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Sap flow dynamics of co-occurring trees in response to seasonal droughts in a subtropical climate

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Introduction: Climate change and extreme rainfall events pose significant challenges to water use strategies for forest species in subtropical regions. Increased degrees of drought and significant seasonal precipitation differences in recent decades in Yunnan Province, China, have exposed forests to high mortality rates. Therefore, there is an urgent need to understand the water use strategies of plants to help develop relevant forest conservation measures in this region.

Methods: In this study, we selected three co-occurring woody species (*Pinus yunnanensis*, *Keteleeria evelyniana*, and *Castanopsis delavayi*). We continuously monitored their sap flow and water potential, as well as environmental factors, to reveal plant water use strategies and to determine how water use strategies relate to environmental factors and vegetation traits.

Results: The results of this study revealed that seasonal water use strategies of plants were significantly different ($P < 0.01$), with J_s lower in the dry season than in the wet season, while the $J_s/J_{s,n}$ was significantly higher in the dry season. Plant water use responded to seasonal environmental factors similarly. SWC was the main limiting factor for J_s in the dry season, and there was a positive correlation between $J_{s,n}$ and VPD; when SWC was sufficient in the wet season, VPD and PAR were the main factors on J_s , and there was a negative correlation between $J_{s,n}$ and VPD. In addition, $J_{s,n}$ during the dry season consisted of E_n and R_e , and E_n accounted for a high percentage (more than 60%). Finally, there are differences in the water use strategies of different species, with *Pinus* having less tight stomatal control in the dry season, possibly related to its deeper roots and relatively smaller leaf area.

Discussion: These findings on the water use strategies and environmental responses of different species complement our knowledge of survival strategies in subtropical forests and provide valuable advice for forest management.

KEYWORDS

subtropical monsoon climate, seasonal drought, sap flow density, water regulation strategies, soil water moisture, vapour pressure deficit

1 Introduction

Against the background of global climate change, interannual or seasonal variability strongly impacts the processes of ecosystem water cycling. Previous studies have highlighted that the variability in precipitation amount, frequency and seasonal distributions has significantly changed during the past several decades (Domingo et al., 2011; Jia et al., 2016; Tarin et al., 2020). This variability could induce soil moisture fluctuations, and thus affect ecosystem processes and functions (Robertson et al., 2008; Niu et al., 2011; Verduzco et al., 2015). Transpiration, the principal pathway for plant water loss, closely couples terrestrial water cycling and energy balance (Ungar et al., 2013; Kumagai et al., 2014) and plays a critical role in the water budget of forest ecosystems (Siegert and Levia, 2011). Although several studies have quantified and compared tree transpiration amongst a diverse range of species at different sites (Yan et al., 2018; Lyu et al., 2020; Kassahun and Renninger, 2021), studies on the differences in transpiration among co-occurring tree species in subtropical forests are rare.

Sap flow is largely influenced by environmental factors, such as air temperature (T_a), photosynthetically active radiation (PAR), relative humidity (RH), water vapour pressure deficit (VPD), soil water moisture (SWC) and wind speed (WS) (Asbjornsen et al., 2007; Loranty et al., 2008; Chen et al., 2018; Hayat et al., 2020). The stomatal conductance is ultimately controlled by these factors. Usually, low or decreasing light, decreasing external humidity and different abiotic stresses, including low temperature and drought stress with reduced cellular water availability, will promote stomatal closure (Zhang et al., 2021; Yang and Qin, 2023). By contrast, high or increasing light, higher humidity and temperature can promote stomatal opening (Zhang et al., 2024a).

In addition, different species may exhibit different stomatal regulation strategies in changing environments (Kannenberg et al., 2021; Wright et al., 2024), with some species showing stronger stomatal control being described as isohydric plants, which reduce plant transpiration at the expense of reduced carbon gain. Other species with less stomatal control are described as anisohydric plants, which regulate transpiration more loosely and are therefore at higher risk of hydraulic damage (Jones and Raynal, 1986; Tardieu and Simonneau, 1998; McDowell et al., 2008). Strong correlations between iso-anisohydric stomatal behaviour and traits, such as specific leaf area (SLA), embolism resistance, woody density and root water uptake depth (Chen et al., 2021; Kaproth et al., 2023). SLA is an important leaf trait (White and Scott, 2006; Hulshof et al., 2013) and is intimately linked to water use strategies (Boucher et al., 2017). It is often applied to evaluate the performance of plants under drought conditions. Strategies with smaller SLA can improve stress resistance and competitive ability in poor environments (Westoby et al., 2002; Long et al., 2011). Root water uptake depth is an important part of

plant water adaptation strategies, it is generally accepted that the different plant water uptake depth is associated with leaf water potential for their water use strategies (Liu et al., 2021). The species with shallower water uptake depth usually exhibited the larger diurnal ranges of leaf water potentials for their transpiration (Ding et al., 2020).

Nocturnal sap flow density ($J_{s,n}$) has contributed to improved tree growth (Caird et al., 2007) and avoidance of tree mortality due to hydraulic failure (Klein et al., 2018; Zeppel et al., 2019). $J_{s,n}$ is influenced by the interaction among several environmental factors, including temperature (T), VPD , wind speed (WS), and soil water content (SWC) (Zeppel et al., 2014; Siddiq and Cao, 2018; Hayat et al., 2021). The temperature can directly affect the rate of $J_{s,m}$ whereas the VPD indirectly regulates $J_{s,n}$, mainly by affecting plant leaf transpiration (Wang et al., 2016). The WS not only affects the rate of evaporation from the plant leaf surface (Schymanski and Or, 2016) but also affects sap flow density by the generation of mechanical stress (Zhao and Fan, 2024). The soil water content determines the effective amount of soil water that can be absorbed by trees (Di et al., 2019). $J_{s,n}$ comprises nocturnal transpiration (E_n) and stem refilling activities (R_e) following daytime water depletion, either occurring alone or concurrently (Daley and Phillips, 2006; Caird et al., 2007; Forster, 2014). Different effects of environmental factors on E_n and R_e also lead to different responses of $J_{s,n}$ to environmental factors. Therefore, we must combine these factors and consider the differences between species (Phillips et al., 2010; Zeppel et al., 2010) to more accurately reveal the formation pattern of $J_{s,n}$.

Despite the increasing research documenting plant transpiration and its relationship with environmental factors, studies on the plant transpiration of the subtropical forest in Yunnan Province of China were rare. This region has a typical “southern subtropical dry and hot valley” climate, with a clear distinction of wet and dry, and is continuously subjected to up to half a year of drought (Luo et al., 2016; Li et al., 2019), which allows for a deeper study of the response of plant transpiration to environmental changes. In addition, this region is a popular area for global biodiversity research with very rich forest types (Pu et al., 2007; Qian et al., 2020), providing more possibilities to better understand the differences in transpiration responses of different species. Under such a situation, we chose the mixed forest formed by *Pinus yunnanensis* with other conifers and broadleaf trees as the research object to study the survival strategy of different species in typical seasonal drought. We investigated the water potential and sap flow changes and along with concurrent observations of climatic variables and the soil water content (SWC) in an experimental forest stand. The objectives of this study were to (1) differentiate the water use strategies in response to seasonal drought among different woody species; (2) identify the distinct meteorological drivers influencing J_s in different species during both the wet and dry seasons; and (3) quantify the composition and use pattern of $J_{s,n}$ of the different tree species during both the wet and dry seasons.

2 Materials and methods

2.1 Site description

The study site is located at the top of Shasongpo in Yongren County, Chuxiong Yi Autonomous Prefecture, northern Yunnan

Abbreviations: J_s , sap flow density; $J_{s,n}$, nocturnal sap flow density; E_n , nocturnal transpiration; R_e , stems refilling activities; Ψ_{leaf} , leaf water potential; $\Psi_{predawn}$, predawn water potential; Ψ_{midday} , midday water potential; T , temperature; VPD , vapour pressure deficit; R_a , solar radiation; P , precipitation; WS , wind speed; SWC , soil water content; DBH , diameter at breast height.

Province (101°43'26"E, 26°5'53"N) (Figure 1), with a southern subtropical monsoon climate. The average rainfall in the study site was 840 mm, the average temperature was 22.6°C, the extremely high temperature on record was 43°C, and the average annual sunshine was 2534h (Zhang et al., 2024b). The site is dominated by the *Pinus yunnanensis* forest, which, in addition to *Pinus yunnanensis*, are accompanied by three species of trees, *Keteleeria evelyniana*, *Castanopsis delavayi*, and *Quercus franchetii*. The *Quercus* in the site were shrubs with numerous tillers, so three other trees were selected for the monitoring study (Table 1).

2.2 Environmental parameters

An integrated ATMOS 41 weather station (METER Group Inc., USA) was mounted on a forestry building at a distance of 100 m from the sample plot. The weather station was programmed to capture meteorological data once every 30 minutes. The observation parameters included solar radiation (R_a , $W \cdot m^{-2}$), precipitation (P , mm), air temperature (T_a , °C), WS ($m \cdot s^{-1}$), photosynthetically active radiation (PAR) ($\mu mol \cdot m^{-2} \cdot s^{-1}$), and VPD (kPa).

The soil volumetric water content was measured every 30 min at depths of 10 and 30 cm in this site via a Hydra Probe II device (Stevens Water Monitoring System, Inc., Portland, OR, USA). The sensors were inserted horizontally into the soil. Measurements were obtained every 10 s, and the 30-min averages were recorded via CR1000 data loggers (Campbell Scientific Inc., Logan, UT, USA). The SWC values ($m^3 \cdot m^{-3}$) analysed in this study were the average measurements at the depths of 10 and 30 cm.

2.3 Xylem water potential

We examined the xylem water potential of the three species (*Pinus*, *Keteleeria*, and *Castanopsis*). Measurements were conducted from December 2022 to May 2023 (dry season) and from July 2023 to November 2023 (wet season). 3–5 trees of each species were measured with a pressure chamber (PMS, Albany, OR, USA). The predawn water potential (Ψ_{pd}) measurements were taken before sunrise (between 05:30 and 06:30), and midday water potential (Ψ_{md}) measurements were taken between 12:00 and 14:00 on the same day. We measured water potential in samples of branches with leaves (*Keteleeria*, *Castanopsis*: because the petiole of leaves is not long enough to fit in the sample holder of the pressure chamber) or leaves (*Pinus*). We used plastic bags and aluminum foil to wrap branches after sunset on the day before measurements; such operations reduced water loss by transpiration and thus equalised the water potential between leaves and branches. Samples were cut and water potential measurements were taken at the site within 15 minutes.

2.4 Sap flow measurements

The sap flow density (J_s) was measured via heat dissipation probes (Granier, 1987), and four individuals of the three species

selected in the study site were instrumented with two thermal dissipation probes (TDPs) mounted at the height of 1.3 m, with a distance of 10 cm between them. To avoid direct sunlight, the sensors were positioned on the shaded side of the trees and covered with radiation protection film. The instantaneous temperature difference between the probes was converted into a voltage value that was recorded via a data logger (Campbell Scientific Inc., Logan, UT, USA). The sap flow data were measured automatically at 30-minute intervals from January 2023 to December 2023.

As a measure of water exchange, sap flow density ($g \text{ H}_2\text{O} \cdot m^{-2}$ sapwood area $\cdot s^{-1}$) was calculated based on an empirical calibration equation (Granier, 1985). Granier found that:

$$J_s = 119 \times 10^{-6} (K^{1.231})$$

where J_s is sap flow density ($m^3 \cdot m^{-2} \cdot s^{-1}$) and K is related to the temperature difference between the two probes:

$$K = \frac{(\Delta T_{max} - \Delta T)}{\Delta T}$$

where K is the sap flow index, ΔT is the temperature difference between heated and reference probe and ΔT_{max} is the temperature when there is no sap flow density ($J_s = 0$).

According to the empirical relationship between sap flow density and the temperature difference between probes established by Granier and revalidated by other researchers (Granier, 1985, 1987; Du et al., 2011), the sap flow density (J_s , $g \cdot m^{-2} \cdot s^{-1}$) was calculated as follows:

$$J_s = 119 \times \left(\frac{\Delta T_{max} - \Delta T}{\Delta T} \right)^{1.231}$$

where ΔT (°C) is the temperature difference between the heated and reference probes, and ΔT_{max} is the maximal temperature difference between the two probes, which was determined as the maximum value of daily ΔT_{max} over a 7–10 day period to avoid the underestimation of the nighttime sap flow (Lu et al., 2004).

2.5 Partitioning of nocturnal sap flow density refilling and nighttime transpiration

J_s was separated into daytime sap flow density ($J_{s,d}$) and nocturnal sap flow density ($J_{s,n}$) components according to solar radiation (R_a) value greater than or less than $5 \text{ W} \cdot m^{-2}$ (Daley and Phillips, 2006). To distinguish the contributions of stem refilling (R_e) and nighttime transpiration (E_n) to the nocturnal sap flow density, the 'forecasted refilling' approach was adopted in this study (Fisher et al., 2007; Yu et al., 2018). This is a time separation method where the declining portion of the diurnal course of J_s is extrapolated forward in time until it reaches zero flow, as expected if there was no nocturnal water loss, thus the area below this forecasted curve is an estimate of refilling (R_e) (Fisher et al., 2007). In turn, the area above the forecasted curve and all $J_{s,n}$ observed after this curve has reached zero, indicates nocturnal water loss (E_n) (Fisher et al., 2007). The proportion attributable to E_n was then calculated as the area above the forecasted refilling curve divided by the total $J_{s,n}$.

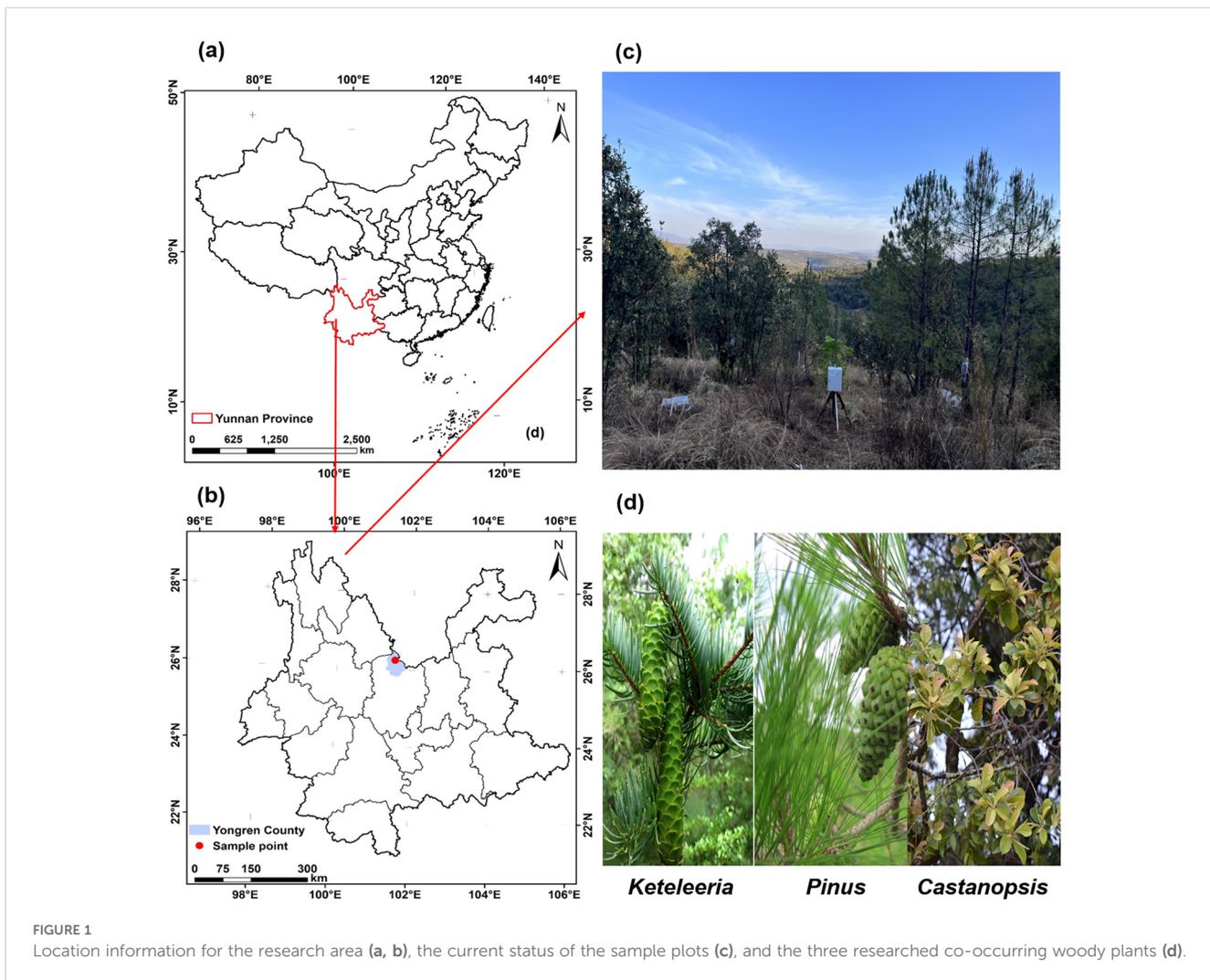


FIGURE 1 Location information for the research area (a, b), the current status of the sample plots (c), and the three researched co-occurring woody plants (d).

TABLE 1 Biometric characteristics of the sap flow sampling trees.

| Species | Group | Leave history | Height (m) | Diameter (cm) |
|-----------------------|------------|---------------|------------|---------------|
| <i>Keteleeria</i> -1 | Gymnosperm | Evergreen | 5.5 | 22.6 |
| <i>Keteleeria</i> -2 | Gymnosperm | Evergreen | 6.4 | 21.3 |
| <i>Keteleeria</i> -3 | Gymnosperm | Evergreen | 5.6 | 22.6 |
| <i>Keteleeria</i> -4 | Gymnosperm | Evergreen | 6.9 | 24.2 |
| <i>Pinus</i> -1 | Gymnosperm | Evergreen | 6.9 | 25.1 |
| <i>Pinus</i> -2 | Gymnosperm | Evergreen | 6.3 | 18.1 |
| <i>Pinus</i> -3 | Gymnosperm | Evergreen | 7 | 19.1 |
| <i>Pinus</i> -4 | Gymnosperm | Evergreen | 7.8 | 20.9 |
| <i>Castanopsis</i> -1 | Angiosperm | Evergreen | 5.5 | 15.8 |
| <i>Castanopsis</i> -2 | Angiosperm | Evergreen | 7.8 | 19.4 |
| <i>Castanopsis</i> -3 | Angiosperm | Evergreen | 4.4 | 17.0 |
| <i>Castanopsis</i> -4 | Angiosperm | Evergreen | 7.1 | 18.3 |

To construct the forecasted curve, we fitted an exponential decay ($J_s(t) = J_s(0) e^{-kt}$) based on the trend of $J_{s,n}$ over time on a typical sunny day in winter, where $t = 0$ was 2 h before sunset. Since SWC is sufficient in winter, when nighttime VPD is minimal, all of the $J_{s,n}$ can be considered to be caused by R_e . When nighttime VPD is high during the dry season, changes in $J_{s,n}$ caused by R_e should follow the same slope and timing pattern as in winter (Fisher et al., 2007).

2.6 Statistical analysis

The different responses of J_s for three co-occurring woody plants to meteorological factors in the dry and wet seasons were fitted by nonlinear functions. We employed analysis of variance (ANOVA) to compare their interactions for the variables Ψ , J_s , $J_{s,n}$, and $J_{s,n}/J_s$. We calculated the contribution of meteorological factors to $J_{s,n}$ by performing multiple linear regressions. All the statistical analyses and plotting were performed via SPSS 13.0 (SPSS, Chicago, IL, USA) and Origin 8.0 (OriginLab, USA), respectively. All the above analyses were performed based on daily average data.

3 Results

3.1 Climate and soil water content

There were significant differences in meteorological factors and soil water content between dry and wet seasons in the research area (Table 2). The precipitation mainly between June to November (wet season) and more than 95% of the total rainfall was concentrated during the wet seasons (Figure 2). The VPD during the dry season (1.25 Kpa) was significantly greater than that during the wet season (0.66Kpa) (Figure 2, Table 2). The dry season exhibits high atmospheric evaporative demand and water scarcity. The SWC is highly consistent with rainfall and differs between the wet and dry seasons. The SWC in the 10-cm soil layer was low during the dry season ($SWC < 0.05 \text{ m}^3 \cdot \text{m}^{-3}$) and recovered during the rainy season ($SWC > 0.1 \text{ m}^3 \cdot \text{m}^{-3}$). The SWC in the 10-cm layer was more sensitive to the timing of short rainfall events than that in the 30-cm layer.

3.2 Seasonal variations in xylem water potential

The xylem water potential of the three woody plants during the wet and dry seasons were significantly different, and Ψ_{pd} and Ψ_{md} were significantly more negative during the dry season than during the wet season for all three woody plants (Figure 3). During the dry season, the Ψ_{pd} values of *Keteleeria* and *Pinus* were greater than that of *Castanopsis*, indicating that these two conifers may access more water for refilling at night. However, there was no significant difference between the three woody plants in terms of either Ψ_{pd} or Ψ_{md} during the wet season.

TABLE 2 Seasonal differences in sap flow (J_s), the proportion of the total sap flow ($J_{s,n}/J_s$) and meteorological factors.

| Factor | Dry season | Wet season | Sig |
|--|----------------|----------------|-------|
| $J_{s,Keteleeria}$ ($\text{g} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$) | 4.36 ± 1.75 | 9.25 ± 2.50 | <0.01 |
| $J_{s,Pinus}$ ($\text{g} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$) | 7.18 ± 1.83 | 11.41 ± 3.29 | <0.01 |
| $J_{s,Castanopsis}$ ($\text{g} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$) | 1.90 ± 0.55 | 4.91 ± 1.48 | <0.01 |
| $J_{s,n,Keteleeria}$ (%) | 40.32 ± 9.50 | 8.05 ± 1.18 | <0.01 |
| $J_{s,n,Pinus-1}$ (%) | 31.19 ± 7.59 | 11.96 ± 3.73 | <0.01 |
| $J_{s,n,Castanopsis-2}$ (%) | 27.37 ± 4.11 | 12.42 ± 3.16 | <0.01 |
| Solar radiation ($\text{W} \cdot \text{m}^{-2}$) | 186.24 ± 30.90 | 167.75 ± 34.76 | 0.003 |
| Temperature ($^{\circ}\text{C}$) | 17.47 ± 2.20 | 19.66 ± 1.33 | <0.01 |
| Precipitation (mm) | 27.38 ± 0.82 | 615.71 ± 70.24 | <0.01 |
| VPD (kPa) | 1.25 ± 0.27 | 0.66 ± 0.11 | <0.01 |
| Soil water content at the 10-cm depth ($\text{m}^3 \cdot \text{m}^{-3}$) | 0.04 ± 0.0004 | 0.26 ± 0.0060 | <0.01 |
| Soil water content at the 30-cm depth ($\text{m}^3 \cdot \text{m}^{-3}$) | 0.10 ± 0.0033 | 0.36 ± 0.0028 | <0.01 |

3.3 Seasonal variations in J_s and controlling factors

There species were significant differences in the sap flow density (J_s) of the three plants between the dry and wet seasons (Figure 4). The J_s of the *Pinus*, *Keteleeria*, and *Castanopsis* were $4.36 \text{ g} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$, $7.18 \text{ g} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ and $1.90 \text{ g} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ in the dry season while $9.25 \text{ g} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$, $11.41 \text{ g} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ and $4.91 \text{ g} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ in the wet season, respectively (Table 2).

The effects of environmental factors on J_s significantly differed between the dry and wet seasons (Figure 5). During the dry season, the soil water content was the main factor influencing J_s , and J_s increased with increasing soil water content (*Keteleeria*, $R^2 = 0.76$; *Pinus*, $R^2 = 0.74$; *Castanopsis*, $R^2 = 0.74$; all P values < 0.01). An increase in the VPD at this time resulted in a decrease in J_s , but this negative correlation was not significant. During the wet season, the VPD, however, was the main factor influencing J_s . Unlike during the dry season, at this time, there was a positive correlation between the VPD and J_s , and J_s increased with increasing VPD (*Keteleeria*, $R^2 = 0.76$; *Pinus*, $R^2 = 0.73$; *Castanopsis*, $R^2 = 0.32$; all p values < 0.01). Additionally, solar radiation attained a significant positive correlation with J_s during the wet season.

3.4 Daily variations in J_s and controlling factors

The three woody plants differed in their daily course of the sap flow density (J_s) on clear days with comparable climatic conditions (Figure 6). On typical sunny days, *Keteleeria* and *Castanopsis*

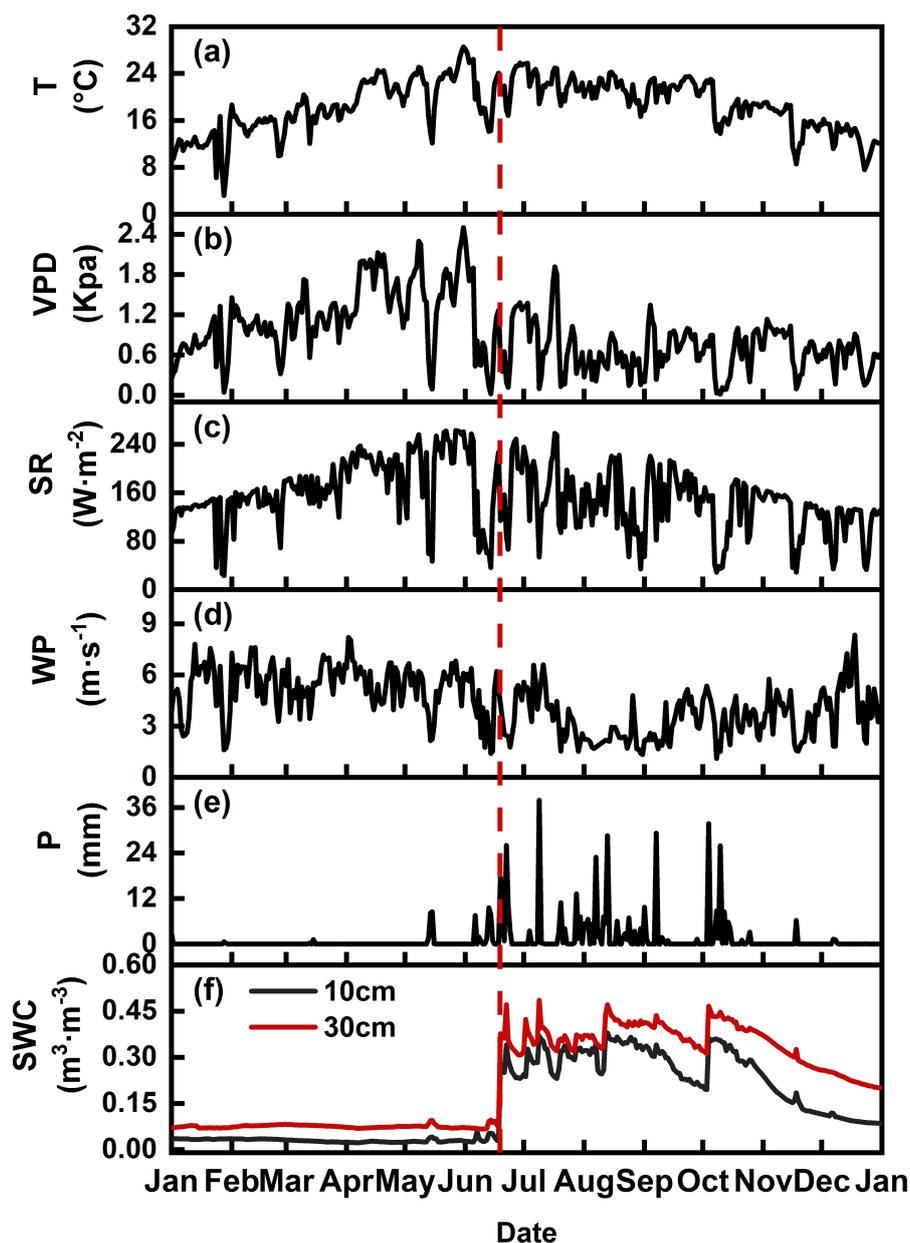


FIGURE 2

Monthly average temperature (T) (a), vapour pressure deficit (VPD) (b), solar radiation (SR) (c), wind speed (WS) (d), precipitation (P) (e) and soil water content (SWC) (f) at a soil depth of 10 cm in the research stand over the study period. The red dotted line represents the first effective rainfall of the year.

showed opposite trends to changes in VPD after sunrise, while *Pinus* remained roughly consistent with changes in VPD. However, *Pinus* showed a midday depression of $J_{s,n}$, which is a typical physiological response to high VPD in the dry season.

3.5 Seasonal variations in $J_{s,n}/J_s$ and controlling factors

The daily percentage of the nocturnal sap flow density ($J_{s,n}/J_s$) in the three co-occurring tree plants increased consistently during the

dry season (with increases of five times for *Keteleeria*, three times for *Pinus*, and more than two times for *Castanopsis*) (Figure 4; Table 2). The $J_{s,n}/J_s$ were significantly higher in *Keteleeria* and *Pinus* than in *Castanopsis* (Figure 4).

The response of $J_{s,n}$ to meteorological factors differed between the dry and wet seasons (Table 3). During the dry season, the SWC was negatively correlated with $J_{s,n}/J_s$, whereas the temperature (T_a), VPD and WS were positively correlated with $J_{s,n}/J_s$ (Table 3). During the wet season, when the relationship between the SWC and $J_{s,n}/J_s$ was not significant, the WS and VPD were negatively correlated with the percentage of the nocturnal sap flow density, whereas the

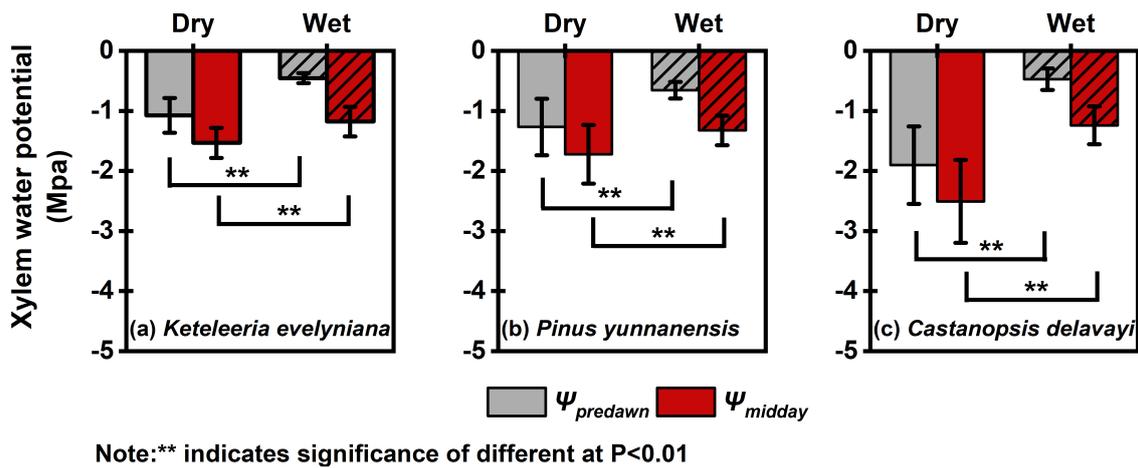


FIGURE 3
 Seasonal changes in the predawn ($\Psi_{predawn}$) and midday (Ψ_{midday}) xylem water potentials of the three tree species: *Keteleeria evelyniana* (a), *Pinus yunnanensis* (b), and *Castanopsis delavayi* (c). The filled shading (diagonal lines) in the figure is used to distinguish between dry and wet seasons. The values are means \pm standard errors (SEs). *** indicates significance of difference at $P < 0.01$.

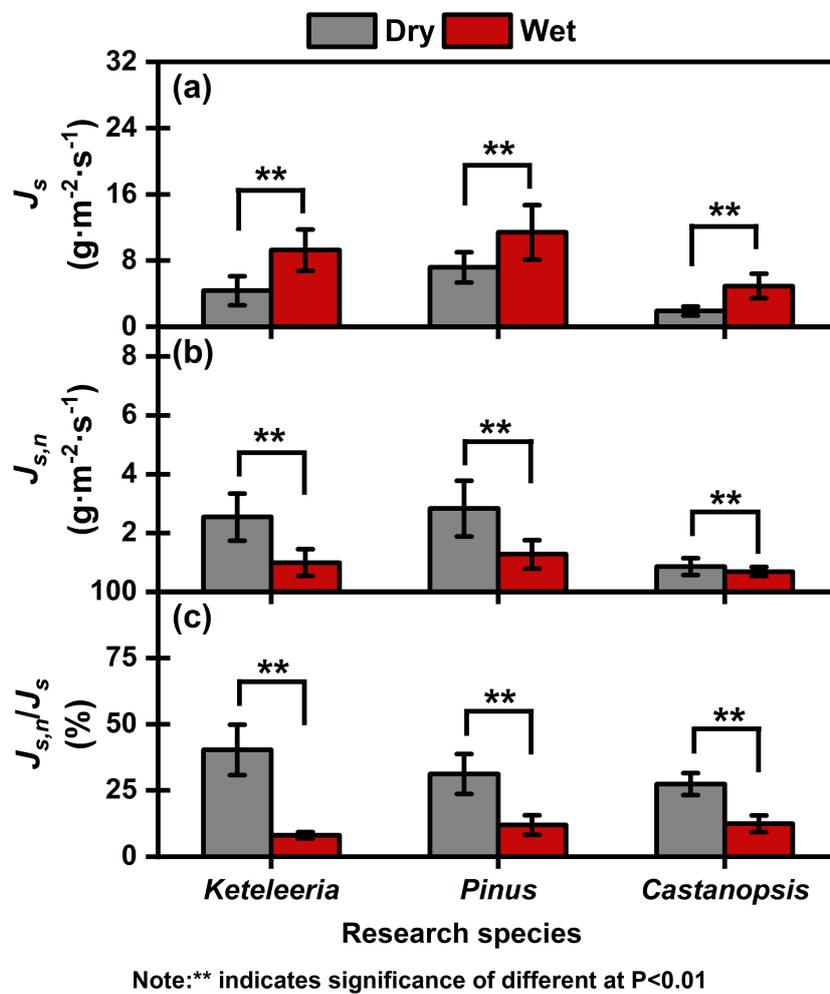


FIGURE 4
 Seasonal mean sap flow density (J_s) (a), nocturnal sap flow density ($J_{s,n}$) (b), and percentage of the nocturnal sap flow density ($J_{s,n}/J_s$) (c) for *Keteleeria*, *Pinus*, and *Castanopsis* during the dry and wet seasons. Different filled colours are used to distinguish between dry and wet seasons. The values are means \pm standard errors (SEs). *** indicates significance of difference at $P < 0.01$.

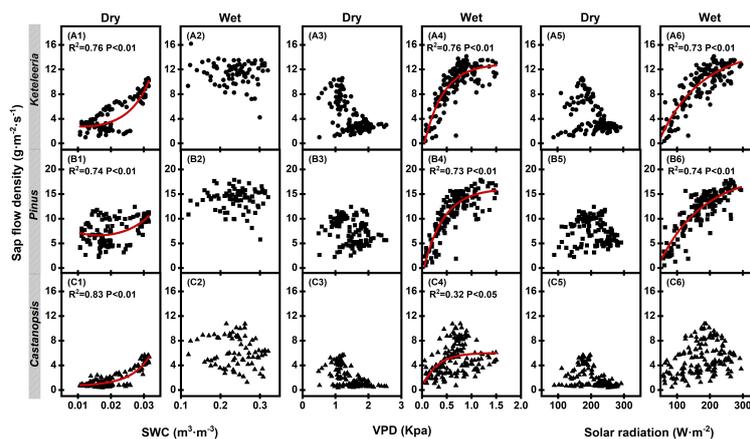


FIGURE 5

Results of nonlinear fitting of plant sap flow density (J_s) to meteorological factors in dry and wet seasons. Relationships between the J_s and the soil water content (SWC), vapour pressure deficit (VPD), and solar radiation (R_a) for *Keteleeria* (A1–A6), *Pinus* (B1–B6), and *Castanopsis* (C1–C6) during the dry and wet seasons. A single point represents the mean of the four sample trees monitored for each tree species. The symbol shapes of circles, squares and triangles represent different species of *Keteleeria*, *Pinus*, *Castanopsis*, respectively. The red curve is the result of nonlinear fitting.

temperature (T_a) was positively correlated with $J_{s,n}/J_s$. The contribution of environmental factors to $J_{s,n}/J_s$ was different among species in the dry season (Figure 7). The contribution of SWC was the largest to the $J_{s,n}/J_s$ for *Castanopsis* and *Pinus*, yet the contribution of VPD was the largest to the $J_{s,n}/J_s$ for *Keteleeria*. During the wet season, it was VPD that contributed the most to the $J_{s,n}/J_s$ for all three species.

3.6 Daily variations in $J_{s,n}$ and the composition

The composition of $J_{s,n}$ differed between the wet and dry seasons. Notably, $J_{s,n}$ during the dry season did not decrease gradually to zero with the decline in R_a (Figure 8). The $J_{s,n}$ comprised a combination of nocturnal transpiration (E_n) and refilling activities (R_e), and a higher proportion of the E_n at night (*Keteleeria*=64.90%; *Pinus*=79.70%; *Castanopsis*=73.01%), whereas during the wet season, it encompassed R_e alone (Figures 8, 9). The percentage of E_n in $J_{s,n}$ was higher in *Pinus* than that in *Keteleeria* and *Castanopsis*.

4 Discussion

Three co-occurring woody plants showed the same seasonal variation in J_s , the mean J_s is lower in the dry season than in the wet season (Figure 4). Our results were consistent with those of Lu et al. (2013), who studied variations in whole-tree transpiration of poplar during the wet and dry seasons. They found that the whole-tree transpiration during the dry season was much lower than in the wet season (only 10–20%). Additionally, the $J_{s,n}/J_s$ of three co-occurring woody plants were higher in the dry season than in the wet season (Figure 4). We suggest that

increasing $J_{s,n}$ in the dry season is a long-term adaptive strategy for plants in this region. $J_{s,n}$ has been proven to occur in a range of woody plants and has important effects on the water balance between soil and plants (Daley and Phillips, 2006; Zeppel et al., 2010; Forster, 2014).

The J_s of three co-occurring woody plants responded similarly to environmental factors in the wet and dry seasons. The SWC was the most significant factor influencing J_s during the dry season and the PAR and VPD were the major factors influencing J_s during the wet season in our study (Figure 5). This similar pattern is consistent with previous results from mixed tropical forests (Meinzer et al., 1995, 1997; O'Brien et al., 2004). More than 85% of the precipitation occurred in wet season during the experimental period, and our study site is second only to Tibet in terms of solar radiation (Figure 2; Table 2). During the dry season, less precipitation and strong light intensity decrease available moisture in soil and/or atmosphere, thus increasing water stress in plants (Wang et al., 2017b). During the wet season, when SWC increased, VPD and PAR were the main environmental factors driving transpiration. Several studies have shown that high VPD and PAR are critical driving variables for transpiration in numerous ecosystems (Wang et al., 2017a; Oogathoo et al., 2020; Ghimire et al., 2022). Ochoa and Abdallah (2023) also showed that VPD is the major environmental factor driving transpiration under higher SWC, and that increased transpiration is enhanced by increased sensitivity of transpiration to PAR.

In our study, SWC affected the response of $J_{s,n}$ to meteorological factors. VPD was positively correlated with $J_{s,n}$ in the dry season, while it was negatively correlated in the wet season (Table 3). Rosado et al. (2012) showed the same results: a positive correlation exists between $J_{s,n}$ and VPD in tropical rainforest plants during the dry season. But Chen et al. (2020) observed a significant negative effect between nocturnal VPD and $J_{s,n}$ in forests with dry soils, while

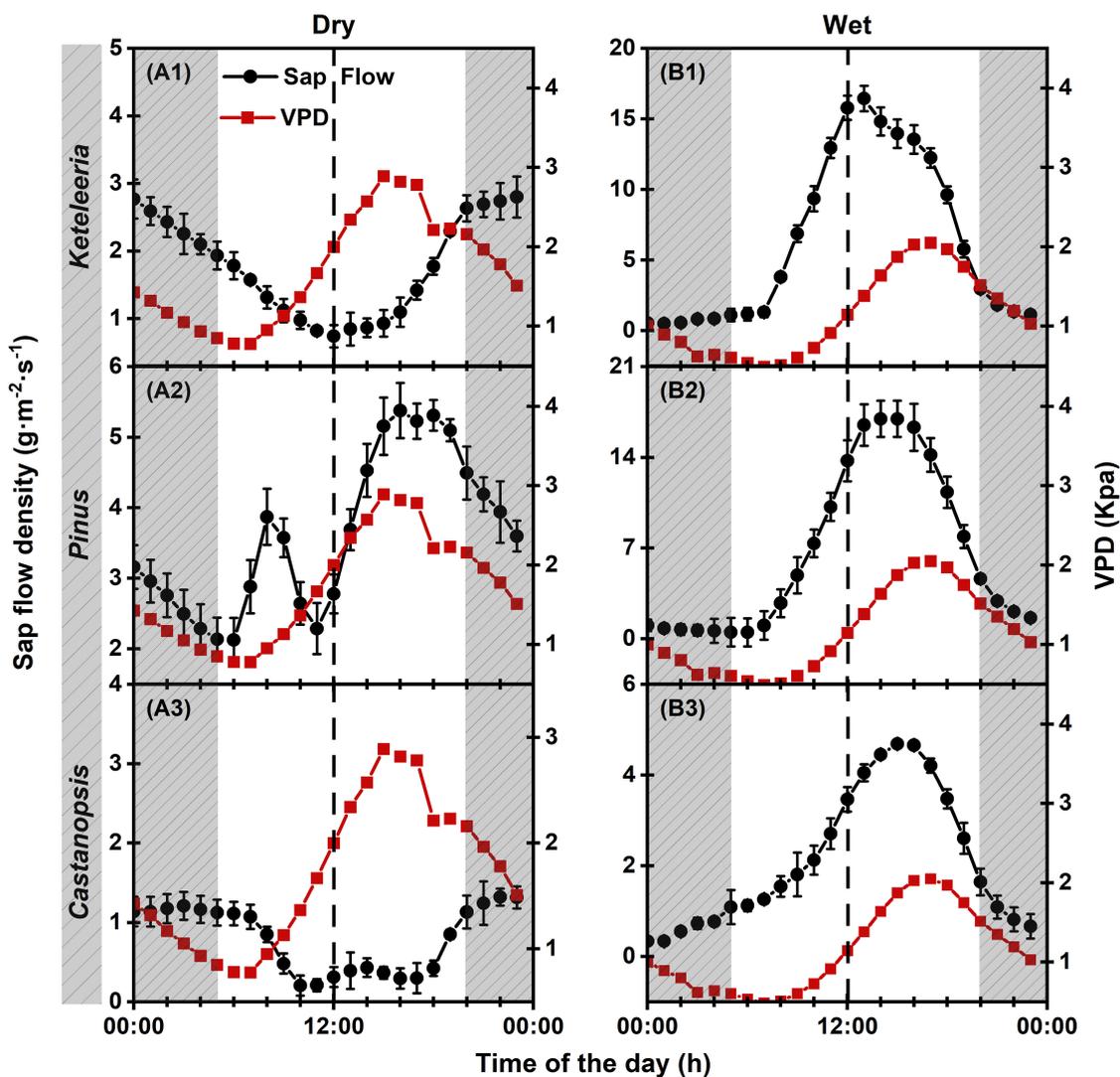
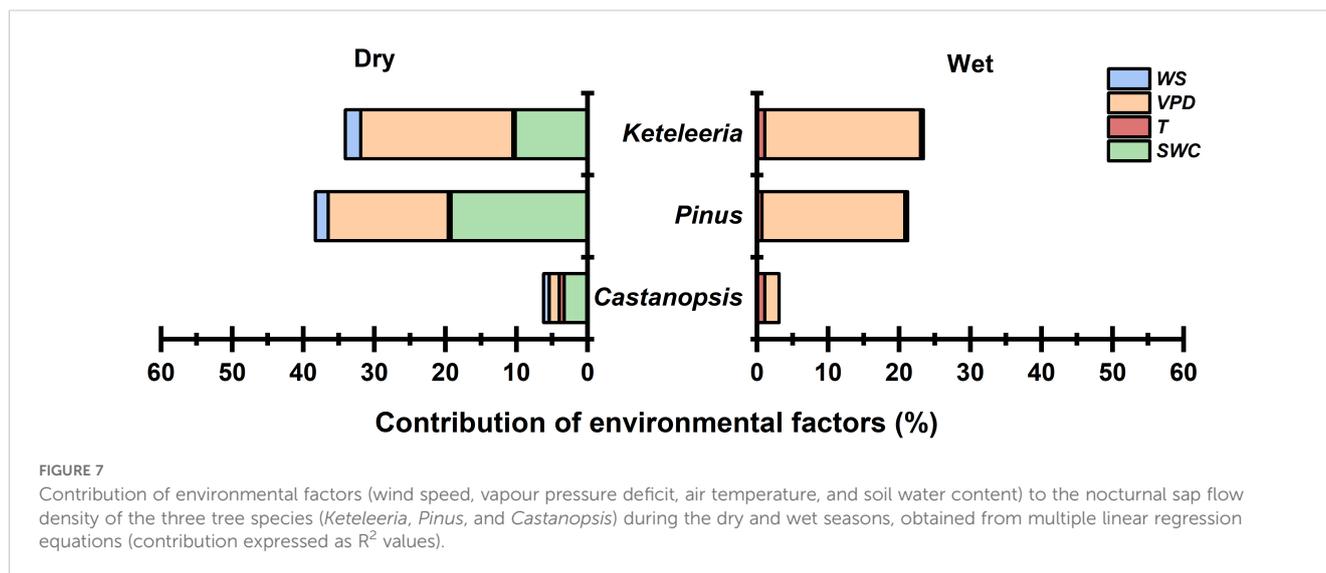


FIGURE 6 Diurnal courses of the VPD and the sap flow density (J_s) for *Keteleeria*, *Pinus*, and *Castanopsis* during the dry (A1–A3) and wet (B1–B3) seasons. The values are the averages of 5–10 representative clear days for each individual. The shaded areas denote nighttime values. The straight line where the circle is located represents plant sap flow. The straight line where the square is located represents VPD. The error bars are the SEs of the repeated samples for each species.

TABLE 3 Standardised regression coefficients between the percentage of nocturnal sap flow and meteorological factors.

| Season | Species | SWC | T | WS | VPD | R ² |
|--------|--------------------|----------|---------|----------|----------|----------------|
| Dry | <i>Keteleeria</i> | -0.212** | 0.803** | 0.334** | 0.107** | 0.341 |
| | <i>Pinus</i> | -0.382** | 0.651** | 0.689** | 0.170** | 0.383 |
| | <i>Castanopsis</i> | -0.360** | 0.964** | 0.649** | 0.156** | 0.062 |
| Wet | <i>Keteleeria</i> | - | 0.106** | -0.217** | -0.059** | 0.234 |
| | <i>Pinus</i> | - | 0.152** | -0.621** | -0.062** | 0.212 |
| | <i>Castanopsis</i> | - | 0.060** | -0.535** | -0.062** | 0.031 |

** indicates significance at P<0.01; - indicates not significant.



there was no correlation between nocturnal VPD and $J_{s,n}$ under wetter soil conditions. Low soil moisture and atmospheric drought trigger stomatal closure (Cavender-Bares et al., 2007; Zeppel et al., 2010; Cirelli et al., 2015). VPD is a major transpiration driver that increases transpiration even when light is absent, thus facilitating J_s in previous studies (Zeppel et al., 2010; Pfautsch et al., 2011). Thus, in the mixed forests of the study area, the physical promotion of VPD on stomatal water loss overwhelmed the inhibition of stomatal opening by soil drought and atmospheric drought. Whereas, in the wet season, sufficient soil moisture avoided plant stomatal opening at night.

Daily variations in water use strategies differed among species unlike the similar seasonal water use for the three co-occurring plants. The changes in hourly J_s with VPD and solar radiation over the day differed for the three woody plants on a typical sunny day in the dry season (Figure 6; Figure 10). This suggests that responses to drought depend on species. The J_s for *Castanopsis* and *Keteleeria* were smaller in daytime than at nighttime, and J_s decreased with increasing VPD after sunrise on typical sunny days in the dry season (Figure 6). This reflects relatively strong stomatal control of *Castanopsis* and *Keteleeria* and is considered isohydric plants. In contrast, the J_s in *Pinus* was greater in daytime than at nighttime, and there was a significant positive correlation between J_s and VPD (Figures 6, 10), which reflects relatively weak stomatal control and is considered an isohydric plant. Previous studies have shown that the relevant traits that determine water strategy are acquisition efficiency (root characteristics) and utilisation efficiency (leaf and stem characteristics) (Wright et al., 2004; Moreno-Gutierrez et al., 2012). In this study, *Castanopsis*, the only broadleaf tree among the three species. Broadleaf species are less resistant to drought-induced cavitation than coniferous species and have less hydraulic safety thresholds (Choat et al.,

2012). This may be due to the coupling differences between leaf and wood phenology, cell (vessel/tracheid) density, or anatomical structure (Vitasse et al., 2019; Tan et al., 2020). *Castanopsis* has higher SLA than *Keteleeria* and *Pinus* (Tang 2025; under review), and higher SLA accelerate water loss (Reich and Cornelissen, 2014; Künzi et al., 2025). However, the findings of this study demonstrate that the transpiration of *Castanopsis* was still smaller than that of the other two conifers during the wet season. Therefore, it can be hypothesised that other environmental or morphological factors may have contributed to the result of lower transpiration of *Castanopsis*. We will continue to explore the plant functional traits of the three species in the hope of explaining in more detail the differences in survival strategies of the three species. The *Keteleeria* is a conifer species, but a previous study showed that *Pinus* could use deeper soil water, and the leaf $\delta^{13}C$ of *Pinus* was higher than that of *Keteleeria*, which had a higher water utilisation efficiency in the dry season (He, 2022). These characteristics enhance the drought resistance of *Pinus*, which has a relatively constant stomatal conductance, ensuring transpiration and making their survival less limited.

Significant differences in the $J_{s,n}/J_s$ among the three species during the dry season (Figure 4), with a higher $J_{s,n}/J_s$ in *Keteleeria* and *Pinus*, and a lower $J_{s,n}/J_s$ in *Castanopsis*, which may be related to their use of different water use strategies. The low $J_{s,n}/J_s$ may reflect low water loss at night due to strict stomatal control (Zeppel et al., 2010). Thus, *Keteleeria* and *Pinus* had less tight stomatal control. The $J_{s,n}$ for three co-occurring woody plants in the dry season was composed of E_n and R_e , and the proportion of E_n was more than 60% in our study (Figure 9). E_n is closely linked to stomatal activity, higher E_n may exacerbate water loss and expose plants to higher hydraulic stress. *Pinus* has the highest percentage of E_n and therefore may be most stressed under future climate change.

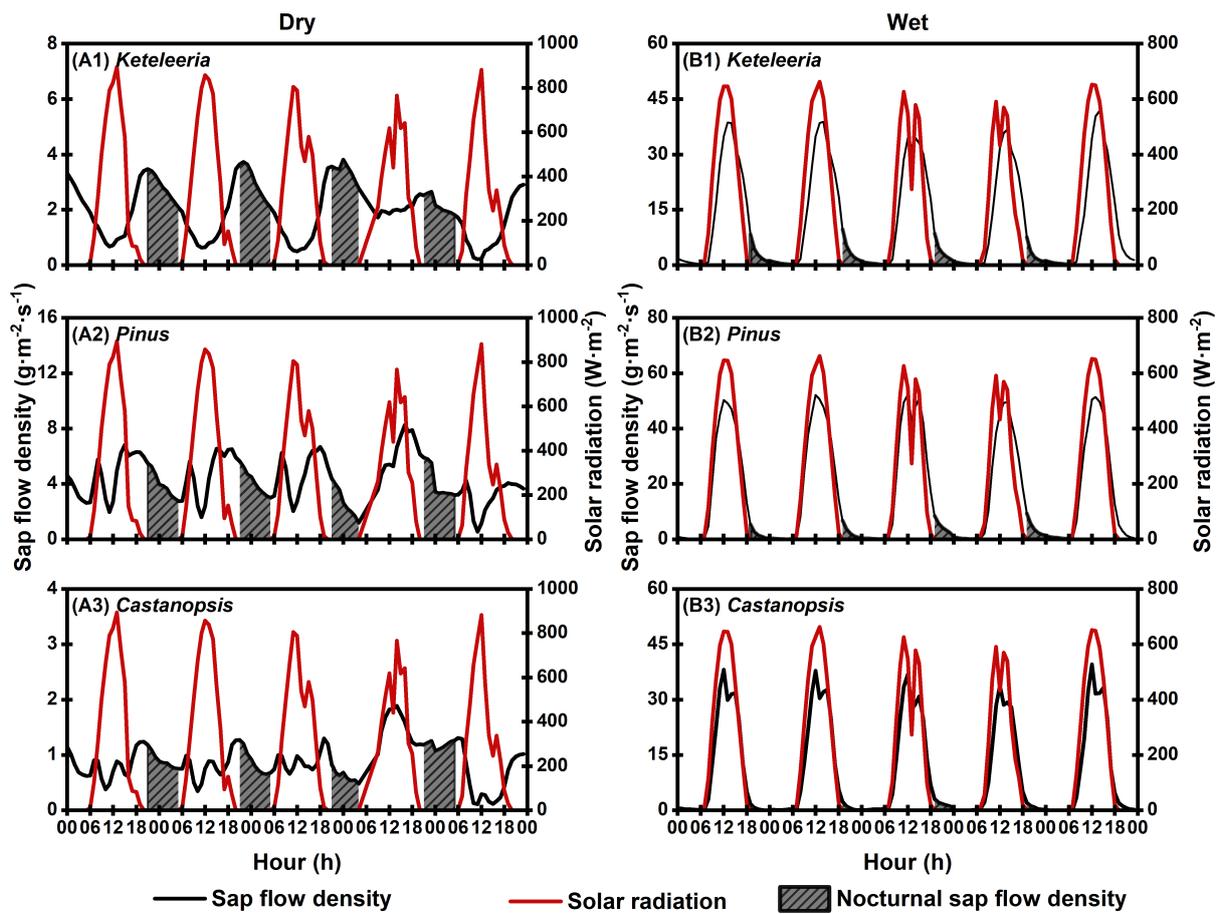


FIGURE 8 Continuous changes in the nocturnal sap flow density of the three species (*Keteleeria*, *Pinus*, and *Castanopsis*) on five typical sunny days during the dry (A1–A3) and wet seasons (B1–B3). The solid black line is plant sap flow. The solid red line is solar radiation. The shaded area is the time period when nocturnal sap flow density occurs.

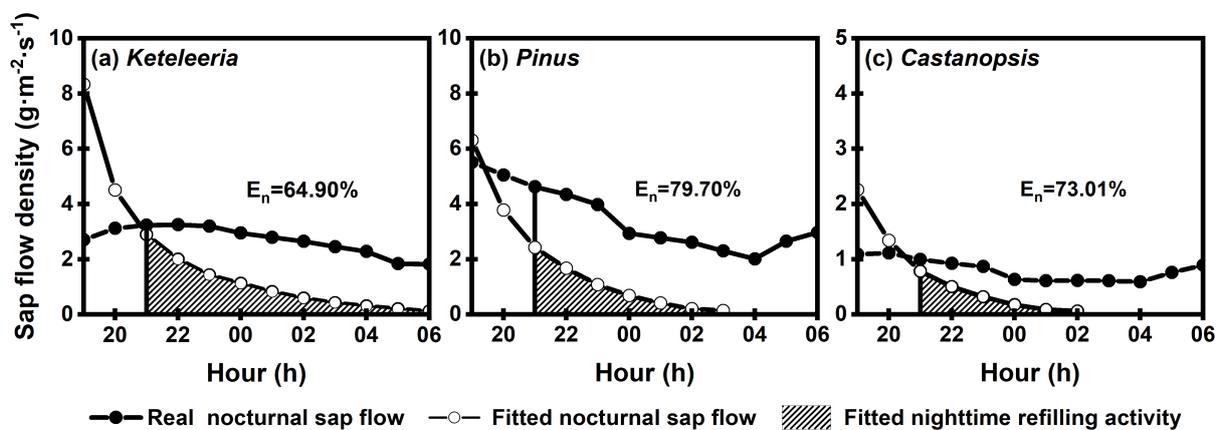
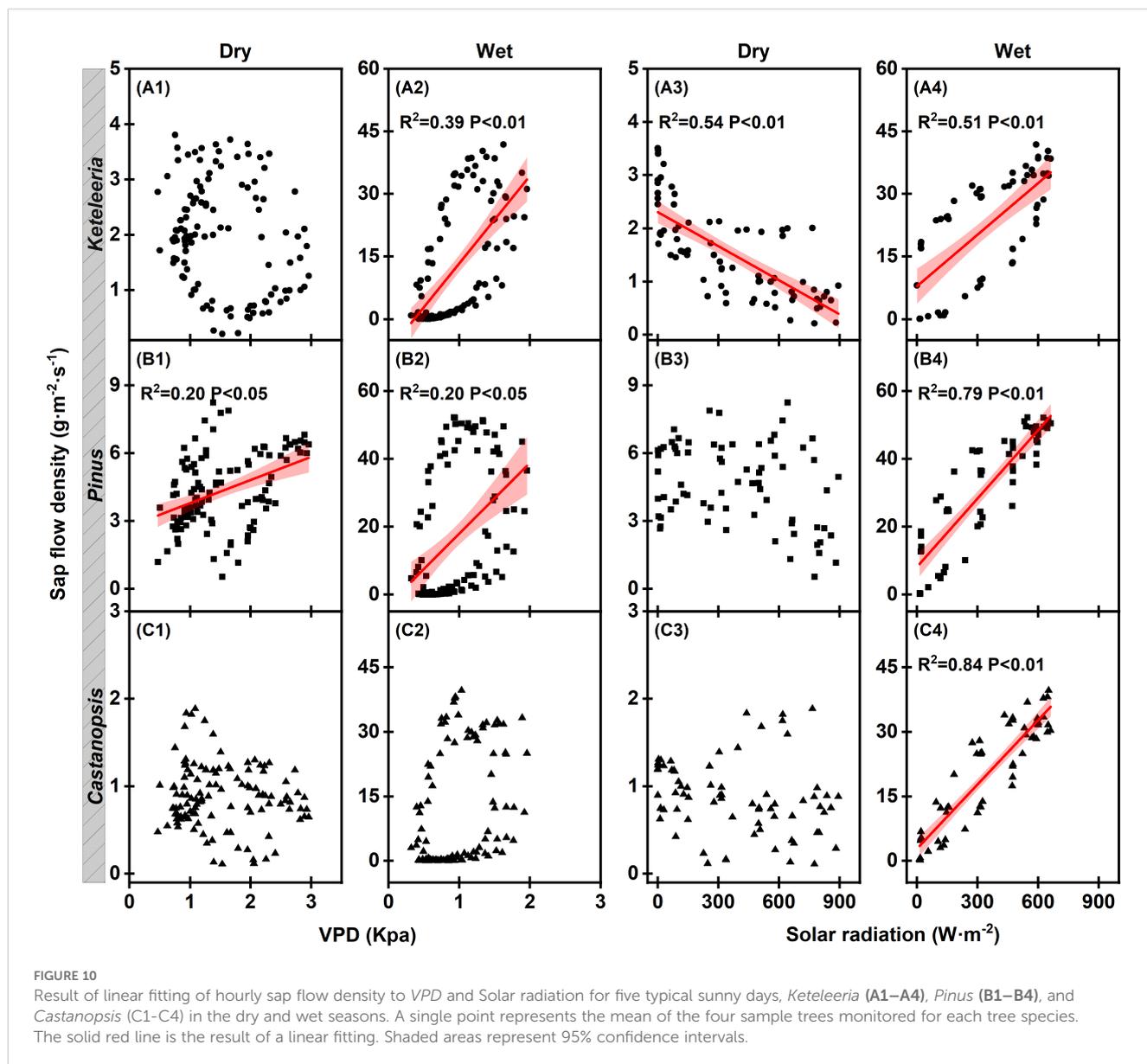


FIGURE 9 Composition of nocturnal sap flow in the three tree species (*Keteleeria* (a), *Pinus* (b), and *Castanopsis* (c)) during the dry season. The solid circular straight line is the real nocturnal sap flow; the dashed circular straight line is the nocturnal sap flow obtained by fitting. The shaded area is the area below the fitted curve and represents nighttime refilling activity.



5 Conclusions

There were seasonal and species differences in sap flow and water potential of three co-occurring woody species (*Keteleeria evelyniana*, *Pinus yunnanensis*, and *Castanopsis delavayi*) in subtropical forests of Yunnan Province. Seasonal differences in the water use strategies of the three species were characterised by significantly smaller sap flow in the dry season than in the wet season and a significantly larger percentage of nocturnal sap flow in the dry season. The seasonal response of the sap flow to environmental factors was shown that SWC was the main influence factor in the dry season, and nocturnal sap flow was negatively correlated with VPD; while in the wet season, when there was sufficient soil moisture, VPD and PAR were the main influence factors, and nocturnal sap flow was negatively correlated

with VPD. In addition, *Pinus*, which has less tight control of stomata conductance, may suffer higher hydraulic stress during the dry season. The sap flow of *Pinus* increased with increasing VPD on typical sunny days during the dry season and had the highest percentage of nocturnal sap flow. The results of the fitted exponential decay equations showed that the *Pinus* had the highest percentage of nocturnal transpiration. Our results provide greater insights into the water use strategies of plants in this region, highlighting the physiological and ecological significance of plant water use strategies and nocturnal sap flow during the different seasons. The results could help to more accurately predict plant feedback to the environment and changes in survival strategies, especially within the context of climate change, with increasing nighttime temperatures and more frequent droughts.

Data availability statement

The original contributions presented in the study are included in the article. Further inquiries can be directed to the corresponding author.

Author contributions

JT: Data curation, Investigation, Methodology, Software, Writing – original draft, Writing – review & editing. ZD: Investigation, Methodology, Writing – review & editing. GW: Investigation, Methodology, Writing – review & editing. YW: Investigation, Methodology, Writing – review & editing.

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