

## A 14-year experiment emphasizes the important role of heat factors in regulating tree transpiration, growth, and water use efficiency of *Schima superba* in South China

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### ABSTRACT

Research results on the effects of environmental factors on tree water use, growth, and water use efficiency vary latitudinally and geographically and the conclusions remain controversial. In this study, we investigated the tree transpiration ( $E_t$ ), basal area increment (BAI), and water use efficiency (WUE) of a typical plantation tree species, *Schima superba*, in South China, aiming to identify the dominant environmental factors in regulating and affecting the tree water use and growth. Datasets including the continuously measured sap flow and meteorological parameters, as well as the periodically measured diameter at breast height and height of observed sample trees, were collected during the period from 2008 to 2021. The redundancy analysis results indicated the significant effects of air temperature (T) and humidity (RH) on tree  $E_t$ , BAI, and WUE. According to Pearson correlations among the environmental factors, we divided them into “Heat group” and “Water group”, and conducted the variation partitioning analysis. Results highlighted that it was the heat factors including air temperature and solar radiation rather than the water factors that explained the larger variations of  $E_t$ , BAI, and WUE. The abundant total precipitation in South China and the ability to take advantage of deep soil moisture of *S. superba* weakened the role of water but emphasized the effect of heat. Considering the current growth and the water use of *S. superba*, and the obvious climate changes in recent decades in South China, it is concluded that this species can maintain its growth under the current climate conditions. Overall, our study demonstrates a more important role of heat factors compared to water factors in regulating tree water use, growth and WUE in subtropical *S. superba* plantations, which could offer a promising implication for the management of subtropical plantations under future climate trajectories.

### 1. Introduction

Nowadays, global climate change due to the increase of greenhouse gases such as atmospheric CO<sub>2</sub> and the resulting rise in air temperature have altered precipitation patterns. The changing temperature and precipitation patterns can trigger frequent and severe droughts in semi-arid and arid regions (Spinoni et al., 2018), even in some subtropical areas like South China that receive abundant rain (Ouyang et al., 2020). These changes will influence tree physiology and forest ecology by altering the plants' carbon-water relationships (Körner, 2000).

Tree transpiration is the process of water movement from roots to leaves where the moisture evaporates into the air. It connects leaf carbon assimilation and ecosystem functions, and can indicate the forest responses to climatic changes and soil water status (Lu et al., 2020; Zhou et al., 2011). It is jointly controlled by the climatic and environmental variables, such as vapor pressure deficit (VPD), net radiation (Rn), air temperature (T), precipitation (P), and soil moisture (SM) (Ouyang et al., 2020, 2022b; Novick et al., 2016; Grossiord et al., 2018). For instance, Liu and Bondi (2020) reported that the sap flow based transpiration of pines growing in Nevada was mainly limited by evaporative

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demands when water resources are abundant, while soil moisture became the dominant factor when water availability decreased. Wang et al. (2011) aimed to sort out the contributions of heat, water, and pollutant variables to the transpiration of six urban tree species in Beijing in North China, and found that the heat and water factors rather than the atmospheric pollutants mainly regulated the tree transpiration. Whereas, our previous study on tree water use along an urban - rural environmental gradient demonstrated that the pollutant emission exerted more impact on sap flow than climatic factors in South China (Ouyang et al., 2022a). Though it is widely accepted that tree-level sap flux at daily or longer temporal scales is generally controlled by VPD variations and soil moisture, the relative sensitivity of sap flux to these factors under long-term environmental conditions has rarely been determined experimentally (Grossiord et al., 2018). Similarly, tree growth is also determined by air temperature, radiation, potential evapotranspiration, precipitation, and the seasonal patterns of these climatic variables (Zuidema et al., 2022; Fyllas et al., 2017). For instance, the annual woody biomass growth responds positively to dry-season precipitation, but negatively to dry-season maximum temperature, and the responding degree to these dry-season climate factors varies among sites (Zuidema et al., 2022). Generally, sufficient water supply, moderate temperatures, and high humidity could favor fast biomass accumulations, while extreme temperature or drought usually leads to less or decreased biomass increment. In this context, the dominant role of environmental variables and the degree of their influence on transpiration and tree growth always vary with climatic region, time, and tree species. Therefore, no definite conclusions have been reached over the long term scale and further research in this respect is needed.

Water use efficiency (WUE), defined as the ratio of the increased biomass to the water transpired during a given period, provides a necessary multi-scale reflection of the coupling of water transpiration and carbon assimilation (Bogeat-Triboulot et al., 2019). Previous literature has systematically analyzed the drivers of carbon gain process and water use (Jiang et al., 2022; Mathias and Thomas, 2021), and showed the crucial roles of water and energy on WUE (Chen et al., 2022). In arid or semi-arid regions, the significant increase in intrinsic WUE could be attributed to the decrease of stomatal conductance as temperature increased or soil moisture decreased (Jia et al., 2022). Nevertheless, research results from Wang et al. (2020) showed significant positive relationships between temperature or precipitation and annual WUE in the Tibetan Plateau. Another study had proposed that the climate changes would have a negative effect on WUE in South China but a positive effect in North China in the future, emphasizing the zonal difference of climate (Zhu et al., 2011). Recently, there is an ongoing controversy on the relative role of VPD and SM in determining the ecosystem production efficiency, and different viewpoints were reported (Liu et al., 2020; Lu et al., 2020). These works highlighted the challenge and necessity for disentangling of respective effects of environmental factors on ecosystem processes (Lu et al., 2020). Since WUE is a key indicator linking plant productivity and water resources, quantifying the spatiotemporal variations in WUE and clarifying the dominant drivers could better understand the response of ecosystem to the current and future climatic conditions, and also improve the prediction of climate impacts on forest ecosystems (Jiang et al., 2022).

Differing from other subtropical drylands, China has the largest subtropical evergreen broadleaf forest which has been considered as an important carbon sink (Song et al., 2020). Meanwhile, subtropical China is sensitive to global changes and has experienced obvious regional climate change (Zhou et al., 2011). Generally, the climate changes including air temperature and precipitation patterns vary latitudinally and geographically, suggesting different effects of climate changes on subtropical forest water use (Schlaepfer et al., 2017), while related studies mainly focused on the arid and semi-arid regions (Qin et al., 2022; Jia et al., 2022). In addition, plantations had been widely planted to recover the degraded hilly lands since the 1980 s in South China.

Benefiting from the wide ecological niche, timber application, and fire resistance, the native species *Schima superba* is commonly planted and often regarded as a pioneer species for ecological restoration in barren hills, shrubs, and forests. However, how this species will perform trade-off between its water use and growth to adapt to the changing environment in a long term remains uncertain.

In this study, we collected the data of continuously monitored sap flow and periodically measured growth (in term of basal area increment, BAI) of *S. superba* trees, and local environmental factors during 2008–2021. The objectives were to investigate the temporal dynamic changes in transpiration, tree growth, and WUE of *S. superba* in such long-term experiment, and therefore, to clarify their dominant driving factors. Given the fact that the extension of dry season with more severe aridity has occurred in South China within the recent 30 years (Hu et al., 2018), we hypothesized that the local soil water availability, especially in the dry season, plays an equally important role as solar radiation and air temperature in determining transpiration, growth, and WUE of *S. superba*.

## 2. Materials and methods

### 2.1. Site description

The experiment was conducted in a *S. superba* plantation (planted in the mid-1980 s) located in the South China Botanical Garden, Guangzhou, Guangdong Province, China (23°10'N, 113°21' E) from January 2008 to December 2021. Characterized by a subtropical oceanic monsoon climate, Guangzhou has a mean annual temperature of 22 °C and receives mean annual precipitation of about 1700 mm. Generally, more than 75% of the precipitation fall in the wet season (from April to September), and less raining occurs in the dry season (from October to March of the next year). The *S. superba* trees were planted with an average plant spacing of 2.5 m × 2.5 m, and have experienced no human disturbance since planting. The current stand grows in a gentle slope with a density of 603 trees per hectare. The leaf area index of the plantation generally ranged from 3 to 4 m<sup>2</sup> m<sup>-2</sup>. Soil texture of the experimental site was loam, with a soil pH value of 3.95 ± 0.22 and topsoil (0–20 cm) organic matter content of 22.52 ± 4.61 g kg<sup>-1</sup>, respectively. The total nitrogen (N) content, available phosphorous (P) content, and available potassium (K) of the topsoil were 0.68 ± 0.27 g kg<sup>-1</sup>, 1.74 ± 0.57 mg kg<sup>-1</sup>, and 29.59 ± 9.27 mg kg<sup>-1</sup>, respectively.

### 2.2. Environmental parameters

The meteorological data, including net radiation (Rn, MJ/m<sup>2</sup>), air temperature (T, °C), relative humidity (RH, %), and precipitation (P, mm) were hourly recorded at a nearby meteorological station (Wushan Meteorological Station, about 2 km away from the experimental site). Vapor pressure deficit (VPD, kPa) was calculated from T and RH using the equation described in Campbell and Norman (1998) as follows:

$$VPD = a \times \exp(b \times T / (T + c)) \times (1 - RH) \quad (1)$$

where *a*, *b* and *c* are constants set to 0.611, 17.502 and 240.97, respectively. Daily potential evapotranspiration (PET) is estimated following the Hamon's method (Hamon, 1963; Federer and Brook, 1978):

$$PET = 0.1651 \times D \times V_d \quad (2)$$

where *D* is the time from sunrise to sunset in multiples of 12 h, and was also obtained from the Wushan Meteorological Station. *V<sub>d</sub>* is the saturated vapor density (g m<sup>-3</sup>) at the daily mean temperature (*T<sub>daily</sub>*) and is calculated by the equation of  $V_d = 216.7 \times V_s / (T + 273.3)$ . *V<sub>s</sub>* is the saturated vapor pressure (Mb) and is calculated by  $V_s = 6.108 \times \exp[17.26939 \times T / (T + 237.3)]$ . Once the estimated PET is obtained, we can calculate the monthly and annual P/PET (dryness index, Federer

and Brook, 1978; Zhou et al., 2015). Soil water content (SWC) was continuously monitored using three soil water probes (SM300, Delta-T Devices, Ltd., Cambridge, UK) that were buried at the depth of 30 cm beneath the soil surface.

### 2.3. Sap flow measurement

Total of twenty-one sample trees of good health and different diameters at breast height (DBH) in the experimental plot were chosen as the sample trees for the sap flow measurements. Sample tree distribution was displayed in [Supplementary Figure 1](#) according to an inventory survey within the experimental site. We used lab-made thermal dissipation probes (TDPs) according to the prototype of Granier's TDP to monitor the sap flux density. A pair of TDP sensors were, vertically 10–13 cm apart, inserted into the xylem of sample trees at the breast height (1.3 above the ground) and 2 cm deep on the north side of the stem. The upper probe consisted of a copper-constantan thermocouple and a heating element of constantan that was heated by a constant DC of 120 mA, while the lower one remained unheated and served as a temperature reference. The probes were covered by a plastic cover and an aluminum reflective foil to protect against mechanical disturbance, radiation and rain. The monitoring of sap flow was carried out from 2008 to 2021. Detailed information for the sap flow measurement was

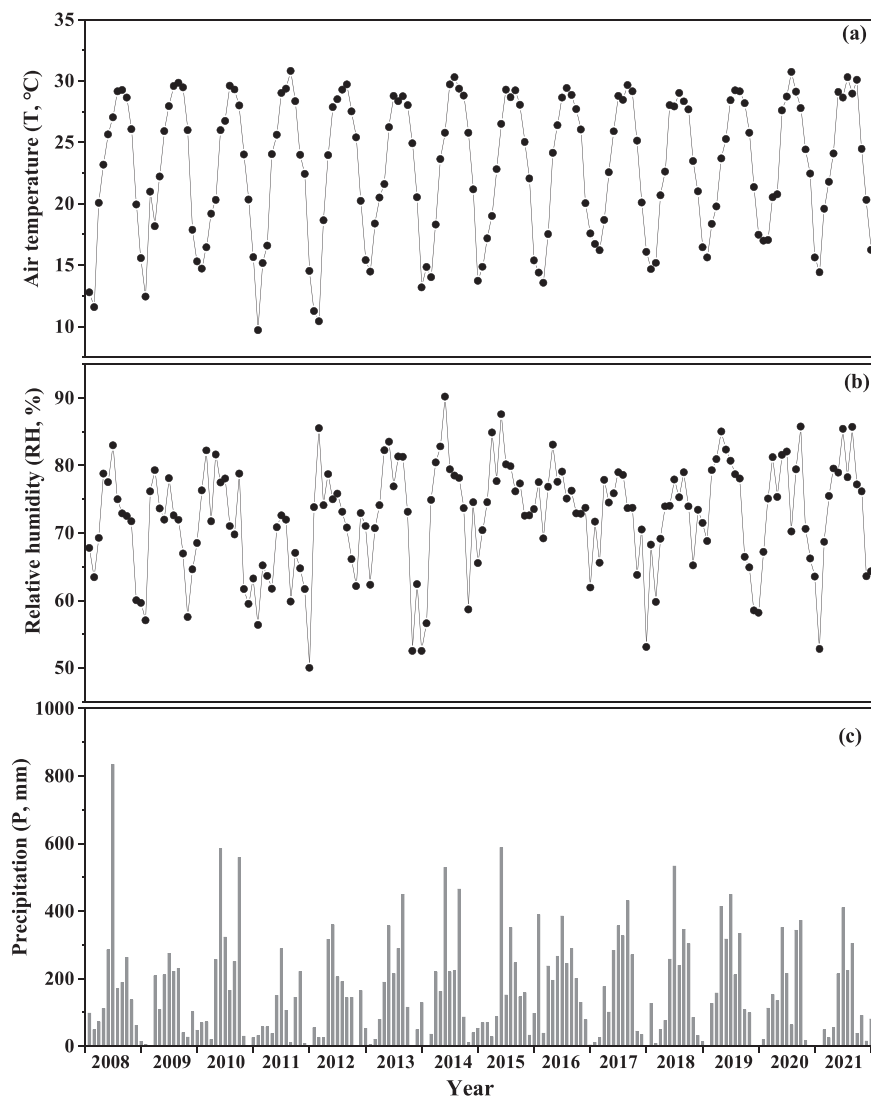
described in [Ouyang et al. \(2020\)](#), and the sap flux density ( $J_s$ ,  $\text{g H}_2\text{O m}^{-1} \text{s}^{-1}$ ) was calculated by the following equation ([Granier, 1987](#)):

$$J_s = 119 \left( \frac{\Delta T_m - \Delta T}{\Delta T} \right)^{1.231} \quad (3)$$

where  $\Delta T_m$  is the maximum temperature difference under zero-flux conditions, and  $\Delta T$  is the instantaneous temperature difference between the heated and the unheated probes. The original voltage difference (in proportion to the temperature difference) between the two probes were read every 30 s, and averaged every 10 min and recorded by a Delta-T data loggers (DL2e, Delta-T Devices, Ltd., Cambridge, UK), and then converted to  $J_s$  using Baseline 3.0 program.

### 2.4. Tree transpiration, tree growth, and water use efficiency

We chose seven non-sampled trees with different DBH within the plot and drilled wood cores using a borer of 5 mm in diameter. The sapwood depths were directly measured from the cores by distinguishing the different colors between sapwood and heartwood. The DBH and tree height (H) of sampled trees were annually hand-measured. The allometric equation between DBH and  $A_s$  was established and used to calculate the sapwood area of the sampled trees. We had performed a



**Fig. 1.** Mean monthly values of (a) air temperature (T), (b) relative humidity (RH), and (c) precipitation (P) during the experimental period of January 2008 - December 2021.

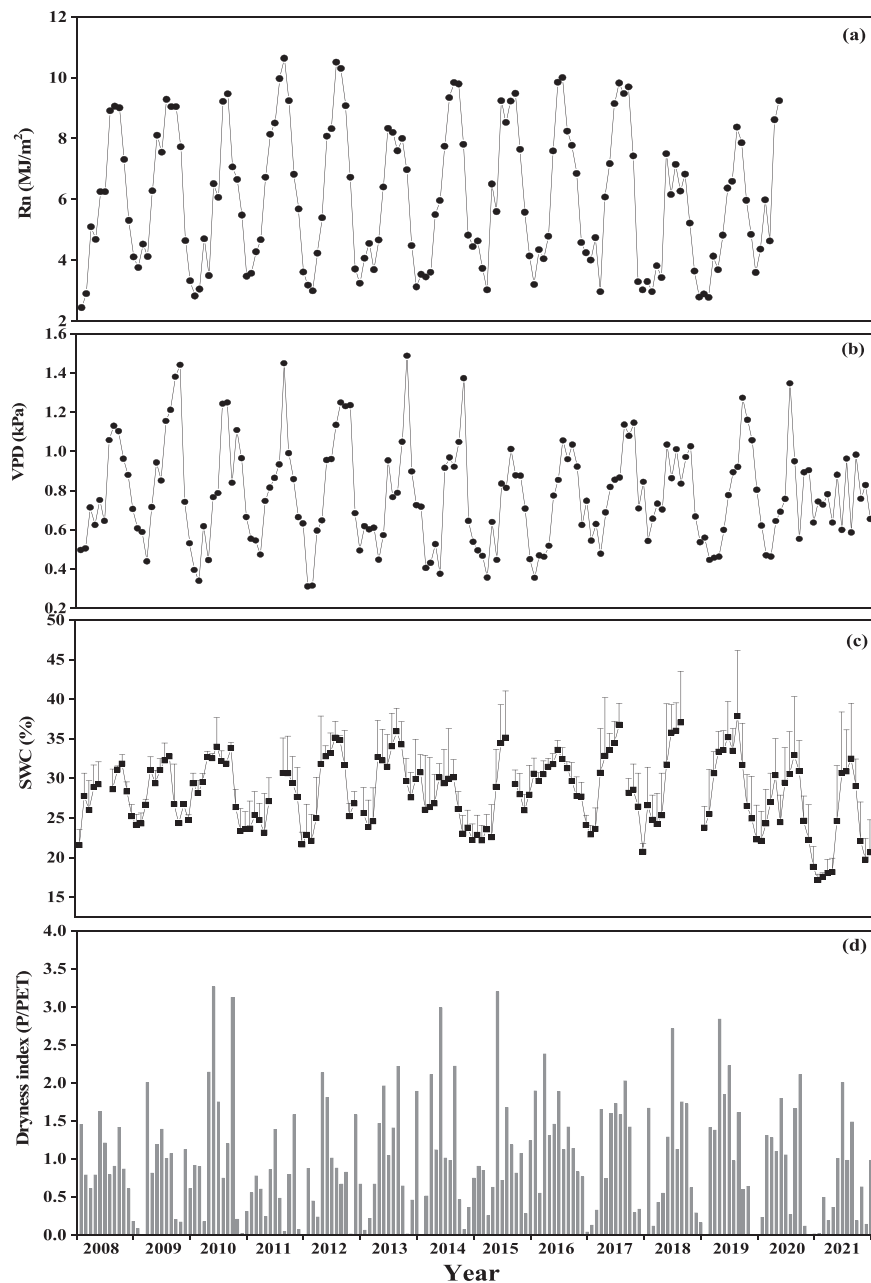


Fig. 2. Mean monthly values of (a) net radiation (Rn), (b) vapor pressure deficit (VPD), (c) soil water content (SWC), and (d) dryness index (P/PET) during the experimental period of January 2008 - December 2021. Rn data from May 2020 to December 2021 are not available because the Wushan Meteorological Station has not sorted out.

measurement to study the radial variation of sap flow of *S. superba*. The results at the same site showed that significant difference in  $J_s$  in different sapwood depths was observed ( $p < 0.0001$ ). The Duncan test results showed that the  $J_s$  of *S. superba* was similar when sapwood depth is less than 4 cm, but decreased to 45% of that at the most outer 0–2 cm depth when the sapwood depth was greater than 4 cm (Mei et al., 2010). Therefore, in this study the whole-tree transpiration was estimated by using the equation:  $E = J_{s(0-4\text{ cm})} \times A_s(0-4\text{ cm}) + 0.45 \times J_{s(>4\text{ cm})} \times A_s(>4\text{ cm})$ . To remove the effect of tree size on whole-tree transpiration, we adopted a normalized tree transpiration ( $E_t$ ) expressed as  $E/DBH$  proposed by Besson et al. (2014).

Data missing is a common and inevitable problem when conducting a long-term sap flow measurement due to probe or power failure. To fill the missing data, we firstly established the linear or exponential saturation regressions between the  $J_s$  and the monitored photosynthetically

active radiation (PAR) or VPD using the available data for every single tree within each month. The  $J_s$  and PAR readings were collected with 10-min resolution by the Delta-T data loggers at our own micro meteorological station on an observation tower within the stand, and thus the sample size of the data is large enough to establish the linear or exponential regressions with significant regression relationships ( $R^2 > 0.5$ ,  $p < 0.05$ ). Secondly, we calculated the missing  $J_s$  values based on the established regression equations. Lastly, the complete  $J_s$  data can be scaled up to obtain the monthly and annual transpiration.

Because of its smaller dependence on tree age, the annual basal area increment (BAI,  $\text{cm}^2 \text{ year}^{-1}$ ) is generally regarded as an indicator of tree growth (Battipaglia et al., 2013). Studies proposed that the BAI can increase the accuracy in the climate response of tree growth (Ding et al., 2021; Mohr et al., 2019). We calculated the BAI as follows:

$$\text{BAI} = \pi(r_n^2 - r_{n-1}^2) \quad (4)$$

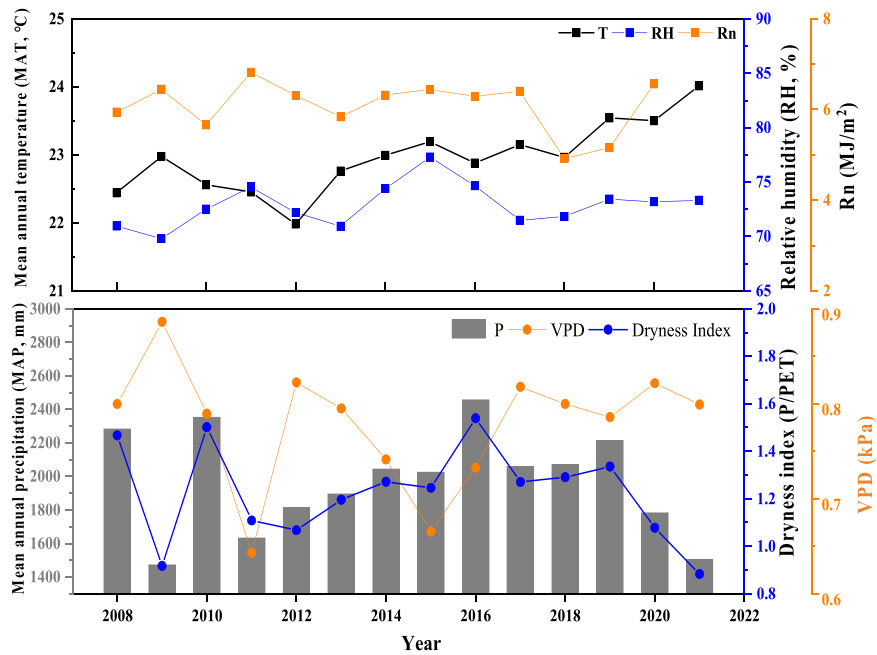


Fig. 3. Annual values of climatic variables derived from Figs. 1 and 2 during the time period of 2008–2021.

where  $r$  is the tree radius at breast height, and  $n$  is the year. Since it is strictly forbidden to cut down any trees in the South China Botanical Garden, the biomass of our sample trees was calculated by the allometric equation between tree biomass and DBH/H established from a *S. superba*

stand of similar age in the Heshan National Field Research Station of Forest Ecosystem ( $22^{\circ}41' N$ ,  $112^{\circ}54' E$ ), which is near Guangzhou city and shares a similar climate and soil conditions. Specifically, we fell down seven *S. superba* trees of different DBH at the station, measured the

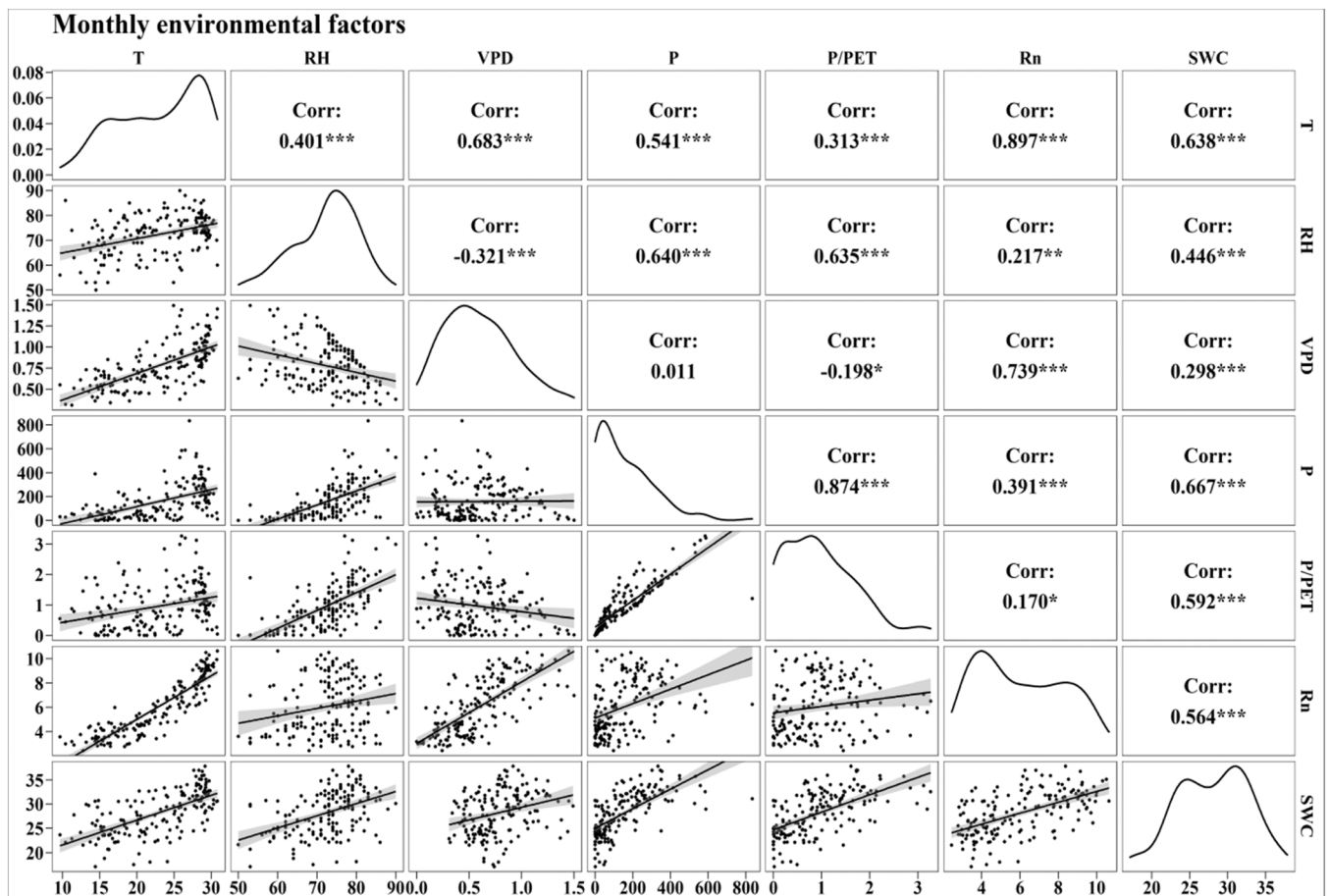


Fig. 4. Pearson correlation coefficient between the monthly environmental factors.



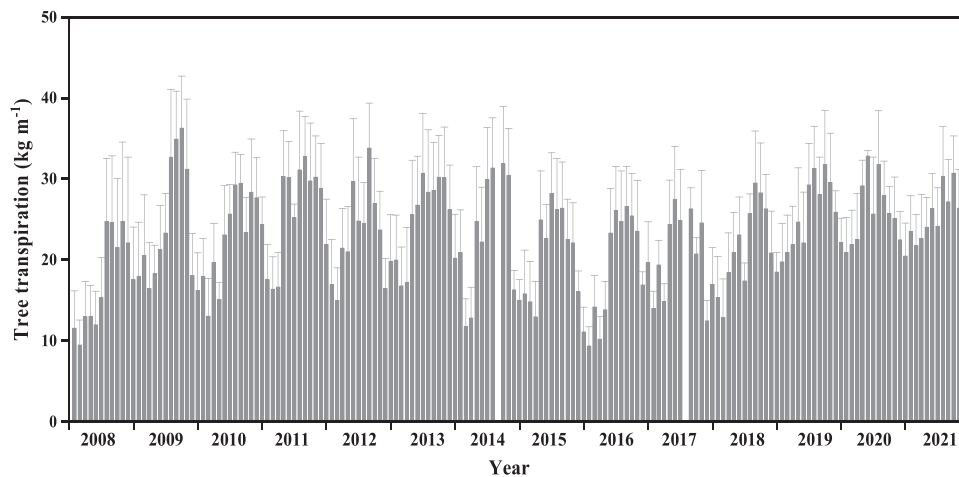


Fig. 5. Mean monthly transpiration of *Schima superba* during the experimental period of January 2008 - December 2021.

DBH, tree height (H), and oven-dried and weighed the leaf, stem, branch, and root biomass of the felled trees. Then, the allometric equations were established and listed as follows:

$$\text{Above-ground biomass} = 0.1521 \times (\text{DBH}^2 \cdot \text{H})^{0.8068} \quad (n=7, R^2=0.89) \quad (5)$$

$$\text{Under-ground biomass} = 0.0879 \times (\text{DBH}^2 \cdot \text{H})^{0.6701} \quad (n=7, R^2=0.91) \quad (6)$$

Therefore, we can calculate the biomass of sampled trees every year based on their DBH and H. Water use efficiency (WUE) was calculated as the ratio of the increment of whole tree biomass to the whole tree transpiration in every year ( $\Delta\text{Biomass}/E$ ).

### 2.5. Statistical analysis

Linear regressions were used to indicate the linear trends of mean annual temperature (MAT) and WUE, as well as the relationships between monthly transpiration/annual WUE and environmental factors during the whole experimental period. Pearson correlation coefficients were calculated among the environmental factors including T, RH, P, Rn, VPD, SWC, and P/PET. We conducted a series of redundancy analyses (RDA) according to a both-side selection option to clarify the dominant drivers on tree transpiration, growth, and WUE. Only the significant environmental variables identified in this process were included in subsequent analyses. The collinearity between the environmental variables usually complicates the assessment of environment-induced impacts on tree water use. Therefore, the collinear factors will be classified into two groups, namely "Heat group" and "Water group", to explore their combined effects according to the results of linear regression matrix. Specifically, those parameters that refer to the energy, such as net radiation and air temperature, were classified as "Heat group", while the relative humidity, soil moisture, and precipitation were regarded as "Water group" (Wang et al., 2011). Then, the variation partitioning was performed to obtain the partition variance of tree transpiration, annual BAI, and annual WUE. We plotted the environmental factors,  $E_t$ , BAI, and WUE by Origin 18.0. All the statistical analysis and related figures were conducted using R version 3.5.3 (R Development Core Team, 2018), and we denoted significant differences at  $p < 0.05$ .

## 3. Results

### 3.1. Environmental factors

The values of T, RH, P, Rn, VPD, and SWC in the wet season were generally higher than those in the dry season, showing clear seasonal variations during the whole experimental period (Figs. 1 and 2). The

MAT was between 22.0 and 24.0 °C, and the mean temperature ranged from 16.3 to 21.0 °C in the dry season and from 26.6 to 28.5 °C in the wet season, respectively. Mean annual precipitation (MAP) ranged from 1472 mm (2011) to 2457 mm (2016), and the precipitation in the wet season accounted for more than 70% of the annual total. The Rn in dry season ranged from 3.62 to 4.99 MJ m<sup>-2</sup> but increased to the values between 6.22 and 8.87 MJ m<sup>-2</sup> in the wet season. The largest and lowest averaged annual VPD occurred in 2009 and 2011, being 0.89 kPa and 0.64 kPa, respectively. Similar temporal changes of SWC were also observed. Resulting from the abundant rainfall, SWC reached the seasonal maximum of 28~35% during the wet months, whereas the values dropped to about 20% during the dry months. In terms of the annual dryness index (P/PET), we found only the year 2009 and 2021 experienced a value of less than 1, indicating a potential drought. Because of uneven distribution of the precipitation in the whole year, monthly P/PET showed an obvious seasonal variation, with potential drought mainly occurring in winter. Furthermore, the MAT during the period from 2008–2021 showed a significant increasing trend ( $p < 0.05$ ), while the other parameters just fluctuated within a certain range (Fig. 3). Pearson correlation coefficients showed the collinear relationships among the environmental variables (Fig. 4). The results indicated that T, VPD, and Rn were highly correlated with each other ( $p < 0.001$ ). Similarly, significant positive correlations were also presented among precipitation, relative humidity and dryness index, while the soil water content was mainly related to precipitation ( $p < 0.001$ ).

### 3.2. Tree transpiration, BAI, and WUE

Seasonal changes in  $E_t$  from 2008 to 2021 were shown in Fig. 5. Within every single year,  $E_t$  gradually increased to a seasonal maximum during the wet season, and then decreased due to unfavorable environmental conditions (water, light, or heat availability) and leaf senescence. The greatest tree transpiration usually occurred in the summer and early autumn (from June to October), reaching values of more than 30 kg m<sup>-1</sup>. Limited by the lower air temperature, soil moisture, and solar radiation,  $E_t$  values were generally lower during the winter, with values mainly ranging from 10 to 20 kg m<sup>-1</sup>. During the whole experimental period, the lowest annual whole tree transpiration occurred in 2008, while trees in 2011 had the strongest transpiration, and all the  $E_t$  values fluctuated between 200 and 310 kg m<sup>-1</sup> (Fig. 6a).

Annual DBH, H, and BAI experienced relatively significant increases throughout the experimental years (Fig. 6b and c). For example, the values of annual BAI were less than 30 cm<sup>2</sup> year<sup>-1</sup> at the early stage, while the increment values reached more than 30 cm<sup>2</sup> year<sup>-1</sup> during the recent 2 years. Due to the relatively stable tree transpiration and the increase in the biomass increment, annual WUE also significantly

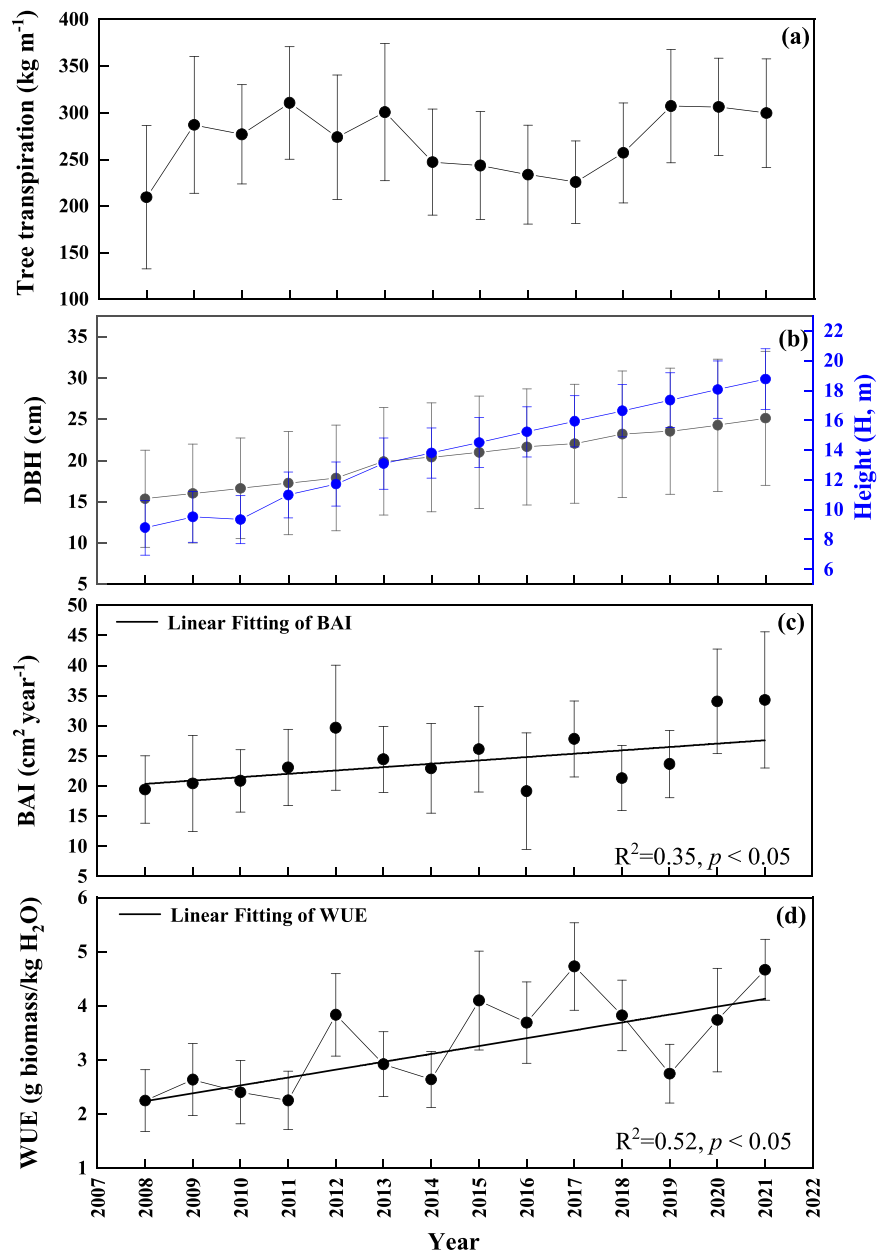


Fig. 6. a) Annual averaged tree transpiration, b) diameters at breast height (DBH) and height (H), c) basal area increment (BAI), and d) water use efficiency (WUE) of *Schima superba* from 2008 to 2021.

increased over the years (Fig. 6d,  $p < 0.05$ ). Results showed that the minimum WUE occurred in 2008 with values of  $2.25 \pm 0.57$  g biomass/kg H<sub>2</sub>O, while the WUE values have increased to  $4.73 \pm 0.81$  in 2017 and  $4.67 \pm 0.56$  g biomass/kg H<sub>2</sub>O in 2021, respectively.

### 3.3. Relationships of $E_b$ , BAI, and WUE with environmental factors

We established the linear relationships between monthly  $E_t$  and all environmental factors (Fig. 7). Results indicated significant positive correlations between monthly  $E_t$  and air temperature, VPD, Rn and SWC, with the  $R^2$  values ranging from 0.13 to 0.54 ( $p < 0.05$ ). Nevertheless, the linear relationships between transpiration and other factors, including precipitation, relative humidity, dryness index were not significant (data not shown).

Differing from monthly transpiration, annual BAI only presented significant linear correlations with air temperature and SWC in the dry season (Fig. 8,  $p < 0.05$ ). With smaller variations in annual VPD and Rn,

linear relationships were not significant between these factors and BAI. In addition, on the larger time scale, the linear regression relationships between annual WUE and most monitored environmental factors were not significant. Only annual mean air temperature and averaged SWC in the dry season showed significantly positive linear relationships with annual WUE, with  $R^2$  values between 0.34 and 0.59 (Fig. 9,  $p < 0.05$ ).

### 3.4. Variation partitioning analyses on $E_b$ , BAI, and WUE

Redundancy analysis (RDA) results showed that the T and RH were the main factors significantly affecting monthly transpiration, annual BAI, and WUE ( $p < 0.05$ ). According to the strong correlations of environmental variables shown in Fig. 4, we classified T and Rn as “Heat group”, and RH, P, and SWC as “Water group”. As presented in Fig. 10, when the variance of monthly transpiration was decomposed, the heat (T and Rn) and the water (RH, P, and SWC) variables accounted for an average variance of 50% and 9%, respectively. The shared effects of heat

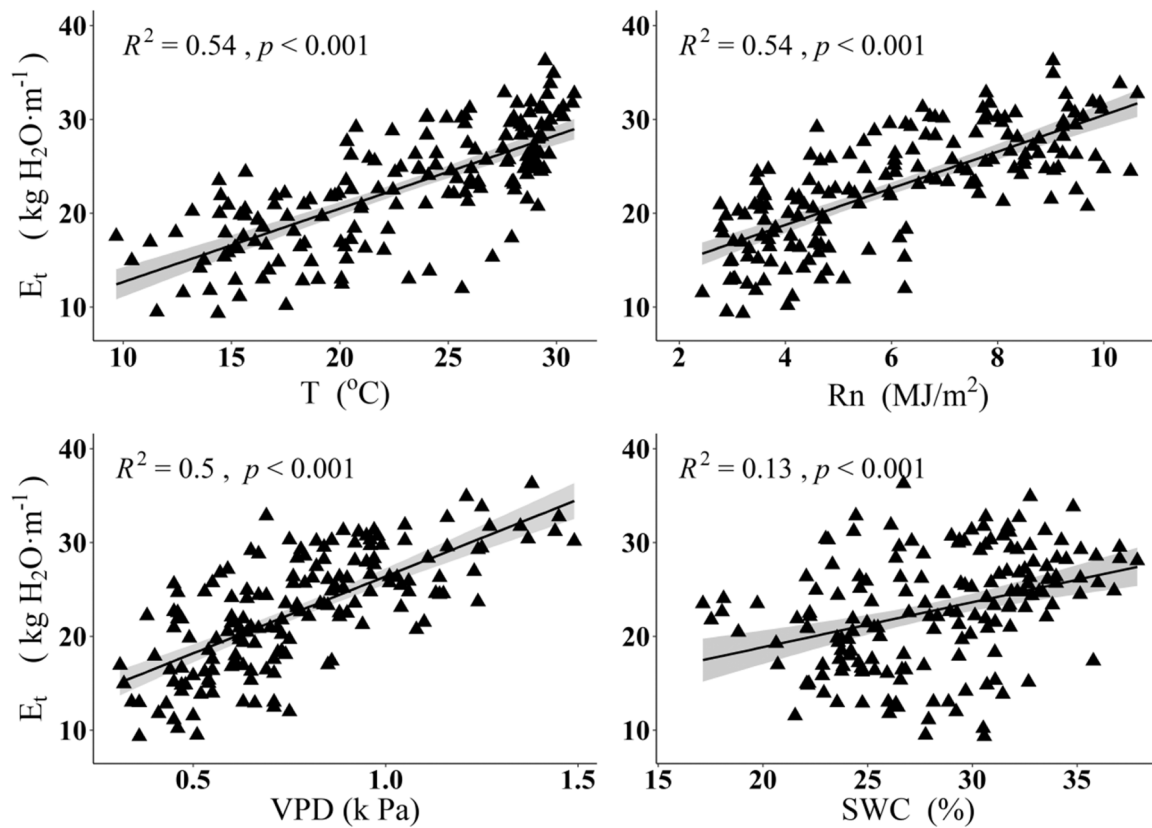


Fig. 7. Linear response of monthly transpiration ( $E_t$ ) to mean monthly air temperature ( $T$ ), net radiation ( $R_n$ ), vapour pressure deficit ( $VPD$ ) and soil water content ( $SWC$ ).

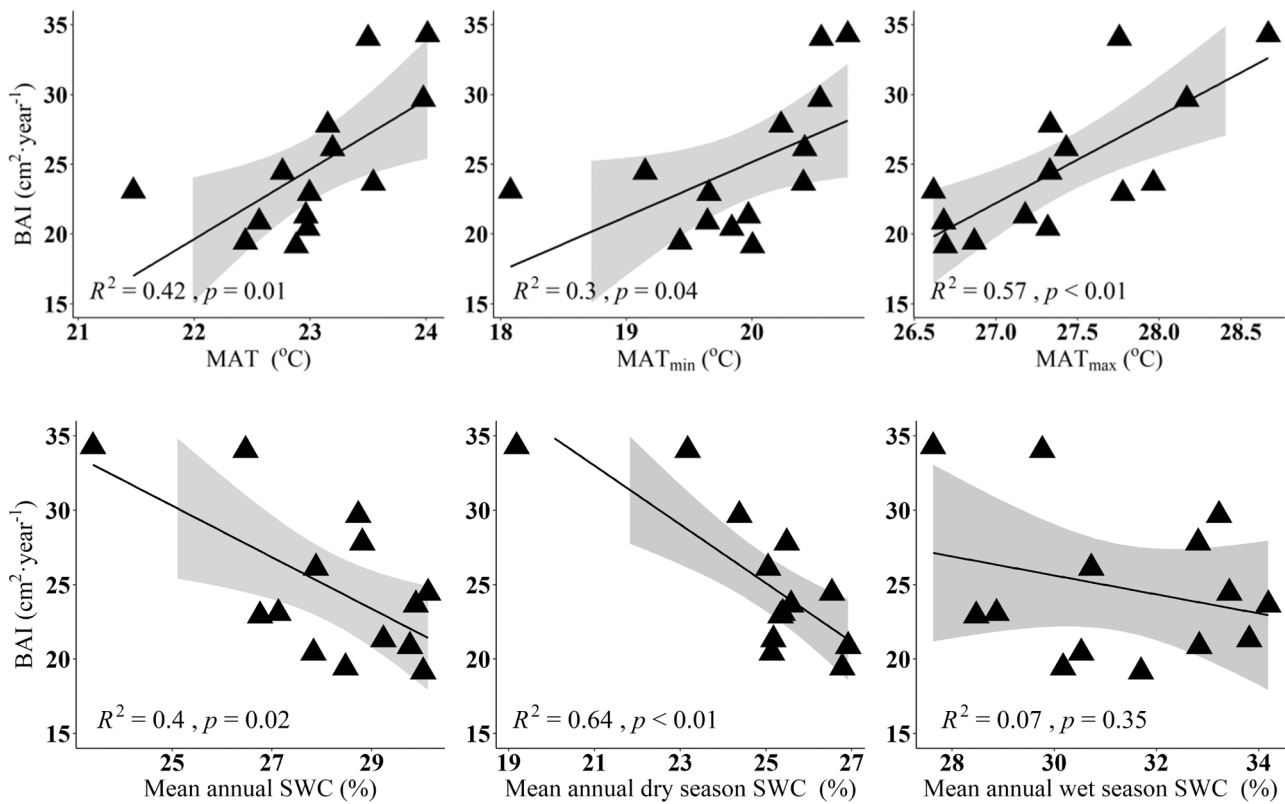


Fig. 8. Linear response of annual basal area increment ( $BAI$ ) to mean annual air temperature ( $MAT$ ), annual minimum temperature ( $MAT_{min}$ ), annual maximum temperature ( $MAT_{max}$ ), annual averaged soil water content ( $SWC$ ), as well as to averaged  $SWC$  in dry season and in wet season, respectively.



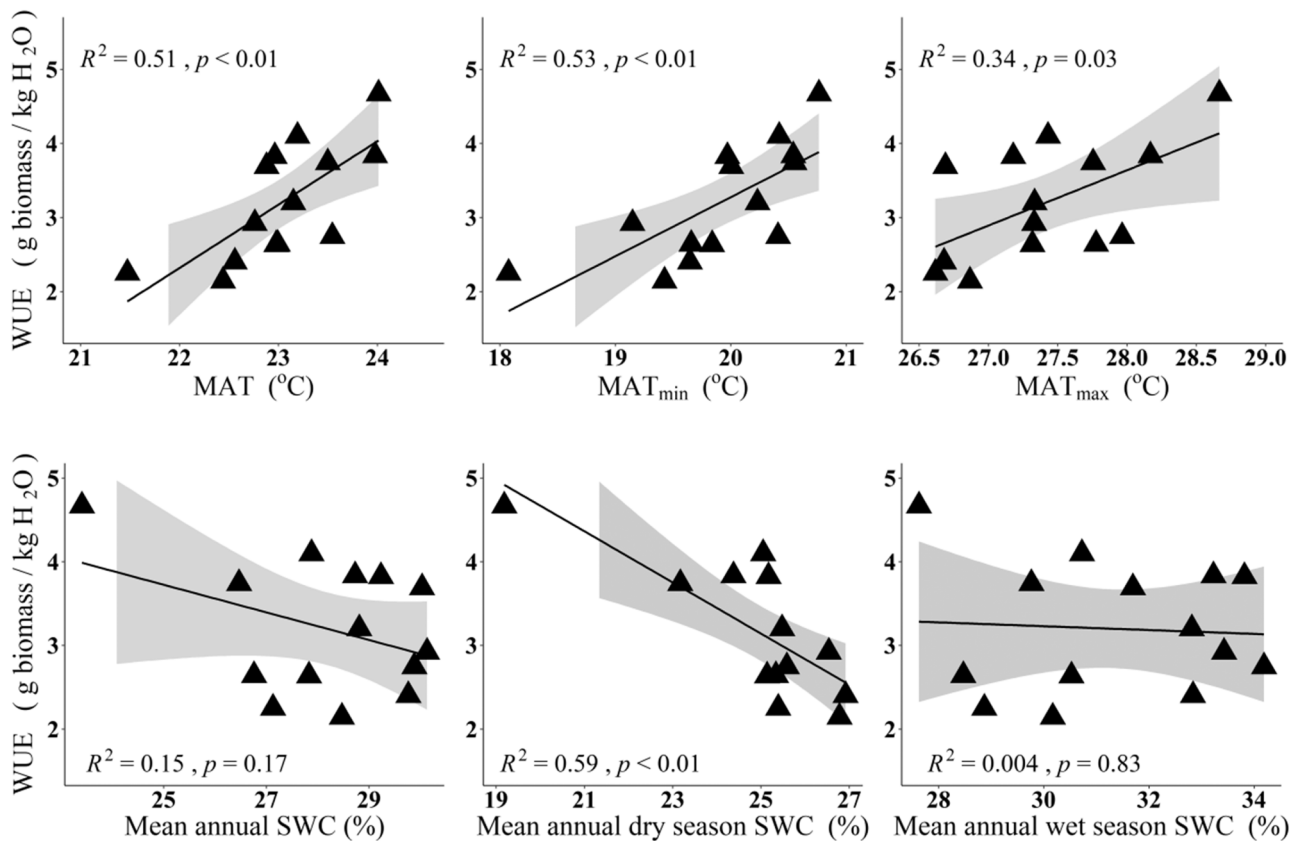


Fig. 9. Linear response of annual water use efficiency (WUE) to mean annual air temperature (MAT), annual minimum temperature ( $MAT_{min}$ ), annual maximum temperature ( $MAT_{max}$ ), annual averaged soil water content (SWC), as well as to averaged SWC in dry season and in wet season, respectively.

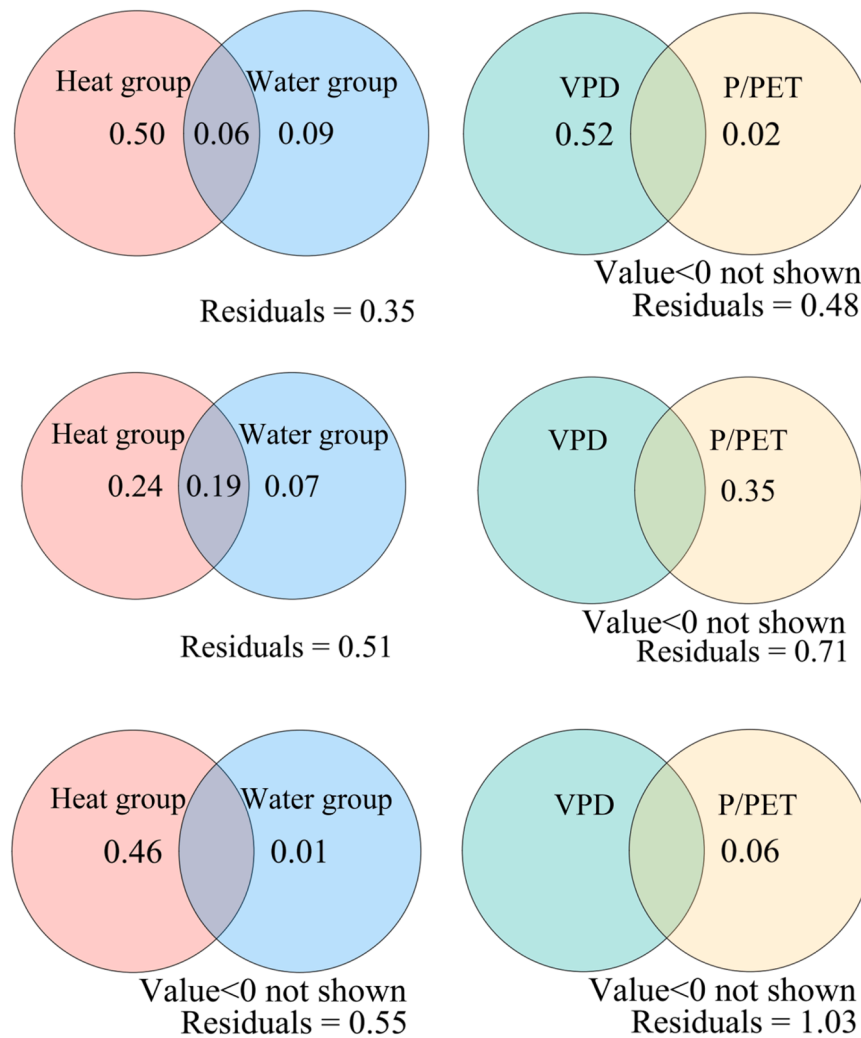
and water groups were 6% on the variance of  $E_t$ , and the amount of variation captured by all of the selected explanatory variables was collectively 65%. Since VPD and P/PET were calculated from the aforementioned factors, their effects were separately listed. Benefiting from the combination of T and RH, the explanation of VPD for  $E_t$  was relatively high with a value being 52%, while P/PET had weak individual effects and only explained 2% of the variation for monthly transpiration. In addition, the heat and water groups explained 24% and 7% of the variance of annual BAI, respectively, while VPD and P/PET just showed weak explanations. Similar to the effect on  $E_t$ , the heat variables still ranked as the greatest ones in influencing annual WUE with a contribution rate of 46%. Whereas, the water group had a weak individual effects (1%) on annual WUE and no shared effects were observed. Moreover, the proportions of variances of VPD and P/PET for WUE accounted for only 6% (Fig. 10).

#### 4. Discussion

In this study, the seasonal variation of transpiration could be attributed to the changing climatic and SWC conditions, which was supported by the established linear relationships between  $E_t$  and the related factors (Fig. 7). Under higher air temperature, more sufficient solar radiation, and sufficient soil water supply, trees generally transpired more water in the wet and the early stage of dry season, which in accordance with many previous studies (Obojes et al., 2018; Ouyang et al., 2022b). Differing from our hypothesis, the water-related factors such as precipitation rarely exerted significant explanation on tree monthly  $E_t$  from 2008 to 2021, implying no water limitation on *S. superba* plantations in this region. Moreover, the variation partitioning analysis highlighted the importance of heat factor, such as air temperature and net radiation, rather than the water factors on tree monthly transpiration. A similar result reported that these two variables were the

potential important predictors for the daily transpiration of tested tree species in Beijing in North China (Wang et al., 2011). Also, several studies have indicated that evapotranspiration was mainly driven by radiation in humid regions (Jiang et al., 2022; Aguilos et al., 2019). The most reliable explanation for our results could be attributed to the regional climatic characteristics. On one hand, water is the main limiting factor for forests in semi-arid and arid areas. Reduced precipitation and decreased soil moisture generally resulted in less transpiration (Grossiord et al., 2018; Wang et al., 2017; Pangle et al., 2015). However, in our study, the abundant precipitation (total annual precipitation ranging from 1400 mm to 2300 mm) keeps the SWC values around ~20% even in dry seasons, which were still higher than those of arid areas. On the other hand, our previous study showed that *S. superba* trees have roots as deep as 50 ~60 cm and were proved to be able to take advantage of deeper soil moisture (40 ~ 60 cm) under dry conditions according to the estimated xylem water  $\delta^{18}O$  values (Ouyang et al., 2020). Therefore, the plenty of rainfall and the ability to utilize deep soil water make the water-related factors less crucial and thus highlight the role of the heat factors.

A remarkable result in our study is that the tree BAI positively and negatively responded to the MAT and SWC, respectively ( $p < 0.05$ ). The heat and water groups accounted for 19% shared effects on the variance of BAI, suggesting a combined effect of water and heat. Both positive and negative effects of air temperature on tree growth have also been reported (Jia et al., 2022; Dixit et al., 2022; Chen et al., 2022; Fu et al., 2020). For instance, air temperature is the main limiting factor for tree growth in permafrost regions (Zhang et al., 2016; McMahon et al., 2010), and thus, an extension of the growing season caused by the increase in temperature can facilitate tree growth (Oishi et al., 2018). Jia et al. (2015) also proposed that a warmer climate accompanied by less water stress at the end of the growing season can benefit carbon storage for the following growing season. In our case, with abundant rainfall and



**Fig. 10.** Individual and shared effects of “Heat group”, “Water group”, vapor pressure deficit (VPD), and dryness index (precipitation/potential evapotranspiration, P/PET) on tree transpiration (the upper row), annual basal area increment (BAI) (the middle row), and annual water use efficiency (WUE) (the bottom row) as derived from variation partitioning analysis.

the above-mentioned ability to utilize deep soil water, a higher temperature can promote *S. superba* trees to capture carbon resources for biomass increment even in the autumn and winter, and the carbon storage might facilitate the formation of the earlywood in the next year (Litton et al., 2007). The sufficient radiation in the Autumn is also conducive to the wood growth of trees, which was confirmed by a dendroecological study in the same area of this research (Li et al., 2020). The relatively favorable environment finally leads to the positive effect of air temperature on the tree growth of *S. superba*. However, the negative relationship between BAI and SWC was unexpected, and a similar result was observed by Xie et al. (2016) who reported a negative relationship between precipitation and gross ecosystem production in spring. Also, Zuidema et al. (2022) conducted a pantropical tree-ring network research and found a weak negative response of tree growth to precipitation occurring at sites with relatively high water availability. Research has proposed that the negative response may reflect radiation limitation of photosynthesis, as the radiation limitation is thought to occur when MAP > 2000 mm (Wagner et al., 2016), in other words, frequent cloudy and rainy weather reduced the stomatal opening and, therefore, decreased the CO<sub>2</sub> uptake. Despite the unexpected result, we tend to think that it was the MAT, not the SWC, dominated the change in BAI. Such effect of SWC on annual BAI is likely to be overestimated due to the reason of scale effect (i.e., annual growth) and was supported by the fact that only 1% of the variation on BAI explained by water factors.

Unlike the previous studies which reported the decoupled relationship between BAI and WUE (Giguere-Croteau et al., 2019; Lévesque et al., 2014), we found that both BAI and WUE experienced an increasing trend throughout the experimental period. Researchers attributed the decoupling of BAI with WUE to the more vulnerable xylem conduits and the unsustainable growth resulting from the low carbon assimilation rate (Zadworny et al., 2019), as well as the inaccessibility of deep water under water-limited conditions (Jia et al., 2022). However, such conditions hardly occurred in our study. As shown in Fig. 5, the transpiration of *S. superba* remained relatively vigorous especially in the recent three years (2018–2021) even in the dry season. Meanwhile, proved by the values of SWC and the previously measured root depth, the *S. superba* was less likely to suffer from a severe drought compared with those species of other studies. As a result, *S. superba* was able to maintain relatively stable transpiration, promote the increase of WUE, and ultimately improve its growth even under the condition of dry season (Fig. 6). Similar to the BAI, annual tree WUE was positively correlated with the MAT, but negatively correlated with SWC in the dry season (Fig. 9), confirming the viewpoint stressing the role of dry-season climate variability in driving the trade-off between tree water use and growth (Zuidema et al., 2022). It is widely accepted that decreased soil water can lead to tight stomatal control and limited transpiration rates (Fu et al., 2020). Trees are prone to improve the WUE to cope with the potential drought when soil water supply decreases. While the increase

of MAT increased biomass as previously discussed, and consequently led to higher WUE values under such conditions (Urrutia-Jalabert et al., 2015). The responses of tree growth and transpiration to environmental variables over a long term determined the variations in WUE, and the heat factors also showed a relatively stronger explanation for the WUE compared with the water factors (Fig. 10). Therefore, we proposed that in rainy South China, air temperature and solar radiation that explained more variance variability in  $E_t$  played more important roles in regulating the tree's water use efficiency.

Climate changes have induced a warmer atmosphere and obvious changes in rainfall patterns. The observed correlations between climate and typical tree species' growth at a given climatic zone are often used to estimate tree health and growth in the future (Charney et al., 2016). Whether the potential benefits of high WUE can offset the negative impacts of climate change remains uncertain (Friedlingstein et al., 2013). This study provided 14 years of monitored data about the water transpiration and growth of the native *S. superba* trees and the responses to the climate factors and soil water content. Differing from our hypothesis, the results emphasized the importance of heat factors especially air temperature to tree water use, growth, and WUE, and possible reasons were due to the climate condition in South China and the water use strategy of *S. superba*. In addition, the increasing trend of BAI indicated the *S. superba* is still in a good situation under current climatic conditions as proposed that trees' BAI trend would not decrease unless trees begin to senesce (Duchesne et al., 2003; Jia et al., 2022). Owing to the relatively deeper root depth and the sufficient soil water supply in South China, we can expect that *S. superba* could have an advantage in maintaining its growth when facing the possibly prolonged drought and small increases in atmospheric temperature in the future. Further research should focus on the sensitivity of the functional traits, especially those related to photosynthesis and water use efficiency, of typical tree species to the climatic and environmental drivers (Bauman et al., 2022).

## 5. Conclusion

Our study investigated the sap flow-based transpiration, tree growth, and water use efficiency of the native *S. superba* plantation during the period from 2008 to 2021 in subtropical South China. The annual transpiration was vigorous and fluctuated, while the BAI and WUE showed a significant increase trend during the whole period. The temporal change of monthly  $E_t$  has been affected by a variety of environmental factors, such as air temperature,  $R_n$ , VPD, and SWC. The annual BAI and WUE presented significant linear regressions with MAT and SWC in the dry season. We have demonstrated the significant effects of T and RH on  $E_t$ , BAI, and WUE, and divided the environmental factors into two groups "Heat group" and "Water group" based on their Pearson correlations. The variation partitioning analysis indicated that the heat factors including air temperature and solar radiation explained larger variations of  $E_t$ , BAI, and WUE than the water factors, whereas the VPD and dryness index rarely influence the BAI and WUE. Therefore, our results suggested that it was the heat factors, especially air temperature, rather than the water factors that regulate the tree transpiration, growth, and WUE of *S. superba*. Additionally, due to the advantages in obtaining deeper soil water, the *S. superba* trees can deal with the current climate conditions such as uneven distribution of rainfall to maintain their growth. The climate responses of the typical subtropical tree growth and WUE elucidated from this study can enhance the understanding of how the water- and carbon-related plant physiological processes will respond to the future climate dynamic changes.

## Declaration of Competing Interest

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

## Data Availability

Data will be made available on request.

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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.agwat.2022.107902.

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