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Partition of nocturnal sap flow in *Acacia mangium* and its implication for estimating the whole-tree transpiration

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Abstract We analyzed the partition of nocturnal sap flow into refilling of internal water storage and transpiration in *Acacia mangium*. Sap flow of trees was monitored continuously with Granier's sensors for estimating the whole-tree transpiration. Possible night transpiration and stomatal conductance at the leaf level in the canopy were measured with a LI-6400 photosynthesis measuring system. For nocturnal leaf transpiration and stomatal conductance were weak, nocturnal sap flow of mature *A. mangium* trees was mainly associated with water recharge in the trunk. No significant change in night water recharge of the trunk was found at both seasonal and inter-annual scales. Morphological features of trees including diameter at the breast height (DBH), tree height, and canopy size could explain variances of night water recharge. Furthermore, although the contribution of nocturnal sap flow to the total transpiration varied among seasons and DBH classes, the error caused by night water recharge on whole-tree transpiration was negligible.

Keywords *Acacia mangium*, Granier's thermal dissipation probe method, nocturnal sap flow, nocturnal transpiration

1 Introduction

Water use of trees is essential to study functions and process of forest ecosystem. Long time ago, the whole-tree and stand water use were estimated by scaling up from the

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leaf and wattle transpiration measurement, which differed greatly with the true value and had great difficulty in practical use (Wang and Ma, 2002). The trunk sap flow measurement system, which has advantages of high accuracy and reliability, non-damage and long-term continuity, can directly estimate the whole-tree transpiration (Ma et al., 2005a; Zhao et al., 2005, 2006a). Owing to its high accuracy and reliability, Granier's thermal dissipation probe method has nowadays become popular in estimating whole tree transpiration and can even accurately measure the slight sap flow, such as nocturnal sap flow (Zhao et al., 2006a). However, little attention was paid to the nocturnal sap flow. Nocturnal sap flow has the following physiological benefits for plants: 1) nighttime sap flow delivers available and mobile N to the roots and transports it rapidly upwards, thus partially compensating for declines in plant N content under CO₂ enrichment that may be attributable to some extent to associated decreases in stomatal conductance and transpiration during the day (McDonald et al., 2002); 2) it can refill the depleted stem and provide the oxygen transfer mechanism for the plant organ respiration (Daley and Phillips, 2006). According to Daley's conclusion, the nocturnal sap flow in *Betula papyrifera*, *Quercus rubra*, *Acer rubrum* was attributed mainly to refill the depleted water recharge compartment, and nocturnal transpiration of *B. papyrifera* might act as the oxygen transfer mechanism in the deeper sapwood (Daley and Phillips, 2006); Lopushinsky (1986) and Caspari et al. (1993) also ascribed the nocturnal sap flow to refill the depleted parts. The research mentioned above noticed the nocturnal sap flow phenomenon, but they did not partition it into nocturnal transpiration and nocturnal water recharge which limited their understanding of the effect of this partition to the total transpiration.

With the help of Granier's thermal dissipation probe method, our primary objectives of this study are: 1) to analyze the partition of the nocturnal sap flow; 2) to discuss nocturnal stem water recharge phenomenon and its possible affecting factors, as well as the inter-annual change; 3) to improve the precision of estimating canopy transpiration and canopy stomatal conductance; and 4) to provide basis for further understanding of the time lag between stem sap flow and canopy transpiration.

2 Materials and methods

2.1 Site description and sample trees

This study was conducted at the Heshan Hilly Land Interdisciplinary Experimental Station, Chinese Academy of Sciences (22°40'N, 112°54'E), Guangdong Province, China. The soil is laterite. The mean annual precipitation is 1700 mm, which is distributed unevenly throughout the year. There is a moderate drought period from November to January in the next year. The mean annual temperature is 21.7°C with the minimum in January and the maximum in July. The mean annual radiation is $4.35 \times 10^5 \text{ cm}^{-2}$. The annual cumulative hour of sunshine is 1797.8 h (Zhao et al., 1990, 2005; Ma et al., 2005a).

The experimental plot was located in a mature *Acacia mangium* plantation on a slope facing east at an elevation of about 80 m above sea level. The plant-to-row spacing is 3 m × 3 m. *A. mangium* which belongs to diffuse porous species with a medium-quality wood of low density is a fast-growing tree species introduced from Australia. Individual trees aged 22 years. The *A. mangium* plantation where the experiment was conducted show a declining trend of growth. Slight defoliation occurs from December to February in the following year. Twelve healthy *A. mangium* in the similar habitats were selected for sampling, which interfered each other somewhat.

2.2 Sap flow

Xylem sap flux density (J_s , $\text{gH}_2\text{O} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$), expressed on a sapwood-area basis, was measured with Granier-type sap flux sensors installed on the trunk at a height of 1.3 m (Granier, 1987; Zhao et al., 2006a). Owing to its high accuracy and reliability and long-term continuity, the data collected is systemic (Granier, 1987). We selected 12 *A. mangium* (number code: 1–12) with DBH ranging from 0.13 to 0.38 m (Ma et al., 2005b; Zhao et al., 2006b). The sap-flow sensor includes two probes, each of them containing a copper-constantan thermocouple. The probes were inserted radially into the trunk with one probe about 10–15 cm above the other. The upper probe was heated by providing a constant direct current of 0.12 mA and the lower one was left unheated. Every four probes were inserted in the east, south, west and north directions in the tree number 1–4. Two probes were inserted in the south and north directions in the tree number 5, others were inserted in the north direction (Zhao et al., 2005). The sapwood depth of samples was usually 1.5–3.0 cm, most of which were 2.0 cm. Therefore, we used the sap flux density in the probe length to represent the sap flux density in the whole sapwood depth (Zhao et al., 2006b; Ma et al., 2007). Plastic cover was used to prevent the probes from mechanical damage. Sun film which was used to mediate the interferences of heat radiation and rain was packed over

the plastic cover (Zhao et al., 2005). The operating principle, installation and programming referred to Ma et al. (2005a) and Zhao et al. (2005, 2006a). The probes used were self-made by Dr. Zhao based on the Granier's theory at the Duke university in the USA. The temperature difference between the two probes was automatically read by Delta-T data logger (Delta-T, UK) every 30 s and averaged and stored every 10 min. Sap flux density which was assumed to be averaged over this distal was derived from the temperature difference of the two probes based on an empirical relationship (Granier, 1987). It was directly calculated using the following equation:

$$J_s = 119 \times 10^{-6} \cdot [(\Delta T_m - \Delta T) / \Delta T]^{1.231}$$

where J_s is the instantaneous sap flux density, ΔT_m is the temperature difference between the heated and the unheated probe when xylem sap flow is zero, and ΔT is the temperature difference between the probes when xylem sap is flowing (Granier, 1987). This equation is applicable to all species. With the aid of the software Baseline 3.0, designed by Dr. Yavor Parashkevov from Duke University, the original voltage data collected from the logger can be converted to the continuous sap flow density (Zhao et al., 2006a).

2.3 Environment monitoring

Soil water content (SWC) was measured with three soil moisture probes (ML2x, Delta-T, Device) within 30 cm depth under soil surface on the study site. Photosynthetically active radiation (PAR), air temperature (T_a) and relative humidity (RH) were monitored in a weather station located 200 m from the study site. T_a and RH were documented using an HMP35E sensor (HMP35E, Vaisala, Finland). PAR was measured with a LI-COR quantum sensor (LI-COR, Lincoln, NE). The meteorological data were sampled at 30 s intervals and averaged and recorded at 10 min intervals so as to match sap flow measurement frequency. The wind speed (v) was provided by the Heshan Hilly Land Interdisciplinary Experimental Station (22°40'N, 112°54'E).

2.4 Estimation of the sapwood cross-sectional area

The sapwood area is a key parameter to calculate the whole-tree transpiration. To avoid the influence on sap flow measurement caused by damaging the samples, twenty-four representative *A. mangium* trees in the surrounding area outside the sap flow-monitoring plot were randomly chosen. The standards for choosing included the identical habitat, good growth status and little reciprocal disturbance. By analyzing the DBH distribution frequency and its corresponding total sapwood area, the trees in the study plot were divided into five classes: $\text{DBH} < 0.15 \text{ m}$, $0.15 \text{ m} < \text{DBH} < 0.20 \text{ m}$, $0.20 \text{ m} <$

DBH < 0.25 m, 0.25 m < DBH < 0.30 m and 0.30 m < DBH. The diameter and the bark thickness were measured. Then, the bark at DBH was removed and cores of 5 mm diameter, the depth of 1/2 diameter were drilled out with an accretion borer. Since the sapwood is easily distinguished from the heartwood, the sapwood thickness in the chosen trees was determined using a ruler on the fresh wood cores (Zhao et al., 2005; Ma et al., 2007). We concluded the relationship between sapwood area and DBH as follows:

$$A_s = m(\text{DBH})^n$$

where m and n are coefficients by non-linear regression (0.1930 and 0.1844). The established formula was used to calculate the sapwood cross-sectional area of sample trees for the sap flow measurements.

2.5 Calculation of nocturnal stem water storage

Nocturnal stem water storage was obtained as follows:

$$W_n = \sum J_s \cdot A_s \cdot t$$

where W_n is the nocturnal stem water storage, $\sum J_s$ is the accumulation of sap flux density when PAR is close to zero ($\text{gH}_2\text{O} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$), A_s is the sapwood cross-sectional area (m^2), t is 600 s (each J_s is averaged and recorded at 10 min intervals).

2.6 Measurement of the leaf conductance and the transpiration rate

To judge the relationship between sap flow and nocturnal transpiration according to the measurement of the leaf conductance and the transpiration rate, every three mature and fully expanded leaves from three trees with good growth status and proper position were randomly sampled. The twigs were pulled down to a certain height so that the leaves on the twigs could be conveniently accessed and measured with the LI-6400 (LI-6400, Li-Cor, USA). The measurements were taken on an hourly basis from 19:00 to

7:00 and a half-hourly basis from 17:00 to 19:00 in the clear night of July 18–19, 2006.

2.7 Statistical analyses

Statistical analysis was carried out using SPSS11.5. The inter-annual differences of nocturnal stem water storage were estimated by One-way ANOVA. Regression relationship between nocturnal stem water recharge and tree form characteristics were determined by curve estimation. Correlations between nocturnal stem water storage, contribution of nocturnal sap flux density and nocturnal water recharge and environmental factors were determined by both partial correlations and regression analysis.

3 Results

3.1 Diurnal pattern of sap flux density

The average sap flux density of all samples, the sap flow densities of the highest and the lowest DBH classes in July, 2004 are shown in Fig. 1. No matter how high the DBH class is, the nocturnal sap flow was observed. Compared with the daytime sap flow, the nocturnal sap flow was much lower and varied less.

3.2 Nocturnal sap flow and canopy transpiration

3.2.1 Nocturnal sap flow and its dependence on VPD and v both in the dry and wet seasons

It has previously been suggested that environmental factors, such as VPD and v significantly affect canopy transpiration. Therefore, the relationship between the nocturnal sap flow and VPD, v can be used to judge whether nocturnal sap flow is mainly attributed to transpiration. If the relationship is significant, adding that the explanation capacity is adequate, the nocturnal sap flow is used for the nocturnal transpiration. If the relationship is not significant, or even significant but that

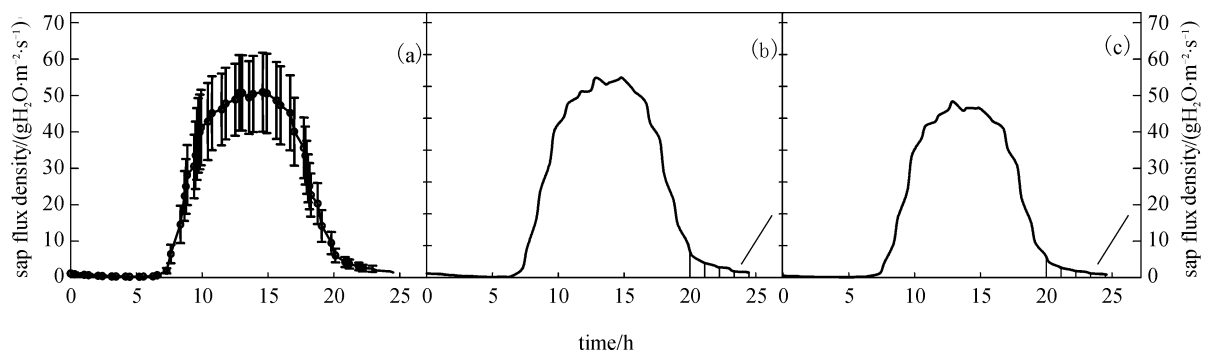


Fig. 1 The diurnal course of the average sap flux density of all samples (a), the sap flow densities of the highest DBH class (b, DBH = 32.9 cm) and the lowest (c, DBH = 16.9 cm) DBH class in July, 2004

the explanation capacity is not adequate, the nocturnal sap flow is used for refilling the depleted stem water storage (Daley and Phillips, 2006; Benyon, 1999).

Correlations between nocturnal sap flux density of *A. mangium* and VPD and v in the dry and wet season of 2005 are shown in Table 1. The positive correlations between nocturnal sap flux density and VPD, v were significant both in the dry season and the wet season, indicating that sap flow contributed partly to nocturnal transpiration. The curve parameter estimation between nocturnal sap flux density and VPD and v are shown in Table 2. Although the significant effect of VPD on nocturnal sap flow of *A. mangium* was observed in this study, VPD did not adequately explain the variation in nocturnal sap flow. The insignificant effect of v on nocturnal sap flow of *A. mangium* was observed in this study and v did not adequately explain the variation in nocturnal sap flow both in the dry and wet season. All in all, environmental factors

such as the VPD and v can affect the amount and the duration of transpiration, but cannot adequately explain the variation in nocturnal sap flow.

3.2.2 Temporal dynamics of nocturnal water use

To illuminate the nocturnal sap flow function of *A. mangium*, the temporal dynamics of nocturnal transpiration rate was measured by LI-6400 on 18–19, July, 2006. At the same time, sap flow data was collected. The results are shown in Figs. 2 and 3. As shown in Fig. 2, nocturnal sap flow gradually decreased as PAR was nearly zero and the stomas were gradually closed during the time period of 17:00–19:00. From 19:00 to 6:00 of the next morning, the stomatal conductance approached zero and the nocturnal sap flow was very low, both of which changed steadily. According to Fig. 3, there existed good correlations between the nighttime sap flow density measured by the

Table 1 Correlations between nocturnal sap flux density of *A. mangium* and vapor pressure deficit, wind speed in the dry and wet season of 2005

nocturnalsap flux density/($\text{gH}_2\text{O}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$)		vapor pressure deficit/kPa	wind speed/($\text{m}\cdot\text{s}^{-1}$)
dry season	Pearson correlation	0.237**	0.118**
	Sig. (2-tailed)	0	0
	<i>N</i>	2015	1961
wet season	Pearson correlation	0.236**	0.101**
	Sig. (2-tailed)	0	0
	<i>N</i>	2196	1300

** Correlation is significant at the 0.01 level (2-tailed).

Table 2 Curve parameter estimation between nocturnal sap flux density and vapor pressure deficit, wind speed

dependent	independent	model fit equation	R^2	<i>p</i>
nocturnal sap flux density/($\text{gH}_2\text{O}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$)	VPD at night in February/kPa	$y = 0.3769 + 0.1119x$	0.156	0
	wind speed at night in February/($\text{m}\cdot\text{s}^{-1}$)	$y = 0.7628 - 0.0293x$	0.005	0.191
	VPD at night in August/kPa	$y = 3.4119 + 0.5615x$	0.061	0.001
	wind speed at night in August/($\text{m}\cdot\text{s}^{-1}$)	$y = 3.9267 + 0.1567x$	0.001	0.699

R^2 : explanatory degree; VPD: vapor pressure deficit

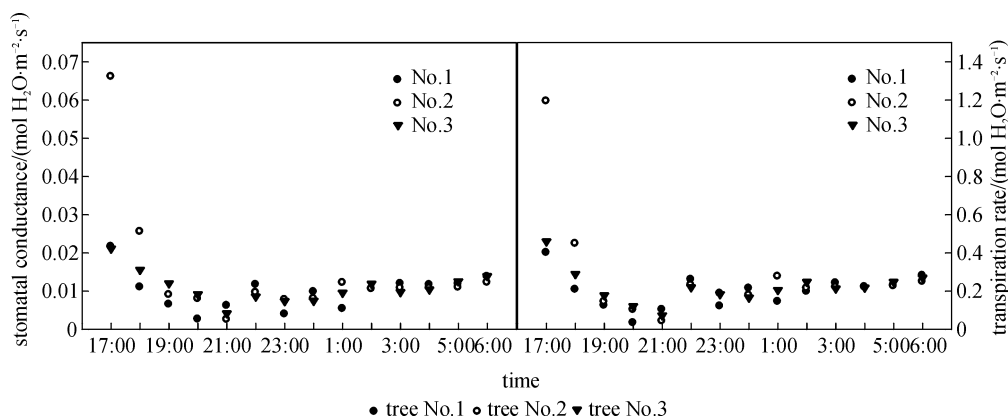


Fig. 2 Variations of leaf stomatal conductance and transpiration rate in *A. mangium* during the nighttime

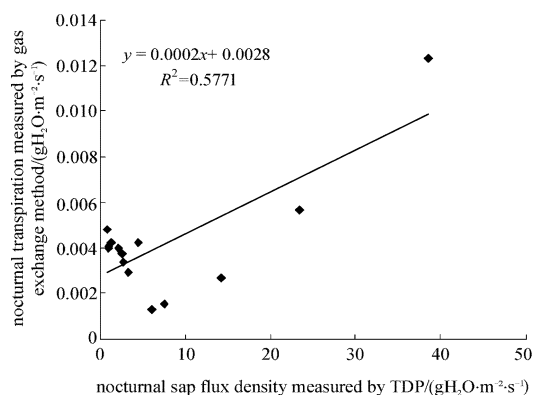


Fig. 3 Regression relationship between the nighttime sap flow density measured by the thermal dissipation probe (TDP) method and nighttime transpiration rate measured by gas exchange method. The unit of nocturnal transpiration rate measured by gas exchange method is $\text{mmol H}_2\text{O}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$. For comparison, the unit of transpiration rate ($\text{mmol H}_2\text{O}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) measured by gas exchange method (LI-6400) is converted into the unit of sap flow density measured by TDP ($\text{g H}_2\text{O}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$).

thermal dissipation probe (TDP) method and nighttime transpiration rate measured by gas exchange method ($R^2=0.577$, $p=0.002$), implying that nocturnal sap flow properly explains the slight transpiration rate measured by Li-6400.

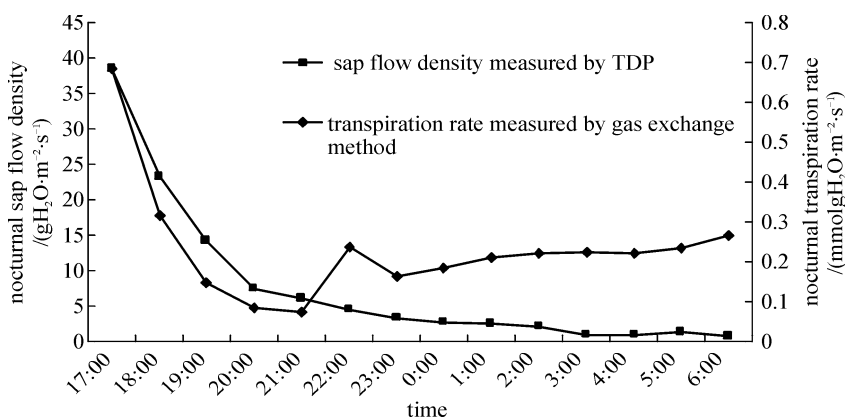


Fig. 4 Temporal dynamics of nocturnal sap flow density measured by the thermal dissipation probe method and nocturnal transpiration rate measured by the gas exchange method

Although the nocturnal transpiration was very little, the temporal dynamics of nocturnal sap flow density measured by the thermal dissipation probe method and nocturnal transpiration rate measured by gas exchange method was presented in the straight-line graph to provide the basis for the stem water storage estimation (Fig. 4). Nocturnal sap flow density measured by the thermal dissipation probe method was much higher than the nocturnal transpiration rate measured by the gas exchange method during most times of night. Considering that the nocturnal transpiration was little, we can reach a conclusion that the nocturnal sap flow we observed was mainly used for refilling the depleted parts, because the high daytime transpiration in July in the wet season could easily cause the depleted stem water storage which needs to be recharged at night.

3.3 Nocturnal stem water recharge and its affecting factors

3.3.1 Inter-annual change of nocturnal stem water recharge

One-way ANOVA on monthly nocturnal water recharge in *A. mangium* trees is presented in Table 3. There were no significant differences among the monthly nocturnal water storages (2004, $p=0.036 < 0.05$). Furthermore, the variance of means was homogenous (2005, $p=0.275 > 0.05$), implying that the environmental factors may have little effect on the nocturnal water recharge.

Table 3 One-way ANOVA on monthly nocturnal water recharge in *A. mangium* trees

year	nocturnal water recharge/($\text{kg}\cdot\text{d}^{-1}$)	sum of squares	df	mean square	F	sig.
2004	between groups	54.171	11	4.925	1.961	0.036
	within groups	361.540	144	2.511	–	–
	total	415.711	155	–	–	–
2005	between groups	40.520	11	3.684	1.228	0.275
	within groups	396.054	132	3.000	–	–
	total	436.574	143	–	–	–

3.3.2 Correlations between nocturnal stem water recharge and the environmental factors

According to Tables 4 and 5, there existed significant correlations between the nocturnal water recharge and SWC, T_a in 2004. Cubic regression fits show a strong correlation between nocturnal J_s and T_a , but they did not adequately explain the variation in nocturnal J_s ($R^2=0.211$; $R^2=0.053$). In other words, although SWC and T_a changed similarly with the nocturnal water recharge, they were not the important factors deciding the nocturnal water recharge. In 2005, there existed significant correlations between the nocturnal water recharge and T_a . Cubic regression fits showing a strong correlation between nocturnal J_s and T_a , but they also did not adequately explain the variation in nocturnal J_s ($R^2=0.064$), implying that T_a was not the important factors deciding the nocturnal water recharge in the climatic conditions of study plot.

3.3.3 Correlates between nocturnal stem water recharge and tree form features

As the above-mentioned nocturnal water storage did not correspond closely with SWC, precipitation, T_a , VPD ($p > 0.05$, at study site), we speculated that nocturnal water recharge was affected mainly by tree characteristics. We chose the curve estimation analysis to depict the regression relationship between the nocturnal stem water recharge and tree form features. The results are shown in Figs. 5–7. The linear regression is in good agreement with the

nocturnal water recharge and DBH ($R^2 = 0.8251$, $p < 0.0001$) (Fig. 5), while the exponential regression in good agreement with the nocturnal water recharge and tree height ($R^2 = 0.2350$, $p < 0.1455$) (Fig. 6). The exponential regression fits the nocturnal water recharge and canopy size ($R^2 = 0.6088$, $p < 0.0017$) (Fig. 7). Therefore, the DBH, tree height and the canopy size can explain the phenomenon that there is insignificant change among inter-annual change of nocturnal stem water recharge.

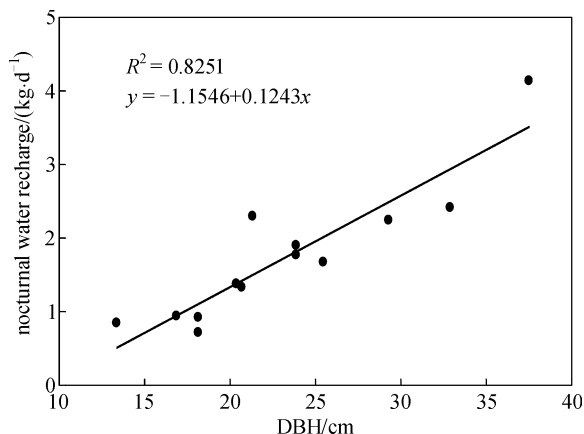


Fig. 5 Regression relationship between nocturnal water recharge amount and DBH

3.4 Annual change of nocturnal stem water recharge

According to Fig. 8, there existed insignificant difference between the nocturnal water recharge in 2004 and 2005

Table 4 Correlations between nocturnal water recharge in *A. mangium* and environmental factors

year	nocturnal water recharge/(kg·d ⁻¹)	soil moisture/(m ³ ·m ⁻³)	air humidity/%	air temperature/°C	vapor pressure deficit/kPa
2004	Pearson correlation	0.459**	0.230**		-0.055
	sig. (2-tailed)	0.000	0.000	0.056	0.388
	N	252	252	252	252
2005	Pearson correlation	-0.004	0.089	0.253**	-0.041
	sig. (2-tailed)	0.956	0.221	0.000	0.594
	N	188	191	191	168

Table 5 Curve estimation between nocturnal water recharge in *A. mangium* and environmental factors

year	dependent	independent	R ²	df	F	p
2004	nocturnal water recharge/(kg·d ⁻¹)	soil moisture/(m ³ ·m ⁻³)	0.211	250	66.85	0
		air humidity/%	0.053	250	13.97	0
		air temperature/°C	0.015	250	3.69	0.056
		vapor pressure deficit/kPa	0.003	250	0.75	0.338
2005	nocturnal water recharge/(kg·d ⁻¹)	soil moisture/(m ³ ·m ⁻³)	0	186	3.1E-03	0.956
		air humidity/%	0.008	189	1.51	0.221
		air temperature/°C	0.064	189	12.89	0
		vapor pressure deficit/kPa	0.002	166	0.29	0.594

R²: explanatory degree

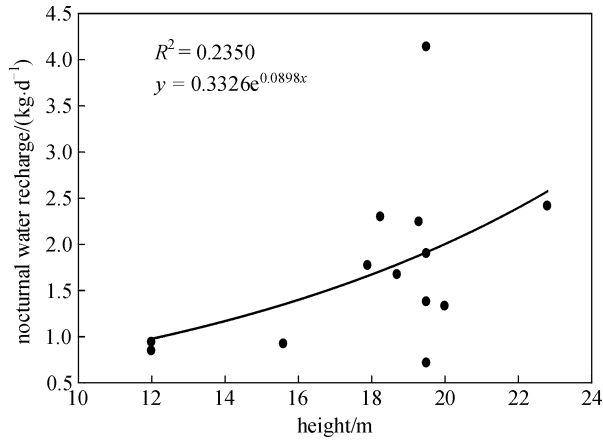


Fig. 6 Regression relationship between nocturnal water recharge amount and tree height

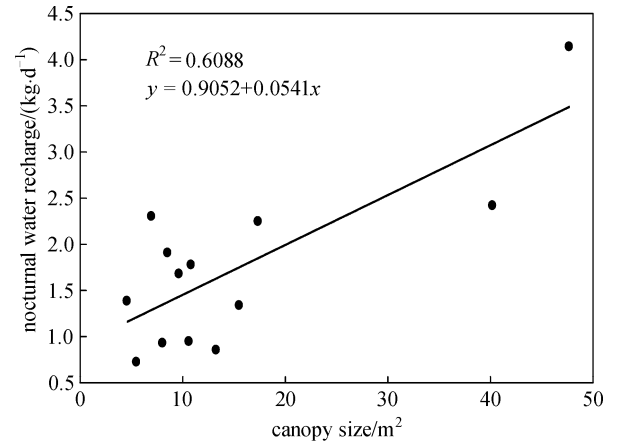


Fig. 7 Regression relationship between nocturnal water recharge amount and canopy sizes

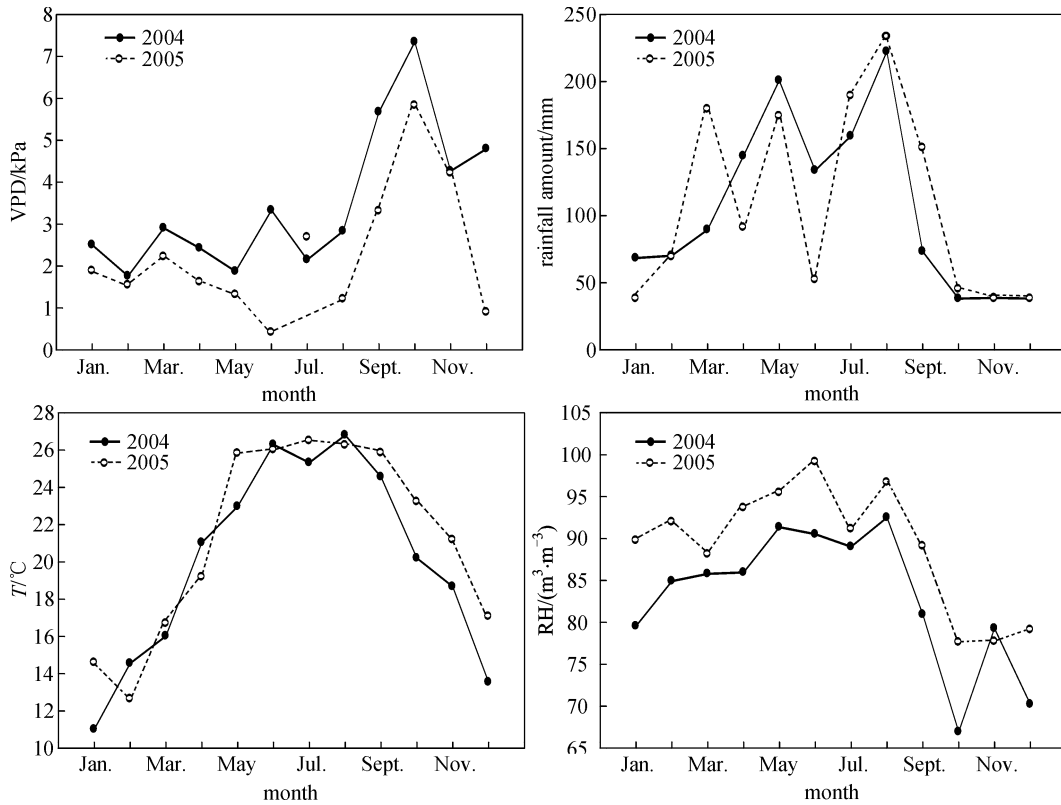


Fig. 8 Comparison of the changes in major environmental factors of the study site in 2004 and 2005

(sig. = 0.223 > 0.05). The above results indicated that the change of the nocturnal water recharge was mainly affected by the tree form characteristics. We also analyzed the environmental change at the study plot in 2004 and 2005 (Fig. 8). The environmental change in 2004 was similar to that in 2005, so they could not cause the difference among annual nocturnal stem water recharge.

3.5 Effect of the nocturnal sap flow on the whole-tree transpiration

3.5.1 Seasonal changes in the ratio of nocturnal water recharge to total transpiration at different breast heights

The ratio of nocturnal water recharge to total transpiration of *A. mangium* in the dry season is higher than in the wet

season, which could be attributed to that the total transpiration amount was less in the dry season than in the wet season, while the nocturnal water recharge was more or less the same in the two seasons (Fig. 9). Compared with trees of higher DBH classes, the ratio of nocturnal water recharge to total transpiration of trees of lower DBH classes was a little higher, implying that the nocturnal water recharge was mainly decided by the tree form, while the physiological activities and nutrient status possibly affected it.

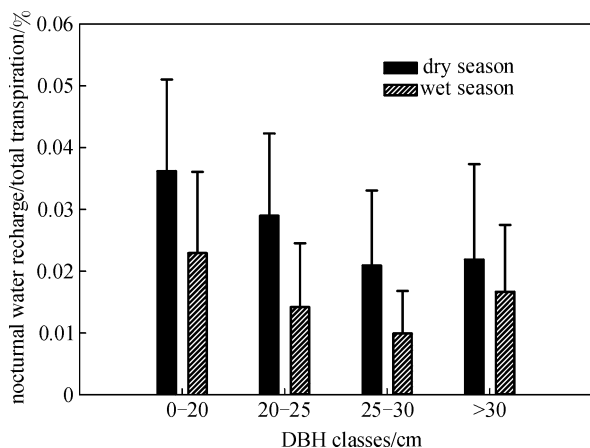


Fig. 9 Seasonal changes in the ratio of nighttime water recharge to total transpiration of *A. mangium* at different breast heights of different DBH classes

3.5.2 The error caused by night water recharge on whole-tree transpiration

It is generally accepted that sap flow measured by the Granier's thermal dissipation probe method can be used to represent the canopy transpiration, which can be calculated and scaled up to the whole-tree and the stand water use (Zhao et al., 2006a). Although the nocturnal sap flow was very low when compared with daytime transpiration, whether it will cause the error in estimation the total transpiration is still uncertain. The total transpiration and the

daytime transpiration (the total transpiration minus the nocturnal transpiration) in 2005 are shown in Fig. 10. Table 7 presents independent samples test between the total sap flow and the sap flow eliminating nighttime sap flow of *A. mangium*, which indicated that the error caused by night water recharge on whole-tree transpiration was negligible.

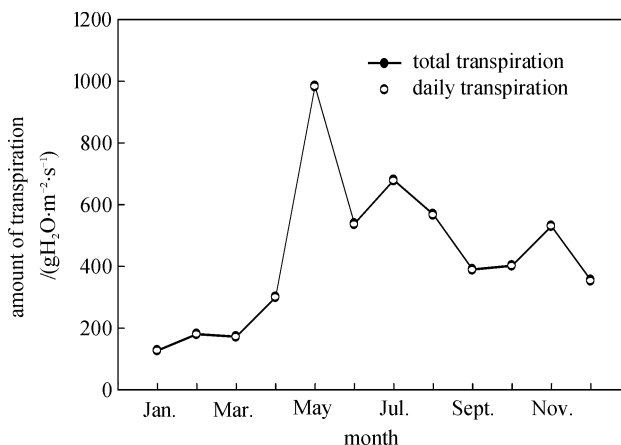


Fig. 10 Inter-annual changes of total transpiration and daily transpiration of *A. mangium*

4 Discussion

4.1 The partition of the nocturnal sap flow

In the previous sap flow studies by thermal dissipation probe method, the nocturnal sap flow was seldom partitioned into the nocturnal transpiration and the water recharge, or it is commonly assumed that transpiration does not occur at night because leaf stomata are closed in the dark. However, there is considerable evidence that the stomata of some species do not completely close during the night, which would allow for nighttime transpiration if there were sufficient environmental driving forces (Daley and Phillips, 2006). Snyder's study revealed that nocturnal stomatal conductance and transpiration in 11 of studied 17 species in North America were observed across life history,

Table 6 Independent samples test on nocturnal water recharge of *A. mangium* in 2004 and 2005

	equal variances	Levene's test for equality of variances		<i>t</i> -test for equality of means	
		<i>F</i>	sig.	<i>t</i>	sig.
nocturnal water recharge/($\text{kg}\cdot\text{d}^{-1}$)	equal variances assumed	0.112	0.741	1.255	–
	equal variances not assumed	–	–	1.255	0.233

Table 7 Independent samples test between the total sap flow and the sap flow eliminating nighttime sap flow of *A. mangium*

	equal variances	Levene's test for equality of variances		<i>t</i> -test for equality of means	
		<i>F</i>	sig.	<i>t</i>	sig.
the total sap flow vs the sap flow	equal variances assumed	0	0.997	0.020	0.984
eliminating nighttime sap flow	equal variances not assumed	–	–	0.020	0.984

photosynthesis pathway and habitats (Snyder et al., 2003). In our study, there existed slight nocturnal transpiration and stoma conductance of *A. mangium* and both were maintained at a steady level. Environmental factors such as VPD and ν could affect the amount of the nocturnal transpiration, which can explain the sap flow variation of *Eucalyptus grandis*, *Malus sylvestris*, *Actinidia deliciosa* and birch, for the nocturnal sap flow of these species was mainly used for the nocturnal transpiration (Green et al., 1989; Benyon, 1999; Daley and Phillips, 2006). Contrary to the above results, Daley and Phillips found that VPD could not explain the nocturnal sap flow variation of red oak and red maple, implying that the sap flow was mainly used for refilling the depleted stem water storage. Our findings revealed that VPD and ν cannot explain the sap flow variation adequately, implying that there was significant water flow into or out of tissue storage compartments.

Although both the leaf transpiration and the stem water recharge were observed, whether the leaf transpiration partly came from the stem water recharge was not clear, which needs the sap flow measurement on branches and further analysis.

4.2 Nocturnal water recharge

There has been much work on the relationship between the sap flow and the tree form (Zhao et al., 2006a). Researches on the water use of *Anacardium excelsum*, *Cordia alliodora*, *Ficus insipida*, *Schefflera morototoni* indicated that total daily water use increases sharply with tree size ranging from 46 kg/d in the 0.34 m diameter individual of *Cordia alliodora* to 750 kg/d in the 0.98 m diameter individual of *Anacardium excelsum* (Meinzer et al., 2003). Researches on sap flow of three evergreen species and two deciduous species (*Anacardium excelsum*, *Cecropia longipes*, *Ficus insipida*, *Spondias mombi* and *Luehea seemanni*) revealed that the diurnal storage capacity and basal sapwood area, tree height were positively correlated (Goldstein et al., 1998). However, limited information on nocturnal water recharge was available in Goldstein's study. In our study, the nocturnal water recharge of *A. mangium* did not differ significantly among months and between years. Our analysis on the relationship showed that the environmental factors can affect the nocturnal water storage, but cannot adequately explain it. Therefore, we speculated that tree form features could explain the nocturnal water recharge reasonably, which is consistent with our findings.

4.3 The implication of the nocturnal water recharge

Water stored in plant tissues has long been recognized as an important factor in plant–water relations. Estimates of the contribution of stored water to daily transpiration vary

widely, ranging from 10 to 20% (Lostau et al., 1996; Tanaka and Kobayashi, 2001; Phillips et al., 2003), and to as much as 30%–50% (Waring et al., 1979; Holbrook, 2004). However, little information was available for tropical trees (Goldstein et al., 1998). The contribution of the internal water storage to daily transpiration was related to environmental factors. For example, the amount of water stored in the trunk of *Pinus pinaster* accounted for 12% of the daily transpiration when soil water was abundant, but increased to 25% of the daily transpiration at the end of summer following a period of drought (Lostau et al., 1996). Consistent with the results above, the contribution of nocturnal stem water storage to the total daily transpiration of *A. mangium* in the dry season was larger than in the wet season and affected by the environmental factors, indicating that it could reflect the contribution of the nocturnal water recharge to the daily transpiration.

It is assumed that the nocturnal water loss was zero or its estimate was included into the total transpiration when making use of the sap flow measurement system. The error caused by night water recharge on whole-tree transpiration of *A. mangium* was negligible, but the error may become large if it was scaled up to stand level.

5 Conclusions

By means of the Granier's thermal dissipation probe method, adding the canopy leaf transpiration rate measured by Li6400 gas exchange method, our measurements and analyses suggest a greater allocation of nocturnal sap flow to the refilling of depleted water storage and that it did not cause obvious error on the whole-tree transpiration amount. Nocturnal water recharge was more strongly affected by tree features than by environmental factors. For the lack of sap flow measurement of the branch end, there still existed localization in the partition mechanism. For *A. mangium*, a tropical pioneer species, the partition mechanism and the ecological meaning deserves further investigation.

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