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RESEARCH ARTICLE

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Nocturnal sap flow characteristics and stem water recharge of *Acacia mangium*

Abstract In this paper, we studied the nocturnal stem water recharge of *Acacia mangium*. It is helpful to improve the precision of canopy transpiration estimation and canopy stomatal conductance, and to further understand the lag time of canopy transpiration to stem sap flow. In this study, the whole-tree sap flow in an *A. mangium* forest was measured by using Granier's thermal dissipation probe for over two years in the hilly land of South China. The environmental factors, including relative humidity (RH), precipitation, vapor pressure deficit (VPD), photosynthetically active radiation (PAR), and air temperature (T_a) were recorded simultaneously. The stem water recharge of *A. mangium* was analyzed on both daily and monthly scales. Sap flux density was lower at night than during the day. The time range of nighttime sap flux density was longer in the dry season than in the wet season. The water recharging mainly occurred from sunset to midnight. No significant differences were observed among inter-annual nighttime water recharges. Nighttime water recharge had no significant correlation with environmental factors, but was well correlated with the diameter at breast height, tree height, and crown size. In the dry season the contribution of nighttime water recharge to total transpiration had significant correlations with daytime transpiration, total transpiration, VPD, PAR and T_a, while in the wet season it was significantly correlated with daily transpiration and total transpiration.

Keywords *Acacia mangium*, Granier's thermal dissipation probe method, nocturnal stem water recharge, environmental factors

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1 Introduction

Transpiration plays an important role in the plant-water relationship. Among the numerous methods, heat balance, heat pulse technique, thermal dissipation probe method and so forth are indirect methods for estimating tree transpiration (Ma et al., 2005a). Granier's thermal dissipation probe method, which was assumed to get the average value over a distal of 2 cm, has become popular in estimating whole tree transpiration in both tropical and temperate areas, owing to its simplicity, high accuracy and reliability, and relatively low cost (Granier et al., 1992; Lostau et al., 1996). The theory of Granier's method is that the sap flow across sapwood can be regarded as the whole-tree transpiration amount (Cohen et al., 1981). Using this method, the nocturnal sap flow of *A. mangium* was found to be very low but above zero. As air humidity increased and air temperature decreased at night, the vapor pressure deficit (VPD) and the canopy stomatal conductance were approaching zero, thereby indicating that the sap flow measured with TDP could not necessarily be nocturnal transpiration (Wang et al., 2002; Yu et al., 2003). Goldstein et al. (1998) found that for the same species, under similar weather condition, a positive value of the difference between crown sap flow and basal sap flow meant that water transpiration was preferentially withdrawn from the stem water storage, and a negative value meant that water was refilling stem. Because the nocturnal canopy transpiration of *A. mangium* was zero, and the difference between nocturnal canopy transpiration and basal sap flow was negative, nocturnal sap flow measured with TDP can be used to estimate nocturnal stem water recharge, which has particularly meaning as follows: 1) It provides the contribution information of internal water storage to the total daily water consumption; 2) Exchange of water between transpiration and stem storage may result in a considerable lag time between fluctuations of canopy transpiration and those of sap flow near the base of the stem (Lostau et al., 1996; Martin et al., 1997; Saugier et al., 1997; Goldstein et al., 1998); 3) Stored water has a marked effect on surface energy budget during periods of plant water stress (Carlson and Lynn, 1991); 4) A possible explanation for the limitation of tree height growth (Fan et al., 2005); 5) Understanding the refilling of depleted stem water storage caused by the daytime transpiration (Wang et al., 2002).

Dynamic changes of discharge and recharge of water stored in sapwood had been studied (Waring et al., 1978; 1979), however, the results were mainly focused on seasonal and diurnal changes. Information on nocturnal stem water recharge has not been reported. With the help of Granier's thermal dissipation probe method, our primary goals for this study were: 1) To analyze the characteristics of nocturnal sap flow; 2) To discuss nocturnal stem water recharge phenomenon and its possible affecting factors; 3) To improve the precision of estimating canopy transpiration and canopy stomatal conductance; 4) To provide basis for further understanding 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′07′′–22°41′07′′N, 112°53′15′′–112°54′00′′E, at elevation 80 m). The soil is laterite. Mean annual precipitation is 1700 mm, which is distributed unevenly throughout the year. There is a moderate drought period from November to January. Mean annual temperature is 21.7°C, with the minimum in January and the maximum in July. Mean annual radiation is 4.35×10^5 J/cm^2. Annual cumulative hour of sunshine is 1797.8 h (Ma et al., 2005a; Zhao et al., 2005).

The experimental plot was located in a mature *A. mangium* plantation covering an area of 640.5 m^2 (36.6 m × 17.5 m). The plant-to-row spacing is 3 m × 3 m. *A. mangium*, belonging to diffuse porous species with a medium-quality wood of low density, is a fast-growing tree species introduced from Australia (Peh et al., 1984). Individual trees aged 22 years. The *A. mangium* plantation where the experiment was conducted showed a decline trend of growth. Slight defoliation occurs from December to February. Tree height ranged from 12 to 22. 8 m. Tree diameter at the breast height ranged from 13.4 to 37.5 m. Canopy width was from 4.6 to 47.7 m (Ma et al., 2005a).

2.2 Sap flow

Thirteen *A. mangium* sample trees were selected for measurements of sap flow. Xylem sap flux density, expressed on a sapwood-area basis, was measured with Granier-type sap flux sensors installed on trunks at a height of 1.3 m (Granier, 1987). The sap-flow sensor includes two probes, each of them containing a copper-constantan thermocouple. The constantan ends of the two thermocouples are connected to measure the temperature difference between the two probes at the ends of the copper wires. The probes were inserted into the trunk, with one probe about 10–15 cm above the other. The upper probe was continuously heated at constant power (0.2 W) while the lower one was left unheated to measure the ambient temperature of the wood tissue and acted as a reference probe (Granier, 1987). The probes were 2 cm long with the distal of 2 cm long being the effective sensing part. Plastic cover was used to prevent the probes from mechanical damage. Solar film, which was used to mediate the interferences of heat radiation and rain, was packed over the plastic cover (Zhao et al., 2005). Sap flux density, assumed to get the average value over this distal, was derived from the temperature difference of the two probes based on an empirical relationship (Granier, 1987; Lu et al., 2003). It was directly calculated using the following equation:

$$J_s = 118.99 \times 10^{-6}[(\Delta T_m - \Delta T)/\Delta T]^{1.231} \qquad (1)$$

where J_s is xylem sap flux density (g $H_2O \cdot m^{-2} \cdot s^{-1}$); ΔT_m is the temperature difference between a heated and an unheated probe when xylem sap flow is zero, and ΔT is the temperature difference between the probes when xylem sap is flowing (Granier, 1987).

2.3 Environment factors monitoring

Soil water content (*SWC*) was measured with three soil moisture probes (ML2x, Delta-T, Device) within the 30 cm depth below the soil surface. A meteorological station, 200 m away from the study site, was equipped with environmental monitoring sensors to measure solar radiation (R_s), photosynthetically active radiation (*PAR*), air temperature (T_a), relative humidity (*RH*), wind speed (*w*). Air temperature and relative humidity were measured with HMP35E sensor (HMP35E, Vailsal). Photosynthetically active radiation 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.

2.4 Calculation of nocturnal stem water storage

Nocturnal stem water storage was obtained as follows:

$$W_n = \Sigma\ J_s A_{st} \qquad (2)$$

where W_n is nocturnal stem water storage, ΣJ_s is the accumulation of sap flux density when *PAR* is close to zero (g $H_2O \cdot m^{-2} \cdot s^{-1}$), A_s is sapwood cross-sectional area (m^2), t is 600 s (each J_s is averaged and recorded at 10-min intervals).

2.5 Statistical analyses

Statistical analysis was carried out using SPSS11.5. Both the inter-annual differences of nocturnal stem water storage and contribution of nocturnal water recharge to the total daily transpiration were estimated by One-way ANOVA. Regression relationship between nocturnal stem water recharge and tree form characteristics were determined by curve estimation. Correlation between nocturnal stem water storage, contribution of nocturnal water recharge to the total daily transpiration and environmental factors were determined by partial correlation analysis.

3 Results

3.1 Diurnal pattern of sap flow

Compared with the daytime sap flow, nocturnal sap flow was much lower as showed in Fig. 1. After 20:00, nocturnal sap flow approached zero as the *PAR* nears zero. During this time, the nocturnal sap flow was refilling stem, meaning it was refilling the depletion of water caused by strong transpiration during the daytime (Wang et al., 2002) according to the conclusion of Goldstein et al. (1998).

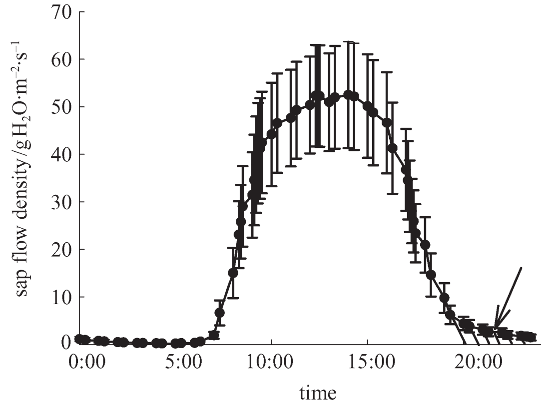

Fig. 1 Daily variations of average stem sap flux density of *A. mangium* in July, 2004

3.2 Nocturnal pattern of sap flow

February and July represent the dry and wet season of hilly land in south China, respectively. Nocturnal sap flow in February and July were presented in Figs. 2 and 3. It showed that the sap flow before midnight was much higher and changed more than that after midnight. The after midnight sap flow became steadier and changed less, implying that the trunk was refilled and the water storage compartment was saturated. Here, we speculated that stem water recharging mainly occurred before midnight. At first, the nocturnal sap flow was much higher in the dry season than that in the wet season, however, the period only lasted one hour. Furthermore, the time period for recharging in the dry season was somewhat longer than that in the wet season. Therefore, as for the total amount of nocturnal stem water recharge, there may be no significant differences between the dry season and the wet season.

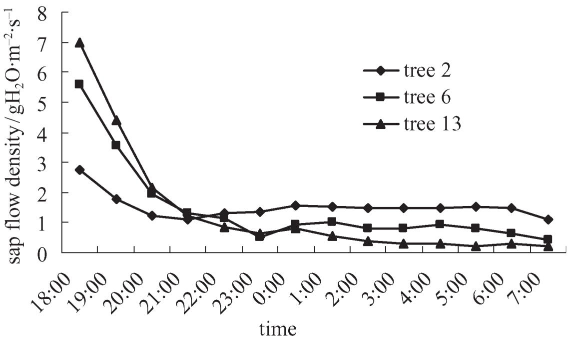

Fig. 2 Variations of average night stem sap flux density of three trees on three clear days in February, 2004

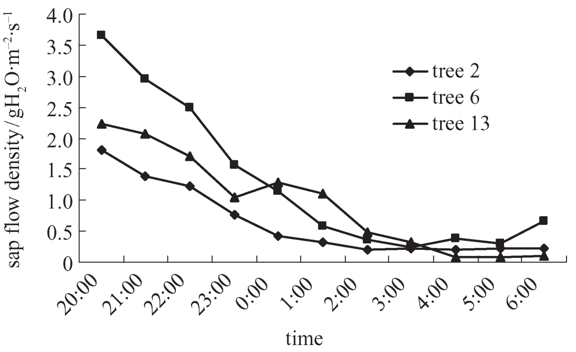

Fig. 3 Variations of average night sap flux density of three trees on three clear days in July, 2004

As nocturnal sap flow was getting steady, the stem was gradually refilled. The nocturnal sap flow after midnight may be due to the lenticel and cutin transpirations of mature leaf, adding that sap flow after midnight in the dry season was higher than that in the wet season, which conformed to the higher transpiration in the dry season comparing with that in the wet season.

3.3 Nocturnal stem water recharge

3.3.1 Inter-annual change of nocturnal stem water recharge

There were no significant differences among the monthly nocturnal water storages ($P = 0.036 < 0.05$) (Table 1), and the variance was homogenous ($P = 0.153 > 0.05$), implying that the samplings were representative for the whole *A. mangium* stand. Because water recharging was an important component of nocturnal water storage, and water storage was mainly determined by capacitance (the ratio of change in water content to change in water potential of a tissue), we speculated that nocturnal water recharging was mainly affected by tree form features. Due to the fact that the precipitation amount was obviously higher in 2005 than that in the other year, we attributed no significant differences among the monthly nocturnal water storage to the slight drought intimidation.

Table 1 One-way ANOVA on monthly nocturnal water storage of *A. mangium* in 2005

item	sum of squares	*df*	mean square	*F*	*Sig.*
Between groups	54.171	11	4.925	1.961	0.036
Within groups	361.540	144	2.511	–	–
Total	415.711	155	–	–	–

3.3.2 Correlation between nocturnal stem water recharge and *SWC*, precipitation, T_a, *VPD*

For analyzing the correlation between nocturnal stem water recharge and *SWC*, precipitation, T_a, *VPD*, and considering the inter-relationship among the environmental factors, we choose the partial correlations analysis. Partial coefficients between nocturnal stem water recharge and environmental factors were −0.27284, −0.27284, −0.54054, 0.37364 and −0.39084, while the significance probability were 0.601, 0.286, 0.466, 0.444 ($P > 0.05$) respectively as shown in Table 2.

3.3.3 Correlation between nocturnal stem water recharge and tree form features

As mentioned above, nocturnal water storage did not correspond closely with *SWC*, precipitation, T_a, and *VPD* ($P > 0.05$) at the study site. We speculated that nocturnal water recharge was mainly affected by tree characteristics. Therefore, results show that exponential regression between the nocturnal water recharge and tree height performed well ($R^2 = 0.36$, $P < 0.05$) (Fig. 4). Cubic curve regression between the nocturnal water recharge and DBH had a good fit ($R^2 = 0.85$, $P < 0.01$) (Fig. 5), as well as between the nocturnal water recharge and canopy breadth ($R^2 = 0.65$, $P < 0.05$) (Fig. 6).

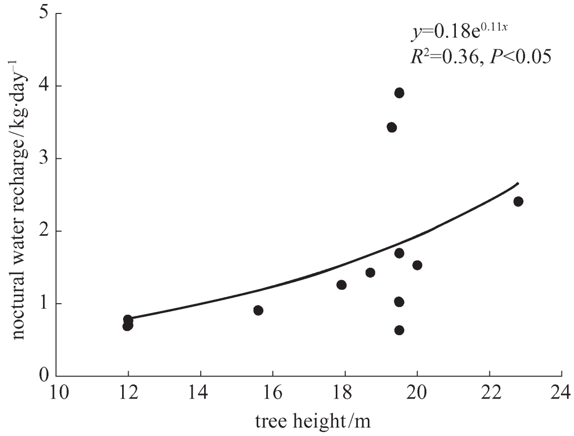

Fig. 4 Regression relationship between nocturnal water recharge and height of *A. mangium*

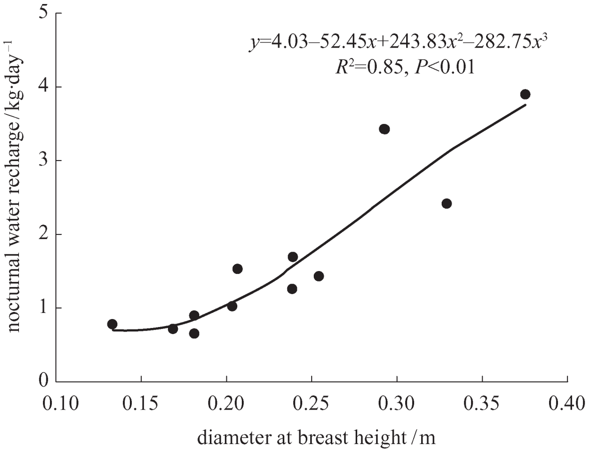

Fig. 5 Regression relationship between nocturnal water recharge and diameter at the breast height of *A. mangium*

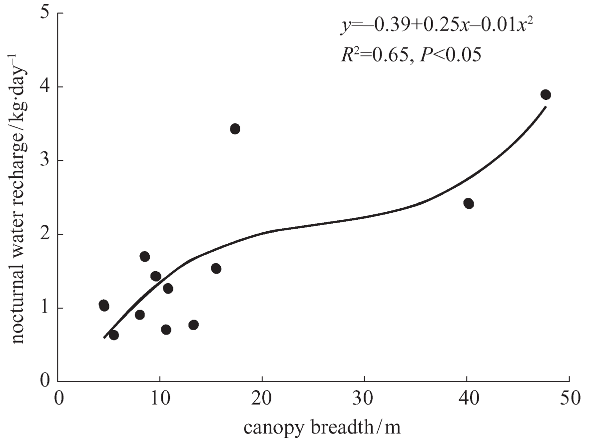

Fig. 6 Regression relationship between nocturnal water recharge and canopy breadth of *A. mangium*

Table 2 Analysis on partial correlations between nocturnal water storage and *SWC*, precipitation, T_a, *VPD* of *A. mangium* in 2005

nocturnal water recharge	*SWC*	precipitation	T_a	*VPD*
Partial correlation coefficient	−0.27(**)	−0.54(**)	0.37	−0.39
Sig. (2-tailed)	0.60	0.29	0.47	0.44

Note: ** Correlation is significant at the 0.01 level (two-tailed test).

3.4 Contribution of nocturnal water recharge to the total transpiration

3.4.1 Inter-annual change of contribution of nocturnal water recharge to the total transpiration

The inter-annual contribution of nocturnal water recharge to the total daily transpiration differed significantly ($P = 0.000 < 0.0001$) (Table 3). And due to the variance homogeneity ($P = 0.057 > 0.05$), the sampling trees represented well for the *A. mangium* stand.

Table 3 One-way ANOVA on the contribution of nocturnal water recharge to the total daily transpiration of *A. mangium* in 2005

item	sum of squares	*df*	mean square	*F*	*P*
Between groups	0.052	11	0.005	10.220	0.000
Within groups	0.061	132	0.000	–	–
Total	0.113	143	–	–	–

3.4.2 Seasonal change of contribution of nocturnal water recharge to the total transpiration

Due to the relatively low T_a and *PAR*, sap flux density in February is lower than that in May, July and October. Therefore, the contribution of nocturnal water recharge to the total daily transpiration in February was obviously higher than that in May, July and October, implying that the nocturnal water recharge may play a more important role on the plant-water relation in February compared with that in the other months (Fig. 7). 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 (Loustau et al., 1996).

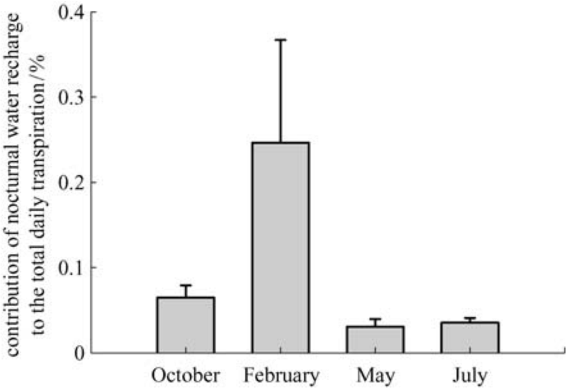

Fig. 7 Seasonal change of the contribution of nocturnal water recharge to the total daily transpiration of *A. mangium*

3.4.3 Correlation between contribution of nocturnal water recharge to the total transpiration and mainly affecting factors

The correlations between the contribution of nocturnal water recharge to the total transpiration and nocturnal stem water recharge, total transpiration, daily transpiration, *SWC*, precipitation, *VPD*, *PAR*, T_a in the dry season were different from those in the wet season in 2005. In the dry season, the contribution of nocturnal water recharge to the total daily transpiration was significantly affected by daily transpiration, total transpiration, *VPD*, *PAR* and T_a (Table 4). The correlations between the contribution of nocturnal water recharge to the total daily transpiration and *PAR*, T_a and *VPD* were negative, and ranked as follows: daily transpiration> total transpiration> $PAR > T_a > VPD$ according to the Pearson correlation coefficients. *PAR*, T_a and *VPD* were positively correlated with sap flux density (Ma et al., 2005b). Since the inter-annual nocturnal water recharge didn't differ significantly, the higher the total transpiration, the less the contribution of nocturnal water recharge to the total transpiration. In the wet season, the contribution of nocturnal water recharge to the total daily transpiration was significantly affected by daily transpiration and total transpiration (Table 4). Furthermore, both in the dry and wet season, the correlations between the contribution of nocturnal water recharge to the total daily transpiration and total transpiration, daily transpiration were negative.

4 Discussion

With the help of TDP method, it is easy to measure the nocturnal stem water recharging and to discuss the phenomenon of *A. mangium*. We found that both in the dry and wet seasons the nocturnal sap flows were low. Sap flow before midnight was much higher and changed more than that after midnight, implying that the major period for recharging was before midnight. The nocturnal sap flux density after repletion was for the lenticel and cutin transpirations of mature leaf. The research on total water use of *A. excelsum*, *C. alliodora*, *F. insipida*, *S. morototoni* indicated that total daily water use increased sharply with tree size from 46 kg·day^{-1} in the individual of *C. alliodora* with DBH of 0.34 m to 750 kg·day^{-1} in the individual of *A. excelsum* with DBH of 0.98 m (Meinzer et al., 2003; Phillips et al., 2003). Studies of Goldstein et al. (1998) on diurnal storage capacity of three evergreen species and two deciduous species (*Cecropia longipes*, *Anacardium excelsum*, *Ficus insipida*, *Luehea seemannii* and *Spondias mombin*) showed that their diurnal storage capacities were different. They conformed to a common linear relationship between

Table 4 Correlations between the contribution of nocturnal water recharge to the total daily transpiration and mainly affecting factors in dry and wet seasons in 2005

item	contribution in dry season			contribution in wet season		
	Pearson correlation	*Sig.*	*n*	Pearson correlation	*Sig.*	*n*
Nocturnal water recharge	0.062	0.907	6	−0.001	0.999	6
Total transpiration	−0.936(**)	0.006	6	−0.929(**)	0.007	6
Daily transpiration	−0.937(**)	0.006	6	−0.929(**)	0.007	6
SWC	0.563	0.244	6	−0.253	0.629	6
Precipitation	0.395	0.438	6	−0.141	0.79	6
VPD	−0.900(*)	0.014	6	−0.123	0.816	6
PAR	−0.929(**)	0.007	6	−0.583	0.225	6
T_a	−0.921(**)	0.009	6	−0.403	0.428	6

Notes: ** means correlation is significant at the 0.01 level (two-tailed test). * means correlation is significant at the 0.05 level (two-tailed test).

diurnal storage capacity and basal sapwood area, a common exponential relationship between diurnal storage capacity and tree height (Goldstein et al., 1998). However, few researches on the relationship between the nocturnal water storage and the tree characteristics were conducted. In this study, we found that the inter-annual nocturnal stem water storage, which did not differ significantly, was mainly dependent on tree form features.

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; Goldstein et al., 1998; Kobayashi et al., 2001), and to as much as 30%–50% (Waring et al., 1979; Tyree et al., 1990; Holbrook et al., 1992). However, few information existed in the 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 (Loustau et al., 1996). Therefore, the contribution of nocturnal stem water storage to the total daily transpiration of *A. mangium* in the dry season was significantly affected by daily transpiration, total transpiration, *VPD*, *PAR*, and T_a. In the wet season, the contribution of nocturnal stem water storage to the total daily transpiration was affected by daily transpiration and total transpiration which may be due to the limiting effect of the environmental factors. Another explanation may be attributed to the fact that the effect that the high total transpiration covered up the effect of other factors in the wet season.

Additional research is necessary to fully understand the possible error caused by nocturnal stem water recharge on the estimation of whole-tree transpiration and canopy stomatal conductance. In addition, whether nocturnal water recharge differs significantly on the year scale or not and its affecting factors deserve further study. Like for example, whether drought intimidation causes significant difference on the yearly scale.

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