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Phenology-related water-use efficiency and its responses to site heterogeneity in rubber plantations in Southwest China

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ABSTRACT

The survival strategy and ecophysiological process of rubber trees (*Hevea brasiliensis*), in which water-use efficiency (*WUE*) represents a vital indicator linking the carbon and water cycles, are mediated by phenology and can be severely affected by a low fruit-set rate and cold stress. However, the phenology-related *WUE* and its temporal variation as well as its responses to site heterogeneity in rubber plantations remain poorly understood. In this study, we used a four-year (2013–2016) continuous dataset of biometric survey, sap flow and phenology of rubber trees to examine the *WUE* in response to phenological changes and cold stress. The planting density and stand age, factors exhibiting a considerable difference and contributing to site heterogeneity, were explored to reveal their effects on the *WUE* of rubber plantations in Yunnan Province of Southwest China. Unexpectedly, the response of the *WUE* to phenological changes was characterized by the peak value (2.73 ± 0.59 g C kg^{-1} H_2O) that occurred simultaneously with the fruiting period (P_f), and the *WUE* values during the P_f were significantly higher than that of other phenological periods ($P<0.01$), indicating that the survival strategy adopted by the rubber trees to cope with the low fruit-set rate as well as cold stress during the defoliation period (P_d) and adapt to the local climate might be very effective. However, this effectiveness might be reduced to some extent, since the *WUE* was significantly affected by the planting density ($df=2$, F-value$=11.51$) and stand age ($df=3$, F-value$=22.84$) indicated by one-way analysis of variance ($P<0.01$). These findings can provide a deeper understanding for the adaptation strategies to adverse climate and the cultivation and management of rubber plantations.

1. Introduction

Water-use efficiency (*WUE*) is a crucial indicator for evaluating the relative rates of coupled processes such as the assimilation of carbon from the atmosphere and the transpiration of water to the atmosphere (Baldocchi, 1994; Beer et al., 2009; deWit, 1958; Ponton et al., 2006; Yang et al., 2013; Yu et al., 2004). However, the *WUE* has not only been examined to gain a deeper understanding of the responses of terrestrial ecosystems to climate change, which is exerting a profound influence on the tightly coupled carbon and water cycles involved in ecosystem functions and processes (Huxman et al., 2004; Keenan et al., 2013; Mu et al., 2011; Ong and Huxley, 1996), but also widely used to assess the impacts of plant growth on water resources as well as environmental factors on plant water-use strategies (Donovan and Ehleringer, 1991; Tong et al., 2014). Furthermore, these processes can be profoundly influenced by plant physiological characteristics such as stand age and likely depend on site conditions (Day et al., 2001; Helman et al., 2017; Jassal et al., 2009; Köstner et al., 2002; Liu et al., 2018; Zheng et al., 2012). Moreover, the phase, timing and magnitude of ecosystem carbon sequestration and hydrological processes have been demonstrated to be affected by the variation in plant phenology (Obrist et al., 2003; Qiu, 2009). However, many processes that involve water use, particularly those related to the cycling of both carbon and water in plants which have apparent phenological changes, are directly mediated by

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phenology, and the seasonality of these processes is implicitly phenological (Gu et al., 2003; Noormets, 2009). Therefore, phenology related to both the timing and causes of recurrent biological events as well as the interrelation among phases of different species (Lieth, 1974) has been emphasized because phenology mediates vegetation feedback to the atmosphere and climate systems via various sets of processes and mechanisms (Noormets, 2009; Richardson et al., 2013).

Although the patterns of change in the *WUE* and its controlling factors have been well studied from the individual species level to the whole ecosystem level at different temporal and spatial scales in recent years (Beer et al., 2009; Brienen et al., 2017; Conte et al., 2018; González de Andrés et al., 2018; Lin et al., 2018a; Mizunuma et al., 2013; Tan et al., 2015; Xiao et al., 2013), previous studies have focused only on the impacts of global change on plant phenology, such as leaf-out, flowering, fruiting, senescence and abscission (Morisette et al., 2009; Pau et al., 2011; Polgar and Primack, 2011). Furthermore, the *WUE* and its underlying processes involving in both carbon and water cycling are periodic since these processes might exhibit various responses to phenological changes, however, the phenology-related *WUE* still receives little attention. This lack of attention might be due to the difficulties involved not only in the observations of phenology, but also in the uncertainties in referencing changes in the seasonal timing of ecosystem carbon, water and energy exchanges to traditional phenological events (Noormets, 2009; Song et al., 2017). Therefore, increasing attention should be paid to studies related to the phenological *WUE*.

Rubber trees (*Hevea brasiliensis*) are widely known to have high economic and defensive values, therefore, approximately 2 million ha were planted between 2010 and 2017 in considered sub-optimal for rubber cultivation (FAOSTAT, 2017), i.e., Xishuangbanna in southwest China, where the average rubber yield of 1800 kg ha^{-1} $year^{-1}$ was amongst the highest global yields (Deng, 2005; Fox and Castella, 2013); the rubber plantation area in Xishuangbanna was estimated at 3.76×10^5 ha until 2014 (Liao et al., 2014), but an area of 7.01×10^4 ha decreased thereafter because of the sharp decline in the rubber price (Zhang et al., 2019). Although rubber trees have recently been reported to be large carbon sinks (Chen et al., 2011; Song et al., 2014), the environmental consequences associated with these conversions have resulted in rubber plantations gaining the reputation as “water pumps”, and this crop has been blamed for water shortages in local areas (Giambelluca et al., 2016; Lin et al., 2016; Qiu, 2009, 2010; Tan et al., 2011). In addition, limited research has been conducted in rubber plantations, as assessments of growth and water use are tedious for rubber trees (Priyadarshan, 2017); few studies have measured water use in rubber agroforestry systems while continuously evaluating them at different anthropocentrically divided temporal scales (Lin et al., 2018a; Rodrigo et al., 2005; Wu et al., 2016). Therefore, little is known about how the ecohydrological and coupled processes between the carbon gain and water consumption (*WUE*) of rubber plantations respond to phenological changes and site heterogeneity, i.e., the planting density and stand age. Moreover, since rubber trees have a naturally low fruit-set rate (Rao, 1961; Warmke, 1951) as well as a drastic response to cold stress characterized by intense defoliation and dormancy (Lin et al., 2018a, 2018b), the survival strategy adopted by rubber trees to cope with these disadvantages and adapt to local climates and environments remains unknown.

Our general objective of this study was to explore the responses of the carbon-water coupling of rubber plantation to phenological changes, stand ages, planting densities, as well as hydrothermal conditions, and the specific aims were (1) to divide the annual life cycle (P_{lc}) of rubber trees into different phenological periods according to the phenological observations, (2) to explore the dynamic pattern in the *WUE* of rubber plantations and to reveal the survival strategy of rubber trees in terms of *WUE* in response to phenological changes as well as cold stress, and (3) to analyze the influences of site heterogeneity and hydrothermal conditions on the *WUE* of rubber plantations.

2. Materials and methods

2.1. Study site

Our study site is located 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 in Xishuangbanna Prefecture is an extension of the tropical forest of Southeast Asia (Zhu and Yan, 2009), but much of this forest has been replaced by rubber plantations after 2012. According to the observation of the climate in a flux tower set up in one of the studied rubber plantations, the multiyear (2010–2018) mean annual precipitation is 1353 mm, and approximately 79% of the rainfall occurs during the rainy season. The mean monthly rainfall during the dry season, which can be divided into the fog-cool (between November and February) and dry-hot (March and April) seasons (Zhang, 1963), is less than 50 mm; the mean annual temperature is 22.1°C, and the mean monthly values range from 14.9°C to 26.4°C; the annual total photosynthetically active radiation is between 6979 and 9310 mol m^{-2}; the mean monthly surface soil water content ranges from 21.45% to 35.05% (Lin, 2019; Lin et al., 2022). The general topography consists of hilly terrain and lateritic soil (pH 5.6) derived from siliceous rocks.

The characteristics of the four stand-age rubber plantations (plots) are showed in Table 1. The rubber trees grown in this region are considered to be adapted to the local growing conditions as they are cold-resistant clones (PB86 and RRIM600), and were planted 2 m apart in rows with mixed spacing, varying from 4 m to 12 m. The main rubber-tapping period coincides with the rainy season and extends from April 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), and understory weeds and seedlings were removed by hand or using herbicides. The rubber trees strongly responded to cold stress, with a pattern characterized by intense defoliation and dormancy for approximately 50 days between January and February as well as a slow recovery from dormancy in March (Lin et al., 2018a, 2018b).

2.2. Data collection

2.2.1. Observations of hydrothermal conditions and phenology

The surface soil water content (*SWC*, %) and air temperature (T_a, °C) of the four stand-age rubber plantations were monitored by soil moisture (SM150, Delta-T Devices, England) and temperature (ON-940 series, Omega, USA) sensors twice per month from 2014 to 2016, respectively. The phenology of rubber trees at a stand age of 34 years planted in 1982 was estimated based on a digital camera (W80, Pentax Ricoh Imaging Co., Japan), visual observation, and the measurement of litterfall. In addition, the leaf area index (*LAI*, m^2 m^{-2}) was measured using Plant Canopy Analyzers (LAI-2000/2200, Li-Cor, USA) near litter traps established in each stand-age rubber plantation.

2.2.2. Biomass measurements

We randomly selected six rubber trees within each of the four stand-age rubber plantations and observed their monthly diameter at breast height (*DBH*, m) using metal bands from 2013 to 2016. Meanwhile, we collected the total dry weight of litterfall (*L*, g) by establishing ten randomly placed litter traps (area of 0.5 m^2 each) in each of the four stand-age rubber plantations. The dry weight of the litterfall of rubber trees (L_w, kg $tree^{-1}$) was calculated as follows:

$$L_w = L \times 2000/1000/N \tag{1}$$

where *L* is the total dry weight of the litterfall (g) collected from the ten litter traps, and *N* is the planting density of rubber plantations (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:

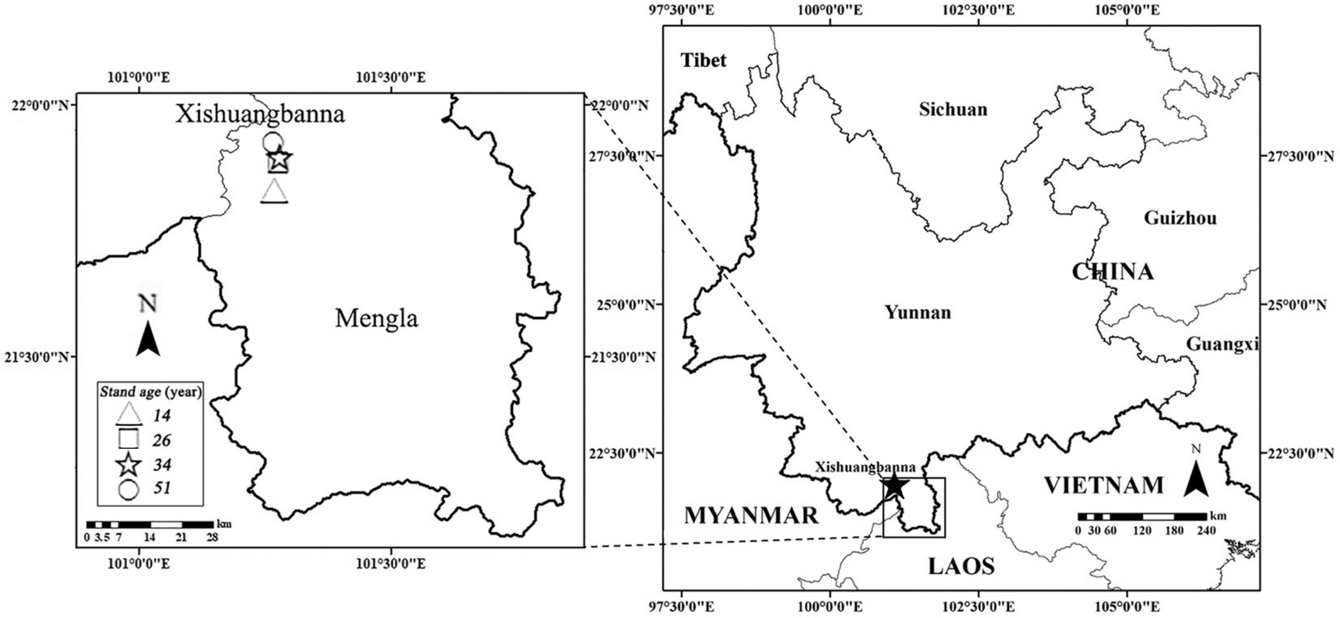

Fig. 1. Geographic location of the study site (star). The symbols of hollow triangle, square, star and circular on the left panel represent the stand age of rubber plantations at 14, 26, 34 and 51 years old, respectively.

Table 1
Characteristics of the four stand-age rubber plantations.

	Stand age (year)			
	14	*26*	*34*	*51*
Latitude	21°50′29″ N	21°54′21″ N	21°54′41″ N	21°55′33″ N
Longitude	101°15′50″ E	101°16′15″ E	101°16′22″ E	101°15′58″ E
Altitude (m)	776	565	592	570
Plot area (m^2)	20×20	20×20	20×20	20×20
Samples (tree)	6	6	6	6
*Distance** (km)	12.13	1.13	0	2.25
Slope	29°	24°	17°	5°
Aspect	NW297°	NW276°	SW266°	SW219°
Soil water content (% $year^{-1}$)	38.56 ± 1.72^a	38.16 ± 1.41^a	37.06 ± 0.81^a	33.24 ± 1.98^b
Air temperature (°C $year^{-1}$)	22.1 ± 0.3^b	21.0 ± 0.14^b	23.5 ± 0.3^a	23.3 ± 0.6^a
Soil temperature (°C $year^{-1}$)	20.9 ± 0.1^c	21.6 ± 0.1^b	22.0 ± 0.1^a	21.7 ± 0.1^b
Relative humidity (% $year^{-1}$)	84 ± 9^a	87 ± 6^a	85 ± 5^a	83 ± 6^a
Planting density (tree ha^{-1})	431 ± 107^{ab}	581 ± 107^a	346 ± 81^b	300 ± 127^b
Canopy height (m)	11.9	12.4	15.0	16.5
Tree height (m)	17.64	18.26	21.87	24.33
Leaf area index (m^2 m^{-2} $year^{-1}$)	3.23 ± 0.20^a	3.31 ± 0.17^a	3.16 ± 0.32^a	2.78 ± 0.77^a
Litterfall (kg $tree^{-1}$ $year^{-1}$)	14.50 ± 3.00^b	13.12 ± 1.72^b	24.70 ± 7.18^{ab}	33.47 ± 9.47^a
Diameter at breast height (cm)	23.64 ± 1.73^c	22.04 ± 4.53^c	31.95 ± 2.64^b	45.24 ± 5.06^a
Number of years of tapping (year)	6	18	26	40 (*stop tapping*)

Note that "*" indicates the distance between the plot and micrometeorological tower and "±" indicates the mean (multiyear average during the three-/four-year observations) plus/minus standard deviation. The multiple comparisons of related factors were performed by one-way analysis of variance (*ANOVA*) and tested using the *Tukey* test. Each group of values not marked with the same lowercase letters indicates statistical significance at the 0.05 level.

$$W = 0.136 \times DBH^{2.437} \tag{2}$$

where W is the total biomass of rubber trees (kg $tree^{-1}$). According to the studies reported by Pang (2009) and Wang et al. (2011), the mean carbon content of rubber trees and latex are 48.6% and 30.0%, respectively. Thus, the incremental carbon sequestration (ΔC, kg $tree^{-1}$) could be calculated as follows:

$$\Delta C_m = (W_m - W_{m-1} + L_{W_m}) \times 0.486 + W_{latex} \times 0.30 \times n_m \tag{3}$$

where

ΔC_m is the incremental carbon sequestration (carbon gain) for a specific month;

W_m and $W_{m\text{-}1}$ represent the biomass values of the corresponding month and the last value in that month, respectively;

W_{latex} is the total rubber latex that rubber trees can produce per tree per year (according to multiyear observations, the latex yield is 18 kg $tree^{-1}$ $year^{-1}$); and

n_m (%) is the weight coefficient of latex for specific months from April to November according to the investigations (see Fig. S1).

2.2.3. *Sap flow measurements*

The sap flow density (J_s, g m^{-2} s^{-1}) of the same six rubber trees in each of the four stand-age rubber plantations was measured using custom-made heat dissipation probes (Granier, 1985) from 2013 to 2016. Pairs of 20-mm-long and 2-mm-diametral probes were inserted into the same-facing side of the trunk of each rubber tree at a height

1.3 m above the stem base. The upper probe was heated with a constant power of approximately 0.2 W, while the lower probe was not heated and served as a reference for the upper probe. The distance between the two probes was maintained at approximately 10 cm to avoid thermal interference, and the two probes were shielded from solar radiation, thermal gradients and rainfall by reflective insulation. The temperature difference between the two probes was recorded with copper-constantan thermocouples via a data logger (CR10X/CR10XTD, Campbell Scientific, USA), after which the difference was used to calculate the J_s, which was estimated according to the empirical calibration equation reported by Granier (1985):

$$J_s = 119 \times [(\Delta T_m - \Delta T)/\Delta T]^{1.231} \tag{4}$$

where ΔT_m is the maximum temperature difference (°C) at which the J_s reaches its minimum value and ΔT is the instantaneous temperature difference (°C) between the two probes. Here, we used our previously reported relationship (Zhao et al., 2014) to obtain the sapwood area (A_s, m^2) as follows:

$$A_s = 0.18776 \times DBH - 0.01638 \tag{5}$$

Therefore, the instantaneous transpiration rate (E_r, g s^{-1}) of a rubber tree could be calculated as follows:

$$E_r = J_s \times A_s \tag{6}$$

Thus, the transpiration (E, kg H_2O $tree^{-1}$) could be calculated as follows:

$$E_m = \overline{E_{r_m}} \times 60 \times 60 \times 24 \times d_m/1000 \tag{7}$$

Where E_m is the transpiration during a specific month (kg H_2O $tree^{-1}$ $month^{-1}$), $\overline{E_{r_m}}$ is the mean transpiration rate of a rubber tree during the same month (g s^{-1}), and d_m is the number of days during that month.

2.2.4. Calculation of WUE

The *WUE* of rubber trees was calculated as the water consumption per unit carbon gain at the single-tree scale (Tu, 2007) during a phenological period (based on the monthly time scale), which was similar to the ratio of net primary productivity (*NPP*) to transpiration at the plant community scale previously reported (El Aou-Ouad et al., 2015; Medrano et al., 2015). The calculation formula is as follows:

$$WUE_p = \Delta C_p \Big/ E_p = \sum_{m=from}^{m=to} \Delta C_m \Big/ \sum_{m=from}^{m=to} E_m \times 1000 \tag{8}$$

where WUE_p is the water-use efficiency (g C kg^{-1} H_2O) on a per-tree basis during a specific phenological period; ΔC_p and E_p are the incremental carbon sequestration (kg C $tree^{-1}$) and transpiration (kg H_2O $tree^{-1}$) during the same phenological period, respectively; and *m*, *from* and *to* represent those months that were included in the specific phenological period.

2.3. Statistical analysis

All data entry and collation were performed using the Microsoft Excel Software 2016. Comparisons between the environmental, biological factors and site heterogeneity as well as the *WUE* at the four stand-age rubber plantations were performed by one-way analysis of variance/covariance (*ANOVA*/*ANCOVA*) and tested by *Tukey* using SPSS 16.0. The interactive effects of the T_a and *SWC* on the *WUE* were tested using R Core Team (2020). Regression between the *WUE* and site heterogeneity (stand age, planting density, T_a, and *SWC*) was performed with Origin 8.0.

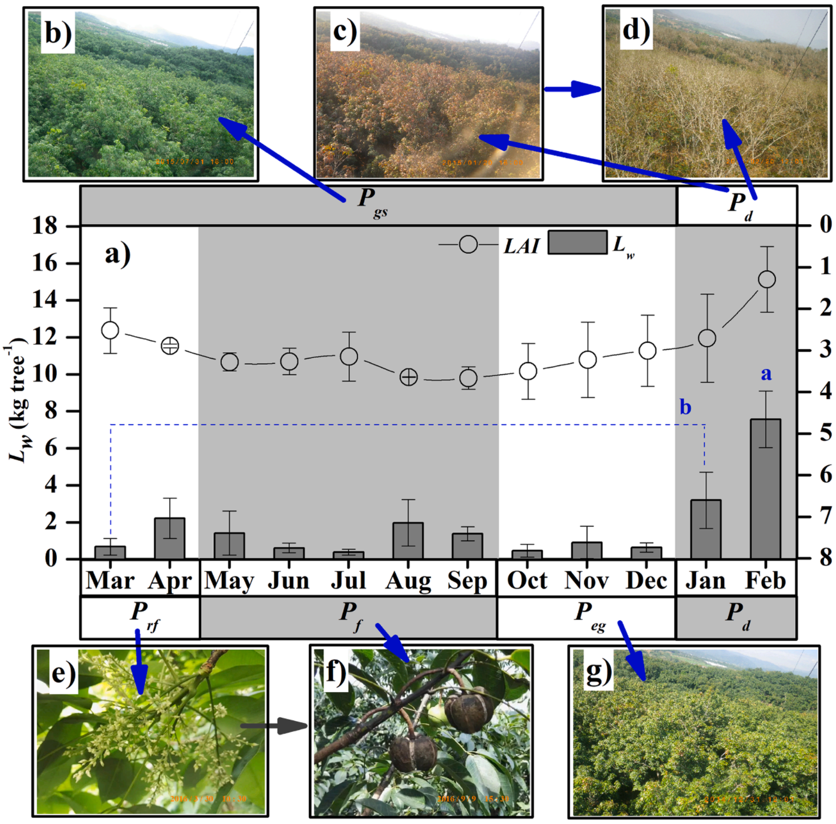

Fig. 2. Annual variation of the phenology in rubber plantations. (a) Monthly mean (plus/minus standard deviations) values of the dry weight of litterfall (L_w) and leaf area index (*LAI*) from March 2013 to February 2016, and the phenological periods of (b) the growing season (P_{gs}), (c-d) the defoliation period (P_d), (e) the refoliation and flowering period (P_{rf}), (f) the fruiting period (P_f), and (g) the end of the growing period (P_{eg}). The values not marked with the same lowercase letters indicate statistical significance at the 0.05 level.

3. Results

3.1. The P_{lc} of rubber trees in Xishuangbanna

The monthly *LAI* trend was opposite to that of the L_w (Fig. S3a), however, both variables showed important synchronous phenological events during the P_{lc} of rubber trees, i.e., the events of flowering, fruiting and defoliation (Fig. 2a). Although there were no significant differences in the L_w between the months of the whole year except for February ($P > 0.05$), the division of the P_{lc} into four periods was more reasonable and accurate when considering certain important phenological events mentioned above: 1) the refoliation and flowering period (P_{rf}), during which the rubber trees refoliated and flowered quickly in March and April (Fig. 2a and e); 2) the fruiting period (P_f), during which the rubber trees developed fruits slowly from May to September (Fig. 2a and f); 3) the end of the growing season (P_{eg}), which occurred between October and December (Fig. 2a and g); and 4) the defoliation period (the non-growing season, P_d), which usually occurred between January and February, when the rubber trees displayed intense leaf defoliation (Fig. 2a, c and d). We defined the growing season (P_{gs}) of rubber trees as March until December, which consisted of the P_{rf}, P_f and P_{eg} (Fig. 2a and b).

3.2. Temporal variability in the WUE of the four stand-age rubber plantations

The similarity between the annual pattern of the *WUE* and *NPP* was greater than that of the J_s (Fig. 3a, S2 and S3b). During the P_{gs}, the *WUE* of the four stand-age rubber plantations generally showed the same trend, which was characterized by the minimum mean *WUE* values of 0.46 g C kg^{-1} H_2O occurring in March, and by the maximum values ranging from 1.87 to 5.66 g C kg^{-1} H_2O occurring between August and September (Fig. 3). However, the *WUE* of rubber plantations was highly over-estimated due to the huge inputs of the L_w during the P_d, with a mean *WUE* value of 6.64 g C kg^{-1} H_2O occurring in February (Figs. 2a and 3a), therefore we no longer investigated any characteristics during the P_d hereafter.

Among the four-year observations, the *WUE* of the four stand-age rubber plantations showed a similar variation tendency, with a peak value occurring during the P_f in the growing season (Fig. 4), and the *SWC* and T_a were generally and significantly higher during the P_f than during the P_{rf} and P_{eg} ($P < 0.05$) (Table S1). In particular, the significant difference in the *WUE* between the P_f and other phenological periods (P_{rf} and P_{eg}) during the P_{gs} was observed at the stand age of 14, 26 and 34 years ($P < 0.05$) (Fig. 4b). Additionally, no significant differences in the *WUE* were observed between the P_{eg} and P_{lc}($P > 0.05$); the same results occurred for the *SWC* and T_a as a whole (Fig. 4b; Table S1). In general, the mean *WUE* values (±standard deviation) of the four stand-age rubber plantations in Xishuangbanna during the P_{rf}, P_f, P_{eg}, P_{gs} and P_{lc} were 1.27±0.40, 2.58±0.90, 1.85±0.84, 2.08±0.68 and 2.27±0.70 g C kg^{-1} H_2O, respectively.

3.3. Variation in site heterogeneity related to the WUE of rubber plantations

Among the heterogeneity of the four stand-age rubber plantations, the planting density and stand age significantly affected the *WUE* of rubber plantations separately ($P < 0.01$) (Table 2 and S2), but their effects on the *WUE* differed when they were considered together: regardless of whether the stand age was analyzed as a covariate or not, the planting density always exhibited highly significant effects on the *WUE* rubber plantations ($P < 0.001$) (Table 2).

The *WUE* of rubber trees at the stand ages of 14 and 51 years was significantly higher than that at the stand ages of 34 and 26 years ($P < 0.05$), and the *WUE* of rubber trees at a stand age of 34 years was significantly higher than that at the stand age of 26 years ($P < 0.05$) (Fig. 5a). Moreover, the *SWC* of the rubber plantation at a stand age of 51 years was much lower than that of the other stand-age rubber plantations, while the T_a was generally higher than that of the other stand-age rubber plantations ($P < 0.05$) (Table S3). The mean *WUE* values of the four stand-age rubber plantations in Xishuangbanna during the P_{lc} ranged from 1.42 to 3.00 g C kg^{-1} H_2O.

The *WUE* of rubber plantations at a planting density of 581 tree ha^{-1} was significantly lower than that at the densities of 300, 346 and 431 tree ha^{-1} ($P < 0.05$), and no significant differences in the *WUE* of rubber plantations occurred among the planting densities of 300 and 431 tree

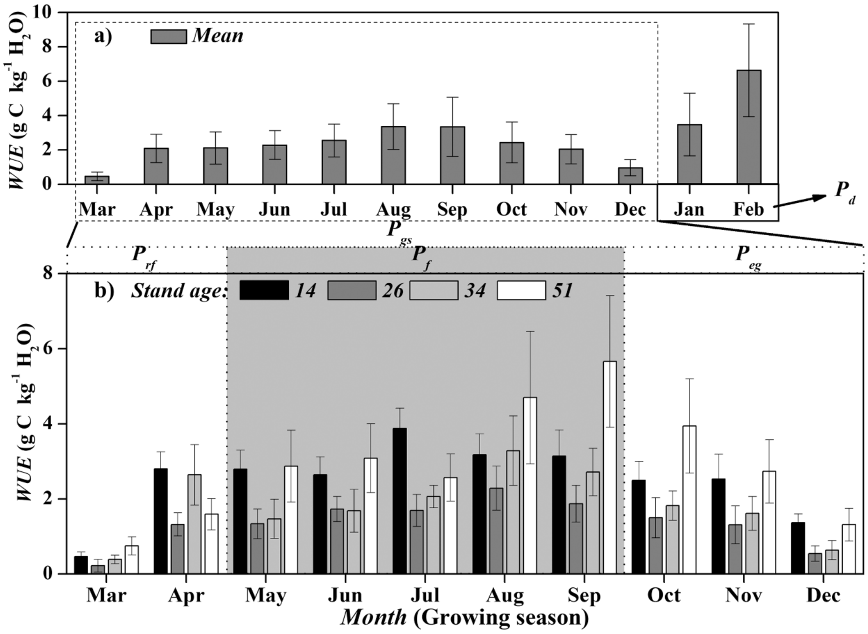

Fig. 3. Annual variation (mean plus/minus standard deviations) of water-use efficiency (*WUE*) of the four stand-age rubber plantations from 2013 to 2016. (a) Monthly variation in the *WUE* of the four stand-age rubber plantations, and (b) the *WUE* variation of each stand-age rubber plantation during the growing season (P_{gs}).

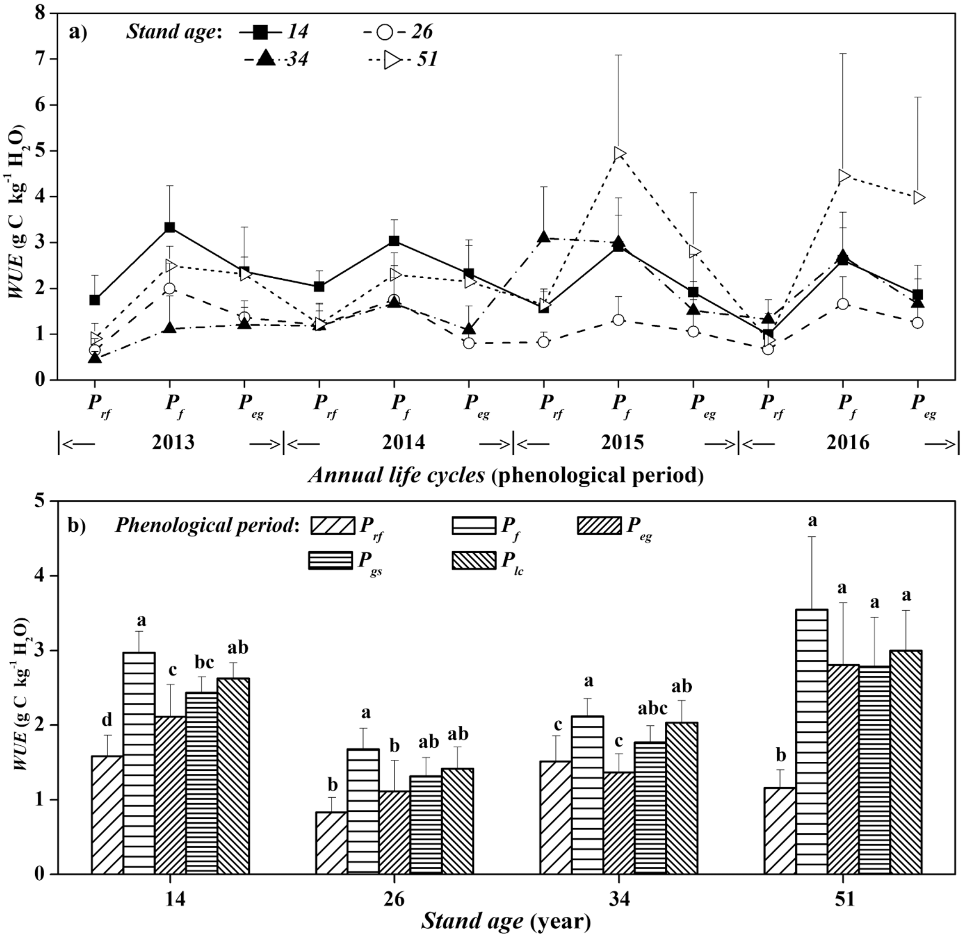

Fig. 4. Temporal variation (mean plus standard deviations) in water-use efficiency (*WUE*) of rubber plantations in Xishuangbanna. (a) The *WUE* of the four stand-age rubber plantations during different phenological periods from 2013 to 2016; (b) multiple comparisons of the *WUE* during different phenological periods in each stand-age rubber plantation. Each group of values not marked with the same lowercase letters indicates statistical significance at the 0.05 level.

Table 2

Effects of site heterogeneity on the *WUE* of rubber plantations.

Test effect	*Site heterogeneity*	*df*	*Sum Sq*	*Mean Sq*	*F value*
One-way ANOVA	*Stand age*	3	8.64	2.88	22.84**
	Planting density	2	5.84	2.92	11.51**
One-way ANCOVA	*Planting density (covariant)*	1	4.396	4.396	34.85**
	Stand age	2	4.246	2.123	16.83**
	Stand age (covariant)	1	1.216	1.216	9.644**
	Planting density	2	7.425	3.713	29.438**

Note that the levels of specific site heterogeneity are classified according to the results of multiple comparisons, which were obtained from the four stand-age rubber plantations and are showed in Table 1; *df*, *Sum Sq* and *Mean Sq* represent the degree of freedom, sum and mean of square for deviation, respectively; and "**" indicates statistical significance at the 0.001 level.

ha^{-1} (Fig. 5b). The mean *WUE* values during the P_{lc} of rubber plantations at the planting densities of 300, 346, 431 and 581 tree ha^{-1} were 3.00, 2.03, 2.62 and 1.42 g C kg^{-1} H_2O, respectively. Additionally, the increases in the planting density tended to reduce the *WUE*, especially when the planting density was over 433 tree ha^{-1} (R^2=0.36, P<0.05), while the relationship between the stand age and *WUE* was much more complex, with the *WUE* values decreased before the stand age of 26 years then increased hereafter (R^2=0.48, P<0.01) (Fig. 5a and b).

The *WUE* values of the four stand-age rubber plantations generally increased as the T_a increased, and the variance in the *WUE* explained by the T_a ranged from 10% to 45% (Fig. 5c, d, e and f). Moreover, the *WUE* of the four stand-age rubber plantations first increased but then decreased as the *SWC* increased, although little variation in the *WUE* could be explained by the *SWC* (R^2=0.01–0.11) (Fig. 5c, e and f). However, a strong relationship was observed between the *WUE* and *SWC* at the stand age of 26 years, and the *SWC* explained 39% of the variance in the *WUE* (P<0.05) (Fig. 5d). Furthermore, the results of linear models showed that neither the main effects of hydrothermal conditions nor the interactive effects (coefficients) on the *WUE* occurred (P>0.05), although the model for the stand age of 26 years was significant (Table 3).

4. Discussion

4.1. Phenological pattern of rubber trees in Xishuangbanna

According to the combined observations of the phenology and L_w as well as *LAI* of rubber trees (Fig. 2), we divided the P_{lc} of the rubber trees into four phenological periods: the P_{rf}, P_f, P_{eg} and P_d. With the exception of February, no significant differences in the L_w between any two months were observed (P>0.05), which indicated that the calculations of the ΔC and *WUE* based on the monthly *DBH* and L_w values were somewhat reasonable (Fig. 2a). The following reasons may explain this finding: 1) the growth of the rubber trees, i.e., the *DBH* and ΔC, may take place using carbohydrate reserves that accumulated previously and thus are controlled by phenology (Gu et al., 2003; Noormets, 2009; Song et al., 2017); 2) some certain phenological time nodes, i.e., the events of

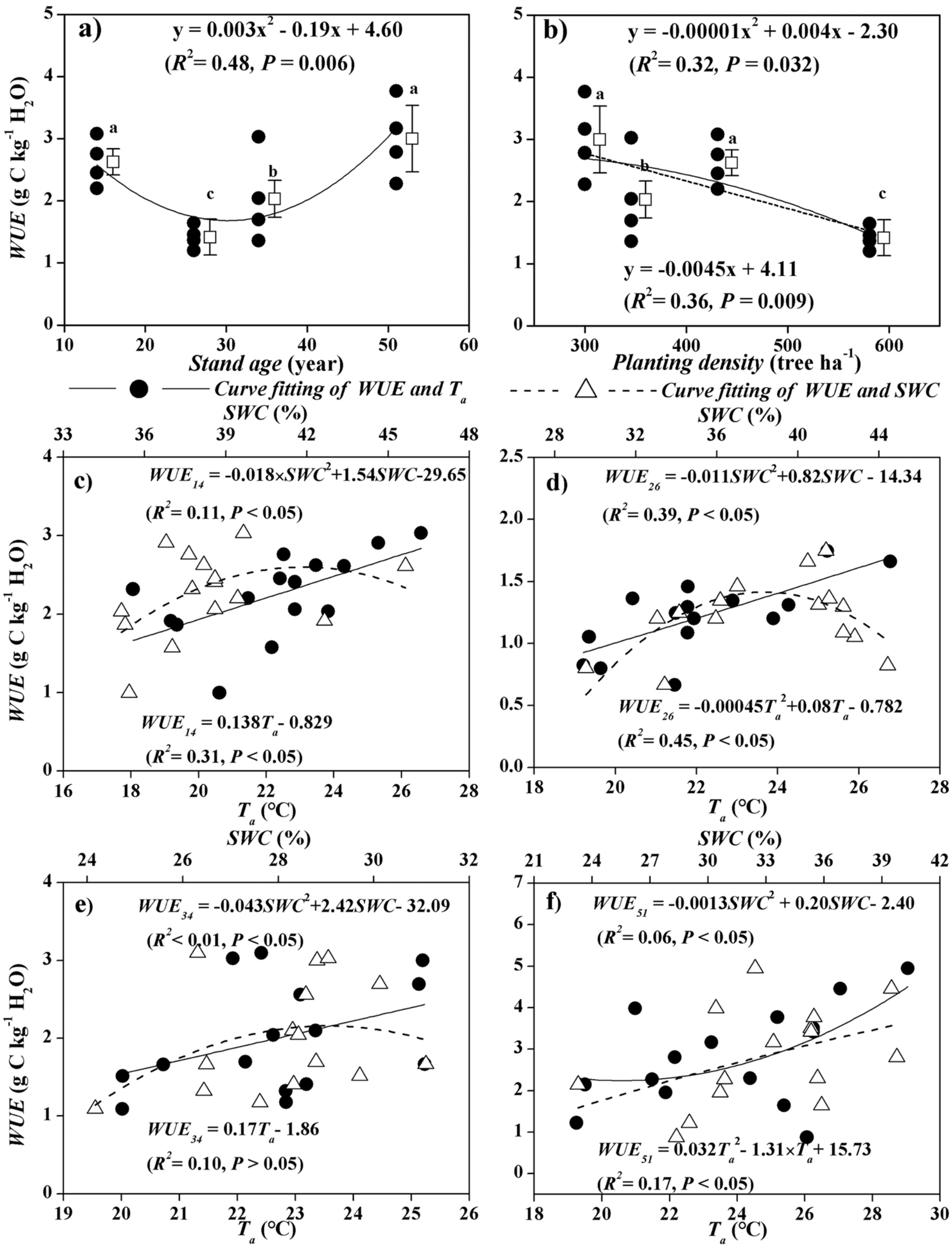

Fig. 5. Relationships between water-use efficiency (*WUE*) of rubber plantations and site heterogeneity. (a) Relationship between the *WUE* and stand age, (b) relationship between the *WUE* and planting density, and (c, d, e and f) relationships of the *WUE* with air temperature (T_a) and surface soil water content (*SWC*) in rubber plantations at the stand ages of 14, 26, 34 and 51 years from 2014 to 2016. Each group of values not marked with the same lowercase letters indicates statistical significance at the 0.05 level.

refoliation, flowering and fruiting (Morisette et al., 2009; Pau et al., 2011; Polgar and Primack, 2011; Sarvas, 1972), can be identified from the annual L_w and *LAI* dynamics (Fig. 2a); and 3) the intense defoliation of rubber plantations in January and February critically affects the physiological activities and yields of the rubber trees (Lin et al., 2018a, 2018b; Priyadarshan, 2017), i.e., photosynthesis and transpiration. In general, it might be more reasonable and accurate to divide the P_{lc} of the rubber trees into periods of the P_{rf}, P_f, P_{eg} and P_d in accordance with the changes in canopy phenology, rather than the rainy, fog-cool and dry-hot seasons which were not suitable for the further exploration of the ecophysiological characteristics (Fig. 4b and S4), of which were phenologically periodic (Morisette et al., 2009; Noormets, 2009; Pau

Table 3
Interactive effects of the T_a and *SWC* on the *WUE* of the four stand-age rubber plantations.

Stand age	*Coefficient*				*Statistical value*			
	Intercept	T_a	*SWC*	$T_a \times SWC$	*N*	*df*	*Multiple* R^2	*F-statistic*
14	-7.154	0.332	0.169	-0.005	15	11	0.4294	2.759
26	0.796	-0.017	-0.042	0.003	15	11	0.5966	5.422*
34	-30.783	1.463	1.014	-0.045	15	11	0.2123	0.9883
51	18.72	-0.809	-0.619	0.030	15	11	0.3698	2.151

Note that "*" indicates statistical significance at the 0.05 level, "×" represents the interaction term between the two factors, *N* is the total number of the dataset obtained from the P_{rf}, P_f, P_{eg}, P_{gs} and P_{lc} during 2014–2016, and *df* is the degree of freedom.

et al., 2011; Polgar and Primack, 2011).

4.2. The WUE of rubber trees in response to phenological changes

Previous studies have reported that the *WUE* values of the rubber trees estimated from leaf δ^{13}C values are higher during the dry-hot season than during the rainy season (Wu et al., 2016) and the *WUE* values improve during the drier seasons and years (Ehleringer and Cooper, 1988; Krishnan et al., 2006; Rytter, 2005; Song et al., 2017). These findings are suggested to contribute to soil water deficit (Moreno and Cubera, 2008; Wu et al., 2016), and a relatively larger response of the reduced water consumption than that of the carbon gain occurs under these conditions (Song et al., 2017). However, the rubber trees introduced into Xishuangbanna show drastic response to cold stress characterized by intense defoliation and dormancy during the P_d (Lin et al., 2018a, 2018b); this response can severely impact the yield, growth and ecophysiological processes of rubber trees (Lin et al., 2018a, 2018b; Priyadarshan, 2017). Furthermore, this response might result in highly over-estimated *WUE* (3.48–6.64 g C kg^{-1} H_2O) in January and February due to the enormous inputs of the L_w during the P_d (Figs. 2a and 3), whereas it would cause slightly under-estimated *WUE* in March on a monthly scale as the rubber trees recovered from dormancy slowly (Figs. 2a and 3). Therefore, it was unreasonable that the rubber trees had the highest *WUE* during the period between January and March as reported by Wu et al. (2016) and as showed by the similar results reported in this study (Fig. 3). Hence, we no longer discussed the *WUE* during the P_d thereafter; however, a more effective method needed to be developed to explore the *WUE* during this dormancy period of rubber trees. Moreover, no significant differences in the *WUE* of the four stand-age rubber plantations were observed between the P_{gs} and P_{lc} during the four-year observations (P>0.05) (Fig. 4b); in other words, the over-estimated *WUE* values during the P_d resulting from intense defoliation could be ignored, which indicated that the *WUE* values calculated from the growing season on the monthly and phenological-period scales used in this study were reasonable (Fig. 4b and S4).

Among the four-year observations throughout the growing season, the *WUE* of the four stand-age rubber plantations was generally and significantly higher during the P_f than during the P_{rf} and P_{eg} (P<0.05) (Fig. 4). The highest *WUE* values occurred during the P_f, which was the phenological period that the rubber trees developed fruits, and this result was similar to our previous reports that the peak *WUE* values usually occurred in each year around August during the growing season (Fig. 3) (Lin et al., 2018a). The strengthened coupling processes between the carbon and water cycles (*WUE*) of rubber trees occurred synchronously with the P_f, indicating that it might be one of the most effective plant survival strategies to guarantee reproduction in response to possible adverse conditions, especially for the rubber trees had encountered cold stress and then entered dormancy during the P_d (Lin et al., 2018a, 2018b). Moreover, it has been reported that the rubber trees have a naturally low fruit-set rate even with artificial pollination (Ghandimathi and Yeang, 1984; Rao, 1961; Warmke, 1951; Yeang, 2007). Therefore, this survival strategy could help to guarantee the fruit-set rate and might be a long-term adaptation to the local climates and environments in Xishuangbanna, where the rubber trees experienced multiple environmental stresses, including cold and drought stresses (Priyadarshan, 2017).

4.3. Effects of site heterogeneity on the WUE of rubber plantations

According to the four-year observations, significant relationships of the *WUE* with planting density and stand age were observed (P < 0.05), with the higher planting density tended to reduce the *WUE*, while the *WUE* in response to stand age with the *WUE* first decreased and then increased with the increase of stand age (Fig. 5a and b). Without considering the rubber plantation at a stand age of 14 years, which suffered less damage from latex tapping (6 years) (Fig. 5a; Table 1) and benefited from moderate planting density (431 tree ha^{-1}) (Eastham et al., 1988; Kumagai et al., 2013; Martín-Benito et al., 2010; Yoda et al., 1963) and also had the most vigorous stand age (14 years) to maintain the highest photosynthesis and the strongest carbon and water coupling to satisfy rapid growth (Zheng et al., 2012), the *WUE* tended to increase as the stand age increased, which was consistent with the previous studies (Chen et al., 2004; Jassal et al., 2009). However, the *WUE* was significantly affected by the effects of planting density as well as the interactive effects between planting density and stand age (P<0.01) (Fig. 5b; Table 2 and S2), and the productivity and growth of rubber plantation at a stand age of 26 years (581 tree ha^{-1}) might be strongly restricted by the density effects (Eastham et al., 1988; Kumagai et al., 2013; Yoda et al., 1963) via intensified intraspecies competition for soil moisture, nutrients and light (Fig. 5b and d; Table 1), whereas the *WUE* of the rubber plantation at a stand age of 51 years showed greater variability and might recover to a slightly higher value because they were not tapped for approximately 10 years (Figs. 4b and 5a; Table 1). Therefore, the positive relationship between the *WUE* and stand age could be reversed, showing that the *WUE* decreased as stand age increased, which was similar to other studies (Chen et al., 2004; Köstner et al., 2002). This result can be explained by the decrease in photosynthetic capacity as the stand age increases (Chen et al., 2004; Day et al., 2001; Köstner et al., 2002; Zheng et al., 2012), whereas the transpiration generally increases as the stand age increases (Chen et al., 2004; Lin et al., 2016); therefore, the *WUE* decreases as the stand age increases. These results indicated that the pattern of the coupled processes between the carbon and water cycles of rubber trees could be strongly affected by the stand age and planting density as well as their interactive effects (Table 3).

Our results showed that the *WUE* generally increased as the T_a increased, which supported the similar positive and linear relationship showed in our previous analyses based on the monthly time scales during the growing season (Lin et al., 2018a), and this trend seemed clear when the T_a was greater than approximately 23 °C. In addition, the T_a could explain between 10% and 45% of the variance in the *WUE* among the four stand-age rubber plantations. In contrast, the *SWC* was weakly related to the *WUE*, and no interactive effects between the T_a and *SWC* on the *WUE* generally occurred (P>0.05) (Fig. 5c, d, e and f; Table S3), indicating that the strength of the coupling processes between the carbon and water cycles of rubber plantations in Southwest China might be mainly controlled by temperature rather than water status, and that climate warming might promote the *WUE* values of the rubber trees in this area. Similar relationships between the *WUE* and T_a have been reported in subtropical and temperate forests (Zhu et al., 2014; Song et al., 2017), as the T_a may improve both photosynthesis and transpiration, which is similar to previous reports (Xiao et al., 2013; Yu et al., 2008), but T_a may largely stimulate photosynthesis more than transpiration when photosynthesis is not suppressed by T_a (Yu et al., 2008). However, the stand age of 14 years of rubber plantation was a unique case, as the *SWC* could explain approximately 40% of the variance in the *WUE* ($P<0.05$) (Fig. 5d). Among the four stand-age rubber plantations, the planting density of 581 tree ha^{-1} played a crucial role in the strong relationship between the *WUE* and hydrothermal conditions (Fig. 5b and d; Tables 1, 2, S1, S2 and S3). The density effect reported for the stand age of 26 years (581 tree ha^{-1}) of rubber plantation in this study might result in competition for limited resources of light, nutrients and soil moisture (Kumagai et al., 2013; Martín-Benito et al., 2010); therefore, this stand age of rubber trees presented low tree height (18.26 m), canopy height (12.4 m), *DBH* (22.04 cm) and *WUE* (1.42 g C kg^{-1} H_2O) values, which were slightly higher or even lower than those at the stand age of 14 years (Figs. 3, 4 and 5a; Table 1).

In general, the *WUE* of rubber plantations in Xishuangbanna ranged from 1.42 to 3.00 g C kg^{-1} H_2O, which was similar to values (0.67–2.34 g C kg^{-1} H_2O) reported previously for rubber plantations (Dey and Vijayakumar, 2005; Lin et al., 2018a; Nugawela et al., 1995; Priyadarshan, 2017; Rodrigo et al., 2005). Compared with the *WUE* values of trees originating in the wet tropics, these low values may have occurred because the lower T_a and *SWC* did not favour the dry matter production (Priyadarshan, 2017). Moreover, the relationship between the *WUE* and stand age was strongly influenced by the planting density, especially for the stand age of 26 years (581 tree ha^{-1}) of rubber plantation (Fig. 5a and b; Table 2 and S2). Therefore, the pattern of the ratio of the carbon gain to water consumption (*WUE*) was rather site specific and dependent on plot heterogeneity; as such, comparison of this pattern with that in other studies was difficult (Ong and Huxley, 1996; Rodrigo et al., 2005), as it could be profoundly affected by the physiology and community structure, i.e., the planting density and stand age (Fig. 5a and b; Table 2 and S2).

5. Conclusion

The results of our study showed that the division of the P_{lc} of the rubber trees into four phenological periods rather than into months or seasons was more appropriate for exploring the ecophysiological characteristics of the rubber trees. In particular, the *WUE* values of the rubber trees were generally and significantly higher during the fruiting period (P_f) than during other phenological periods, implying that this tree species might adjust its survival strategy to strengthen the carbon and water coupling (*WUE*) in response to the low fruit-set rate and cold stress to adapt to the local climate and environment. However, the effectiveness of the survival strategy and the growth of the rubber trees was significantly depressed by the planting density and its interactive effect with stand age. Therefore, the planting density and stand age must be well considered during the cultivation and management of rubber plantations in Southwest China.

CRediT authorship contribution statement

Youxing Lin: Validation, Investigation, Data curation, Formal analysis, Writing – original draft preparation. **Yiping Zhang:** Supervision, Conceptualization, Methodology, Project administration, Funding acquisition. **Liguo Zhou:** Validation, Investigation. **Jing Li:** Validation, Investigation, Writing – reviewing and editing. **Ruiwu Zhou:** Validation, Investigation. **Huiling Guan:** Validation, Investigation. **Jin Zhang:** Validation, Investigation. **Liqing Sha:** Supervision, Conceptualization. **Qinghai Song:** Visualization, Writing – reviewing and editing.

Declaration of Competing Interest

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

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.eja.2022.126519.

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