82(0.02)	5.65(0.06)
BD (g.m ⁻³)	1.02(0.03)	1.13(0.02)	1.34(0.02)	1.37(0.03)	1.30(0.01)

SOM (%)	2.37(0.21)	1.47(0.15)	1.29(0.06)	0.90(0.08)	0.91(0.15)
TN(g·kg ⁻¹)	1.36(0.07)	1.08(0.02)	0.93(0.02)	0.82(0.02)	0.67(0.03)
TP(g·kg ⁻¹)	0.94(0.11)	0.77(0.04)	0.84(0.04)	0.75(0.05)	0.78(0.05)
TK(g·kg ⁻¹)	4.12(0.53)	3.46(0.32)	3.80(0.59)	4.16(0.93)	4.40(0.45)
AN (mg·kg ⁻¹)	335.23(13.59)	319.22(36.60)	334.31(20.06)	265.48(14.16)	216.78(22.59)
AP (mg·kg ⁻¹)	2.37(0.56)	2.92(0.32)	4.8(0.79)	2.81(0.35)	5.42(0.16)
AK (mg·kg ⁻¹)	18.20(2.91)	15.22(1.14)	12.48(1.16)	12.38(0.30)	14.52(0.88)

Note: BD, bulk density; SOM, soil organic matter; TN, total nitrogen; TP, total phosphorus; TK, total potassium; AN, available nitrogen; AP, available phosphorus; AK, available potassium. Values in parentheses represent standard errors of three replicate plots in the *E. urophylla* × *E. grandis* plantation.

2.2 Meteorological factors and soil water content measurement

Meteorological factors were continuously monitored using an automatic meteorological observation system set up in an open area near the eucalyptus plantation. Among the meteorological parameters, Ta (°C) and RH (%) were measured with a thermo recorder (HMP155A, Vaisala, Helsinki, Finland); the solar radiation (Rs, W·m⁻²) was measured by a photon sensor (LI-200R, LICOR, Lincoln, NE, USA); wind speed (WS; m·s⁻¹) was measured with an anemometer (ATMOS 22, Decagon, Pullman, WA, USA); and precipitation (P; mm) measured with a tilting rain gauge (TE525MM, Campbell, Logan, UT, USA). All meteorological data were collected at 1 min intervals, averaged every 10 min, and recorded using a data logger (CR3000; Campbell, USA). The vapor pressure deficit (VPD, kPa) was calculated from Ta and RH according to the following equation (Campbell & Norman, 1998):

$$VPD = 0.611 \times e^{\frac{17.502Ta}{Ta+240.97}} \times (1-RH) \quad (1)$$

Soil water content (SWC) was measured using six soil moisture sensors (CS616, Campbell, Logan, UT, USA) installed near the sap flow monitoring sample trees at different soil depths (10, 20, 40, 60, 80 and 100 cm). Measurements were recorded every 30 min by a data logger (CR1000, Campbell, Logan, UT, USA) synchronized with sap flow monitoring of the trees as described below.

2.3. Sap flow estimation methods and sapwood area determination

Six trees that cover the DBH range in the plantation (Table 2) were selected each year to measure sap flow (Di et al., 2019; Han et al., 2019; Pei et al., 2023). This sampling strategy, as indicated by the close correspondence between the biometric characteristics of the sap flow sampled trees and the stand, was satisfactory in representing the individual variability of the stand under study (Chen et al., 2020). In particular, only trees with symmetric stems and no branch or bark defects within 15 cm above or below breast height (1.3m) were selected (Chen et al., 2020).

The sap flow density ($\text{cm}\cdot\text{min}^{-1}$) of sample trees was monitored continuously from January 2019 to December 2021 using thermal dissipation probes (TDP) (SF-G; Ecomatik, Munich, Bavaria, Germany). To ensure accurate determination of sap density, and thus a more accurate distinction between Tn and Re, four TDP probes were inserted into the active xylem of each sample tree in four directions from south-east to north-west at trunk height at breast height (1.3 m) to avoid differences in the direction of sap flow in the sample trees, and covered with radiation-shielding aluminum foil to avoid solar radiation and reduce the effects of ambient temperature fluctuations and rain. The connection between S_0 (heated probe) and S_1 (reference probe) provides the difference in their temperature (ΔT), which was recorded at 30 min intervals using the data logger (CR1000; Campbell, USA). Then, the ΔT was converted into sap flow density, based on the calibration equation (Granier, 1987):

$$J_d = 0.714 \times \left(\frac{\Delta T_{\max} - \Delta T}{\Delta T} \right)^{1.231} \quad (2)$$

where J_d is the sap flow density in one direction of the measured tree ($\text{cm}\cdot\text{min}^{-1}$), and ΔT_{\max} is the maximum ΔT when the xylem sap flow density is near zero. However, since the sap flow density cannot reach zero every day, the maximum value of ΔT obtained over a period of 7–10 days was considered as ΔT_{\max} to avoid underestimating the nocturnal sap flow (Lu et al., 2004). Ultimately, the sap flow density of the measure tree was averaged over four directions.

Calculating the water consumption of trees through sap flow density requires the data of their sapwood area (SA, cm^2). Assuming circular stem cross-sections, individual values of SA were calculated by measuring the heartwood and sapwood thickness of 18 non-sample trees per DBH class in the experimental forest, and then the cross-section at breast height was measured by

felling. The color difference between sapwood and heartwood was used to identify their boundaries. Based on the SA and DBH data of 18 trees, the empirical power function between SA and DBH of the test stand was established as follows (Figure S1):

$$SA=0.3519 DBH^{2.018}, R^2=0.965, P<0.0001 \quad (3)$$

The tree water use (Q) at stand level was calculated as follows (Kumagai et al., 2005):

$$Q=\sum J_C \left(\frac{SA_{plot}}{A_E \times 1000} \right) \times 30 \quad (4)$$

where Q (mm) is the total water use in a certain time period; J_C ($\text{cm} \cdot \text{min}^{-1}$) is the stand mean sap flow density which was computed as the sapwood area weighted average of sap flow density for each DBH class, 30 is the recording interval of sap flow density in minutes; SA_{plot} (cm^2) is the total SA of all trees in the experimental plot; and A_E (m^2) is the area of the experimental plot.

Table 2

*Details of the Sample Trees of *E. urophylla* × *E. grandis* Used in Each Year for Measuring Sap Flow.*

Year	Sample tree number	DBH (cm) ^a	Tree height (m)	Crown width (m×m) ^b	Sapwood area (cm ²)
2019	1	12.1	14.3	2.5×3.0	53.89
	2	13.7	14.6	3.2×3.5	69.23
	3	14.9	15.4	2.8×3.7	82.02
	4	15.5	15.3	3.1×3.8	88.82
	5	16.2	16.1	3.2×3.6	97.10
	6	17.2	17.6	3.8×4.0	109.58
2020	1	13.6	15.7	2.4×3.5	68.22
	2	14.6	19.3	3.7×3.5	78.72
	3	15.7	20.6	3.9×4.0	91.15
	4	16.5	19.4	3.5×3.2	100.76
	5	17.8	20.0	4.4×3.9	117.43
	6	18.5	20.2	4.8×3.2	126.93
2021	1	14.2	18.7	3.0×2.9	74.43
	2	16.0	19.0	3.7×3.5	94.70

3	16.6	20.4	3.6×3.0	102.00
4	17.6	20.3	3.3×3.6	114.78
5	18.7	21.0	4.1×4.6	129.72
6	20.9	20.2	5.6×5.9	162.36

^aDBH, diameter at breast height.

^bCrown width indicates measurements taken in east-west direction × north-south direction.

2.4. Measurement of diurnal variation in DBH

A circumference dendrometer (DC3; Ecomatik, Germany) was installed on the northeast side of the stem of each sample tree at 1.3 m height to measure the variation in stem circumference, which in turn converted into the variation in stem diameter. The installation of sensors at the same height minimized the potential effects of vertical variation in stem swelling and shrinking. Each sensor was mounted using a stem embracing cable wire, which consisted of a special material (purpose-specific alloy) with the lowest thermal expansion coefficient available. Pressure was applied to the sensors through the stem embracing wire to generate change in resistance for measuring stem diameter variation. The measuring range of the sensor was 25mm, and the measuring accuracy was $\pm 3.3 \mu\text{m}$. Data were recorded every 30 min with a datalogger (CR1000; Campbell, USA).

2.5 The method of partitioning nocturnal sap flow

The nocturnal sap flow was partitioned into Re and Tn using the following method. First, several representative days were selected in each year, when daytime transpiration was weak due to cloudiness or rain, resulting in no stem water deficit or little stem water deficit but can filling to saturate it quickly, while considerable VPD exists at night, implying that sufficient transpiration driving force exists at night (Chowdhury et al., 2022; Di et al., 2019, 2022). Figure 2 shows the continuous variation of sap flow and DBH on one of the selected typical special days. Since the short-term change in diameter was shown to be proportional related to changes in the volume of water within the stem tissues (Corell et al., 2019; Vilas et al., 2019; Xue et al., 2022; Zweifel et al., 2000, 2016), we can determine the state of stem water deficit by making high-precision observations of diameter. For example, during the red cover period in Figure 2, stem diameter reached a short-term maximum, representing a period when stem water reached saturation,

resulting in an inability for the stem refill at night and therefore the diameter to remain stable (Dietrich et al., 2018; Herzog et al., 1995). The sap flow density monitored during this period was considered as the nocturnal transpiration rate. Conversely, during the grey cover period in Figure 2, stem diameter did not reach its maximum value at saturation, implying that the stem was in a state of water deficit (Dietrich et al., 2018; Zweifel et al., 2001). The diameter was still increasing due to continuous Re. The sap flow monitored during this period was used for both Tn and Re. Subsequently, we used the sap flow density during the nocturnal stem saturation period to establish a high explanatory fitted equation with Tn drivers to obtain a predictive model for Tn. This model, combined with the nocturnal environmental factors, allowed us to calculate the Tn rate for any given time. The difference between the actual measured nocturnal sap flow density and the calculated Tn rate is the Re rate.

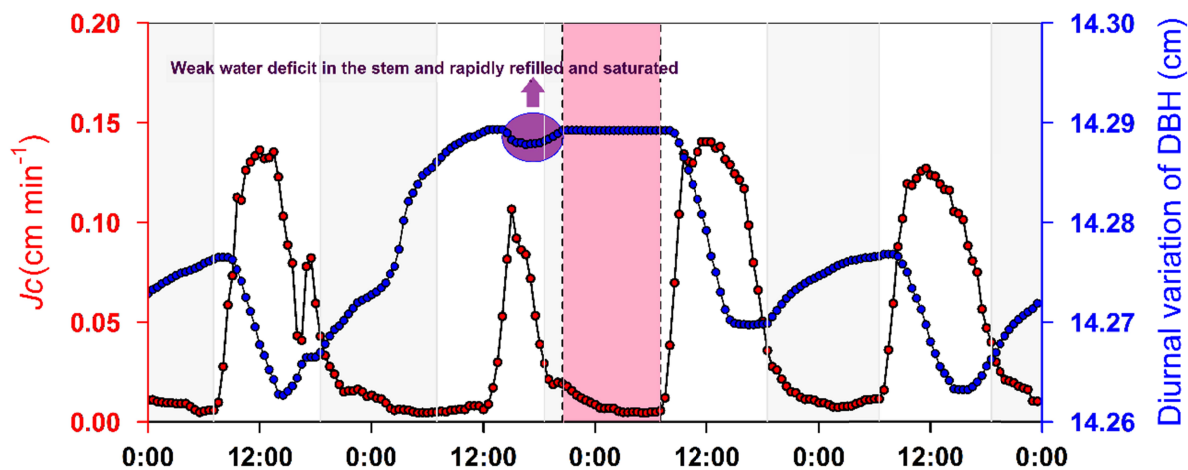


Figure 2. An example of a selected special day with diurnal variation in J_C and DBH. The gray-covered area is the period when the stem has a water deficit at night and is being refilled, when the monitored sap flow represents both stem refilling and nocturnal transpiration. The red covered area is the period when the stem reaches saturation and cannot be refilled, when the monitored sap flow represents only nocturnal transpiration.

2.6 Statistical Analyses

One-way analysis of variance (ANOVA) was used to examine the differences in diurnal and nocturnal environmental factors and water use as well as differences in Re ratios, soil moisture Q_{daily} , Q_{day} and R_{night} between the dry and wet seasons. Linear regression analysis was performed

to examine the response of nocturnal J_c to different environmental factors, and the correspondence between the measured and predicted T_n values. Regression was used to fit a power function curve and a polynomial curve to quantify the relationship between S_A and DBH and the relationship between Re and nocturnal diameter increase, respectively. Stepwise regression analysis was performed with 5% and 10% confidence levels as the threshold values for selection and rejection, respectively, to develop a multivariate linear model of T_n and VPD , T_a , RH and their interactions. Nighttime and daytime were defined as periods when the solar radiation was less and more than $5.0 \text{ W}\cdot\text{m}^{-2}$, respectively (Di et al., 2019; Wang et al., 2012). The R statistical program 4.2.2 (R Development Core Team 2022) was used to perform all statistical analyses and generate the figures.

3 Results

3.1 Variations in environmental conditions

Daily climate variables over the 3-year experimental period showed a similar interannual variability as well as seasonal variations (Figure 3). The mean daily R_s was $241.99 \text{ W}\cdot\text{m}^{-2}$ in 2019, $241.96 \text{ W}\cdot\text{m}^{-2}$ in 2020 and $249.48 \text{ W}\cdot\text{m}^{-2}$ in 2021. Due to the lack of typhoon rains in recent years, the total annual P during the monitoring period was lower than the long-term average, with 1319.5 mm in 2019, 1579.4 mm in 2020, and only 1208.4 mm in 2021. In all three years, more than 80% of the P occurred between May and October (rainy season) (Figure 3). Due to the influence by P , the mean daily SWC was lower ($P<0.001$) in each dry season (18.97%, 18.43% and 20.27% in 2019, 2020, and 2021, respectively) than in the corresponding wet season (23.75%, 22.24%, and 22.99%). The mean daytime T_a was 25.67°C in 2019, 24.99°C in 2020, and 25.16°C in 2021, which were significantly greater ($P<0.001$) than the corresponding nighttime values. Similar patterns were also found for VPD and WS (Figure 3). RH , however, showed a completely opposite pattern of magnitude. The mean daytime RH (73.37%, 79.73% and 76.77% in 2019, 2020 and 2021, respectively) was extremely significantly lower ($P<0.001$) than the corresponding nighttime values (86.45%, 91.36% and 88.87%) (Figure 3).

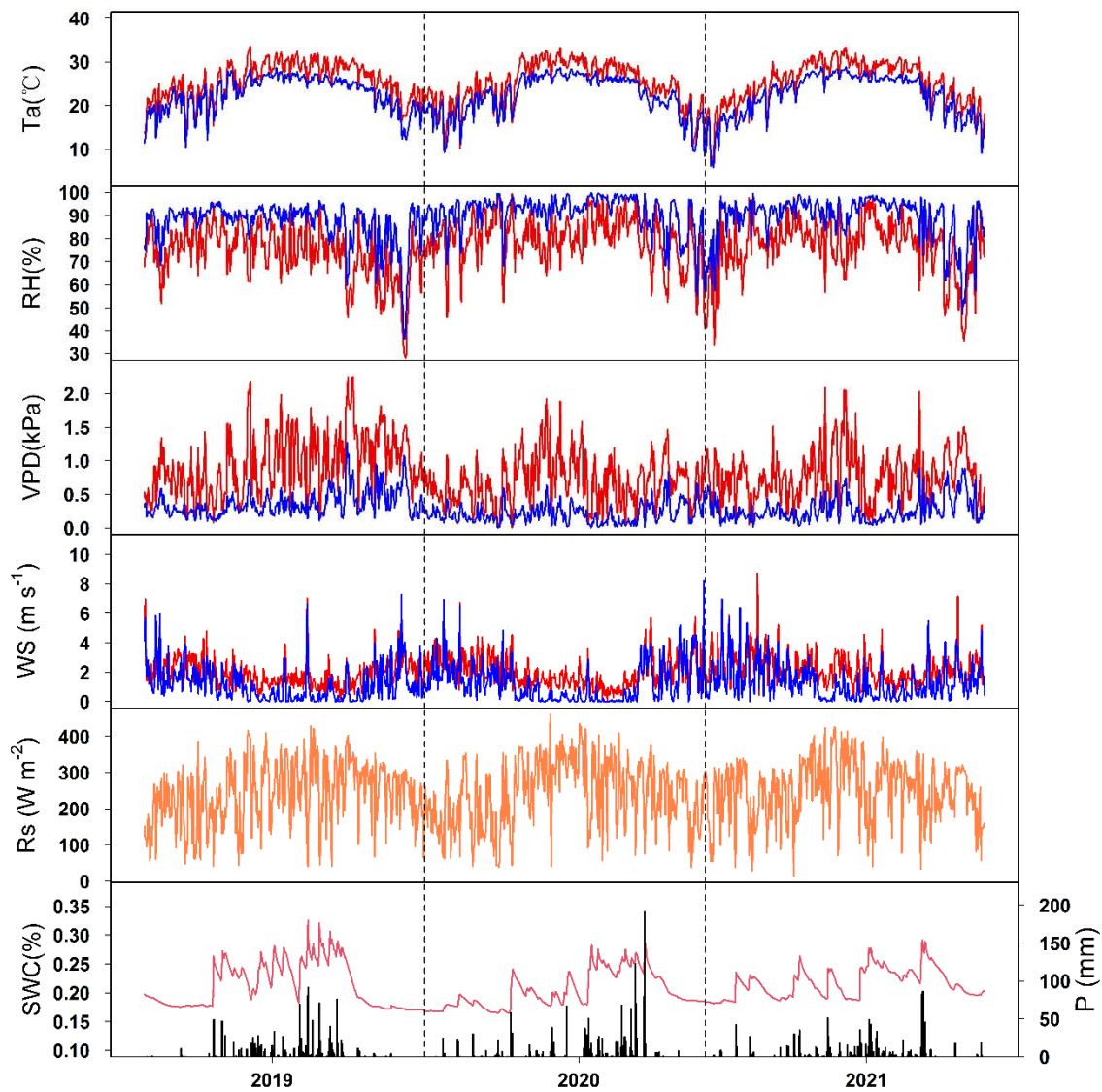


Figure 3. Changes in environmental variables at the experimental sites in 2019, 2020 and 2021. Here P, Ta, Rs, WS, SWC, RH and VPD represent precipitation (mm), air temperature ($^{\circ}\text{C}$), solar radiation ($\text{W}\cdot\text{m}^{-2}$), wind speed ($\text{m}\cdot\text{s}^{-1}$), soil water content (%), relative humidity (%) and vapour pressure difference (kPa), respectively. The red lines in Ta, WS, RH and VPD represent daytime mean values, while the blue lines represent nighttime mean values. And the lines in Rs and SWC represent daily mean values. The bars in P represent the daily cumulative precipitation.

3.2 Seasonal variation in Q_{daily} , Q_{day} , Q_{night} and R_{night}

The pattern of seasonal and interannual variation in Q_{daily} and Q_{day} was similar, with a single peak value appearing in May-July (Figure 4). The mean values of Q_{daily} (1.10 mm·d⁻¹ in 2019, 1.55 mm·d⁻¹ in 2020 and 1.73 mm·d⁻¹ in 2021) and Q_{day} (0.99 mm·d⁻¹ in 2019, 1.45 mm·d⁻¹ in 2020 and 1.63 mm·d⁻¹ in 2021) in the wet season were significantly higher ($P < 0.001$) than the concurrent average Q_{daily} (0.88 mm·d⁻¹ in 2019, 0.94 mm·d⁻¹ in 2020 and 1.25 mm·d⁻¹ in 2021) and Q_{day} (0.79 mm·d⁻¹ in 2019, 0.82 mm·d⁻¹ in 2020 and 1.16 mm·d⁻¹ in 2021) in the dry season. The annual mean Q_{daily} was 0.98 mm·d⁻¹ in 2019, 1.23 mm·d⁻¹ in 2020, and 1.49 mm·d⁻¹ in 2021. The concurrent Q_{day} was 0.89 mm·d⁻¹ in 2019, 1.12 mm·d⁻¹ in 2020, and 1.39 mm·d⁻¹ in 2021, and was significantly higher ($P < 0.001$) than the Q_{night} value (0.124 mm·d⁻¹ in 2019, 0.159 mm·d⁻¹ in 2020, and 0.171 mm·d⁻¹ in 2021). There was no obvious tendency in the seasonal variation of Q_{night} . The R_{night} (Q_{night}/Q_{daily}) ranged from 0.5% to 57.6% throughout the study period, with mean values of 12.66% in 2019, 12.96% in 2020, and 11.43% in 2021. The R_{night} followed a seasonal trend, first decreasing and then increasing, with the mean values in the dry season (14.9% in 2019, 16.9% in 2020, and 13.1% in 2021) being significantly greater ($P < 0.001$) than the mean values in the wet season (10.3% in 2019, 8.5% in 2020, and 9.7% in 2021) (Figure 4).

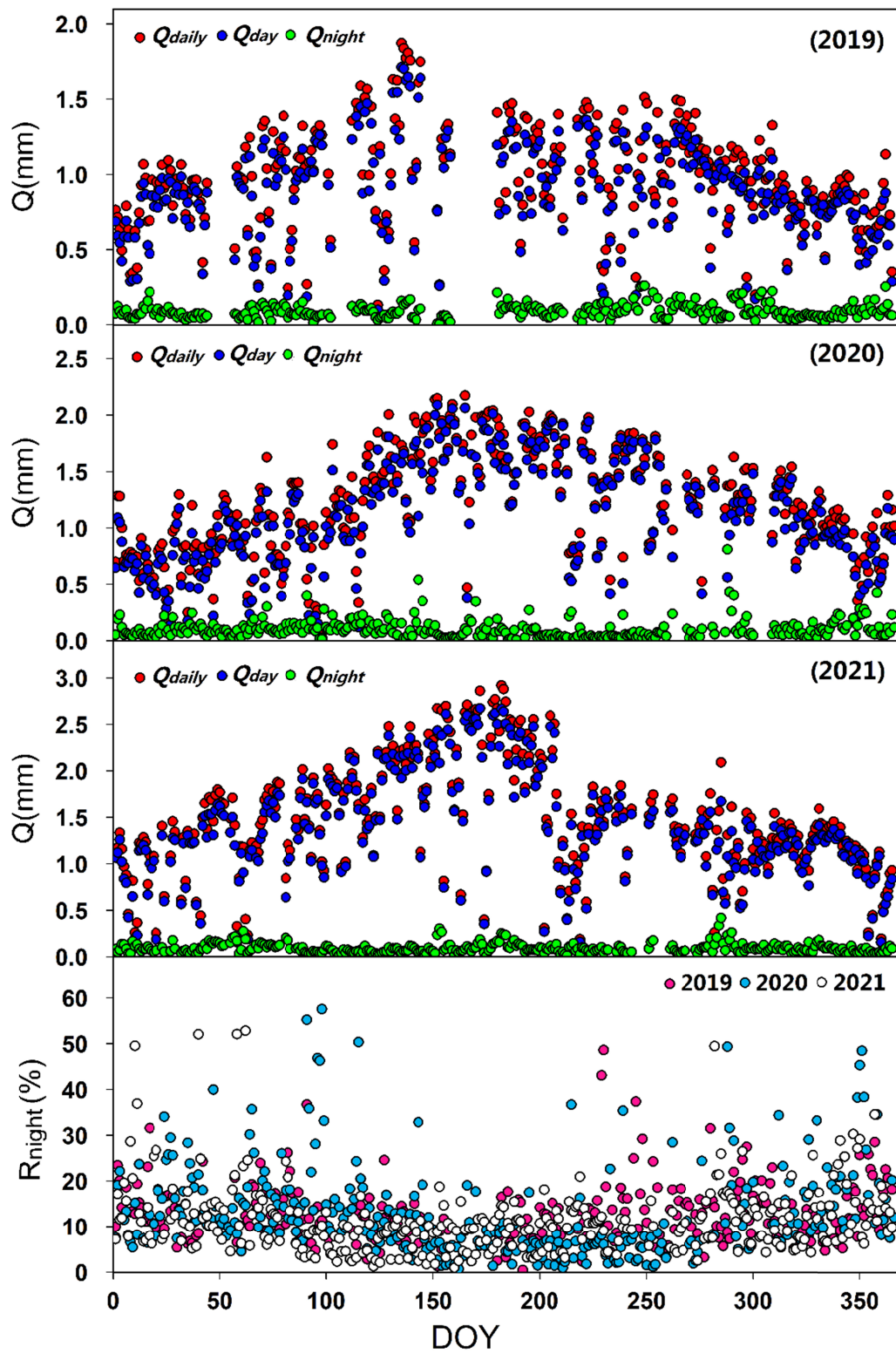


Figure 4. Annual variation in daily water use (Q_{daily}), daytime water use (Q_{day}), nocturnal water use (Q_{night}), the ratio of nocturnal to daily water use ($R_{night}=Q_{night}/Q_{daily}$) in 2019, 2020 and 2021, with some data missing for 2019 due to power supply issues. DOY is day of year.

3.3 Factors affecting Tn and predictive modelling

Significant and positive linear correlations ($P<0.001$) were found between nocturnal J_C and VPD ($R^2=0.427$ in 2019, 0.402 in 2020, and 0.428 in 2021) (Figure 5a), with an overall fit R^2 of 0.459 for all data in 3 years. Nocturnal J_C was significant and positively related to Ta ($R^2=0.081$ in 2019, 0.119 in 2020, 0.018 in 2021, and 0.063 for all data in 3 years) (Figure 5b). There was a significant and negative linear correlation ($P<0.001$) between nocturnal J_C and RH ($R^2=0.227$ in 2019, 0.200 in 2020, 0.204 in 2021, and 0.205 for all data in three years) (Figure 5c). No significant correlation was found between nocturnal J_C and SWC and WS in *E. urophylla* × *E. grandis* plantation over the 3-year study period.

The above analyses found that environmental factors had a low interpretation of nocturnal J_C , which is mainly due to the fact that nocturnal J_C is not only caused by Tn, but also by Re. To develop a highly explanatory model for predicting Tn, we screened all nocturnal J_C and corresponding VPD, Ta, RH data during the nocturnal stem water saturation period in each year based on daily diameter variation to reduce the confounding effect of Re (see 2.5 in Materials and methods). A new dataset was created by randomly selecting a portion of the screened data from each year, which was used to fit a multiple regression model (i.e., the Tn prediction model), and the remaining portion of the data from each year was used to validate the model. Regression analysis showed that excluding Re significantly improved the explanation of the nocturnal J_C fit of VPD, Ta and RH, increasing the explanations to 80.54%, 39.88% and 42.41%, respectively (Table 3). Furthermore, compared to the regression model of VPD and Tn, the introduction of Ta and RH (where RH was rejected) in the multiple regression increased the explained variance by only 1.3%. When the interaction between VPD, Ta and RH is then introduced (only RH·VPD was incorporated), the variance explained by the multiple regression can be increased to 82.65%, an increase of 2.11% over VPD alone (Table 3). In such a case, VPD could be considered as the main driver of Tn, with Ta having an independent but weak influence, while Ta and RH more predominantly affect Tn by influencing VPD.

The average T_n for remaining portion of the data in 2019, 2020, and 2021 calculated using the predictive model 5 in Table 3 was $0.00488 \text{ cm} \cdot \text{min}^{-1}$, $0.00483 \text{ cm} \cdot \text{min}^{-1}$ and $0.00343 \text{ cm} \cdot \text{min}^{-1}$, which was 102.62%, 94.29%, and 106.72% of their actual measured values, respectively, with a slight overestimation of the model when the measured T_n was less than $0.005 \text{ cm} \cdot \text{min}^{-1}$ and, conversely, a slight underestimation (Figure 6). The Nash and Sutcliffe coefficient was 0.868 for 2019, 0.948 for 2020, and 0.915 for 2021. In addition, the slopes of the linear fit between the measured and predicted sets of values for 2019, 2020 and 2021 were 0.905, 0.864 and 0.807, respectively, with corresponding R^2 values of 0.866, 0.966 and 0.938, respectively (Figure 6), indicating excellent agreement between these two sets of values. These results thus provide ample evidence to support the established model for predicting T_n .

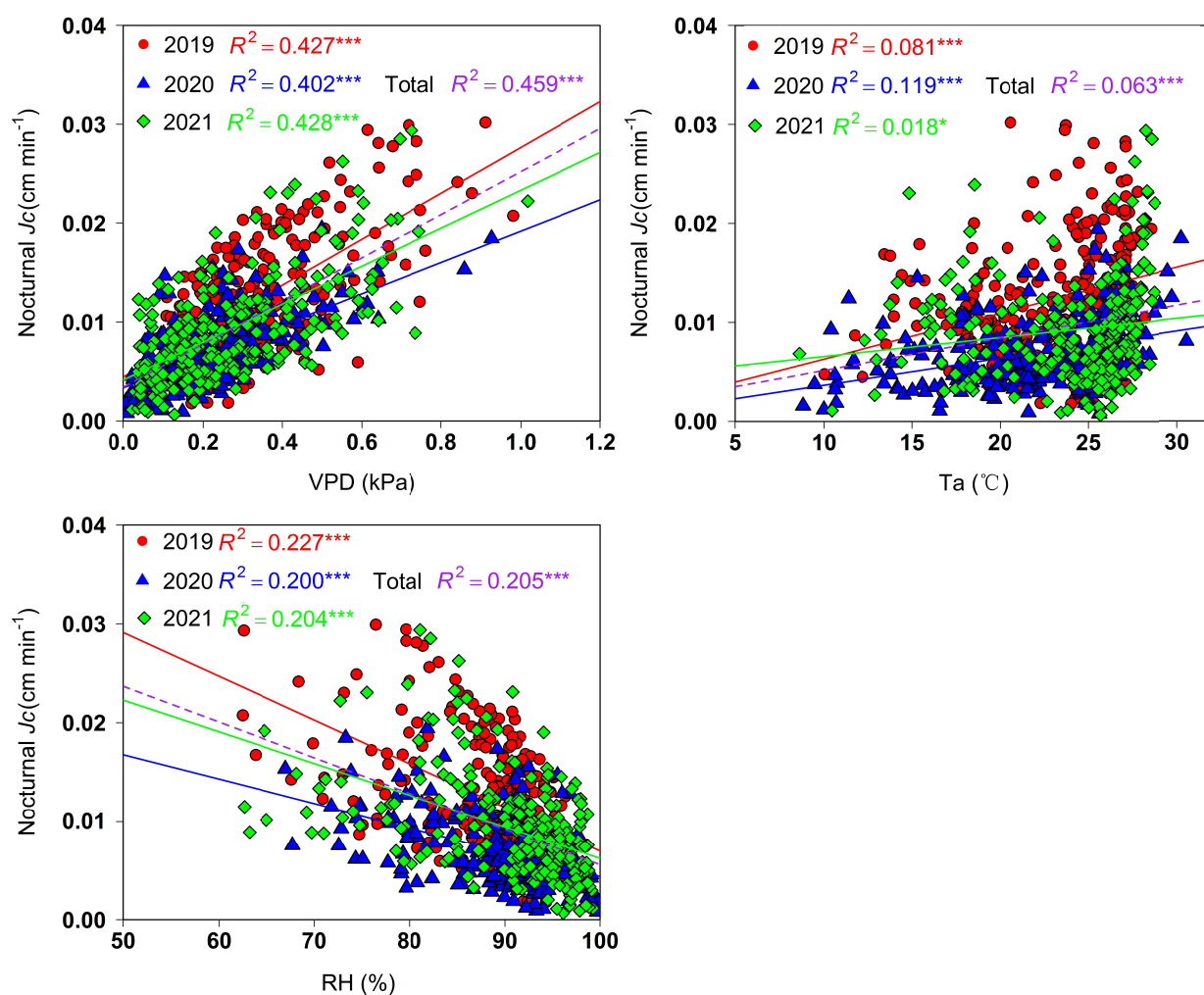


Figure 5. Relationship of between nocturnal sap flow density (J_c) with nocturnal mean vapor pressure deficit (VPD)(a), nocturnal mean atmospheric temperature (T_a)(b), nocturnal mean

relative humidity (RH)(c). The red, blue, and green dots and lines represent the data and regression lines for 2019, 2020, and 2021, respectively. The purple dashed line is the regression of all data in 3 years. * represents $P < 0.05$, *** represents $P < 0.001$.

Table 3

Stepwise Regression Analysis Models of Nocturnal Transpiration Rate (T_n ; Nocturnal Sap Flow Density Measured when the Tree Stem Saturated with Water Storage) Versus Vapor Pressure Deficit (VPD), Nocturnal Mean Atmospheric Temperature (T_a) and Nocturnal Mean Relative Humidity (RH).

Number	T_n prediction model	R^2
1	$T_n = \mathbf{0.0314} \cdot \text{VPD} - 0.0048$	0.8054***
2	$T_n = \mathbf{0.00079} \cdot T_a - 0.011$	0.3988***
3	$T_n = \mathbf{-0.00075} \cdot \text{RH} + 0.070$	0.4241***
4	$T_n = \mathbf{0.0282} \cdot \text{VPD} + \mathbf{0.000185} \cdot T_a - 0.00754$	0.8184***
5	$T_n = \mathbf{0.1148} \cdot \text{VPD} + \mathbf{0.000412} \cdot T_a - \mathbf{0.00115} \cdot \text{VPD} \cdot \text{RH} - 0.00825$	0.8265***

Note: partial regression slopes in bold are significant ($P < 0.01$), *** represents $P < 0.001$.

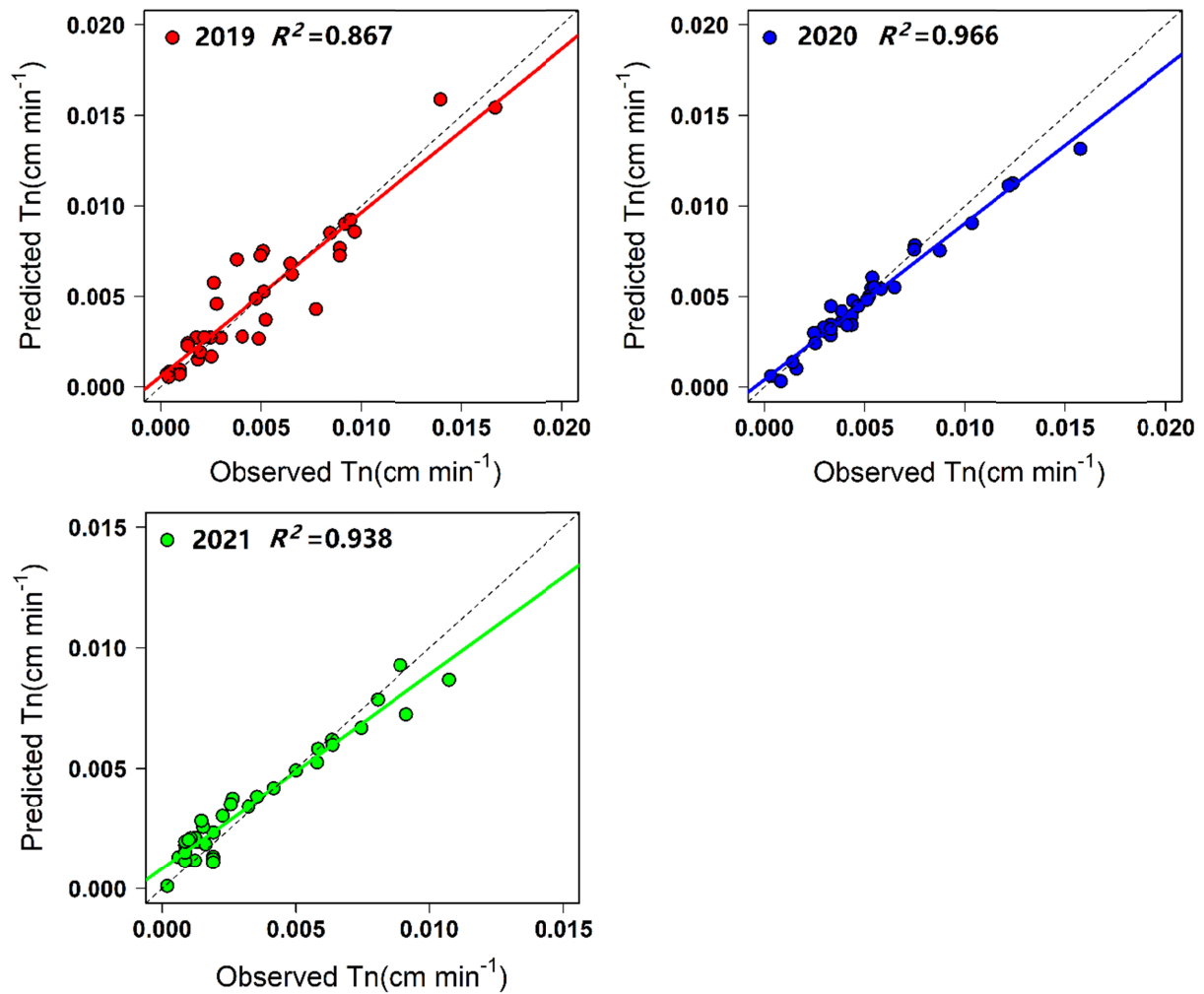


Figure 6. The predicted Tn (cm min⁻¹) plotted against the corresponding observed Tn (J_C during nocturnal stem saturation period, cm min⁻¹) of *E. urophylla* × *E. grandis* in 2019, 2020 and 2021. Note: The dotted line denotes the 1:1 relationship, and the solid line indicates the actual relationship between the predicted and observed values.

3.4 Nocturnal J_C components in typical weather conditions

The composition of nocturnal J_C varied greatly with weather conditions. When both days and nights were sunny (e.g., 25-26 August 2021; Fig. 7a-b), nocturnal J_C was related to a combination of Tn and Re. Re tended to start in the afternoon when transpiration rates decrease to coincide with root uptake rates, at which time diameter reaches its minimum value for the day (18: 00 in Figure 7a). As the rate of transpiration continued to decrease, the rate of Re gradually

increased, followed by a decreasing stem water deficit due to stem water refilling, resulting in a gradual decrease in the rate of R_e . Thus, the rate of R_e increased and then decreased from the onset of R_e and throughout the night thereafter. Looking only at the night, both R_e and T_n decrease gradually (Figure 7b). During rainy days and sunny nights (e.g., 29-30 August 2021; Figures 7c-d), the stem water deficit was minimal due to the low daytime transpiration and could be rapidly refilled to saturation (Figure 7c). At this time there was essentially no R_e at night and simultaneously sufficient VPD (0.13 kPa-0.24 kPa, mean 0.18 kPa) to drive transpiration, so that the vast majority of the monitored nocturnal J_c was T_n (Figure 7d). This situation also underlies the distinction between T_n and R_e in this study. During sunny days and rainy nights (e.g., 3-4 May 2021, Figures 7e-f), the stem water deficit was substantial due to high daytime transpiration (Figure 7e), while at night, due to rainy weather, VPD was minimal and insufficient to drive T_n (0.028 kPa - 0.059 kPa, mean 0.037 kPa), so that all nocturnal J_c during this period was caused by R_e (Figure 7f).

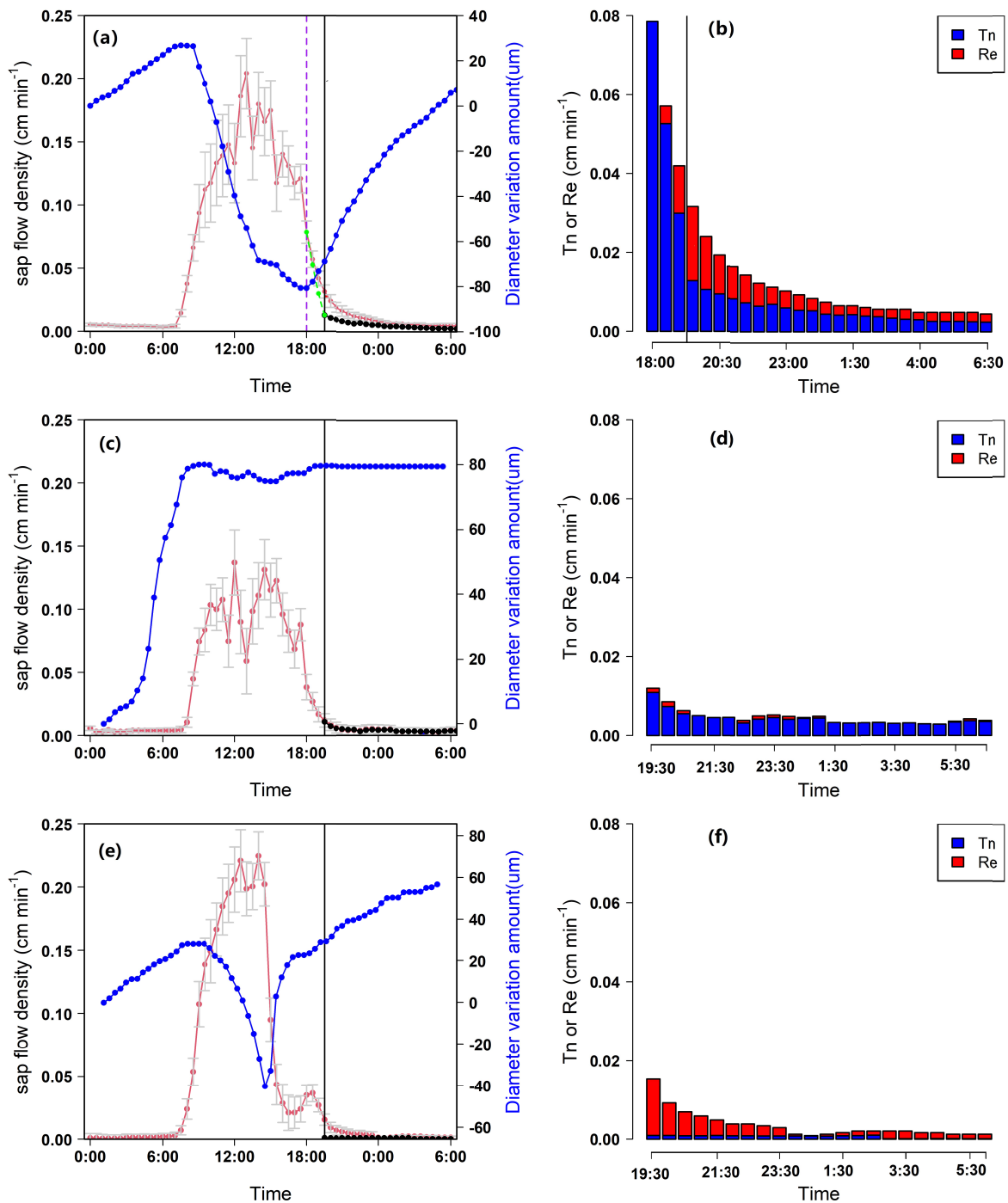


Figure 7. Daily variation of sap flow and tree diameter during sunny days and nights(a), rainy days and sunny nights(c), sunny days and rainy nights(e). The black vertical line is the boundary between day and night. The black dots and lines are the model's calculation of Tn variation. The purple vertical dashed line in (a) is the point at which the diameter begins to increase and

nocturnal refilling begins. The green dots and lines in (a) are the actual transpiration rates after estimating the refilling rate from the rate of change in diameter (assuming a linear relationship between the rate of change in diameter and the refilling rate). (b), (d) and (f) are the distribution of transpiration and refilling rates, respectively, corresponding to typical weather conditions on the right (where (b) is drawn from the time when refilling begins and the others from the beginning of the night).

3.5 Contribution of Tn and Re to nocturnal J_c

The contribution of Tn and Re to nocturnal J_c in the *E. urophylla* × *E. grandis* plantation varied considerably among months and even slightly between years (Figure 8). Monthly mean contribution of Tn to nocturnal J_c ranged from 28.6% (March) to 85.1% (December) with an annual mean of 55.28% in 2019, 34.3% (March) to 82.1% (April) with an annual mean of 60.29% in 2020, and 18.8% (August) to 76.7% (June) with an annual mean of 61.51% in 2021 (Figure 8). Over the 3-year study period, mean contribution of Tn to nocturnal J_c was 58.63%, and the mean contribution of Re to J_c was 41.37%. In addition, the total mean contribution of Re to nocturnal J_c was 43.81% in the dry season and 41.13% in the wet season.

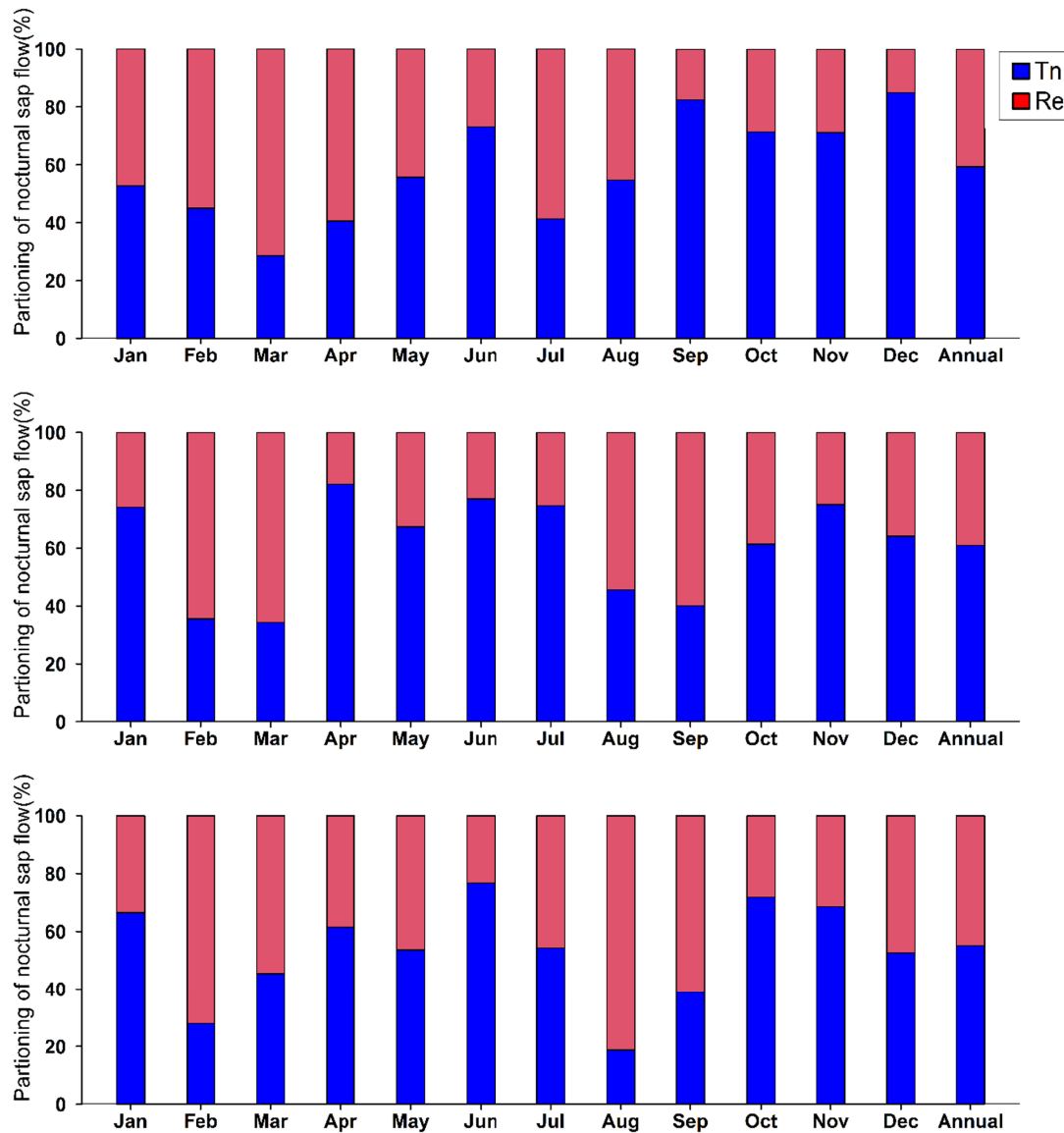


Figure 8. Partitioning of nocturnal sap flow density into nocturnal transpiration and nocturnal stem refilling in 2019 (top), 2020 (middle) and 2021 (bottom), respectively. Red bars represent the contribution ratio of stem refilling, blue bars represent the contribution ratio of nocturnal transpiration.

4 Discussion

4.1 Daily and nocturnal water use of *E. urophylla* × *E. grandis*

During the three years of our investigation, the mean daily transpiration (Q_{daily}) of *E. urophylla* × *E. grandis* ranged from 0.98 to 1.49 mm, with annual values ranging from 358.7 to 545.3 mm at

stand level. These estimates were comparable to the transpiration recorded in *E. urophylla* × *E. grandis* and *E. urophylla* in other regions of China (Morris et al., 2004; Ouyang et al., 2018a; Zhang, 2010) and *E. globulus* in southeastern Australia (Forrester et al., 2010), but was lower than that of *E. urophylla* × *E. grandis* in Brazil (Table S1; 622–879 mm) (Hakamada et al., 2020). The reason for the difference may be a combination of different climatic factors and the higher silvicultural density of *E. globulus* in Brazil (2950 trees ha⁻¹), which resulted in a much higher stand LAI than ours (Table S1). In addition, when compared with other species, *E. urophylla* × *E. grandis* had a higher transpiration than the 19-year-old *Acacia mangium* (Ma et al., 2008), but not high or even low compared with the transpiration of the 22-year-old Chinese Fir (Ouyang et al., 2018b). It is worth noting that the annual transpiration of *E. urophylla* × *E. grandis* averaged only 33.6% of the annual P during our study period, but due to the uneven distribution of P, this proportion increased to 82.51% during the dry season. When understory transpiration and soil evaporation are added, evapotranspiration from the forest stand during the dry season can be greater than the corresponding P, so the impact of eucalyptus water use on water resources during the dry season should be of particular concern.

Nocturnal water use (Q_{night}) is a widespread phenomenon in plants and important for many plant physiological processes (Chen et al., 2020; Chowdhury et al., 2022; Liu et al., 2021; Wu et al., 2020). However, the R_{night} can vary widely among species and different biomes. For example, the value of R_{night} was only 2% and 8% for *red oak* and *red maple* in a mixed New England deciduous forest (Daley & Phillips, 2006), but was 39 % for *Quercus ponderosa* in the Mediterranean region of Prades (Barbeta et al., 2012) and 21% *Pinus ponderosa* in California (Fisher et al., 2007). A study of the nocturnal water use of 98 tree species even found that R_{night} varied from 4.1% to 69% among species (Forster, 2014). In this study, the mean R_{night} of the *E. urophylla* × *E. grandis* plantation was 12.66% in 2019, 12.96% in 2020, and 11.43% in 2021, with a 3-year average of 12.35% (Figure 4). This R_{night} is similar to the results of Forster's R_{night} statistics for the phylogenetic group of Eucalyptus (10.27%). Such differences between tree species may be related to their own biology, as nocturnal stomatal conductance is generally higher in deciduous than in evergreen, in broadleaved than in coniferous, and in C4 than in C3 plants (Caird et al., 2007; Zeppel et al., 2014). However, there were also two studies found that the R_{night} of different tree species growing in the same area did not differ significantly (Phillips et al., 2010; Zeppel et al., 2010). Zeppel (2013) suggest that this may be the result of a tendency for

different plant water uses to show more functional convergence in water-limited areas. From the above, it is clear that the R_{night} of a plant may be influenced by a combination of its own biological characteristics and the environmental conditions.

Furthermore, the R_{night} of *E. urophylla* × *E. grandis* showed a clear pattern of seasonal variation, with higher values in dry season than that in wet season (Figure 4). This is consistent with the previous studies of many of the tree species (Di et al., 2019; Forster, 2014; Siddiq & Cao, 2018). Although this may be due to a higher VPD in the dry season than in the wet season (Forster, 2014), our results are more likely attributable to an insignificant difference in Q_{night} between the dry and wet seasons, coupled with a significantly lower Q_{daily} in the dry season than in the wet season caused by the combined reduction in atmospheric evaporative demand, available energy (Bosch et al., 2014; Han et al., 2019; Huang et al., 2011), soil moisture content (Lagergren & Lindroth, 2002; Ouyang et al., 2018b; Wang et al., 2019) and LAI (Di et al., 2019; Tie et al., 2017) during the dry season. In wet season, R_{night} was low but still as accounted for 9.5% (3-year average), indicating that Q_{night} is a significant contributor to Q_{daily} . Therefore, Q_{night} should be accurately quantified and taken into account to study the water balance of individual farms, parcels, communities or catchments.

4.2 Environmental drivers of nocturnal J_c

The factors affecting the diurnal J_c and nocturnal J_c of *E. urophylla* × *E. grandis* vary considerably. In one of our previous studies, Rs combined with LAI and SWC were found to be the main factors affecting diurnal transpiration (Wang et al., 2022). However, our observations confirm that VPD is the main factor positively influencing nocturnal J_c in *E. urophylla* × *E. grandis*. This may be explained by the fact that VPD can significantly influence the difference in water potential between the leaves and the atmosphere, which contributes to T_n (Zhao et al., 2019). This is also indirect evidence for the existence of T_n in *E. urophylla* × *E. grandis*. Furthermore, the nocturnal J_c of *E. urophylla* × *E. grandis* also showed a close relationship with T_a and RH (Figure 5b, c). However, there was a little improvement in the interpretation of T_n by the multiple regression model when adding T_a , RH and their interactions, compared to VPD alone. Thus, the effects of T_a and RH on nocturnal J_c are also largely mediated by changes in VPD. T_a also had a weak independent effect on T_n (Table 2), which may be related to the fact that increased T_a increases the activity of enzymes involved in transpiration-related

physiological processes (Chen et al., 2020). Some previous studies conducted in other forest ecosystems found that the combination of WS and VPD can better explain the nocturnal J_c (Benyon, 1999; Buckley et al., 2011; Daley & Phillips, 2006; Green et al., 1989; Wu et al., 2020). The theory supporting this conclusion is that increased WS may reduce aerodynamic drag and accelerate the diffusion of water vapor through the cuticle and open stomata from moist canopy air to dry overhead air, thus physically increasing nocturnal water loss (Chen et al., 2020; Fisher et al., 2007; Meinzer et al., 1995; Zhao et al., 2015). However, consistent with studies (Fisher et al., 2007; Siddiq & Cao, 2018; Zeppel et al., 2010), our study showed that nocturnal J_c was independent of WS. There is currently no consistent understanding of how increased WS affects nocturnal water loss (Buckley et al., 2011; Campbell-Clause, 1998; Gutierrez et al., 1994). However, the results of this study may be due to the high nocturnal RH of the air at this study site (Figure 3). Although the increase in WS accelerated canopy and upper canopy air exchange, the improvement in canopy air RH was extremely limited. Previous studies suggest that SWC is also an important factor affecting nocturnal water use (Di et al., 2022; Phillips et al., 2010; Zeppel et al., 2010; Zhao et al., 2017), as it not only affects nocturnal stomatal opening and closing through changes in hydraulic conductivity (Cavender-Bares et al., 2007; Zeppel et al., 2012), which in turn affects T_n , but is also a direct source of nocturnal stem R_e (Chen et al., 2020; Wu et al., 2020). Contrary to these studies, no statistically significant correlation between nocturnal J_c and SWC was found in our study. This may be because the soil water supply at the present study site did not reach the stress threshold required to limit the nocturnal sap flow. SWC restrictions on nocturnal water use may be more pronounced in arid and semi-arid ecosystems (Di et al., 2022).

4.3 The method to separate T_n and R_e

The limited interpretation of environmental factors affecting nocturnal J_c (Figure 5) and the reversible increase in nocturnal diameter (Figure 7a) indicated that the nocturnal J_c of *E. urophylla* × *E. grandis* was the cause of not only T_n but also R_e (Dietrich et al., 2018; Siddiq & Cao, 2018; Tian et al., 2019). Separating these two components is the key for improving the accuracy of stand water loss estimation and providing a strong foundation for further studies on the mechanistic control over crown nocturnal water use (Phillips et al., 2010). Siddiq & Cao (2018) separated T_n from R_e using the difference in nocturnal sap flow between two special days

with similar high daytime VPD and PAR but completely contrasting nocturnal VPD. However, this method can only distinguish nocturnal sap flow on individual days. Limited by the fact that R_e varies with daytime transpiration status, the ratio of T_n to R_e varied considerably between days, so the representativeness of the conclusions from this method still needs to be verified. Zeppel et al. (2010) have differentiated nocturnal sap flow by simultaneously measuring crown and basal sap flow. This method is relatively accurate, but the technique of installing probes in branches or below the main crown is difficult (which is not feasible for many trees) and costly. Fisher et al. (2007) first proposed three concepts for distinguishing between T_n and R_e (Time-separation, back-extrapolation and forecasted refilling, respectively), which have been applied in many studies (Di et al., 2019, 2022). However, Fisher et al. (2007) also found that the results of the three methods varied considerably, with the forecasted refilling method estimated a greater proportion of R_e than the time-separation method, while the back-extrapolation method estimated a smaller proportion of R_e than the time-separation method. Karpul & West (2016) argued that the time-separation and back-extrapolation methods overestimate and underestimate the actual nocturnal sap flow used for R_e , respectively, and that the average of the estimates from the two methods can be used as a more reliable estimate of R_e . Our method integrates the advantages of several of these methods, not only circumventing the technical difficulty and cost of installing probes in branches or below the main crown, but also allowing the inference of T_n and R_e at any given time, unaffected by daily variations in R_e , and with easy access to the relevant parameters. In addition, comparing and verifying with the splitting results of the previous three methods, the R_e obtained by our method, although smaller than the time-separation method and larger than the back-extrapolation method, is similar to the average value of the two (Table S2), so we believe that our method can be more reasonable to split the nocturnal water use into R_e and T_n , and is worthy of further research and application.

The core of our method was to establish a best-fitted T_n prediction model by eliminating the interference from R_e on the relationship between T_n and its driving factors, and the difficulty lies in how to remove the interference of R_e . The only requirement of our method is to make highly accurate observations of the daily variation in the diameter of the sap flow monitoring sample trees. This is because it is difficult to directly observe the status of R_e , but many previous studies have proved that the short-term change in diameter was shown to be proportional related to changes in the volume of water within the stem tissues (Schepper & Steppe, 2010; Zweifel &

Häsler, 2001; Zweifel et al., 2001), and this conclusion is supported by the significant positive correlation between our final R_e and the corresponding nocturnal increase in diameter (Figure S2). Thus, the observation of the nocturnal variations in diameter provides the ability to indirectly understand the real-time status of R_e . Under normal circumstances, the diameter of *E. urophylla* \times *E. grandis* trees increased continuously at night (Figure 7a), indicating that the R_e persisted throughout the night (Dietrich et al., 2018; Vilas et al., 2019; Roman Zweifel, 2016). However, there may still be some special cases in which rainy weather during the day results in R_e being non-existent, or extremely weak but can filling to saturate it quickly (the diameter reaches a short-term maximum and remains constant, as shown in Figure 2 and Figure 7c), while considerable VPD exists at night, in which case the nocturnal J_C monitored is considered to be entirely for T_n (Figure 7c, d). These data were screened to create predictive models of T_n with the corresponding factors (Table 2). The predictive model improved the explanation of T_n to 82.65% after excluding the effect of R_e , and good agreement between the predicted and measured values of T_n under the model were also verified (Figure 6), which proved the reliability of the model in predicting T_n . Nevertheless, 17.35% of T_n remained unexplained, which may be due to the fact that T_n is also subject to the regulatory effects of some as yet unidentified intrinsic physiological processes (Chen et al., 2020). Generally, however, our method's results in splitting T_n and R_e are satisfactory. In addition, the concept and framework of our method can be also used as a reference for predicting T_n for other tree species and vegetation types in different regions, and only needs to be optimized for differences in the drivers of T_n for different tree species in different regions (Chen et al., 2020; Wu et al., 2020). For example, in arid and semi-arid regions the effects of SWC may need to be incorporated into the T_n prediction model (Di et al., 2022), whereas for *Acer truncatum* and *Pinus tabulaeformis* in Beijing, WS may need to be included in the T_n prediction model (Chen et al., 2020; Wu et al., 2020).

4.4 Contribution of T_n and R_e in the nocturnal J_C

This study confirmed that the contribution of T_n and R_e to nocturnal J_C varied considerably both across weather conditions and months (Figures 7, 8). This is mainly due to the fact that the both daytime and nighttime environmental factors can vary considerably from day to day. Unlike T_n , which was mainly affected by nocturnal environmental factors (VPD, T_a and RH; Figure 5), R_e

was influenced by the intensity of daytime transpiration. Because main driving force of R_e is the stem water deficit caused by daytime transpiration (Di et al., 2019; Forster, 2014; Siddiq & Cao, 2018; Zeppel et al., 2010), any factor affecting daytime and nocturnal transpiration intensity can result in large changes in the ratio of T_n and R_e composition. This also implies that it is unreliable to use the ratio of R_e and T_n for only a few specific days to represent the nocturnal water use components of a stand.

The main components of the nocturnal J_C may differ among tree species (Phillips et al., 2010; Siddiq & Cao, 2018; Zeppel et al., 2010). The average ratio of R_e to nocturnal J_C of *E. urophylla* \times *E. grandis* during the 3-year period in this study was 41.37%, which was smaller than the ratio of T_n to nocturnal J_C (58.63%). This result confirmed that the nocturnal J_C observed in the *E. urophylla* \times *E. grandis* plantation was mainly used for nocturnal canopy transpiration, which is consistent with the results of the study on two evergreen temperate woodland species (*E. parramattensis* and *Angophora bakeri*) (Zeppel et al., 2010) and some broadleaf timber species under a tropical seasonal climate (Siddiq & Cao, 2018), but contrasts with the results of the study on a mature poplar plantation (Di et al., 2022) and *Acer truncatum* (Wu et al., 2020).

There were no differences between the dry and wet seasons in the ratio of R_e in the *E. urophylla* \times *E. grandis* plantation. This result rejects our initial conjecture that the ratio of R_e would be higher in the dry season compared to the wet season. Some studies considered that the capacitive discharge of stored water in the stem could reduce the risk of xylem embolism and hydraulic failure (Bucci et al., 2004; McDonald et al., 2002; Phillips et al., 2003; Yi et al., 2017). It could also increase the water potential of stems and leaves before dawn to induce stomatal conductance (Percy, 1988). This can increase the duration of photosynthesis and alleviate the carbon fixation process of plants affected by drought stress (Yu et al., 2016). Thus, the phenomenon of increasing the ratio of R_e in plants under drought stress has been identified in some studies and is considered to be a survival strategy for plants to survive drought (Berbigier et al., 1996). However, in a study of soil moisture dependent nocturnal water use strategy in a mature poplar plantation (Di et al., 2022), there was an opposite variation in the ratio of R_e with soil moisture input, demonstrating that poplars are instead more dependent on stem water storage to sustain rapid diurnal transpiration under wetter soil conditions. The conflicting results may be due to the differences in the biological characteristics among tree species. In this study, the ratio of R_e in *E.*

urophylla × *E. grandis* was greater in some months of dry seasons than in wet seasons, but there were also some months with opposite results (Figure 8), with no significant differences on average overall. Such results may indicate that physiological processes such as diurnal transpiration in the *E. urophylla* × *E. grandis* plantation may not be highly dependent on stem water storage under the soil moisture conditions of this study area.

5 Conclusions

Our results from a 3-year study in *E. urophylla* × *E. grandis* plantations in southern China indicated that annual transpiration ranged from 358.7 mm to 545.3 mm, accounting for 33.6% of annual rainfall. However, the transpiration during the dry season accounted for 82.5% of the corresponding rainfall, implying the effects of water use in dry season on regional water security of eucalyptus in China deserves special attention. In addition, there was also substantial nocturnal water use in the *E. urophylla* × *E. grandis* plantation in south China, accounting for an average of approximately 12.35% of Q_{daily} , and this proportion would increase significantly during the dry season. This implies that nocturnal water use should not be neglected in a multiscale vegetation water balance model. Nocturnal water use of *E. urophylla* × *E. grandis* is used for both T_n and R_e , and T_n is influenced by a combination of nocturnal VPD, T_a and RH, with VPD being the dominant driver. Based on the relationship between daily variation in diameter and stem water storage, we have developed a new method to separated R_e from T_n . The results of the separation showed that the proportion of R_e varied considerably across weather and months. In this study, the 3-year mean of the ratio of R_e for *E. urophylla* × *E. grandis* was 41.37%, which was significant smaller than the value of T_n , indicating that the nocturnal water use in *E. urophylla* × *E. grandis* is mainly used T_n (58.63%) rather than R_e . The lack of variation in R_e ratios between the dry and wet seasons also suggests a low dependence on stem water storage during the dry season for *E. urophylla* × *E. grandis* in this study area. Our results can help to properly understand the processes of nocturnal water use and its control mechanisms, and can also provide a reference for further refinement of multiscale water balance models for *E. urophylla* × *E. grandis*.

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Conflict of 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.

Data Availability Statement

Data on the physico-chemical properties of the soil and information on the sample trees at the test site are given in Tables 1 and 2, respectively. Other analytical data are available at Figshare repository via (Wang et al., 2023) <https://doi.org/10.6084/m9.figshare.24076899.v1> with CC-BY 4.0.

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