

Article

The Relationship between Sap Flow Density and Environmental Factors in the Yangtze River Delta Region of China

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Abstract: Canopy transpiration is an important component of evapotranspiration, integrating physical and biological processes within the water and energy cycles of forests. *Quercus acutissima* and *Cunninghamia lanceolata* are two important, fast-growing and commercial tree species that have been extensively used for vegetation restoration, water conservation and building artificial forests in the Yangtze River Delta region of China. The primary objective of this study was to characterize sap flow densities of the two species by comparing daytime and nocturnal sap flow patterns and their relationships with environmental factors. Sap flow densities (S_d) were measured between September 2012 and August 2013 using the commercially-available thermal dissipation probes. Hourly meteorological data were measured in an open field, located 200 m away from the study site, including photosynthetically-active radiation (P_{ar}), air temperature (T_a), relative air humidity (R_h), vapor pressure deficit (V_{pd}) and precipitation (P). Soil water content (S_{wc}) data were logged hourly in different layers at *Q. acutissima* and *C. lanceolata* forests. Results indicated that the mean S_d in summer was higher than that in spring and autumn. Both the S_d of *Q. acutissima* and *C. lanceolata* showed distinct diurnal patterns. Nocturnal sap flow densities (S_{dn}) were noticeable, and both species followed similar declining patterns during our study period. The daytime sap flow density (S_{dd}) was more sensitive to environmental factors than S_{dn} . Sap flow density was significantly correlated with P_{ar} , V_{pd} and T_a , and P_{ar} and V_{pd} explained the greatest amount of variation in daytime sap flow of *Q. acutissima* and *C. lanceolata*, respectively. Our study will enrich knowledge of plantation forest physical and biological processes and provide valuable information for plantation forest management in the Yangtze River Delta region of China.

Keywords: canopy transpiration; daytime and nocturnal sap flow; vapor pressure deficit; soil water content

1. Introduction

In a forest ecosystem, canopy transpiration, which can be derived empirically from sap flow measurements in the trunk xylem [1], is a physiological metabolism process that is essential to the vitality of tree and also is an important component of evapotranspiration [2–4]. It exerts great influence on the weather patterns, Earth's surface energy balance and water supply to downstream systems [5,6].

Most prior studies indicated that sap flow is strongly influenced by environmental factors [7–9], including solar radiation, vapor pressure deficit, rainfall, air temperature, wind speed and soil water content [10]. For example, in a comparative study, the effect of a flat-roof screen house on banana transpiration showed that reduction in transpiration in the screen house is mainly due to the combined reductions of wind speed and global radiation [11]. There were significant differences in sap flow dynamics of a drought-tolerant plant between the two periods of the day (0:00–15:00 and the remainder) due to the meteorological factors [12]. In the future, climate change likely will increase air temperature, and its variation may be accompanied by similar changes in vapor pressure deficit (V_{pd}), which would influence the canopy transpiration [6]. Therefore, an improved understanding of how these environmental factors interact to influence the sap flow is essential in the Yangtze River Delta region of China.

Transpiration occurs through the stomata, and researchers formerly thought that leaf stomata close at night, so it is generally assumed that transpiration only occurs during the day [13,14], which led to the underestimation of total sap flow [15]. Now, there is a greater awareness that nocturnal sap flow can in fact have a significant contribution to total daily sap flow [16–19]. Most previous work on the nocturnal sap flow has shown by analysis of 98 species that its averaged proportion of the total daily sap flow was 12.03% [16]. Daley and Phillips found that over 10% of the total daily sap flux during the growing season was due to transpiration at night in paper birch [20]. Nighttime sap flow was over 8% of the total daily flow in red oak and 2% in red maple. Integrated crop water loss during the dark, non-photosynthetic hours measured on the lysimeter was 3%–10.8% of total daily water loss [21]. Hence the nocturnal sap flow is significant and needs to be carefully considered in sap flow and related studies [16].

With the rapid growth of the population, China underwent deforestation at an alarming rate during the second half of the 20th century to meet the needs for timber and food production. Almost all natural primary forests have been replaced with secondary forest and fast-growing tree plantations. Plantations currently account for 40% of the total forest area in China [22,23]. *Quercus acutissima* and *Cunninghamia lanceolata* are the most important plantation tree species in China in terms of planted area, yield and timber usage [24–27]. In recent decades, a great deal of pure *Q. acutissima* stands and pure *C. lanceolata* stands were established in the Yangtze River Delta region of China. With the maturation of these plantations, the forest farms faced many problems of management and sustainable development [28–30], such as reasonable use of water. Therefore, accurate calculation of water consumption for the plantation ecosystems is important for forest farm management, which depends on our capacity to quantify the transpiration in plantations. To our knowledge, however, none of the existing studies considered the transpiration of *Q. acutissima* and *C. lanceolata* [31] in the Yangtze River Delta region of China.

Therefore, in this study, we monitored stem sap flow density using thermal dissipation probes (TDPs) in the pure *Q. acutissima* forest and pure *C. lanceolata* forest in the Yangtze River Delta region of China. Our primary objectives were (1) to compare the difference of the sap flow density among the diameters at breast height (DBH), (2) to examine monthly variations of the daily sap flow density and (3) to compare the diurnal and nocturnal sap flow patterns and their relationships with the environmental factors. Our study will enrich knowledge of plantation forest hydrological processes and provide valuable information for plantation forest management in the Yangtze River Delta region of China.

2. Materials and Methods

2.1. Study Site

The study site was located in the Tong Shan forest farm (31°37' N, 118°51' E), Nanjing, China. The altitude of the Tong Shan forest farm ranged from 38 m–388 m. The research area is a mature artificial pure forest of, respectively, *Q. acutissima* pure forest, *C. lanceolata* pure forest or *Phyllostachys edulis* pure forest. It has a subtropical monsoon climate; the annual mean temperature is 16.5 °C, with a monthly mean temperature reaching a maximum of 28.6 °C in July and a minimum

of 3.1 °C in January (Figure 1). Annual cumulative hours of sunshine are 2199.5 h. The annual mean precipitation is 1126.9 mm, and the average precipitation during the rainy season, from June to August is 587.6 mm (Figure 1).

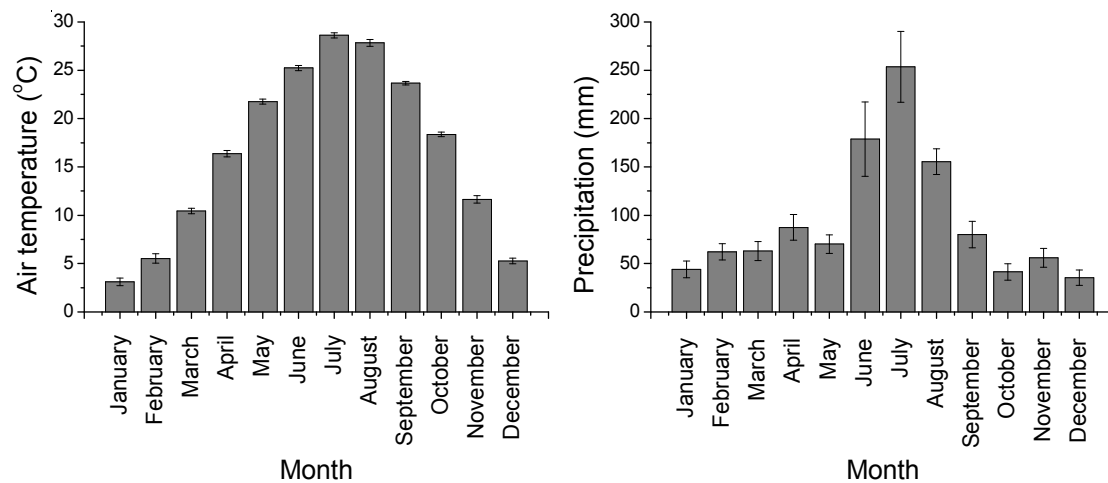


Figure 1. The annual mean air temperature and precipitation of Nanjing from 2000–2015.

The experimental plots were located in *Q. acutissima* deciduous forest and *C. lanceolata* evergreen forest. At the time of the study (2012–2013), the trees were about 45 years old. The averaged tree heights of *Q. acutissima* and *C. lanceolata* were, respectively, 13.8 m and 12.8 m. The stand densities were, respectively, 425 trees ha^{−1} and 850 trees ha^{−1}. The average diameters at breast height (DBH) were, respectively, 25.8 cm and 21.0 cm. The leaf area indices (LAI) of *Q. acutissima* deciduous forest, estimated by an LAI-2200 plant canopy analyzer (LI-COR, Lincoln, USA), was 2.49–3.37 during the growing season, and the LAI of *C. lanceolata* evergreen forest was 1.71–3.12 throughout the year.

2.2. Sap Flow Measurements

Sap flow densities per unit sapwood area (S_d , g·cm^{−2}·h^{−1}) were measured from July 2012 to August 2013 using the commercially-available thermal dissipation probes (Model TDP-30, Dynamax Inc., Houston, TX, USA) [32]. Eight *Q. acutissima* trees and eleven *C. lanceolata* trees, relatively well-grown, were selected based on the growing condition in the experimental site (Table 1). We took a separate sample of 20 trees of the same species distributed across the study area to determine the sapwood area (SA) of the samples. The trees used for the determination of sapwood area were not the same as those used for continuous monitoring of sap flow density, in order to avoid the effects of plant injury on our measurements. Approximately 20 tree ring cores with an average height of 1.3 m were drilled by an increment borer (SY-CO, Haglöf, Långsele, Sweden), after which their heartwood and sapwood were measured [33]. The sapwood area values of the samples were estimated according to the data (Figure 2).

Table 1. Basic parameters of the samples in the two forests.

No.	DBH (mm)	Depth (mm) and Aspects	SA (cm ²)	DBH (mm)	Depth (mm) and Aspects	SA (cm ²)
<i>Q. acutissima</i>				<i>C. lanceolata</i>		
1	187	0–25 at N	142.69	122	0–20 at N	73.64
2	200	0–25 at N	166.49	137	0–20 at N	92.14
3	242	0–25 at N	257.86	188	0–20 at N	169.86
4	252	0–25 at N	282.97	196	0–20 at N	184.11
5	268	0–25 at N	325.91	204	0–20 at N	198.92
6	278	0–25 at N	354.50	208	0–20 at N	206.52
7	308	0–25 at N	448.49	215	0–20 at N	220.17
8	318	0–25 at N	482.61	218	0–20 at N	226.15
9	-	-	-	223	0–20 at N	236.28
10	-	-	-	227	0–20 at N	244.54
11	-	-	-	249	0–20 at N	292.42

DBH, diameter at breast height (1.3m); SA, sapwood area; N, north.

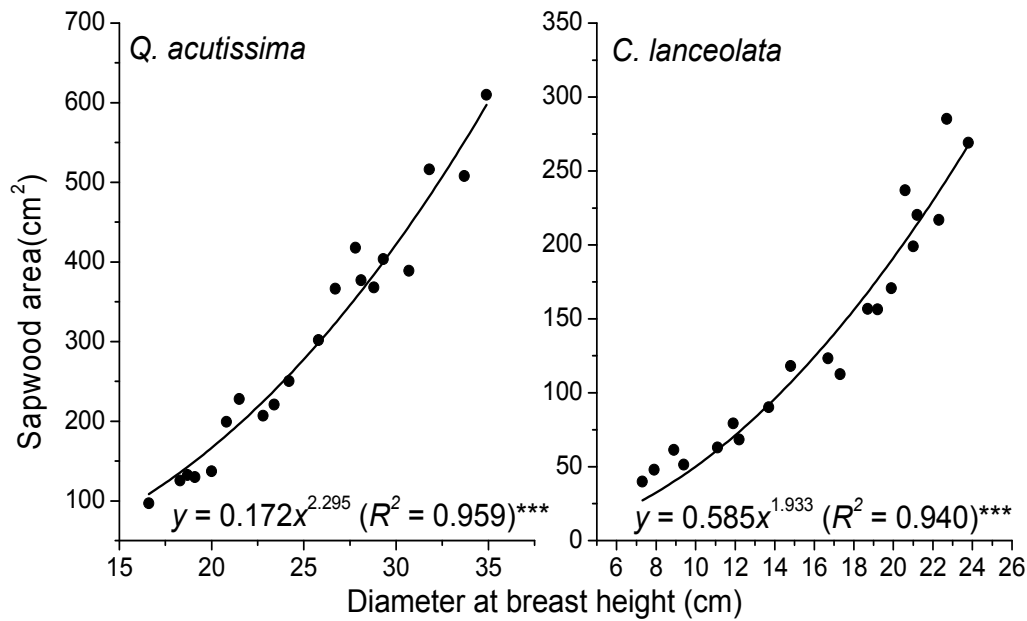


Figure 2. The relationship between diameter at breast height (DBH) and sapwood area (SA).

*** Significant correlation at $p < 0.001$.

Pairs of probes with lengths of 30 mm were inserted in the northern trunk directions at breast height of each sample tree in order to avoid the sun-exposed side of the trunk, the TDP sensor installed according to the instructions recommended by the manufacturer (Copyright 2007, Dynamax Inc.) at the same sapwood depth of the same tree species (Table 1). These probes operated on the constant power principle [34], and the sap flow density was recorded at 10-min intervals. An average value was calculated every 60 min and then recorded in Campbell CR1000 data loggers. Due to loss of electricity supply, the sap flow densities of *C. lanceolata* in May and December were lost.

Sap flow density on a sapwood area basis was calculated based on the temperature difference between the heated and non-heated probe by an empirical equation [34]:

$$S_d = 0.0119 \times 3600 \times [(dT_M - dT) / dT]^{1.231} \quad (1)$$

where S_d is the sap flow density ($\text{g} \cdot \text{cm}^{-2} \cdot \text{h}^{-1}$ or $\text{cm} \cdot \text{h}^{-1}$), dT is differential temperature between the two probes and dT_M is the temperature difference at zero flow. Zeppel et al. used two methods to determine the zero set of each sensor: (1) examining the flow rates at night when V_{pd} and wind speed were ca. zero during the periods and (2) at the end of the study, cutting into the sapwood beneath the sensors in each tree to determine the zero flow rates [35]. They found that there was no significant difference ($p < 0.05$) between the two different methods used to estimate zero flow rates [35]. In our study, zero flow measurements were automatically conducted every six days between the hours of 02:00 and 05:00 because the sap flow velocity can reasonably be considered to be zero or minimal during this period [36]. According to Oishi et al., to account for potential nocturnal sap flows due to both transpiration and recharge, we selected the highest daily dT to represent dT_M if two conditions are satisfied simultaneously: (1) the average, minimum two hours $V_{pd} < 0.05$ kPa, thus assuring that water loss to the atmosphere is negligible, and (2) the standard deviation of the highest dT values $< 0.5\%$ of the mean of these values; such stable measurement of maximum dT ensures that recharge of water above the sensor height is completed or negligible. In our sap flow time series, zero flow nighttime conditions were often not met for several consecutive days [37].

In addition, transpiration was scaled up to the stand level using the following equation [38]:

$$S_t = 10 \times S_{dm} \times SA_{stand} / SG \quad (2)$$

where S_t is stand transpiration ($\text{mm} \cdot \text{h}^{-1}$), S_{dm} is the mean S_d of stand ($\text{g} \cdot \text{cm}^{-2} \cdot \text{h}^{-1}$ or $\text{cm} \cdot \text{h}^{-1}$), SA_{stand} is stand sapwood area (cm^2) and SG is the ground area (cm^2).

2.3. Meteorological and Soil Water Measurements

Hourly meteorological data (EM50, Decagon Devices, Pullman, WA, USA) were measured in an open field, which is 200 m away from the studied stand, including photosynthetically-active radiation (P_{ar} , $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$), air temperature (T_a , $^{\circ}\text{C}$), relative air humidity (R_h , %) and precipitation (P , mm) (Figure 3A,B,C,F). These T_a and R_h data were used to calculate the vapor pressure deficits (V_{pd} , kPa, Figure 3D).

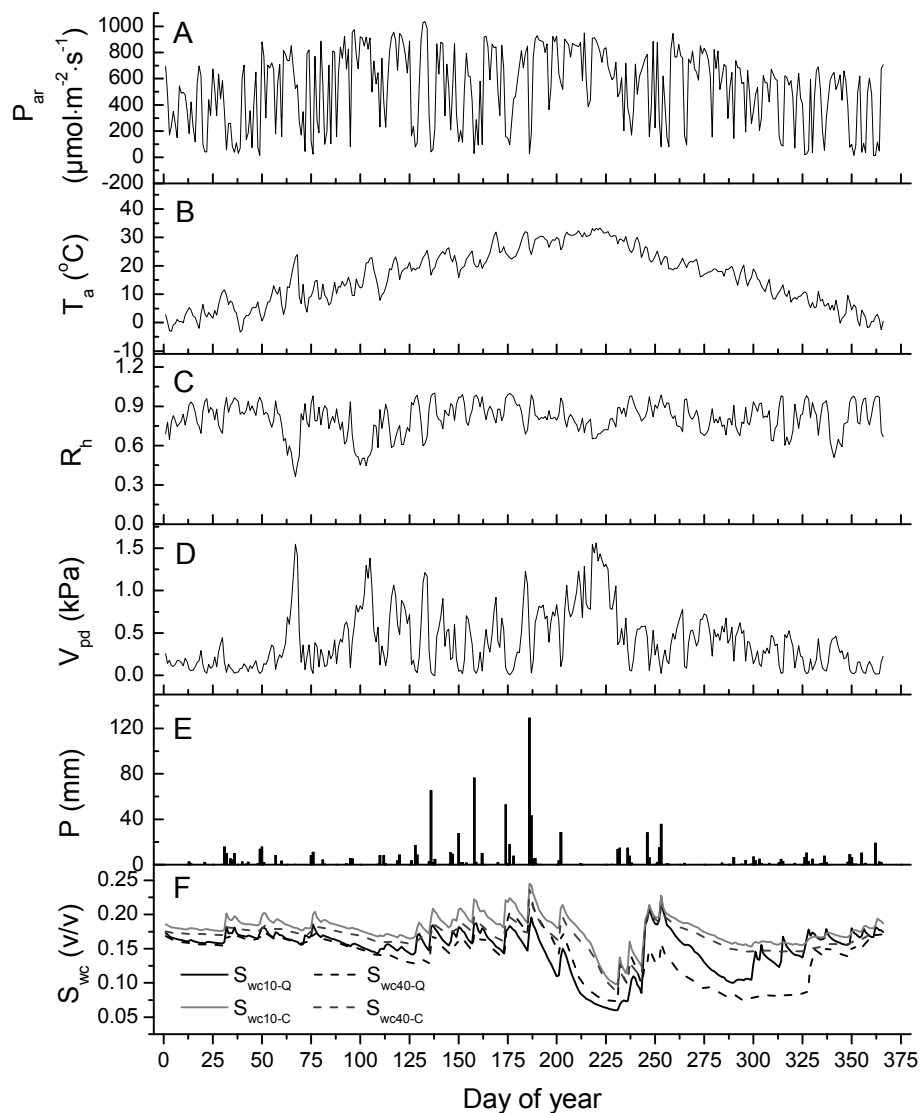


Figure 3. Seasonal course of daily maximum photosynthetically-active radiation (P_{ar}) (A), daily mean air temperature (T_a) (B), mean air relative humidity (R_h) (C), mean vapor pressure deficit (V_{pd}) (D), daily sum of precipitation (P) (E) and daily mean soil water content (S_{wc}) (F) between 9 September 2012 and 8 August 2013.

Soil water content at different soil layers (10 cm and 40 cm) was measured continuously with ECH2O probes (Decagon Devices Inc., Pullman, WA, USA) (Figure 3F).

2.4. Statistical Analyses

All statistical analyses were performed using the SPSS Version 21.0 software (IBM Inc., Armonk, NC, USA). Data plotting was completed with software OriginPro 8.5 (OriginLab Inc., Northampton, MA, USA).

3. Results

3.1. Environmental Variables

The seasonal patterns of environmental variables obtained during the study period (1 September 2012 to 31 August 2013) were representative of the climatic conditions at the study site (Figure 3). The daily maximum photosynthetically-active radiation (P_{ar}), mean air temperature (T_a), mean air relative humidity (R_h) and mean vapor pressure deficit (V_{pd}) had seasonal patterns (Figure 3A,B,C,D). The daily maximum P_{ar} varied from $12.82 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ during December to $1034.55 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ during May (Figure 3A). The daily mean T_a and V_{pd} were highest in August, and the values of July were only a little lower than August. Daily averaged T_a was 15.87°C and varied between -3.31°C (28 February 2013) and 33.28°C (10 August 2013) (Figure 3B,D). The R_h (Figure 3C) was significantly negatively correlated with T_a , and daily averaged R_h was 80.6%.

Rainfall data for the study region were collected from 2012–2013 (Figure 3E). During the data collection period, there were 115 rainy days, which produced a total rainfall of 973.2 mm and an average rainfall of 9.5 mm per day, with individual events ranging from 0.2–129 mm. The distribution of rainfall is shown in Table 2. A light rain event (<10 mm) was most frequent and had the greatest contribution to total rainfall.

Table 2. The distribution of rainfall during our study period.

	The Percentage of Amounts	The Percentage of Events
<10 mm	26.86%	77.39%
10–25 mm	23.28%	14.78%
25–50 mm	16.67%	4.35%
50–100 mm	19.93%	2.61%
>100 mm	13.26%	0.87%

Soil moisture depended significantly on rainfall. Soil water content (S_{wc}) increased with increasing rainfall amount, and the dynamic variation of S_{wc} increased intensely after rainfall, then gradually decreased as a result of evaporation (Figure 3F). Soil water content for the upper 10 cm (S_{wc10}) in most study periods was higher than S_{wc40} . In *Q. acutissima* forest, S_{wc10} averaged 14.97%, and S_{wc40} averaged 13.81%. In *C. lanceolata* forest, S_{wc10} averaged 17.80%, and S_{wc40} averaged 16.59%.

3.2. Sap Flow Densities

Q. acutissima is a deciduous species, and *C. lanceolata* is an evergreen species. We found that the sap flow of *Q. acutissima* obviously rose starting on 8 April and declined starting on 20 November. The sap flow of *C. lanceolata* obviously rose starting in March and declined starting in December. Therefore, the data of *Q. acutissima* used for analyses was from 8 April to 20 November and *C. lanceolata* was from March to November. Mean sap flow density of the two DBH classes (*Q. acutissima*: ≤ 25.8 cm and >25.8 cm (mean DBH of *Q. acutissima* stand); *C. lanceolata*: ≤ 21.0 cm and >21.0 cm (mean DBH of *C. lanceolata* stand)), averaged over the entire study period, is shown for three seasons (Figure 4). The sap flow densities showed no significant difference between two DBH classes of *Q. acutissima* (S_{dQ}) and *C. lanceolata* (S_{dC}), respectively, and the S_{dQ} was higher than that of S_{dC} . In addition, the mean S_{dQ} and S_{dC} in summer were significantly higher than those of the spring and autumn. However, the mean S_{dQ} and S_{dC} showed no significant difference between spring and autumn.

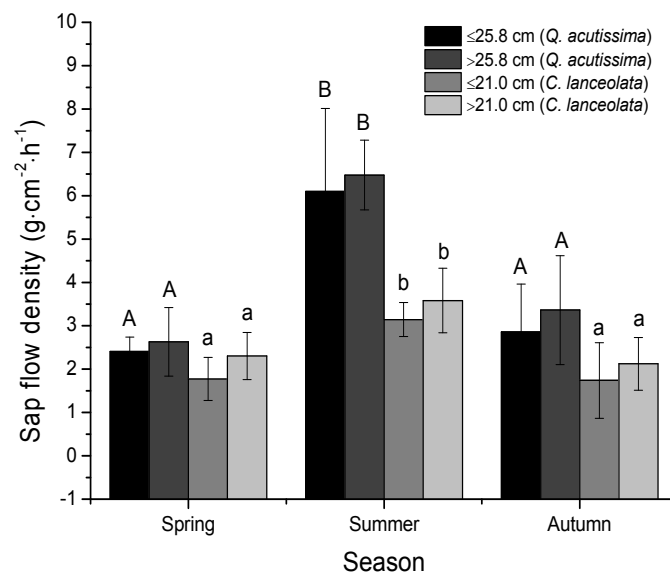


Figure 4. Values of sap flow density ($\text{g}\cdot\text{cm}^{-2}\cdot\text{h}^{-1}$) for each DBH class for four seasons. Error bars show 95% confidence intervals. Vertical columns with the same uppercase (*Q. acutissima*) or lowercase (*C. lanceolata*) letters are not significantly different from each other at $p < 0.05$ according to the Tukey tests.

Daytime sap flow density (S_{dd}) of *Q. acutissima* (S_{ddQ}) started at about 7:00–9:00 a.m. and presented a sustained rise along midday and usually reached a peak at 12 p.m. (Figure 5). Daytime sap flow density of *C. lanceolata* (S_{ddC}) started about one or two hours later than S_{ddQ} . The time that it reached the peak was about two hours later (about 3:00 p.m.). Both the sap flows for *Q. acutissima* and for *C. lanceolata* were highest in July and were lowest in November. To further clarify the differences between *Q. acutissima* and *C. lanceolata*, we calculated the frequency of the S_d peak with sunny days throughout all study periods. The results are presented in Figure 6. On 80.63% of all days over the study period, the maximum S_d ($S_{d,max}$) for *Q. acutissima* occurred between 11:00 a.m. and 1:00 p.m. In contrast, the most frequent occurrence of $S_{d,max}$ for *C. lanceolata* occurred between 2:00 p.m. and 4:00 p.m. (77.23%).

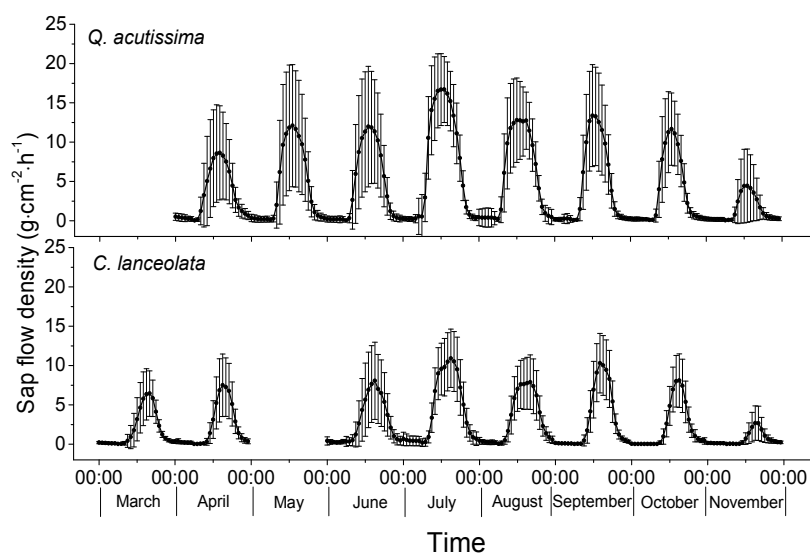


Figure 5. Daily variations of averaged sap flow density in different months.

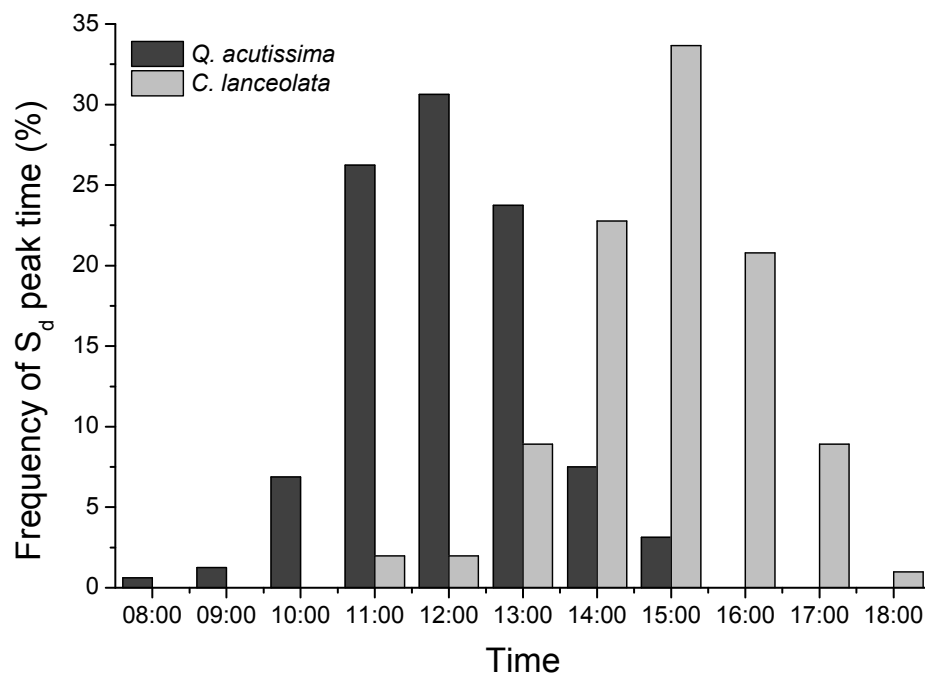


Figure 6. The frequency of time of maximum sap flow density. Data were from the entire sampling period on days with no rainfall.

Both the nocturnal sap flows of *Q. acutissima* and *C. lanceolata* were noticeable and declined slowly at 8:00 a.m.–9:00 p.m. (Figure 7). The nocturnal sap flow density (S_{dn}) showed a strongly declining power function relationship through nights, and all of these power functions passed the variance analysis (Table 3). The nocturnal sap flow density of *Q. acutissima* (S_{dnQ}) and *C. lanceolata* (S_{dnC}) was highest in April ($9.30 \pm 0.85 \text{ g}\cdot\text{cm}^{-2}\cdot\text{d}^{-1}$) and July ($8.16 \pm 1.21 \text{ g}\cdot\text{cm}^{-2}\cdot\text{d}^{-1}$), respectively. The proportions of nocturnal sap flow to the whole-day sap flow for *Q. acutissima* and *C. lanceolata* were, respectively, 2.71% (July)–12.56% (November) and 8.00% (July)–24.29% (November).

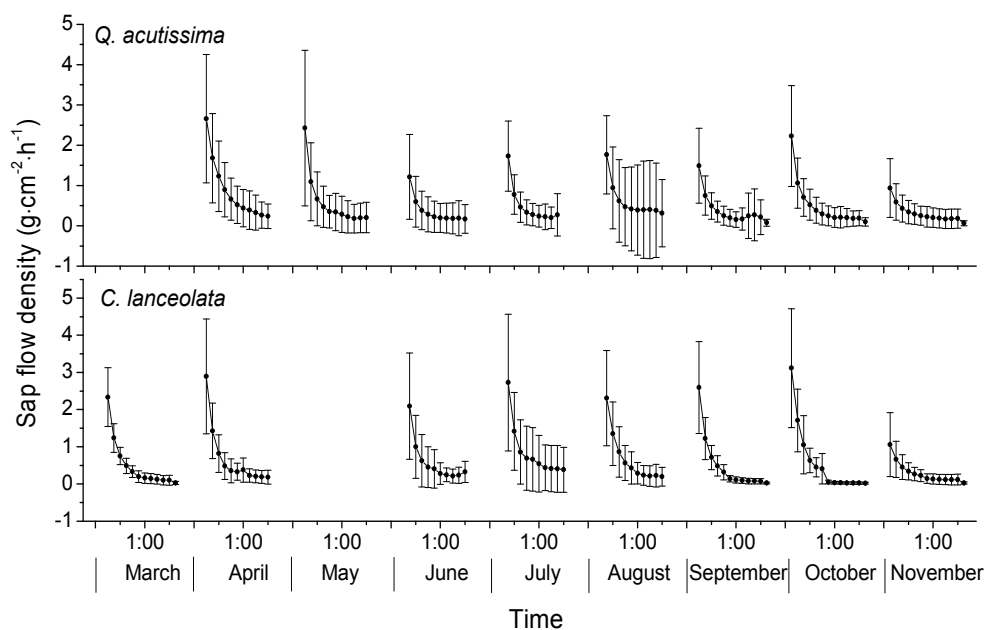


Figure 7. Daily variations of averaged nocturnal sap flow density in different months.

Table 3. The change trends of nocturnal sap flow density from sunset to sunrise.

Month	<i>Q. acutissima</i>	R^2	<i>C. lanceolata</i>	R^2
March	/	/	$y = 3.438 n^{-1.57}$	0.927
April	$y = 3.281 n^{-1.04}$	0.978	$y = 2.889 n^{-1.18}$	0.979
May	$y = 2.274 n^{-1.08}$	0.986	/	/
June	$y = 2.037 n^{-1.11}$	0.929	$y = 1.878 n^{-0.96}$	0.932
July	$y = 1.468 n^{-0.94}$	0.937	$y = 2.547 n^{-0.87}$	0.986
August	$y = 1.497 n^{-0.69}$	0.937	$y = 2.671 n^{-1.16}$	0.979
September	$y = 1.351 n^{-0.93}$	0.829	$y = 3.861 n^{-1.76}$	0.951
October	$y = 2.268 n^{-1.09}$	0.975	$y = 7.988 n^{-2.31}$	0.883
November	$y = 1.041 n^{-0.81}$	0.882	$y = 1.428 n^{-1.14}$	0.862

The time from sunset to sunrise: March and September (7 p.m.–6 a.m., $n = 1$ –12); April and May (7 p.m.–5 a.m., $n = 1$ –11); June and August (8 p.m.–5 a.m., $n = 1$ –10); July (8 p.m.–4 a.m., $n = 1$ –9); October and November (6 p.m.–6 a.m., $n = 1$ –13); n is the integer.

The canopy transpirations of both of *Q. acutissima* and *C. lanceolata* stands were highest in July, and the values were, respectively, 67.42 mm and 56.52 mm (Table 4). The total canopy transpirations were 315.99 mm and 303.55 mm, which were about 32.47% and 31.19% of rainfall, respectively.

Table 4. The canopy transpiration of the stands from March–November (mm).

Month	<i>Q. acutissima</i>	<i>C. lanceolata</i>
March	/	25.25
April	28.18	27.46
May	41.16	43.34
June	40.23	35.47
July	62.72	56.52
August	58.10	39.71
September	40.57	38.56
October	33.52	28.87
November	11.49	8.38
Total	315.99	303.55

3.3. The Relationships between Sap Flow Densities and Environmental Factors

The relationship between daily sap flow density and environmental factors (P_{ar} , T_a , V_{pd} and S_{wc}) in the study periods is shown in Figure 8, in which both the daily sap flow density of *Q. acutissima* and *C. lanceolata* increased with increases in P_{ar} , T_a and V_{pd} (Figure 8A,B,C). There were statistically-significant linear correlations between sap flow density and P_{ar} , T_a or V_{pd} ($p < 0.001$). However, there was no significant correlation between sap flow density and soil water content. To further elucidate the influence of environmental factors on sap flow density, we used the partial regression analysis (Table 5), which showed that P_{ar} explained 25.91% of the variation in daytime hourly sap flow density of *Q. acutissima* and that T_a was a secondary explanatory variable (20.88%). In comparison, V_{pd} was the main explanatory variable for both nocturnal hourly sap flow density of *Q. acutissima* (19.45%) and daytime hourly sap flow density of *C. lanceolata* (35.28%). The nocturnal sap flow density of *C. lanceolata* was not obviously influenced by environmental factors, and the V_{pd} explained only 3.88% of the variation. During the study period, the significance linear relationship between S_{dnC} and S_{ddC} was shown in Figure 9B ($p < 0.01$); but no observed significant correlation of S_{dnQ} to S_{ddQ} was found (Figure 9A).

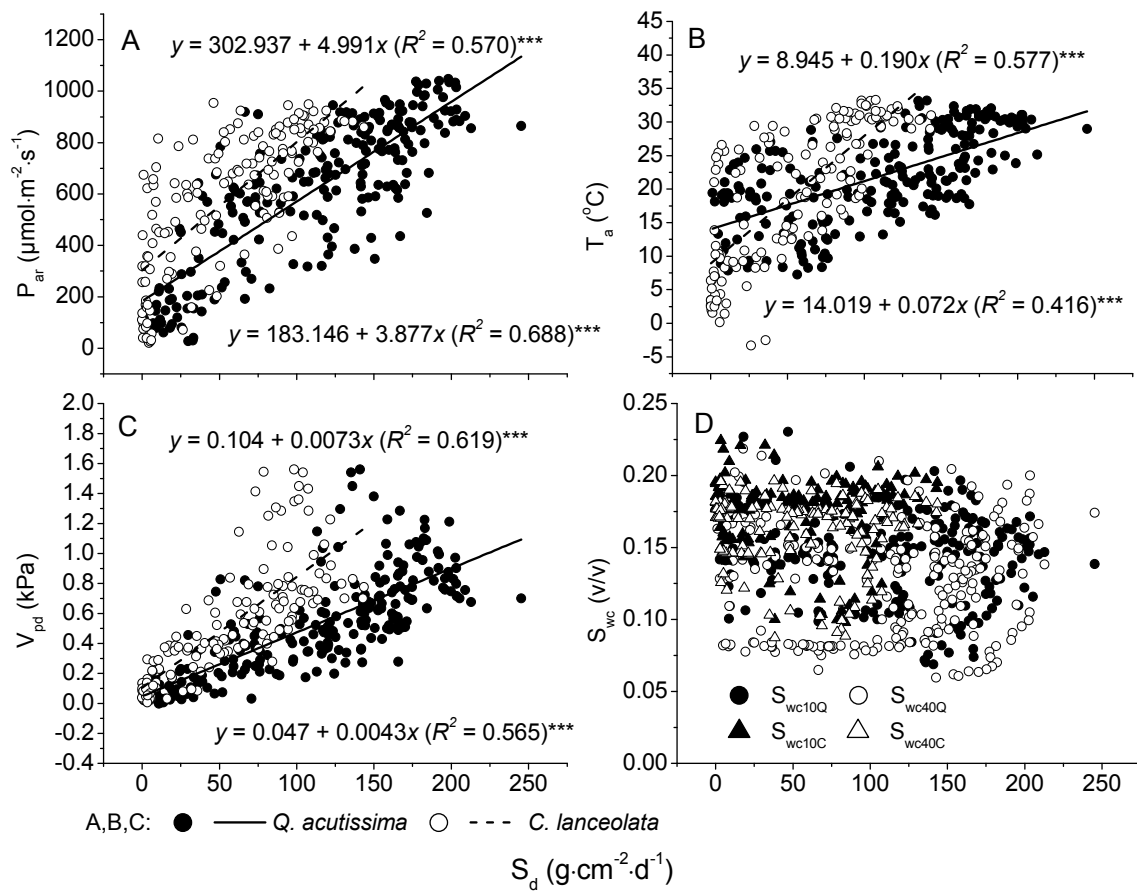


Figure 8. The linear relationship between daily sap flow density and environmental factors. *** Significant correlation at $p < 0.001$.

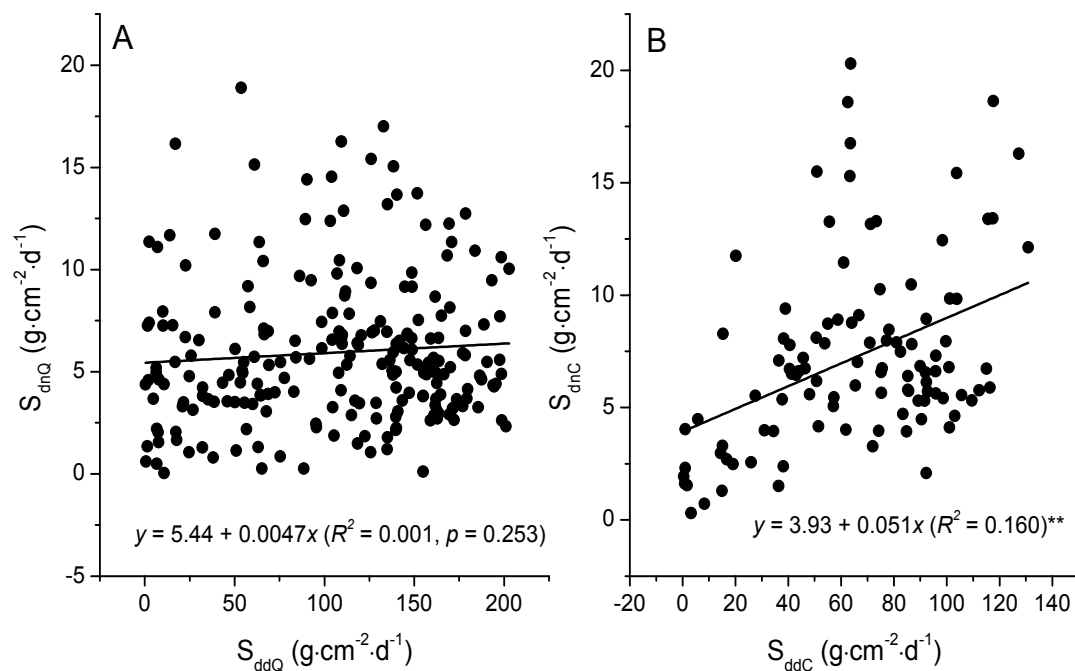


Figure 9. The relationships between daytime sap flow density (S_{dd}) and nocturnal sap flow density (S_{dn}). (A) *Q. acutissima*; (B) *C. lanceolata*. ** Significant correlation at $p < 0.01$.

Table 5. Partial regression analysis of sap flow density versus various explanatory factors.

Factors	S_{ddQ}		S_{dnQ}		S_{ddC}		S_{dnC}	
	PC	VE (%)	PC	VE (%)	PC	VE (%)	PC	VE (%)
P_{ar}	0.51	25.91			−0.07	0.49		
T_a	0.46	20.88	0.01	0.00	0.25	6.45	0.09	0.76
V_{pd}	0.26	6.71	0.44	19.45	0.59	35.28	0.20	3.88
S_{wc10}	0.08	0.67	0.26	6.92	0.06	0.35	0.00	0.00
S_{wc40}	−0.05	0.23	−0.14	1.93	0.03	0.08	−0.01	0.01

S_{ddQ} , daytime sap flow density of *Q. acutissima*; S_{dnQ} , nocturnal sap flow density of *Q. acutissima*; S_{ddC} , daytime sap flow density of *C. lanceolata*; S_{dnC} , nocturnal sap flow density of *C. lanceolata*; PC, partial correlation; VE, variance explained.

In our study, the P_{ar} , T_a and V_{pd} were selected to model and calculate the daily sap flow density. The regression equations are given by:

$$S_{dQ} = 0.103 P_{ar} + 1.579 T_a + 33.178 V_{pd} \quad (R^2 = 0.948) \quad (3)$$

$$S_{dC} = 0.032 P_{ar} + 1.051 T_a + 38.148 V_{pd} \quad (R^2 = 0.908) \quad (4)$$

where S_{dQ} and S_{dC} are the daily sap flow density of *Q. acutissima* and *C. lanceolata* ($\text{g} \cdot \text{cm}^{-2} \cdot \text{d}^{-1}$), P_{ar} is the maximum photosynthetically-active radiation ($\mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$), T_a is the mean air temperature ($^{\circ}\text{C}$) and V_{pd} is the mean vapor pressure deficit (kPa).

4. Discussion

In China, there has been an increasing research focus on the sap flow characteristics in arid and semi-arid regions, where soil water is limited [39–42]. Many people think that water shortage problems only exist in arid or semi-arid regions. However, with the development of regional economy and population, water pollution has gradually increased, and many regions face the serious problem of water quality-induced water shortage [43,44], especially in the Yangtze River Delta region of China. Hence, it is also important and necessary to do research on the sap flow characteristics in water-rich regions in order to plan rational use of the water resources and manage the forest farms.

Measurements of sap flow have been widely used to study the characteristics of transpiration by using the thermal dissipation probe method (TDP) [42,45]. In our study, there was no significant difference between the two DBH classes of *Q. acutissima* and *C. lanceolata*. In spring, summer and autumn, the sap flow density of *Q. acutissima* was greater than that of *C. lanceolata*. The sap flow of *Q. acutissima* and *C. lanceolata* showed similar patterns with solar radiation, which was consistent with the research on *Abies georgei* [33], *Quercus ilex* and *Phillyrea latifolia* [46]. S_{ddQ} started at about 7:00–9:00 a.m., presented a sustained rise during the middle of the day and usually reached a peak at 12:00 p.m. Sap flow velocity of *Abies georgei* increased gradually after 7:00 and reached a peak at approximately 14:00, as shown in Guo et al. [33]. S_{ddC} started later, about one or two hours than S_{ddQ} . The time that it reached the peak was about two hours later (about 3:00 p.m.). Doronila and Forster [47] and Du et al. [48] suggested that species with a peak sap flow at earlier times of the day have greater stomatal sensitivity to V_{pd} , which, in turn, can also affect patterns of carbon uptake and growth rates. Our study species show distinct sap flow peaks at 12:00 p.m. (*Q. acutissima*) and 3:00 p.m. (*C. lanceolata*), respectively. How these times of peak sap flow are related to stomatal opening, photosynthesis, growth rates and even patterns of species co-existence and interaction provides grounds for further research.

In previous studies, nocturnal sap flow has been documented in a wide range of species [16,17]. Zeppel et al. [49] used data from many ecosystems to examine the abiotic factors that may affect the S_{dn} and found that S_{dn} was higher in broad-leaved compared with needle-leaved plants and in tropical compared with temperate species. Our study also demonstrates that S_{dn} accounted for 2.71%–12.56%

(*Q. acutissima*) and 8.00%–24.29% (*C. lanceolata*) of the whole-day sap flow throughout the study period, respectively. S_{dn} was higher in broad-leaved than in evergreen plants. In addition, the proportions of S_{dn} in summer were lower than other seasons, which maybe because the nighttime period during spring and autumn is longer than summer, and therefore, there is more time for nocturnal sap flow to accumulate [16]. Previous studies have also shown that S_{dn} accounted for up to 31%–47% of total daily sap flow in a desert ecosystem [19] and $22.6\% \pm 7.5\%$ for *Q. ilex* and $18.2\% \pm 8.9\%$ for *P. latifolia* in a Mediterranean ecosystem [46]. Comparing the drought regions, the S_{dn} proportion in the Yangtze River Delta region, with its greater water sources, was less, but it was also an important fraction to sap flow of the whole day.

As in previous studies carried out in forests [8,50,51], at our study site, sap flow was also effected by environmental factors, such as P_{ar} , V_{pd} and T_a . Our results indicate that sap flow density was significant linearly correlated with P_{ar} , V_{pd} and T_a . Chang and Zhao, studying a Qinghai spruce forest in northwestern China, reported that daily variation in sap flow was also closely related to changes in P_{ar} , V_{pd} and T_a , and sap flow velocity rose with increasing P_{ar} , V_{pd} and T_a when $P_{ar} < 800 \text{ W} \cdot \text{m}^{-2}$, $V_{pd} < 1.4 \text{ kPa}$ and $T_a < 18.0 \text{ }^\circ\text{C}$ [10]. Among these factors, V_{pd} is a well-known driver of transpiration owing to the water potential gradient and the ability of dry air to pull water from a source of higher water potential [13,19]. Wilson et al. reported that when soil water is plentiful, evaporation generally increases with vapor pressure deficit (V_{pd}) over a wide range of V_{pd} [32]. In our study, P_{ar} and V_{pd} explained the greatest amount of variation in daytime sap flow of *Q. acutissima* and *C. lanceolata*, respectively. In addition, V_{pd} and soil water content (S_{wc}) were the abiotic drivers of nocturnal sap flow [49]. Causally, V_{pd} is also used to determine whether S_{dn} is related to either nocturnal transpiration or stem refilling [16,19,52,53]. Most studies over a wide range of forests indicate that increasing S_{wc} is associated with increased S_{dn} [54]. High S_{wc} will lead to less negative water potentials [54]. For our study site, the V_{pd} was the main explanatory variable for both S_{dnQ} (19.45%) and S_{dnC} (3.88%), and S_{wc10} explained 6.92% of the variation in S_{dnQ} . In addition, the nocturnal sap flow density of *C. lanceolata* was influenced by the S_{ddC} ($R^2 = 0.160$, $p < 0.01$, Figure 9B), but there was no significant correlation between S_{dnQ} and S_{ddQ} ($R^2 = 0.01$, $p > 0.05$, Figure 9A). The results suggest that S_{dnQ} and S_{dnC} were mainly used for transpiration and stem refilling, respectively.

The sap flow density increased gradually with the increase of V_{pd} , but the stomata usually closed with V_{pd} increase [55]. Chen et al. reported that low transpiration was governed by strict physiological regulation and daily V_{pd} exceeding 1 kPa [12]. Sap flow velocity of Qinghai spruce was heightened by increasing the V_{pd} when $V_{pd} < 1.4 \text{ kPa}$ [10]. Deng et al., studying *Hedysarum scoparium* in relation to environmental factors in semiarid northwestern China, reported that the minimum threshold for V_{pd} as a driving force was seen to be around 1.5 kPa [45]. In our study, the S_{dd} also increased gradually with the increase of V_{pd} . When $V_{pd} < 0.6 \text{ kPa}$, it increased significantly. When the $V_{pd} > 1.6 \text{ kPa}$, S_{dd} increased just a little higher than V_{pd} in the interval $1.4 \text{ kPa} \leq V_{pd} < 1.6 \text{ kPa}$ (Figure 10A). When the $V_{pd} > 2.4 \text{ kPa}$ ($V_{pd} > 2.2 \text{ kPa}$), the S_{ddQ} (S_{ddC}) decreased with the increase of V_{pd} . During the nighttime, the V_{pd} in this site ranged from 0–1.5 kPa. When $0.6 < V_{pd} \leq 0.8 \text{ kPa}$, the S_{dnQ} decreased and then increased when $V_{pd} > 1.0 \text{ kPa}$ (Figure 10B). However, when the $V_{pd} > 1.0 \text{ kPa}$, the S_{dnC} decreased. Our studies were carried out on S_{ddQ} and S_{ddC} in the Yangtze River Delta region where optimal V_{pd} values reached 2.4 kPa and 2.2 kPa, respectively.

With these fluctuating rain events, the soil water content frequently increased and diminished (Figure 3E,F). Light rain events ($\leq 10 \text{ mm}$) were most frequent and had the greatest influence on total rainfall in our study site. In a temperate deciduous forest of Korea, the relationship between sap flow of *Quercus serrata* Thunb change and S_{wc} was relatively strong during the drought period, and this relationship was stronger during sunny days [38]. Zhang et al. reported that there was no obvious relationship between monthly sap flow and monthly S_{wc} during the full-leaf periods in a semi-arid black locust plantation, Loess Plateau, China [41]. On the contrary, in arid northwestern China, Chang et al. had established a logistic functional relationship between sap flow and S_{wc} . Sap flow showed an increasing tendency when S_{wc} was increasing, which explained 84% of the variation in sap flow velocity and exhibited great sensitivity [10]. In our study, there was no significant correlation

between both S_{dQ} and S_{dC} (all data) with S_{wc} , because the soil is usually moist during rainy days (115 rain days), when sap flow is low as a result of low P_{ar} , V_{pd} and T_a , which determines the energy available for transpiration [38]. However, in the continuous sunny days (Figure 11), the correlation coefficients between the daily sap flow and soil water contents display very strong positive correlations (Figure 11A,C), which indicates that sap flow decreased with the S_{wc} decreased. Figure 11B,D show that soil water contents gradually decreased with the increase of the cumulative sap flow. All of these results supported the conclusion that transpiration and soil water content influence each other.

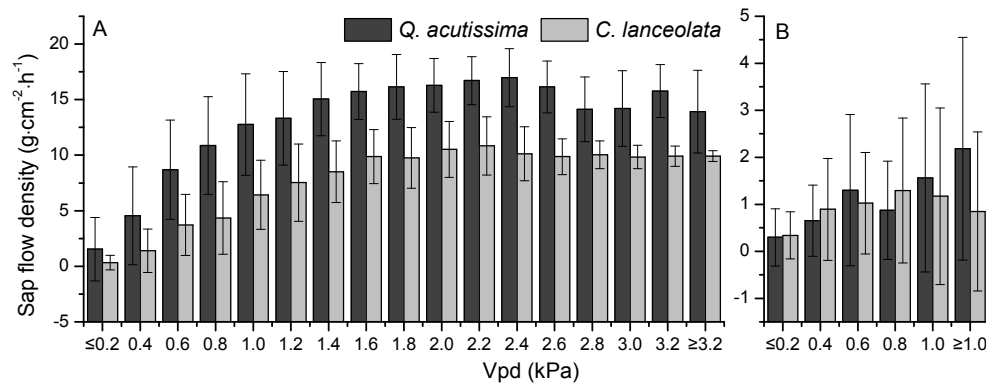


Figure 10. Values of sap flow density ((A) daytime and (B) nighttime) for each V_{pd} stage.

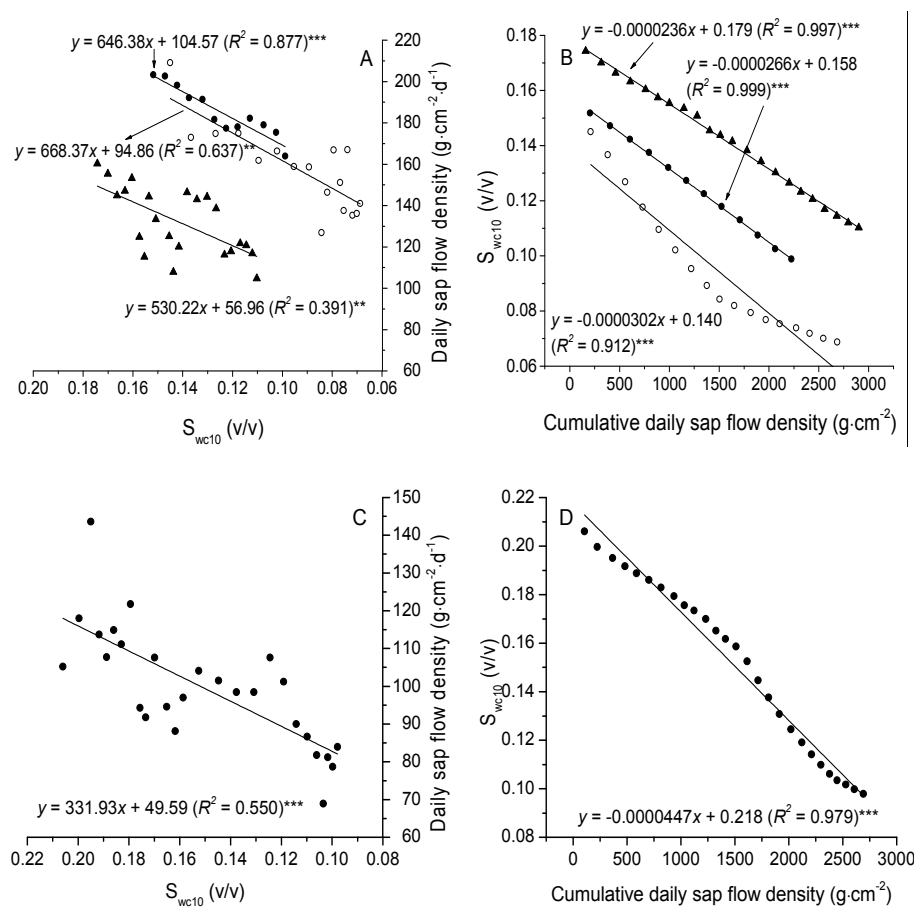


Figure 11. Relations between soil water content and daily sap flow density ((A) *Q. acutissima* and (C) *C. lanceolata*) and cumulative daily sap flow density ((B) *Q. acutissima* and (D) *C. lanceolata*) during continuously sunny periods. The relationship between sap flow density with S_{wc40} was the same as with S_{wc10} . ** and *** mean significant correlation at $p < 0.01$ and $p < 0.001$, respectively.

5. Conclusions

Q. acutissima and *C. lanceolata* are two important, fast-growing, commercial tree species that have been extensively used for vegetation restoration, water conservation and building artificial forests in the Yangtze River Delta region of China. The sap flow densities of trees with different DBH show no significant difference. The sap flow density showed distinct patterns in daytime and nighttime, and S_{dC} reached the peak time about two hours later than S_{dQ} . P_{ar} (25.91%) and V_{pd} (35.28%) explained the greatest amount of variation in daytime sap flow of *Q. acutissima* and *C. lanceolata*, respectively. The amount of nocturnal sap flow was noticeable; the proportions of nocturnal sap flow for *Q. acutissima* and *C. lanceolata* were, respectively, 2.71%–12.56% and 8.00%–24.29%. The total canopy transpirations of the *Q. acutissima* and *C. lanceolata* stands were 315.99 mm and 303.55 mm, which were about 32.47% and 31.19% of rainfall, respectively. The results of this study can be used to estimate the transpiration of *Q. acutissima* and *C. lanceolata* by the regression equations with environmental factors in the Yangtze River Delta region of China.

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