



Sapflow characteristics of mangrove *Avicinia marina* and its affecting factors in Zhangjiang estuary

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ABSTRACT

Xylem sapflow of *Avicinia marina* (Forsk.) Vierh. (*A. marina*) and environment factors were investigated over a year period (June 2011 to May 2012) by continuous sapflow density (SFD) measurements in Zhangjiang estuary in Yunxiao County of Fujian province, China. Diurnal SFD patterns for *A. marina* belonged to single curves following the variation of photosynthetically active radiation (PAR) and vapor pressure deficit (VPD), but time lag between sapflow and PAR as well as VPD in both a wet month (summer) and a dry month (winter) are discussed. PAR exhibited diurnal peak values earlier than sap flow by 30 min (winter) to 60 (summer). However, VPD lagged behind sapflow by 30 min in winter and earlier than sap flow by 30 min in summer. The sapflow rate of *A. marina* was much higher than those of terrestrial tree species. However, the daily water use was still conservative. Daytime half-hourly mean stand sapflow was positively linearly correlated with photosynthetically active radiation (PAR) and vapor pressure deficit (VPD) in during the study period (all $P < 0.001$), whereas daily daytime mean stand transpiration was less tightly coupled to PAR and VPD, especially in the winter. A pronounced hysteresis was observed between stand sapflow and PAR or VPD, but the extent of the hysteresis varied seasonally and between species. However, the mechanisms and ecological implications of mangrove water use deserve further investigation.

Keywords: *Avicennia marina*, sapflow, environment factors, hysteresis

INTRODUCTION

Mangroves as a group have acquired a conservative water use strategy, namely, low xylem water potential^[1], low transpiration rates, high photosynthetic rates and thus high water-use efficiency^[2-4] and so on. But those studies were only based on the leaf-level mechanisms. In the past years, sap flow techniques are widely used for analysis of water-use for woody plant in natural and managed vegetation. However, limited direct evidences (sap flow measurements) have been undertaken to monitor mangrove stands (only several mangrove species: *Avicennia germinans* (L.) Stearn, *Laguncularia racemosa* (L.) Gaertn. f., *Rhizophoramangle* L., *Avicennia* cf. *alba* Blume and *Rhizophora apiculata* Blume)^[5-7], due to the difficulties in instrument maintenance in the mangal environment. And their study results presented that the sap flow characteristics of mangrove species are highly variable and must be considered in relation to local salinity, season and tree size. Nevertheless, no data have been published yet about sap flow of shrub mangroves with very small diameter at breast height (DBH).

In this study, we investigated the sapflow characteristics of *Avicennia marina* (Forsk.) Vierh., the most common native mangrove specie, which widely distributed in the subtropical regions of China. The main objectives of our study were to: (1) quantify the temporal patterns of tree transpiration of *A. marina*; (2) examine control of environment factors (vapor pressure deficit, photosynthetically active radiation) over the water use of mangroves. The results are

expected to contribute not only to the understanding water use strategies of mangrove trees, but also to advance our understandings on environmental controls of water exchange between mangrove forests and atmosphere.

EXPERIMENTAL SECTION

Study site and plant materials

The study was conducted inside the Zhangjiangkou National Mangrove Nature Reserve in Yunxiao county, Fujian province, China (23°55'N, 117°23'E). The unique feature of the mangrove forest in the Zhangjiang estuary is an inter-charge of freshwater from the upstream of Zhangjiang River and the seawater from the downstream of the East China Sea. The tide regime is typical semidiurnal tide. This site is a subtropical maritime monsoon climate zone, rainfall mainly occurs in April to September. The mean annual precipitation and air temperature were 1714.5 mm and 21.2 °C, respectively.

According to the species composition survey, the mangrove forest at the study site was dominated by *K.obovata* and *A. marina*, so *A. marina* with a range of size classes were characterized for their diameters at breast height (DBH), crown dimension, tree density and stand leaf area index (*LAI*). The results were given in Table 1.

Environmental measurements

Meteorological data was measured at 30-min intervals from June, 2011 to May, 2012. Photosynthetically active radiation was measured with a quantum sensor (LI-190SB, Li-COR). Rainfall (TE525MM, Texas Electronics, Texas, USA) was measured with a tipping bucket rain gauge. Temperature and relative humidity (HMP45C, Vaisala, Finland) were monitored at internal and upper canopy. All data were logged using a CR1000X datalogger to automatically record the sensor outputs at half-hourly intervals. The temperature, depth and salinity of the tidal water was monitored by a water gauge (YSI, Yellow Springs, USA) at half-hourly intervals.

Sapflow and transpiration of individual tree

We grouped trees in three diameter size classes (Table 1): namely three small trees (DBH: <4 cm), three middle trees (DBH: <4-6 cm) and three large trees (DBH: >6 cm) The tree class was based on stem diameter rather than tree age since mangrove trees do not form annual rings, which prevents detection of tree age from tree ring cores. Then all trees were selected to install the Granier-type sensors for sapflow measurements^[8-10]. Data were recorded to a multi-channel CR3000 data loggers (Campbell Scientific Inc., Logan, UT, USA) at half-hour intervals. Probes were generally placed on the northeast side of each tree to avoid direct sunlight from sunflecks and covered with aluminium foil.

Xylem sap flux per unit of sapwood area ($\text{gH}_2\text{O m}^{-2}\text{sapwood s}^{-1}$), hereafter referred as sap flow (*SFD*), was determined from diurnal temperature differences between upper and lower probes based on an empirical formula described by^[8,9] that has been revalidated for use in woody stems^[11].

When the sapwood area was calculated, the whole-tree sapflow (E , g s^{-1}) was calculated from *SFD* and sapwood area (A_s).

Sapflow measurements were scaled to stand sapflow from knowledge of species composition and sapwood area. All estimates of sapwood area were adjusted according to known radial variation in sapflow for the individual species^[12]. Then stand sapflow (E_s) (g s^{-1}) was calculated from sapflow measurements performed on sample trees using the equation:

$$E_s = \sum_{i=1}^n E_{ti} = \sum_{i=1}^n (SFD_i \times A_{si})$$

Where SFD_i is the average sapflow density of class i , A_{si} is total sapwood area in class i . E_{ti} is thus the total E_i in class i .

Data analysis

Raw sapflow data analysis was done using SFD-dMax method (supported by Lu P). All statistical analyses (need to be more specific on what type of analyses you performed) were performed with the SPSS and SAS software packages (SPSS 16.0, SAS 9.0). All graphs were made with Sigmaplot software (Sigmaplot10.0, Systat Software Inc, USA).

Table 1 Characteristics of *A. marina* used for the sapflow measurements

Species	Tree size class	DBH (cm)	Height (m)	Crow dimension (cm)		Density (Trees ha ⁻¹)	Plot LAI
				Length	Width		
<i>A. marina</i>	Small (<4 cm)	–	–	–	–	4005	
	Middle (4–6 cm)	4.14–6.0	4.5–6.0	60–200	30–100	1531	1.72–2.19
	Large (>6 cm)	7.01–7.96	5.0–6.0	200–220	130–140	84	

*S, M and L correspond to the size class of branch small, medium and large, respectively DBH: diameter at breast height; LAI: leaf area index; - : no data

RESULTS AND DISCUSSION

Sapflow characteristics of subtropical mangrove *A. marina*

Figure 1 showed that although diurnal *SFD* patterns for *A. marina* belonged to single curves following the variation of *PAR* and *VPD*, they were not necessarily synchronized. Time lag between sapflow and *PAR* as well as *VPD* in both a wet month (summer) and a dry month (winter) are discussed. *PAR* exhibited diurnal peak values earlier than sap flow by 30 min (winter) to 60 (summer). However, *VPD* lagged behind sapflow by 30 in winter and earlier than sap flow by 30 min in summer. And there was a pronounced night sapflow phenomenon for every class of diameter between sunset and midnight. There were significant differences in the magnitude of *SFD* for three classes ($P < 0.05$), i.e., *SFD* for large DBH was the highest in different classes.

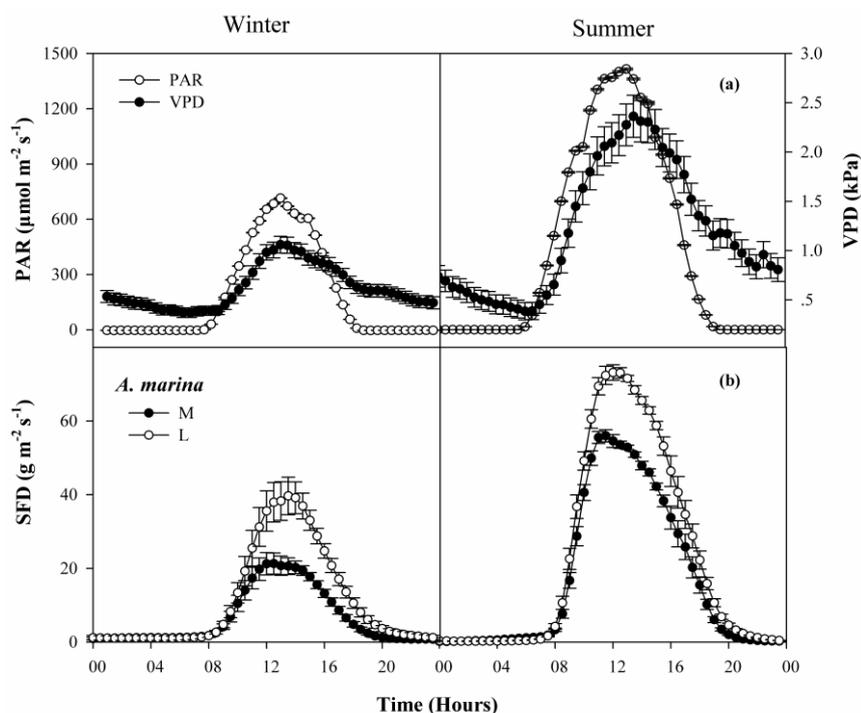


Figure 1 Diurnal patterns of (a) *PAR* (white cycle) and *VPD* (black cycle), (b) *SFD* of DBH-M (black cycle) and L (white cycle) of *A. marina* on several clear days of two seasons
All data were the means over 30 min periods

Although the mangrove trees in the Zhangjiang estuary was mostly in the shrub form with relatively low tree height and small DBH, the sapflow density of *A. marina* even reached a maximum sapflow density of $80 \text{ g m}^{-2} \text{ s}^{-1}$ in summer. Compared with other mangrove species reported before (6.5 to $37.1 \text{ g H}_2\text{O m}^{-2} \text{ s}^{-1}$: *Avicennia germinans* (L.) Stearn, *Laguncularia racemosa* (L.) Gaertn. f., *Rhizophoramangle* L.^[6], 17 to $39 \text{ g H}_2\text{O m}^{-2} \text{ s}^{-1}$: *Avicennia germinans*^[7]), the *SFD* for *A. marina* species in our study were much higher (Figure 1). Furthermore, it was more than twice the *SFD* of forested wet-land tree species investigated-including *Taxodium distichum* (L.) Rich (10 – $20 \text{ g H}_2\text{O m}^{-2} \text{ s}^{-1}$ ^[13]), *Magnolia virginiana* L. (20 – $28 \text{ g H}_2\text{O m}^{-2} \text{ s}^{-1}$ ^[14]) and *Nyssa sylvatica* var. *biflora* (Walt.) Sarg. (30 – $36 \text{ g H}_2\text{O m}^{-2} \text{ s}^{-1}$ ^[14]). Even the *SFD* of *A. marina* was some higher than coniferous forest species (*Pinus taeda*: $72.2 \text{ g H}_2\text{O m}^{-2} \text{ s}^{-1}$ ^[15]) and *Picea crassifolia*: $56 \text{ g H}_2\text{O m}^{-2} \text{ s}^{-1}$ ^[16]), and was commensurate to some deciduous broad-leaf forest species (41.7 – $111.2 \text{ g H}_2\text{O m}^{-2} \text{ s}^{-1}$ for Beech^[17]) and evergreen broad-leaf forest species (40 – $70 \text{ g H}_2\text{O m}^{-2} \text{ s}^{-1}$ for *Acacia mangium*^[18], 60 – $90 \text{ g H}_2\text{O m}^{-2} \text{ s}^{-1}$ for *Quercus glauca*^[19]). Hence, our results further proved that the sapflow density of

A. marina species in subtropical mangrove shrubs appeared to be high.

Species vary in water use maybe one reason for higher *SFD* of mangroves of Zhangjiang estuary. And salinity may be another reason. Salinity is not the special request or necessary request for mangroves. Some mangrove species (e.g. *Rhizophoraceae* and *Rhizophoramucronata* Poir.) grow better with fresh water than saline water. Mangrove was salt resistance, but not like salt. The mean daily salinity was about 10 ppt (data unpublished), which was lower than that at other sites reported before. And that may be more suitable for *A. marina* growing.

Water use of subtropical mangrove *A. marina*

Daily individual tree water use (*F*) for *A. marina* in summer was always significantly higher than that in winter ($p=0.000$) (Figure 2). It is indicated that mean daily water use (*F*) of *A. marina* increased 67-136% compared with that in winter. In winter, both *PAR* and *VPD* were lower than summer and no rainfall occurred, water use patterns were quite stable except for one raining day. However, during summer days, with higher *PAR* and *VPD*, rainfall was distributed intermittently throughout the month, led to water use patterns more variable from one day to the next than during the dry season (e.g. standard deviations in March were twice as high as in November).

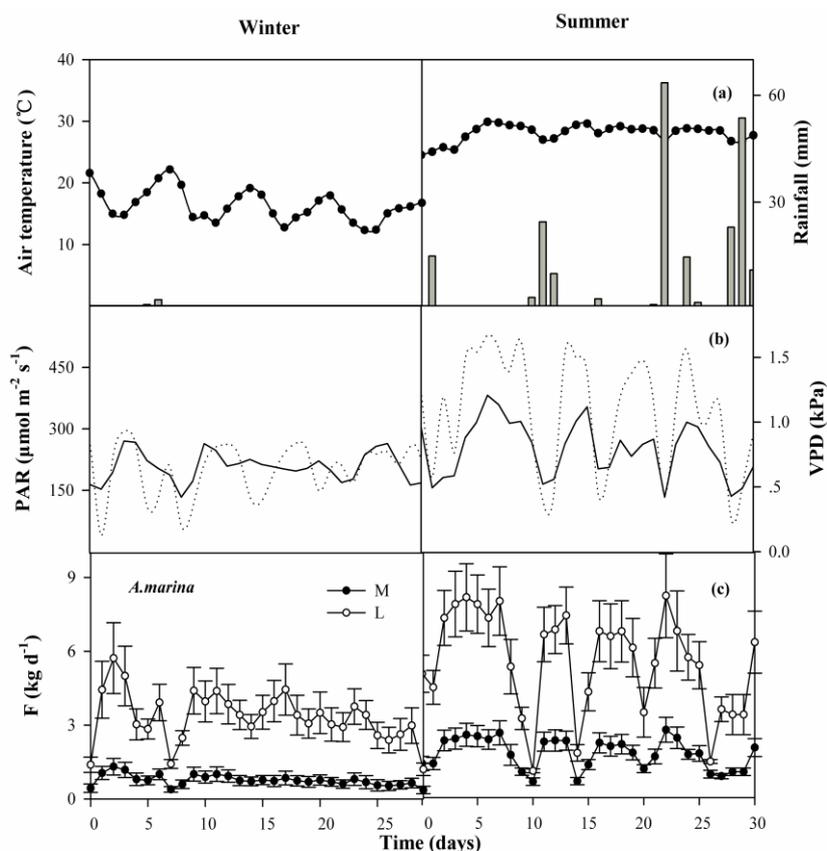


Figure 2 Variations of mean daily (a) air temperature and rainfall, (b) *PAR* (black line) and *VPD* (dotted line), (c) *F* of *A. marina*

Although the *SFD* of *A. marina* measured at a 2-cm depth was much higher, its maximum daily water use was less than 10 kg d^{-1} , which was on the same order of magnitude with other mangrove species in tropical and neotropical zones (DBH<15 cm, 0.31 to $10 \text{ kg H}_2\text{O d}^{-1}$) reported by Muller and Krauss (DBH<15 cm, $F < 10 \text{ kg H}_2\text{O d}^{-1}$)^[6, 7]. This result indicated that mangroves of *A. marina* in Zhangjiang estuary demonstrated conservative daily water use during the study period despite high *SFD* values at a 2-cm depth.

Correlations of stand Sapflow with environmental factors

In addition to physiological factors, environmental factors are the very important factors influencing the Sapflow. For further analysis the relationships between stand sapflow and environment factors, considering the influence of a wet canopy on the energy budget and unstable factors at night, correlation analysis was made between them using daytime half-hourly values excluding the data from rainy days and the day following rain. In this study, dependence of half-hourly stand Sapflow on environmental factors (*PAR* and *VPD*) was evaluated both with and without taking consideration of hysteresis.

Sapflow of *A. marina* was actually very sensitive to small changes in weather conditions (mainly *PAR*, *VPD*) with quasi-simultaneous reactions ($P < 0.001$) as shown in Figure 3 and Table 2. The results indicated that the variation in half-hourly E_s of 55.3–95.1% was explained by *PAR* or *VPD* alone, indicating strong coupling of E_s to the drivers of transpiration at the diurnal scale in both seasons. Taking into consideration of the hysteresis increased the percentage of the variation in E_s explained by *PAR* or *VPD* alone (data not shown). Compared with *VPD*, E_s were more dependent on *PAR* according to the value of the correlation coefficient. And there was a marked seasonal response in half-hourly E_s to environmental factors. During the summer season, the slopes for the regressions of E_s dependent on *PAR* or *VPD* were higher, and value of E_s was higher than winter for a given *PAR* or *VPD*.

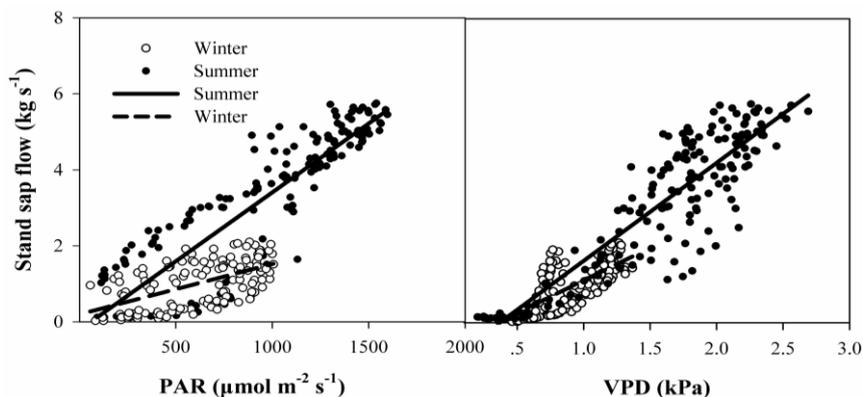


Figure 3 Half-hourly mean daytime values of stand sapflow (E_s) of *A. marina* in relation to (a) *PAR* and (b) *VPD*

Muller *et al.* (2009) firstly reported the regressions between F of mature *A. germinans* individuals and environmental factors (*VPD*, *PAR*, R_n) were not so strong, and regressions were weaker during the rainy season in French^[7], Guiana, but in their study, no hysteresis was considered. The difference between our results and theirs might be caused by difference in (1) climatic conditions, (2) mangrove species-*A. germinans* and (3) salinity between the two study sites.

When E_s dependence on *PAR* and *VPD* was evaluated using daily mean daytime values rather than diurnal half-hourly values, the correlations was greatly reduced. Even there was no significance correlation between them in winter, and the percentage of the variation in E_s explained by environmental factors alone was much reduced, less than 60% of the variation in E_s was explained by *PAR* or *VPD* alone in winter. This might be caused by the daily changes in salinity and flooding condition and reduced range of the variation of the values.

Table 2 Correlation coefficients (R^2) and significant values (P) for the dependence of stand sapflow (E_s) of *A. marina* on *PAR* or *VPD* in each season for the half-hourly and daily mean values

Seasons		Half-hourly values		Daily values	
		R^2	P	R^2	P
Winter	<i>PAR</i>	0.581	0.000	0.473	0.282
	<i>VPD</i>	0.693	0.000	0.496	0.257
Summer	<i>PAR</i>	0.886	0.000	0.943	0.001
	<i>VPD</i>	0.899	0.000	0.817	0.025

Table 3 Hysteresis in the relationship between stand sapflow (E_s) of *A. marina* and *PAR* or *VPD* in two different seasons, Data were the mean values of 7 clear days in each season

Species	Season	Hysteresis (min)*	
		E_s vs. <i>PAR</i>	E_s vs. <i>VPD</i>
<i>A. marina</i>	Winter	-30	+30
	Summer	-60	-30

* “-” indicates that E_s lags *PAR* or *VPD*, while “+” indicates that E_s is ahead of *PAR* or *VPD*

CONCLUSION

This study showed mangrove shrubs *A. marina* of Zhangjiang estuary demonstrated conservative water use despite high sapflow values at a 2-cm depth.

Half-hourly stand sapflow was highly coupled to photosynthetically active radiation and vapor pressure deficit in

each season but its dependence on these factors varied seasonally. During the summer, the levels of stand Sapflow dependent on vapor pressure deficit and radiation was higher than that in winter. And taking consideration of hysteresis, the dependent levels markedly increased in both seasons. Due to interspecies different, the response to environmental factors between two mangroves was some different.

Salinity and flooding were the most important drives for mangroves, a closely investigation is needed to know the influence on water use of mangrove and the response mechanisms in the wild.

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