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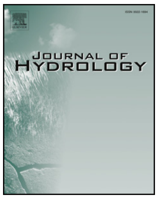

Research papers

Water-use efficiency and its relationship with environmental and biological factors in a rubber plantation

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ABSTRACT

Water-use efficiency (*WUE*) at the whole-plant level plays as an important role as an indicator of both the water-use strategy of the plant, and the ecophysiological processes linking the carbon and water cycles. However, the variation in the annual pattern of *WUE*, the interannual trends, and the regulating factors of *WUE* in rubber plantations remain poorly understood. Here, we used a four-year (2013–2016) continuous biometric survey along with sap flow data recorded at a monthly resolution to examine the annual and interannual dynamics of *WUE* and the relationships of *WUE* with environmental and biological factors in rubber (*Hevea brasiliensis*) plantations in Southwest China. The results showed that (1) there was no definitive pattern in *WUE* between April and December, but the peak *WUE* values generally occurred around August; (2) the multi-year mean *WUE* was $2.34 \pm 0.19\,\mathrm{g\,C{\cdot}kg^{-1}\,H_2O}$, and a negative correlation of *WUE* to photosynthetically active radiation was found at the interannual scale ($r = -0.962$, $P < 0.05$); and (3) a moderate, significant and parabolic relationship of *WUE* with air temperature ($R^2 = 0.40$), net radiation ($R^2 = 0.37$) and growth rate of the diameter at breast height ($R^2 = 0.35$) was observed at the monthly scale during the growing season ($P < 0.001$). These findings indicate that *WUE* might be regulated by factors affecting the carbon sequestration rather than water consumption, and it will provide a deeper understanding of the ecohydrological and coupled processes between the carbon and water cycles of rubber plants.

1. Introduction

The structure and function of terrestrial ecosystems are affected by anthropogenic impacts, e.g., land transformation (Vitousek, 1997). Despite the environmental consequences associated with the conversion of rainforest into rubber tree (*Hevea brasiliensis*) plantations, more than 500,000 ha of rubber plantations in tropical Southeast Asia have been created over several decades to meet market demands (Mann, 2009; Ziegler et al., 2009). Approximately 40% of these plantations occur in the Xishuangbanna Prefecture, Southwest China. There have been reports that since the establishment of these plantations, local people have faced water shortages during the dry season, which seldom occurred prior (Li et al., 2008; Qiu, 2010). Rubber plantations are often considered the cause of such shortages and have acquired the reputation of being “water pumps” due to perceived high levels of water consumption and strong negative impacts on local water resources (Giambelluca et al., 2016; Lin et al., 2016; Tan et al., 2011). Consequently, the coupled processes between the carbon and water cycles are gaining increasing amounts of attention.

Water-use efficiency (*WUE*) is used to describe the coupled processes of assimilating carbon from the atmosphere and transpiring water to the atmosphere (deWit, 1958). *WUE* is a common indicator of the relative rates of these coupled processes (Baldocchi, 1994; Beer et al., 2009; deWit, 1958; Ponton et al., 2006; Yang et al., 2013; Yu et al., 2004), and has been widely used to evaluate the impacts of plant growth on water resources or to evaluate the “water costs” of components of the terrestrial carbon sink (Tong et al., 2014). Moreover, *WUE* can indicate the water-use strategy of plants in different environments (Donovan and Ehleringer, 1991; Tong et al., 2014). Although the application of this important index is partially limited because it has been defined in various ways (McVicar et al., 2002; Stanhill, 1986) and is measured at a variety of spatial and temporal scales using different

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methods (Arneth et al., 2006; Bchir et al., 2016; Beer et al., 2009; Goulden et al., 1996; Nock et al., 2011), these limitations are overcome when the *WUE* is clearly defined. In the present study, both the carbon gain estimated from biometric surveys and biomass models with highly accurate and broadly applicable (Ketterings et al., 2001; Tang et al., 2009), and the water consumption evaluated using simple, accurate and long-term continuous sap flow observations (Granier et al., 1990; Saugier et al., 1997) at the whole-plant scale and on a monthly time scale, were applied to assess the degree of the coupling between the carbon and water cycles. Despite the belief that rubber plantations cause water shortages, little is known regarding the coupling between the carbon and water cycles in the case of rubber trees, although the plantations represent a substantial carbon sink in this part of China (Chen et al., 2011; Song et al., 2016).

Our specific objectives were: (1) to analyse the dynamic patterns of *WUE* during the growing season and the interannual trend of *WUE* in rubber plantations, and (2) to explore the environmental and biological factors that control the variation in monthly *WUE*. The results obtained from this study will (i) provide a baseline for subsequent studies on alternative cropping systems in the area and (ii) enable foresters and hydrologists to make rational decisions about the management of forests in water catchments in the study region and elsewhere in the tropics.

2. Materials and methods

2.1. Study area

Our study site was in the Xishuangbanna Tropical Botanical Garden (XTBG; 21°55′30″N, 101°15′59″E), Yunnan Province, Southwest China (Fig. 1). The original tropical forest of the Xishuangbanna Prefecture is an extension of the tropical forest of Southeast Asia (Zhu and Yan, 2009), but in recent years, much of this forest has been replaced with rubber plantations. The climate is strongly seasonal; two air masses alternate throughout the year (Zhang, 1963). The multi-year (1994–2008) mean annual rainfall is 1504 mm, and approximately 87% of the rainfall occurs during the rainy season; the tropical southern monsoon from the Indian Ocean delivers most (typically ~75%) of the region's annual rainfall from May to October; the remaining rainfall occurs during the dry season, which is dominated by the dry and cold air of the southern edges of the subtropical jet stream (Tan et al., 2010, 2011). The mean monthly rainfall during the dry season, which is sometimes divided into the fog-cool (between November and February) and dry-hot (March and April) seasons (Zhang, 1963), is less than 40 mm. The mean annual temperature is 21.7 °C, and the mean monthly values range from 15.9 to 25.7 °C (Tan et al., 2010). The general topography consists of hilly terrain and lateritic soil (pH 5.6) derived from siliceous rocks.

The characteristics of the four plots of the rubber plantations are shown in Table 1. The rubber trees were planted 2 m apart in rows of mixed spacing between 4 m and 12 m. The main rubber-tapping period was from May to November. Fertilization with mineral fertilizer (containing 15% N as $(NH_2)_2CO$, 15% P as $NH_4H_2PO_4$, and 15% K as KCl) was performed in April and July of each year (Zhou et al., 2016). Understory weeds and seedlings were removed by hand or using herbicides. The rubber trees strongly responded to cold stress, with a pattern of intense defoliation and dormancy for approximately 50 days between January and February as well as a slow recovery from dormancy in March (unpublished data; Figs. 3b, c and S1; Table S1). Therefore, we defined the growing season of rubber trees in Southwest China as April

Fig. 1. Geographic location of the study site (star; plotted using ArcGIS 10.5).

to December (thus defining the non-growing season as January to March), and our analyses related to monthly *WUE* were restricted to these months.

2.2. Data collection

2.2.1. Observations of environmental factors

Environmental variables including precipitation (P_{re}, mm), air temperature (T_a, °C), photosynthetically active radiation (*PAR*, mol·m^{-2}), and net radiation (R_n, MW·m^{-2}) were measured by sensors mounted on a 55-m tall micrometeorological tower that was established in XTBG in 2009. The microclimatic instruments included a rain gauge (Rain Gauge 52203, R. M. Young Co., USA) and sensors for R_n (CNR-1, Kipp & Zonen, NED) and *PAR* (LQS70-10, Apogee, USA) at a height of 28.6 m. The water vapour pressure deficit (*VPD*, hPa) was calculated from T_a and relative humidity (%), which were monitored by a hydrothermograph (HMP45C, Vaisala, Finland) at a height of 28.6 m. The surface soil water content (*SWC*, %) was monitored using a soil water reflectometer (CS616-L, Campbell Sci., USA) at a depth of 5 cm. All meteorological data were collected using a data logger (CR1000, Campbell Sci., USA) every 30 min and averaged or summed to correspond with the monthly biometric survey and sap flow data.

2.2.2. Biomass measurements

We randomly selected six rubber trees in each plot and observed their monthly growth of the diameter at breast height (*DBH*, m) using metal bands. We collected the litterfall by establishing ten randomly placed litter traps (area of 0.5 m^2 each) to obtain the total dry weight of litterfall (*L*, g), and measured the leaf area index (*LAI*, m^2·m^{-2}) (Plant Canopy Analysers LAI-2000/2200, LiCor, USA) near each litter trap. We expressed the growth rate of the *DBH* (D_r,%) as

$$D_{r_i} = (DBH_i - DBH_{i-1})/DBH_{i-1} \times 100\% \tag{1}$$

where D_{ri} is the growth rate (%) of *DBH* in a specific month from January to December in a stated year and where DBH_i and DBH_{i-1} (m) represent the *DBH* value of the corresponding month and last value of that month, respectively. Additionally, the dry weight of litterfall for rubber trees (L_w, kg·tree^{-1}) was calculated as

$$L_{w_i} = L_i \times 2000 \times 1000/N \tag{2}$$

where L_{wi} is the dry weight of litterfall (kg·tree^{-1}) in a specific month, L_i is the total dry weight of litterfall (g) in that month, and N is the planting density (trees·ha^{-1}) of the rubber plantations (see Table 1).

To estimate the biomass of rubber trees, we used the general regression equation from our previous reports (Tang et al., 2009) as follows:

$$W = 0.136 \times DBH^{2.437} \tag{3}$$

where W is the total biomass per rubber tree (kg). According to the studies of Pang (2009) and Wang et al. (2011), the mean carbon content of rubber trees and rubber latex are 48.6% and 30.0%, respectively. Thus, the incremental carbon sequestration (ΔC, kg·tree^{-1}) can be calculated from the following equation:

$$\Delta C_i = (W_i - W_{i-1} + L_{wi}) \times 0.486 + W_{latex} \times 0.30 \times n_i \tag{4}$$

where

ΔC_i is the incremental carbon sequestration (kg·tree^{-1}) in a specific month;

W_i and W_{i-1} represent the biomass (kg·tree^{-1}) value of the corresponding month and the last value of that month, respectively;

W_{latex} is the total rubber latex (kg) that rubber trees can produce per tree per year (according to multi-year observations, the yields of latex are 18 kg·tree^{-1}·year^{-1});

and n_i is the weight coefficient (%) for specific months (from May to November), which is calculated in accordance with the incremental *DBH* during the same period by the following equation:

Table 1
Characteristics of the plant structure and the site of the four plots.

Planting year	*Location*	*Altitude* (m)	*Plot area* (m^2)	*Planting density* (trees·ha^{-1})	*Distance** (km)	*Sampling number* (tree)	*Tree height* (m)	*Diameter at breast height* (cm)	*Sapwood area* (cm^2·tree^{-1})	*Canopy height* (m)	*Leaf area index* (m^2·m^{-2})	*Tapping or not*
2002	21°50′29″ N 101°15′50″ E	776	20 × 20	431 ± 53	~12.13	6	17.64 ± 1.13	19 ± 1	190 ± 1	~11.9	3.00 ± 0.29	Yes
1990	21°54′21″ N 101°16′15″ E	565	20 × 20	581 ± 53	~1.13	6	18.26 ± 0.43	21 ± 2	230 ± 31	~12.4	3.18 ± 0.19	Yes
1982	21°54′41″ N 101°16′22″ E	592	20 × 20	346 ± 33	0	6	21.87 ± 0.16	31 ± 1	420 ± 21	~15.0	3.18 ± 0.15	Yes
1965	21°55′33″ N 101°15′58″ E	570	20 × 20	300 ± 45	~2.25	6	24.33 ± 0.73	43 ± 2	650 ± 33	~16.5	2.80 ± 0.36	No

Note that "*" indicates the distance between the plot and micrometeorological tower, "~" indicates that the values are estimated, and values separated by "±" indicate the mean plus/minus the standard error.

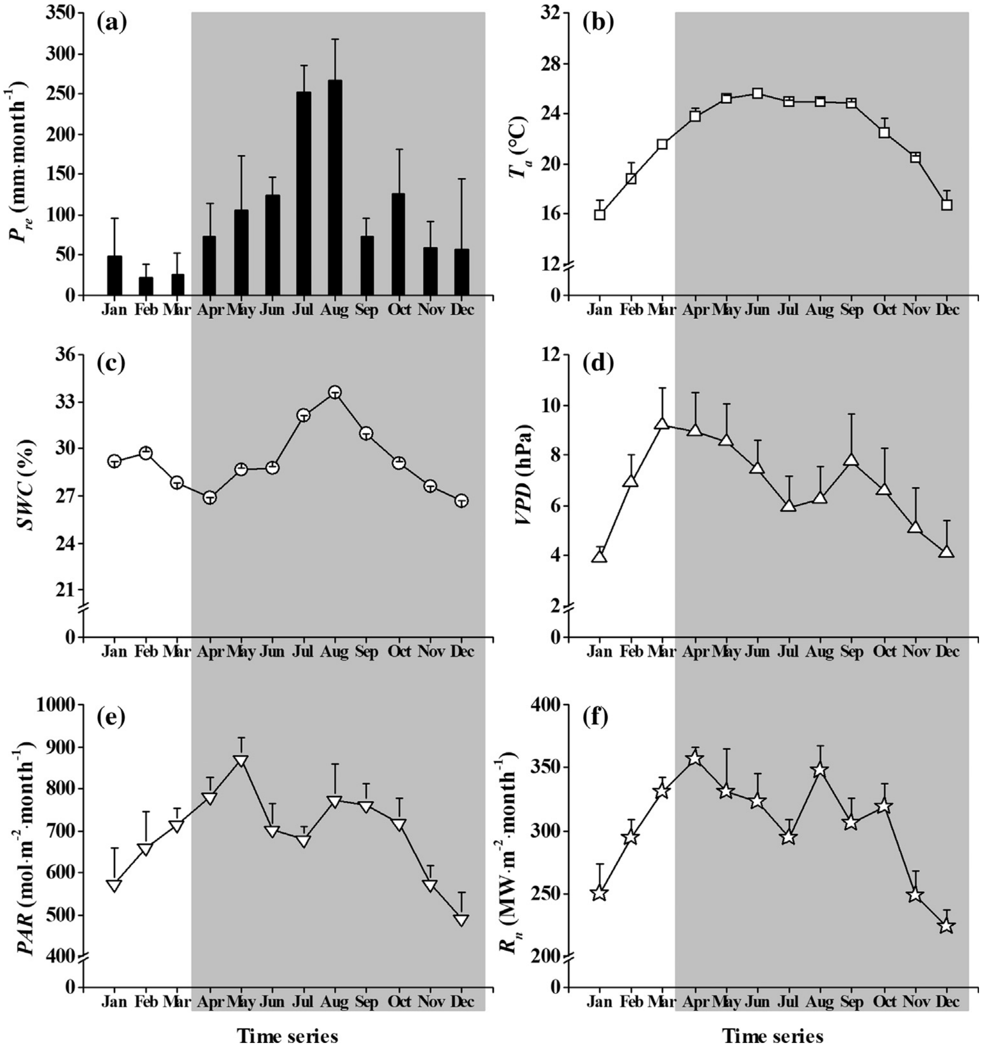

Fig. 2. Annual dynamic (mean plus standard error) of (a) precipitation (P_{re}), (b) air temperature (T_a), (c) surface soil water content (*SWC*), (d) water vapour pressure deficit (*VPD*), (e) photosynthetically active radiation (*PAR*), and (f) net radiation (R_n). Each value represents the average from 2013 to 2016 on a monthly time scale. The light grey and white areas represent the growing season and non-growing season, respectively.

$$n_i = (DBH_i - DBH_{i-1})/\Delta DBH_i \tag{5}$$

where DBH_i and DBH_{i-1} represent the *DBH* (m) values for specific months (from May to November), and ΔDBH is the difference in *DBH* between the months of November and May.

2.2.3. Sap flow measurements

The sap flow density of the same six rubber trees in each plot was measured using custom-made heat dissipation sensors (Granier, 1985). Pairs of 20-mm-long and 2-mm-wide heating probes were inserted into the same-facing side of the trunks of each rubber tree at a 1.3-m height above the stem base and were shielded from solar radiation, thermal gradients and rainfall by reflective insulation. The upper probe was heated with a constant power of 0.2 W, and the lower probe was not heated and served as a reference for the upper probe, with a distance of approximately 10 cm between the two sensor probes to avoid thermal interference. The temperature difference between the two probes was recorded with copper-constantan thermocouples using a data logger (CR10X/CR10XTD, Campbell Sci., USA) to collect the data (averaged and stored every 30 min), after which the difference was used to calculate the sap flow density (J_s, g·m^{-2}·s^{-1}), which was estimated according to the empirical calibration equation reported by Granier (1985):

$$J_s = 119 \times K^{1.231} \tag{6}$$

where *K* is a temperature constant determined as follows:

$$K = (\Delta T_m - \Delta T)/\Delta T \tag{7}$$

where ΔT_m is the maximum temperature difference (°C) at which time the sap flow density has reached its minimum value for a period (typically 7 days in a row) and ΔT is the instantaneous temperature difference (°C) between the two sensor probes. Here, to obtain the sapwood area (A_s, m^2), we used our previous reported correlation relationship (Zhao et al., 2014) as follows:

$$A_s = 0.18776 \times DBH - 0.01638 \tag{8}$$

Accordingly, the instantaneous transpiration rate (E_r, g·s^{-1}) of a rubber tree was calculated as follows:

$$E_r = J_s \times A_s \tag{9}$$

Then, the transpiration (*E*, kg H_2O·tree^{-1}) was calculated as follows:

$$E_i = \overline{E_{r_i}} \times 60 \times 60 \times 24 \times d_i/1000 \tag{10}$$

where E_i is the transpiration in a specific month (kg H_2O·tree^{-1}·month^{-1}), $\overline{E_{ri}}$ is the mean transpiration rate of a rubber tree in that month (g·s^{-1}), and d_i is the number of days in that month.

2.2.4. Calculation of WUE

The *WUE* of a rubber tree was calculated from the water consumption per unit of carbon gain at the single-tree scale (Tu, 2007) during a specific period (month, season, or year) following previous authors (El Aou-Ouad et al., 2015; Medrano et al., 2015). The calculation formula was as follows:

$$WUE_i = \Delta C_i \times 1000 / E_i \tag{11}$$

where WUE_i is the water-use efficiency (g C·kg^{-1} H_2O) in a specific month, ΔC_i is the incremental carbon sequestration in that month (kg C·tree^{-1}·month^{-1}), and E_i is the transpiration in that month (kg H_2O·tree^{-1}·month^{-1}). Thus, we obtained the annual *WUE* and the monthly *WUE* during the growing season from April to December using the above calculations.

2.3 Data analysis

Correlation analysis of the four annual mean values of *WUE* and environmental and biological factors was performed using *Pearson Correlation*, and *2-tailed* tests of significance were used. Linear fitting and multiple linear regression analysis of *WUE* and environmental and biological factors on a monthly time scale during the growing season between April and December were performed with significance testing with *F-statistics*, and plotted using Origin 8.0 software.

3. Results

3.1 Variations in annual and interannual WUE and related factors

During the four years of observations, P_{re}, T_a and *SWC* each showed a pronounced annual pattern, with the highest values occurring in the middle of the growing season (Fig. 2). The lowest *SWC* value occurred in April, but the highest value was in August, reflecting the variability in P_{re}. *VPD*, *PAR* and R_n fluctuated due to the tropical monsoonal P_{re} from May to October. *VPD* increased sharply in response to low P_{re} and T_a during the non-growing season but decreased gradually following the onset of the growing season. Both *PAR* and R_n increased smoothly as the solar azimuth angle increased.

There was a significant annual pattern in D_r; its values were greater than 0.10% per month during the growing season from April to December but close to zero during the non-growing season (Fig. 3b). J_s showed the same pattern as D_r, with both D_r and J_s peaking twice during the growing season (Fig. 3b and c). We found that unlike D_r or J_s, *WUE* did not exhibit a regular pattern; generally, it gradually increased from May until peaking around August during the four years of observations (Fig. 3).

Among the four years of observations, the annual *WUE* ranged from 1.97 to 2.87 g C·kg^{-1} H_2O, and the multi-year mean value was 2.34 g C·kg^{-1} H_2O (Table 2). The annual *SWC*, T_a, *VPD*, R_n, *LAI*, D_r and J_s changed little, with mean values of 29.27%, 22.1 °C, 6.71 hPa, 3730 MW·m^{-2}·year^{-1}, 3.04 m^2·m^{-2}, 2.45% and 13.54 g·m^{-2}·s^{-1}, respectively. However, there was large interannual variation in P_{re} and *PAR*, with values of 1315 ± 269 mm·year^{-1} and 8297 ± 306 mol photons·m^{-2}·year^{-1}, respectively. During the four years of observations, *WUE* had a negative but non-significant correlation with P_{re}, similar to the relationships of *WUE* with J_s and D_r ($P > 0.05$). However, *WUE* significantly decreased with increasing *PAR* ($P < 0.05$).

3.2 Relationships between WUE and related factors at the monthly scale

WUE showed a significant parabolic relationship with *SWC*, T_a, *VPD*, *PAR*, R_n and P_{re} ($P < 0.01$), but the coefficients of determination (R^2) were generally low (Fig. 4). Relatively stronger and highly significant relationships were observed between *WUE* and T_a with a coefficient of determination of $R^2 = 0.40$, and between *WUE* and R_n with a coefficient of determination of $R^2 = 0.37$ ($P < 0.001$) (Fig. 4b and e). The maximum monthly *WUE* occurred when *SWC*, T_a, *VPD*, *PAR*, R_n and P_{re} reached 30.8%, 27 °C, 7.6 hPa, 833 mol photons·m^{-2}·month^{-1}, 340 MW·m^{-2}·month^{-1} and 260 mm·month^{-1}, respectively (Fig. 4). In addition, *WUE* showed a positive correlation with T_a and *PAR*, with coefficients of 0.60 and 0.50, respectively ($P < 0.01$) (Fig. 4b and d).

Regarding the biological factors, J_s and D_r tended to increase with *LAI*, with slopes of J_s and D_r to *LAI* were 2.83 and 0.66, respectively (Fig. 5a and c). However, D_r exhibited a significant parabolic relationship with J_s, with D_r explaining approximately 46% of the variance in J_s ($P < 0.001$) (Fig. 5b). During the growing season from April to December, the monthly D_r and J_s showed similar relationships with *WUE*, with the monthly *WUE* first increasing and then decreasing with increasing D_r and J_s. However, these transformations occurred when the monthly D_r and J_s were approximately 0.45% and 15 g·m^{-2}·s^{-1}, respectively ($P < 0.001$) (Fig. 5e and f). Furthermore, *WUE* increased with D_r, with a correlation coefficient of 0.57 ($P < 0.001$) (Fig. 5e). *WUE* showed a trend of increase with increasing *LAI*, although the relationship was very weak and non-significant ($R^2 = 0.02$, $P = 0.2135$) (Fig. 5d).

Multiple linear regressions of *WUE* as a function of environmental and/or biological factors were performed; the results are shown in Table 3. Regardless of whether the environmental and biological factors were considered separately or together, these factors could only explain approximately 35% of the variation in *WUE* generally, although these regressions were significant ($P < 0.05$). Moreover, the degree of interpretation in the variation in *WUE* among these regressions was equal to or smaller than the degree that could be explained by individual variables (i.e., T_a, R_n and D_r) (Figs. 4 and 5; Table 3).

4. Discussion

4.1 Patterns of annual and interannual WUE

No clear pattern of *WUE* on a monthly time scale during the growing season from April to December was observed in this study, but a peak *WUE* occurred around August during the four years of observations (Fig. 3), which is similar to the results generated in another study based on stable isotope methods (Wu et al., 2016). In general, the coupling between the carbon and water cycles of rubber trees gradually strengthened beginning in May, perhaps to permit more carbon gain to produce fruit around August, as the rubber trees develop leaves rapidly in March (Fig. S1) and then produce flowers around April (Priyadarshan, 2017).

The *WUE* data of selected evergreen broadleaved and tropical forests are summarized in Tables 4: the mean *WUE* of broadleaved forests is 2.78 g C·kg^{-1} H_2O, which is close to the mean value reported by Beer et al. (2009); the mean *WUE* of tropical forests is 2.87 g C·kg^{-1} H_2O, which is much smaller than that reported by Tan et al. (2015). The low variation of *WUE* among broadleaved forests might be due to the similarities among these forests in leaf morphology and structure, e.g., they all have broad leaves with a strongly reflective glabrous surface. Furthermore, these forests presumably evolve where there is an adequate supply of water, without the need for strong water-conserving mechanisms (Tan et al., 2015).

Perhaps due to the advantages of a favourable thermal environment and an ample supply of water, the average *WUE* from tropical forests (2.87 g C·kg^{-1} H_2O) is much higher than the multi-annual mean value reported here for the rubber plantations in Southwest China: 2.34 g C·kg^{-1} H_2O (Table 2). This latter value is greater than the range of 0.67–2.01 g C·kg^{-1} H_2O reported previously for rubber plantations (Dey and Vijayakumar, 2005; Nugawela et al., 1995; Priyadarshan, 2017; Rodrigo et al., 2005). Furthermore, this value is much lower than the nine-year average *WUE* of 3.16 g C·kg^{-1} H_2O obtained previously in a primary tropical rainforest very close to the present study site (Tan et al. 2015). This low value of *WUE* might due to the origin of rubber trees in the wet tropics; the over-saturation in soil moisture did not favour carbon gain (Nugawela et al., 1995; Priyadarshan, 2017).

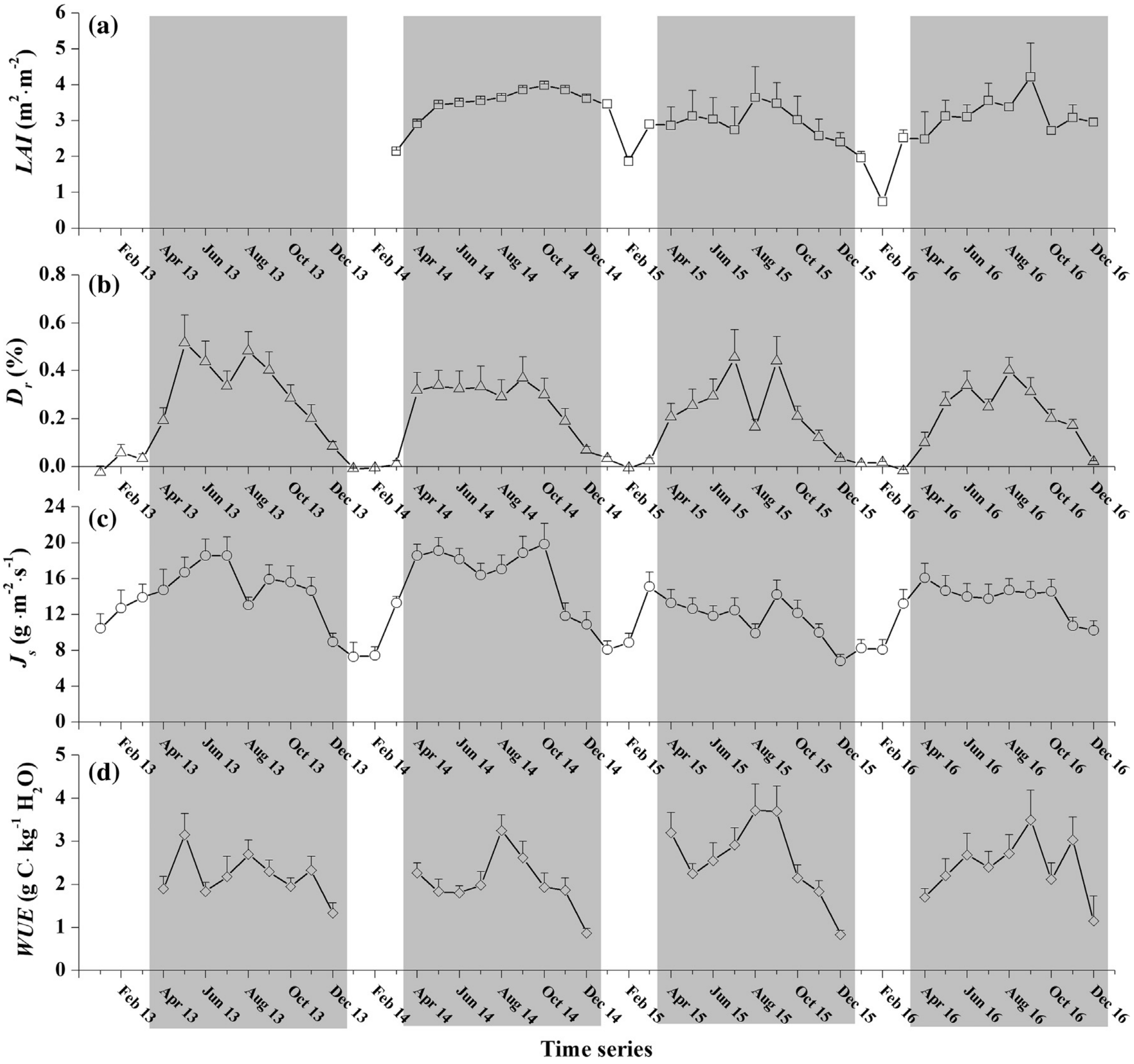

Fig. 3. Mean values (plus standard errors) of (a) the leaf area index (*LAI*), (b) growth rate of the diameter at breast height (D_r), and (c) sap flow density (J_s) on a per-area-of-trunk basis as well as (d) water-use efficiency (*WUE*) on a per-tree basis from 2013 to 2016. The light grey and white areas represent the growing season and non-growing season, respectively.

Table 2
Annual mean and *Pearson Correlation* coefficients of *WUE* and related environmental/biological factors from 2013 to 2016.

	2013	2014	2015	2016	Correlation coefficient
WUE (g C·kg^{-1} H$_2$O)	1.97	2.28	2.87	2.24	1.000
P_{re} (mm·year^{-1})	1641	983	1320	1318	−0.322
SWC (%)	31.28	27.98	29.01	28.82	0.185
T_a (°C)	21.2	22.2	22.1	22.1	−0.473
VPD (hPa)	5.80	6.76	6.03	8.25	−0.140
PAR (mol·m^{-2}·year^{-1})	8660	8370	7910	8250	-0.962^{*}
R_n (MW·m^{-2}·year^{-1})	3690	3840	3770	3620	0.362
LAI (m^2·m^{-2})	—	3.45	2.94	2.73	−0.187
D_r (%)	2.92	2.52	2.22	2.12	−0.651
J_s (g·m^{-2}·s^{-1})	14.68	15.12	11.35	13.02	−0.832

Note that "—" indicates that values were not obtained, and an asterisk indicates statistical significance at the 0.05 level.

Rubber trees have previously been shown to consume more water than other tree species in tropical forests (Giambelluca et al., 2016; Lin et al., 2016; Tan et al., 2011), and the gross primary production of tropical forests has been reported to be greater than that of rubber plantations (Malhi et al., 1999; Song et al., 2014; Tan et al., 2010).

The response of *WUE* to drought is a highly debated topic (Ehleringer and Cooper, 1988; Liu et al., 2015; Niu et al., 2007; Wolf et al., 2013), but we are able to tentatively infer how plants or whole ecosystems might react to drought by comparing data between dry and normal years. A decrease in transpiration can lead to an increase in *WUE* if photosynthesis can still maintain at a high level during a drought (Krishnan et al., 2006; Wolf et al., 2013), although this possibility is debated (Beer et al., 2009; Reichstein et al., 2007). Liu et al. (2015) concluded that moderate and extreme droughts reduced the annual *WUE* in Southern China, while severe droughts slightly increased it. In addition, higher *WUE* is observed under drier conditions (Ehleringer and Cooper, 1988; Liu et al., 2015). Although previous studies reported that the spatial pattern of *WUE* is mainly controlled by P_{re} and that a strong relationship exists between annual *WUE* and P_{re} (Niu et al., 2007; Xiao et al., 2013; Yu et al., 2008), a negative and non-significant correlation ($r = -0.332$, Table 2) was observed between annual *WUE* and P_{re} in the present study. This result might be due to the short period (four years) of observations, which may have been insufficient to reflect the pattern of interannual change. The year 2014 was much drier (983 mm) than the others (Table 2); however, 2014 was not considered as a drought year *per se*, and the decrease in P_{re} in 2014 likely did not result in an increase in *WUE*, as the annual mean *SWC* remained largely stable among the four years of observations (Table 2). Additionally, the rubber plants might adjust their strategy of water use

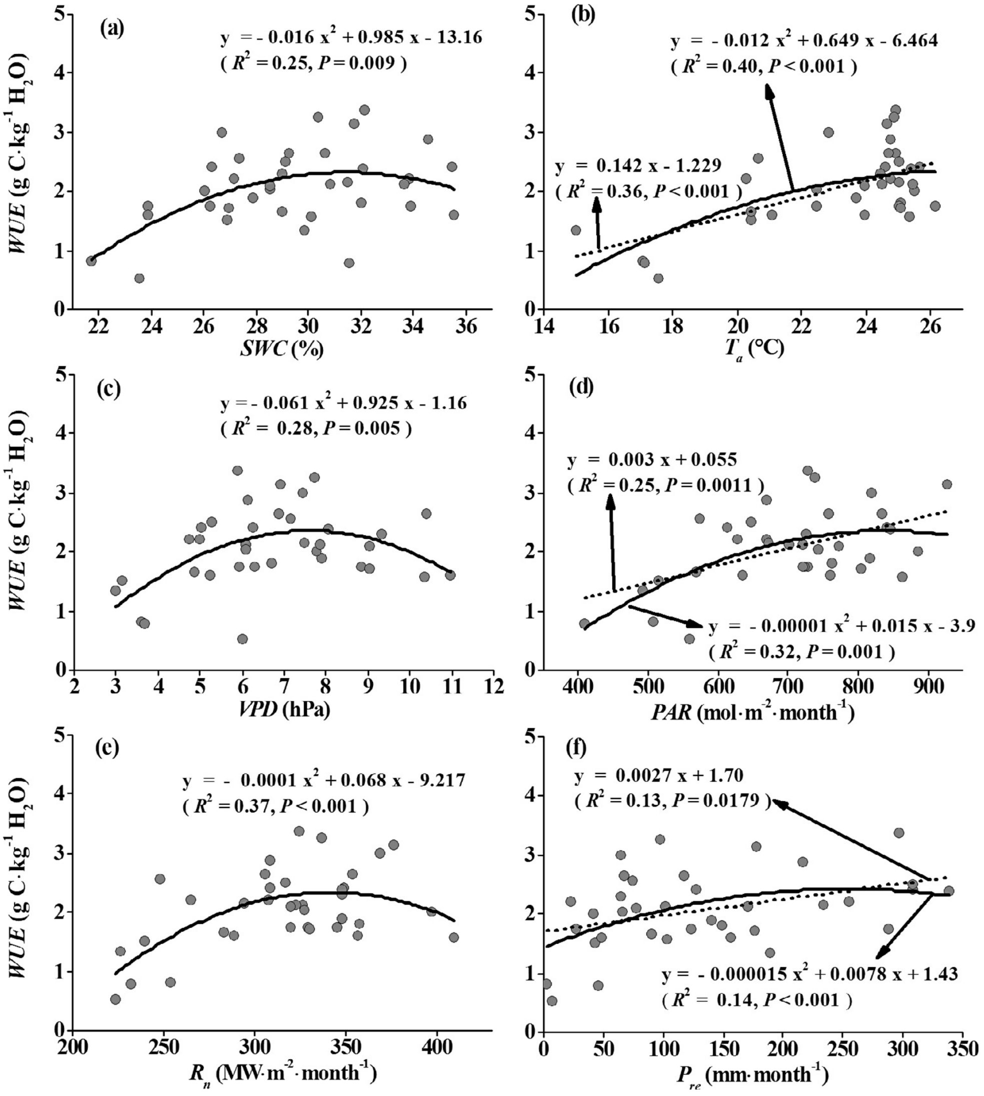

Fig. 4. Relationships between water-use efficiency (*WUE*) on a per-tree basis and environmental factors including (a) surface soil water content (*SWC*), (b) air temperature (T_a), (c) water vapour pressure deficit (*VPD*), (d) photosynthetically active radiation (*PAR*), (e) net radiation (R_n), and (f) precipitation (P_{re}) on a monthly time scale during the growing season from 2013 to 2016.

to reduce transpiration loss and thereby avoid the effects of water stress (Priyadarshan, 2017). Interestingly, rubber trees have a well-developed root system to facilitate the uptake of deep ground water, which they might use during dry seasons or years (Carr, 2012; Lin et al., 2016; Wu et al., 2016; Zhao et al., 2014).

4.2 Factors controlling WUE on the monthly time scale

One difficulty in analysing *WUE* on a monthly time scale involves the fact that growth may take place using carbohydrate reserves that were accumulated by photosynthesis in previous months. The results of the analyses at the monthly scale for the growing season between April and December should therefore be viewed as suggestive rather than definitive; however, these results are valuable, since little was previously known about the patterns of *WUE* and related factors in rubber plantations and a limited amount of work had been conducted due to challenges involved in assessing growth and water use in *Hevea* rubber plants (Priyadarshan, 2017).

To investigate the possible controls of *WUE* in the present case, environmental variables were related to *WUE* by curve fitting (Fig. 4). Previous studies reported strong relationships of *WUE* with both T_a and P_{re} at the interannual scale (Niu et al., 2007; Xiao et al., 2013; Yu et al., 2008). However, in the current study, the only environmental variables to show significant relationships with *WUE* were T_a and R_n, which showed moderately strong parabolic relationships with *WUE* at the monthly time scale (Fig. 4b and e). The net flux of radiant energy, R_n, is often closely correlated with T_a; thus, it is not surprising that *WUE* was similarly correlated with T_a and R_n. However, *WUE* generally increased as T_a increased (Fig. 4b), similar to reports in temperate and subtropical forests (Song et al., 2017; Zhu et al., 2014) but in contrast to findings in tropical and subtropical forests (Tan et al., 2015; Zhu et al., 2014). Moreover, the increases in T_a and *PAR* might have enhanced *WUE* on a monthly scale, whereas the other environmental factors were only weakly correlated with *WUE* or had suppressing effects on *WUE* (Fig. 4). A potential explanation for these results is that these other factors controlled *WUE* on a smaller time scale. For example, Tan et al. (2015) and Yang et al. (2009) reported that the *WUE* strongly depended on *VPD* on the daily time scale. However, the strong correlation between *WUE* and T_a might reflect the expansion of rubber cultivation to sub-optimal areas where the effect of *SWC* or P_{re} on growth (D_r) is smaller than that of T_a (Table S2). In addition, neither the thermal environment nor the water supply was superior to that of native regions (Priyadarshan, 2017).

Regarding the biological factors, *WUE* showed a stronger correlation

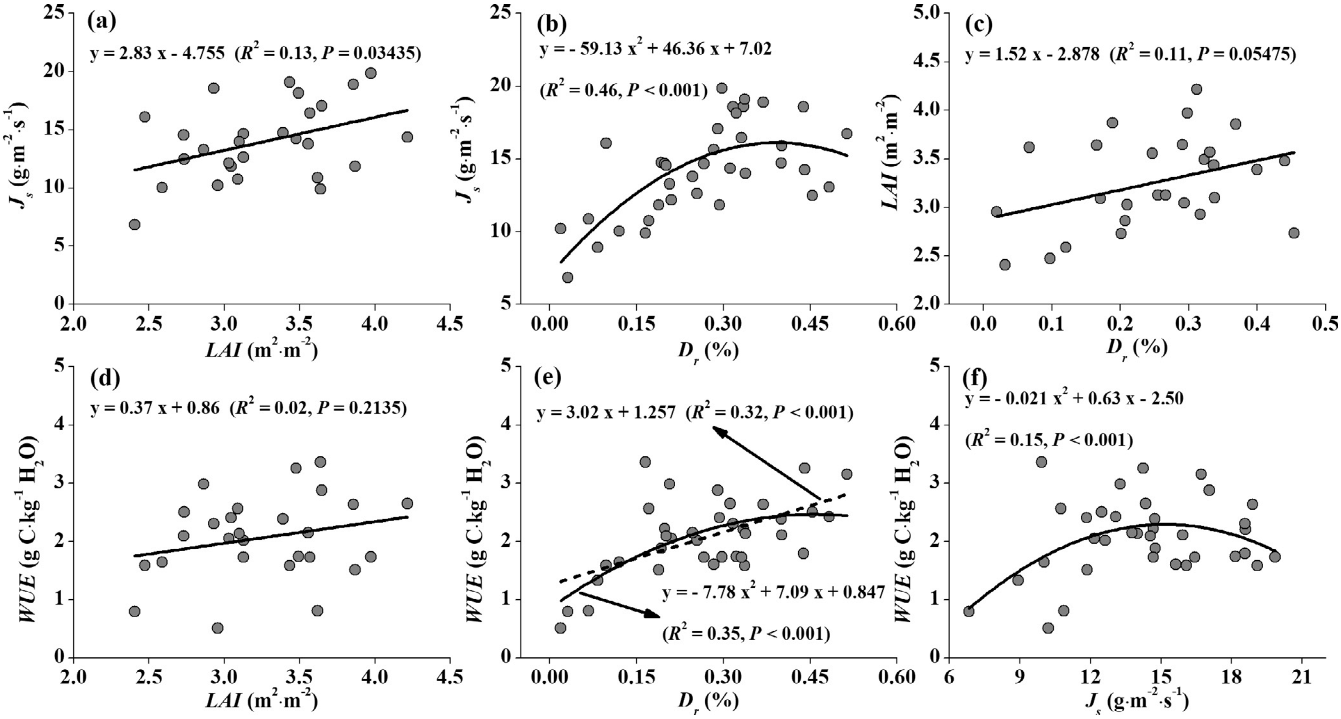

Fig. 5. Relationships between water-use efficiency (*WUE*) on a per-tree basis and biological factors. Regressions of sap flow density (J_s) on a per-area-of trunk basis with (a) the leaf area index (*LAI*) and (b) growth rate of the diameter at breast height (D_r); of (c) *LAI* and D_r; and of *WUE* with (d) *LAI*, (e) D_r and (f) J_s are shown. All the regression analyses were based on a monthly time scale during the growing season between April and December from 2013 to 2016.

Table 3
Multiple linear regressions of *WUE* and environmental and biological factors.

Expression of the regression relation	R^2	P	Eq.
$WUE_{bio} = 0.13 \times LAI + 4.36 \times D_r{}^{**} - 0.06 \times J_s + 1.35$	0.3111	0.0088	(12)
$WUE_{env} = 0.002 \times PAR + 0.20 \times T_a{}^{*} + 0.06 \times SWC - 0.09 \times VPD - 0.006 \times R_n - 0.01 \times P_{re} - 3.52^{*}$	0.3680	0.0152	(13)
$WUE_{gen} = 0.18 \times LAI + 1.6 \times D_r - 0.10 \times J_s + 0.002 \times PAR + 0.17 \times T_a + 0.06 \times SWC - 0.03 \times VPD - 0.003 \times R_n - 0.002 \times P_{re} - 3.4$	0.3676	0.0383	(14)

Note that "*" and "**" indicate that the coefficients of a variable or constant are statistically significant at the 0.05 and 0.01 levels, respectively, and that Eqs. (12–14) represent the multiple linear regressions of *WUE* with biological, environmental and all factors, respectively.

with D_r than that with *LAI* at the monthly scale (Fig. 5). This result conflicts with reports that *LAI* was the crucial factor controlling *WUE* (Beer et al., 2009; Hu et al., 2012). Although *LAI* was more strongly correlated with J_s than that with D_r (Fig. 5a and c), it showed no significant relationship with *WUE* (Fig. 5d). The power of all the factors together in explaining the variation in *WUE* was smaller than the power of the individual variables (Fig. 4; Table 3), i.e., T_a, which is an environmental factor. Both T_a and D_r could explain most of the variance in *WUE*, and T_a was found to be the most correlated with D_r (Figs. 4b and 5e; Table S2); thus, T_a might control D_r and hence *WUE*. Since D_r and J_s generally reflect the extent of carbon gain and transpiration of rubber trees, respectively, *WUE* showed a stronger correlation with D_r than with the remaining biological factors, although it tended to be compromised when J_s exceed a certain threshold (Fig. 5e and f). Furthermore, *WUE* and D_r generally exhibited the strongest correlations with T_a (Fig. 4b; Table S2). These findings indicate that the coupling processes between the carbon and water cycles (*WUE*) of the rubber plantations were mainly controlled by factors (i.e., T_a, R_n and *PAR*) that affect the carbon sequestration rather than water consumption in Southwest China.

Table 4
Mean annual *WUE* for different forest zones and forest types according to the Whittaker Biome Diagram and International Geosphere-Biosphere Program, respectively.

Forest types	*Number of sites*	*WUE* (g C·kg^{-1} H$_2$O)	*Forest zones*	*Number of sites*	*WUE* (g C·kg^{-1} H$_2$O)
Evergreen broadleaved	11	2.78 ± 0.15^{a}	*Tropical*	4	2.87 ± 0.20^{a}
	6	$2.95 \pm 0.23^{b,c}$		2	3.16 ± 0.00^{b}
Evergreen needle	16	$3.47 \pm 0.24^{b,c}$	*Subtropical*	3	2.25 ± 0.33^{b}
Deciduous broadleaved	7	$4.14 \pm 0.45^{b,c}$	*Temperate*	13	4.30 ± 1.13^{b}
Mixed	4	$3.86 \pm 0.51^{b,c}$	*Boreal*	5	3.25 ± 0.50^{b}

Note that the *WUE* values represent the mean plus/minus the standard error. Sources are a: this study (calculated from the data in Table S3), b: Tan et al. (2015), and c: Beer et al. (2009).

5. Conclusions

A pattern in annual *WUE* characterized by peak values generally occurring around August was observed during the growing season from April to December. The multi-year mean *WUE* of rubber plantations was markedly lower than the annual mean *WUE* values reported for evergreen broadleaved and tropical forests. However, no definitive interannual pattern of *WUE* was observed other than a negative correlation between *WUE* and *PAR*. *WUE* was controlled more by T_a, R_n and D_r than by other factors. Regarding the biological factors, D_r was more correlated with T_a as well as it could explain more of the variation in *WUE* than J_s. Our results indicate that the coupling processes between the carbon and water cycles of the rubber plantations might be mainly controlled by factors that affect the carbon sequestration rather than water consumption in Southwest China, while the latter might tend to decrease the strength of the coupling processes when it exceeded a certain threshold.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.jhydrol.2018.05.026.

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