

# River Mangrove Maintains Certain Level Na<sup>+</sup> and Cl<sup>-</sup> in Leaves to Adapt Seasonal Freshwater

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## Research

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## Abstract

**Background:** Mangrove environments are often characterized by large fluctuations in salinity, ranging from freshwater to hypersaline conditions. Most reports have focused on the mechanisms by which mangroves adapt to high salinity. However, how mangroves cope with seasonal freshwater habitats has seldom been studied. To address this question, we surveyed the river salinity and leaf traits (chlorophyll fluorescence, ion concentrations, carbon isotope ratios and osmolality) of *Aegiceras corniculatum* (L.) Blanco (river mangrove) along a freshwater-dominated river.

**Results:** *Aegiceras corniculatum* at the upstream site was subjected to low salinity, being in fresh water for a long period (up to 310 h) in the wet season and experiencing a short term of low salinity in the dry season. The actual photosystem II efficiency ( $\Phi_{PSII}$ ) and electron transport rates (ETR) of the leaves at the upstream site decreased in the wet season, and recovered substantially in the dry season. Quenching analysis indicated that there was only a down-regulation of photoprotection, but no photoinhibition at the upstream site in the wet season. An explanation for this is that high levels of  $\text{Na}^+$  and  $\text{Cl}^-$  were maintained in the leaves in the wet season.

**Conclusions:** Long-term freshwater is a stressful environment for *A. corniculatum*. *Aegiceras corniculatum* maintains certain level  $\text{Na}^+$  and  $\text{Cl}^-$  to adapt the seasonal freshwater.

## Introduction

Mangroves are halophytic woody plants that are distributed in tropical and sub-tropical intertidal zones (Hutchings and Saenger 1987; Tomlinson 2016). Their environments are often characterized by large spatial and temporal (daily, monthly, and seasonal) fluctuations in salinity, often from freshwater to hypersaline conditions, particularly in tropical estuaries (Bazihizina et al. 2012; Ewe et al. 2007; Ridd and Stieglitz 2002). These fluctuations can also be intensified during changes in the climate or environment (Bompy et al. 2015; Eslami-Andargoli et al. 2009; Lovelock et al. 2017; Moon et al. 2015; Widlansky et al. 2015). Additionally, artificial disturbances such as dam construction and channel opening or closing can also contribute to salinity fluctuations (Jaramillo et al. 2018; Wemple et al. 2018).

One striking feature of mangroves is their great ability to adapt to fluctuating salinities (Bompy et al. 2014; Krauss and Ball 2013; Tomlinson 2016). Salinity has long been recognized as a vital factor regulating the growth and distribution of mangroves (Ball 2002; Duke et al. 1998; Hayes et al. 2019; Krauss and Ball 2013; Robert et al. 2009). Extremely low levels of salinity, such as under prolonged freshwater, may occur in mangrove habitats during abnormal climatic events, but the effects thereof on mangroves have not yet been elucidated (Bompy et al. 2015; Lovelock et al. 2017). Prolonged drought or tidal surges can lead to more rapid rises or decreases in water/soil salinity, resulting in larger fluctuations in water/soil salinity, which could affect the ecophysiology and survival of mangroves (Bompy et al. 2015; Islam and Gnauck 2007; Jaramillo et al. 2018; Komiyama et al. 2019; Munns 2002). Massive mangrove mortality resulting from the modification of hydrologic connectivity and consequent hypersaline conditions has been previously reported (Duke et al. 2017; Jaramillo et al. 2018; Lovelock et al. 2017). Abnormal long-term freshwater flooding has also caused extensive mangrove forest death (Erftemeijer and Hamerlynck 2005).

Most of our present knowledge of mangrove salt tolerance originates from controlled experiments under constant salinity (Bazihizina et al. 2012; Parida and Jha 2010; Wang et al. 2011). However, mangroves grown under constant salinities in greenhouses or under controlled experiments are unlikely to behave in the same way as in field situations with fluctuating salinities (Beckett et al. 1995; Bompy et al. 2014; Lin and Sternberg 1993; Reef et al. 2015). Few studies have assessed the effects of fluctuations in salinity on mangroves under field conditions (Ball and Farquhar 1984a; Bompy et al. 2014; Lin and Sternberg 1993). An improved understanding of the adaptation of mangroves to salinity fluctuations can assist in mangrove conservation, as mangroves are greatly threatened by developments such as dam construction (Alcérreca-Huerta et al. 2019).

The salt tolerance mechanisms of mangroves have been extensively evaluated (reviewed in Parida and Jha 2010). While most reports have focused on the mechanisms by which mangroves adapt to hypersaline environments (Krauss and Ball 2013; Méndez-Alonzo et al. 2016; Munns 2002; Nguyen et al. 2017; Parida and Jha 2010), few have assessed the manner in which mangroves tolerate seasonal freshwater conditions in their natural environment and their associated ecophysiological responses (Tuffers et al. 2001; Werner and Stelzer 1990).

*Aegiceras corniculatum* (L.) Blanco, commonly known as river mangrove, has a shrub- or small tree-like growth form and is commonly found in estuarine areas, in the region of India to South China, as well as a part of Australia (Tomlinson 2016). It is the most dominant mangrove species in China and is classified as a pioneer in mangrove succession (Wang and Wang 2007). It can grow under contrasting salinities, from fresh to brackish water to seawater (Ball 1988; Mallery and Teas 1984). Our earlier study documented its natural distribution from the river mouth to the most upstream location along the Huangzhu River: a freshwater-dominated river in the monsoonal subtropics of southwestern China that is characterized by different mangrove growth and environmental conditions (Xu et al. 2019). Given the wide fluctuations in substrate salinity experienced by *A. corniculatum*, we hypothesized that: (1) long-term freshwater constitutes a physiological stress to mangroves, and (2) under seasonal freshwater, mangroves maintain homeostasis by actively accumulating salts. To test these hypotheses, we compared the photosynthetic performance (chlorophyll fluorescence), osmotic adjustment, and ion concentrations of mangrove plants among an upstream site characterized by long-term inundation with fresh water, an intermediate site with medium salinity, and a downstream site with high salinity.

## Materials And Methods

### Study area

The Huangzhu River, a freshwater-dominated river enters into Pearl Bay, Guangxi (21°31'~21°37'N, 108°00'~108°16'E), in the monsoonal subtropics of southwestern China. The average temperature and salinity of sea water in Pearl Bay are 23.5 °C and 19.6‰, respectively. Annual rainfall is 2221 mm, with

maximal rainfall in the wet season (from May through September, with monthly mean greater than 300 mm) and a minimum rainfall in the dry season (from November through February, with monthly mean less than 32 mm). The river experiences a diurnal tide.

## Sampling sites

From the river mouth to the upstream limit of the mangrove distribution, the riverine bank was divided into three parts, namely upstream, intermediate, and downstream, according to the method of Duke et al. (1998). A proportional distance from the river mouth was used to classify the riverine parts, where downstream represented the lower third of the estuary (including no-estuary stands), intermediate represented the middle third of the estuary, and upstream represented the upper third. Downstream therefore runs from 67% to 100% of the river length, intermediate runs from 33% to 67%, and upstream runs from 0% to 33% (Fig. 1). Three sites (Site 1, Site 2 and Site 3) were established according to the hydrological and topographical features to monitor the environmental factors and eco-physiological features of *A. corniculatum* during two contrasting seasons, including the driest month of the dry season (January 2008) and the wettest month of the wet season (August 2008). This was done in order to capture one set of extreme dry or wet conditions that might be limiting the species distribution. Site 1, about 9.0 km away from the river mouth in the upstream section, was located at the upstream limit of the *A. corniculatum* distribution. The dominant mangroves here include *Excoecaria agallocha* L. and some mangrove associates such as *Hibiscus tiliaceus* L. and *Pongamia pinnata* (L.) Pierre, with *A. corniculatum* occurring occasionally at the waterward fringe of the mangrove forests. Site 2, in the intermediate section, is located approximately 5.0 km away from the river mouth and is dominated by *A. corniculatum*. Site 3 is located at the river mouth in the downstream section where large areas of mangrove exist, with *Avicennia marina* (Forssk.) Vierh. and *Bruguiera gymnorhiza* (L.) Lam. being the dominant species, while *A. corniculatum* and *Kandelia obovata* Sheue, H.Y. Liu & J. Yong occur occasionally. At each site, three 5 m × 5 m quadrats parallel to the river bank were established for plant species survey. In each quadrat, the height and base diameter of each mature *A. corniculatum* tree were measured. Three healthy *A. corniculatum* trees (more than 5 years old) with uniform growth conditions at each quadrat were selected for further measurements.

## Salinity measurements

The surface water salinities of the three sites were measured using three conductivity loggers (HOBO U24-002-C, Onset, USA) at 60-min intervals. At each quadrat, the soil sample at a depth of 10–15 cm was collected during low tide. The soil was weighed and air-dried. Ten grams of dry soil powder was suspended in 50 mL distilled water and shaken well, and the salinity was measured by mobile salinity meters (Star 3, Thermo Orion, USA).

## Nitrogen and phosphorous concentration measurements

The nitrogen (N) and phosphorus (P) concentrations of the soils at a depth of 10–15 cm were sampled under each selected tree during low tide in the dry season. Leaves and soils were digested in sulfuric acid-hydrogen peroxide. N concentration was determined using the micro-Kjeldahl method (Yoshida et al. 1976), while P was determined by the ascorbic acid-antimony reduced phosphate colorimetric method (Murphy and Riley 1962).

## Chlorophyll fluorescence measurements

Chlorophyll fluorescence was measured on selected tree leaves of sunward external canopy (PAR at leaves was about 1000  $\mu\text{mol m}^{-2}\text{s}^{-1}$ ), by a portable fluorometer (PAM 2100, Walz, Germany) following dark adaptation for 30 min (Yuan et al. 2012). Measurements were randomly made from 9:00 to 11:00 AM on 20–32 *A. corniculatum* trees (5–8 mature leaves tree<sup>-1</sup>) at each site, respectively. Fluorescence parameters were calculated according to Maxwell and Johnson (2000).

## Carbon isotope composition ( $\delta^{13}\text{C}$ ) measurements

The leaf samples were collected from the selected trees at each quadrat and washed with distilled water, blotted dry, weighed, and oven-dried at 80°C for 48 h. Dry samples were weighed and ground into powder.  $\delta^{13}\text{C}$  values were determined with an isotope ratio mass spectrometer (model delta S, Finnigan MAT, San Jose, CA, USA). The  $\delta^{13}\text{C}$  was used as an indicator of the long-term water use efficiency (WUE).

## Osmolality and ion concentration measurements

The extracted leaf sap from selected trees at each site was used to measure sap osmolality with a pressure vapor osmometer (5520, Wescor Inc., Logan, UT). The concentrations of Chloride ( $\text{Cl}^-$ ), Sodium ( $\text{Na}^+$ ), potassium ( $\text{K}^+$ ), and calcium ( $\text{Ca}^{2+}$ ) in leaves were determined by inductively coupled plasma-mass spectrometry (ICP-MS, ELAN DRC-e, Perkin Elmer Inc., USA), according to Parida et al. (2004). The ion concentrations of the leaf sap were calculated on the basis of the leaf water content. Soil samples were collected at 10–15 cm depth under each sampled tree during low tide. After oven-drying at 60°C to constant weight, the contents of  $\text{K}^+$ ,  $\text{Na}^+$ ,  $\text{Ca}^{2+}$ , and  $\text{Mg}^{2+}$  were determined by ICP-MS after microwave-assisted digestion in  $\text{HNO}_3$ , HF, and  $\text{H}_2\text{O}_2$  (Parida et al. 2004).

## Statistical analysis

One-way ANOVA (Turkey test) was used to compare salinity, tree height, N and P concentrations among sites, and osmotic potential (Table 1, Table 2, Fig. 5). Two-way ANOVA (Turkey test) was used to analyze the data of photosynthetic parameters, carbon stable isotope, ion concentrations, and ion enrichment ratios among sites and seasons (Table 3, Table 4, Fig. 3, Fig. 4). All statistical analyses were performed with the SPSS statistical package version 10.0 (ver. 10.0, Inc., Chicago, IL, USA).

## Results

### Changes in salinity along the Huangzhu River

Surface water salinity measured over the course of a six-month period along the Huangzhu River differed significantly between the dry and wet seasons, as well as among the three sampling sites (Table 1, Fig. 2). The salinity of the soil interstitial water also showed significant seasonal variation, being 12.0, 18.9, and 33.5‰ in the dry season and declining to 0.5, 4.9, and 20.2‰ in the wet season (Table 1). These results showed that there were significant spatial and temporal (daily and seasonal) variations in water salinity of the Huangzhu River. The water salinity regime also suggests that the Huangzhu River is a freshwater-dominated river, and mangroves growing at the upstream site suffered from long-term (up to 310 h) exposure to freshwater in the wet season.

### Tree height

*Aegiceras corniculatum* trees were tallest at the intermediate site, with a mean height of  $4.9 \pm 0.3$  m. In contrast, the river mangroves at the upstream and downstream sites were comparatively shorter, with heights of  $2.5 \pm 0.3$  m and  $1.1 \pm 0.2$  m, respectively (Table 1).

Table 1  
Water salinity, and height of *Aegiceras corniculatum* along the Huangzhu River

Site	River water			Soil interstitial water salinity (‰)		Tree height (m)
	Mean salinity (‰)	Maximal freshwater duration (h)	Percentage of freshwater time (%)	Wet season	Dry season	
Upstream	1.4	310	67.2	$0.5 \pm 0.2^a$	$12.0 \pm 1.1^a$	$2.5 \pm 0.3^a$
Intermediate	5.9	173	14.7	$4.9 \pm 0.5^b$	$18.9 \pm 0.6^b$	$4.9 \pm 0.3^b$
Downstream	19.6	0	0	$20.2 \pm 3.7^c$	$33.5 \pm 1.9^c$	$1.1 \pm 0.2^c$

Note: Different letters within the same column indicate significant differences ( $P < 0.05$ )

### N and P concentrations

The N and P concentrations decreased with increasing salinity levels in the soil (Table 2) at all sites, but there were no significant differences in N and P concentrations in the mature leaves ( $P > 0.05$ ). These results suggest that N and P were not the key factors influencing the growth differences of *A. corniculatum* in our study.

Table 2  
Nitrogen (N) and phosphorus (P) concentrations of the soil and mature leaves of *Aegiceras corniculatum*

Site	Soil ( $\text{mg g}^{-1}$ )		Leaf ( $\text{mg g}^{-1}$ )	
	N	P	N	P
Upstream	$1.0 \pm 0.36^a$	$0.19 \pm 0.04^a$	$17.03 \pm 2.97^a$	$1.41 \pm 0.42^b$
Intermediate	$1.0 \pm 0.01^a$	$0.22 \pm 0.02^a$	$14.65 \pm 0.92^a$	$1.05 \pm 0.05^b$
Downstream	$0.6 \pm 0.05^b$	$0.12 \pm 0.01^b$	$13.65 \pm 1.08^a$	$0.96 \pm 1.03^b$

Note: Data are mean values  $\pm$  SE,  $n = 3$ . Different letters within the same column indicate significant differences ( $P < 0.05$ )

### Chlorophyll fluorescence

The maximal quantum yield of photosystem II (PSII) photochemistry ( $F_v/F_m$ ) measured in dark-adapted leaves declined significantly at the downstream site, but no significant difference was detected between the upstream and intermediate sites in both seasons ( $P > 0.05$ ) (Fig. 3a). In the dry season, ETR and  $\Phi_{\text{PSII}}$  decreased from upstream through to the intermediate to downstream sites (Fig. 3b, c). ETR at the upstream ( $69.9 \mu\text{mol m}^{-2}\text{s}^{-1}$ ) and intermediate ( $65.4 \mu\text{mol m}^{-2}\text{s}^{-1}$ ) sites was significantly higher than at the downstream site ( $43.1 \mu\text{mol m}^{-2}\text{s}^{-1}$ ) ( $P < 0.05$ ), but there were no differences between the upstream and intermediate sites.  $\Phi_{\text{PSII}}$  also showed the same trend. However, in the wet season, ETR and  $\Phi_{\text{PSII}}$  were significantly higher at the intermediate site ( $P < 0.05$ ) where the soil salinity was moderate (4.9‰). The ETR and  $\Phi_{\text{PSII}}$  values were much lower at the upstream site with a low salinity (ETR:  $83.9 \mu\text{mol m}^{-2}\text{s}^{-1}$ ;  $\Phi_{\text{PSII}}$ : 0.154) and the downstream site with a high salinity (ETR:  $82.5 \mu\text{mol m}^{-2}\text{s}^{-1}$ ;  $\Phi_{\text{PSII}}$ : 0.152) than in the intermediate site, and there was no difference

between the downstream and upstream sites. These data demonstrated that significant spatial and temporal variation in *A. corniculatum* photochemical efficiency in PSII exists along the Huangzhu River. The proportion for closed PSII reaction centers ( $1 - qP$ ) at the upstream site was lower than that at the intermediate site in the dry season but was significantly higher than the intermediate site in the wet season ( $P < 0.05$ ) (Fig. 3d; Table 3). Non-photochemical quenching (NPQ) at the intermediate site was lower than at the downstream site in both seasons. In the dry season, the upstream and intermediate sites had similar NPQ values. However, in the wet season, NPQ at the upstream site was higher than at the intermediate site, and there were no significant differences between the upstream and downstream sites ( $P > 0.05$ ) (Fig. 3e). The  $1 - qP$  and NPQ of the downstream site were higher than the other sites in both seasons ( $P < 0.05$ ).

## $\delta^{13}C$

The  $\delta^{13}C$  of *A. corniculatum* ranged from  $-30.6$  to  $-26.8$ ‰ and did not differ significantly between the dry and wet season ( $P > 0.05$ ). In the dry season,  $\delta^{13}C$  at the downstream site was higher than at the upstream and intermediate sites (Fig. 4; Table 3).

## Ion concentrations

The ion ( $Na^+$  and  $Cl^-$ ) concentrations of the soil interstitial water showed significant seasonal and spatial changes ( $P < 0.05$ ) (Table 3, 4). All ion concentrations of the soil interstitial water were higher in the dry season than in the wet season (Table 3, 4). At the upstream site, the  $Na^+$  and  $Cl^-$  levels in the dry season were 43 and 26 times higher than those in the wet season, respectively. At the downstream site, the  $Na^+$  and  $Cl^-$  levels in the dry season were only 0.7 and 0.8 times higher than in the wet season, respectively. In addition, all ion concentrations ( $Na^+$ ,  $Cl^-$ ,  $K^+$ ,  $Ca^{2+}$ ) also increased significantly from upstream to downstream ( $P < 0.05$ ) (Table 4), suggesting that the mangroves growing at the upstream site suffered a long-term (from April to October) very-low-salinity environment in the wet season.

In contrast to the significant seasonal and spatial changes in the water salinity and ion concentration of the soil, the ion concentrations of the leaf sap showed much less seasonal and spatial variation (Table 3, 4). The  $Na^+$  and  $Cl^-$  concentrations of the leaves remained at a high level in the wet season at all sites. At the upstream site, there were no differences in leaf  $Na^+$  and  $Cl^-$  concentrations between the two seasons ( $P > 0.05$ ).

In the dry season, the  $Na^+$  and  $Cl^-$  enrichment ratios at all three sites were less than 1. However, in the wet season, the enrichment ratio of  $Na^+$  and  $Cl^-$  at the upstream site was 45- and 30-fold higher than in the dry season. The enrichment ratios of  $Na^+$ ,  $Cl^-$ ,  $K^+$  and  $Ca^{2+}$  decreased from the upstream site to the downstream site, and the enrichment ratios of  $K^+$  and  $Ca^{2+}$  at the upstream site were higher by 104.8% and 170.6% compared to  $Na^+$  and  $Cl^-$ , respectively ( $P < 0.05$ ) (Table 4).

## Leaf sap osmolality

Leaf sap osmolality at the downstream site was significantly higher compared to the intermediate and upstream sites in both seasons ( $P < 0.05$ ) (Fig. 5). In the dry season, the leaf sap osmolality decreased by 35.8% at the upstream site and 37.8% at the intermediate site compared to that at the downstream site. There were no significant seasonal and spatial differences in leaf sap osmolality between the intermediate and upstream sites ( $P > 0.05$ ) (Fig. 5, Table 3).

Table 3  
Summary of two-way ANOVA analyses on the effects of sites and seasons

Factor	Chlorophyll fluorescence				$\delta^{13}C$	Osmolality	Ion concentrations of soil interstitial water				Ion concentrations of leaves				Ion enrichment ratios of leaves			
	$F_v/F_m$	$\Phi_{PSII}$	$1 - qP$	NPQ			$Cl^-$	$Na^+$	$K^+$	$Ca^{2+}$	$Cl^-$	$Na^+$	$K^+$	$Ca^{2+}$	$Cl^-$	$Na^+$	$K^+$	$Ca^{2+}$
Season (A)	*	**	**	**	ns.	*	**	**	**	**	ns.	ns.	ns.	**	**	**	**	**
Site (B)	**	**	*	**	**	**	**	**	**	**	**	**	**	ns.	**	**	**	**
A × B	ns.	**	*	**	ns.	ns.	ns.	**	**	ns.	*	ns.	ns.	ns.	**	**	**	**

Note:  $\delta^{13}C$  represents leaf carbon isotope composition. Symbols reflect the significance levels: ns,  $P > 0.05$ ; \*  $0.05 > P > 0.01$ ; \*\*  $0.01 > P > 0.001$

Table 4  
Ion enrichment ratios of *Aegiceras corniculatum* leaves during the dry and wet seasons

Element	Site	Interstitial water (mM)		Leaf sap (mM)		Enrichment ratios (%)	
		Wet season	Dry season	Wet season	Dry season	Wet season	Dry season
	U	4.2 ± 4.5 <sup>a</sup>	187.6 ± 19.2 <sup>a</sup>	193.0 ± 32.4 <sup>a</sup>	186.5 ± 33.5 <sup>a</sup>	45.7 ± 7.7 <sup>a</sup>	1.0 ± 0.1 <sup>a</sup>
Cl <sup>-</sup>	I	70.1 ± 10.7 <sup>b</sup>	283.4 ± 7.6 <sup>b</sup>	242.0 ± 31.0 <sup>b</sup>	203.7 ± 30.4 <sup>a</sup>	3.5 ± 0.8 <sup>b</sup>	0.8 ± 0.2 <sup>b</sup>
	D	289.6 ± 64.2 <sup>c</sup>	503.4 ± 32.4 <sup>c</sup>	231.8 ± 35.8 <sup>b</sup>	334.1 ± 44.2 <sup>b</sup>	0.8 ± 0.1 <sup>c</sup>	0.7 ± 0.1 <sup>b</sup>
Na <sup>+</sup>	U	6.5 ± 2.2 <sup>a</sup>	169.1 ± 14.4 <sup>a</sup>	153.9 ± 35.7 <sup>a</sup>	143.5 ± 33.9 <sup>a</sup>	25.2 ± 6.0 <sup>a</sup>	0.8 ± 0.2 <sup>a</sup>
	I	137.8 ± 3.5 <sup>b</sup>	230.4 ± 9.1 <sup>b</sup>	236.1 ± 25.2 <sup>b</sup>	182.6 ± 11.7 <sup>b</sup>	1.7 ± 0.2 <sup>b</sup>	0.8 ± 0.1 <sup>a</sup>
	D	227.0 ± 18.3 <sup>c</sup>	413.0 ± 43.5 <sup>c</sup>	247.0 ± 53.9 <sup>b</sup>	310.4 ± 28.7 <sup>c</sup>	1.1 ± 0.2 <sup>b</sup>	0.7 ± 0.0 <sup>a</sup>
	U	1.0 ± 0.3 <sup>a</sup>	4.6 ± 0.8 <sup>a</sup>	102.6 ± 14.9 <sup>a</sup>	141.0 ± 28.0 <sup>a</sup>	104.8 ± 15.5 <sup>a</sup>	32.8 ± 3.1 <sup>a</sup>
K <sup>+</sup>	I	4.9 ± 0.3 <sup>b</sup>	6.4 ± 1.0 <sup>b</sup>	86.4 ± 9.0 <sup>b</sup>	81.3 ± 8.0 <sup>b</sup>	18.0 ± 2.8 <sup>b</sup>	12.7 ± 2.2 <sup>b</sup>
	D	3.8 ± 0.5 <sup>c</sup>	10.3 ± 1.3 <sup>c</sup>	71.0 ± 10.3 <sup>c</sup>	85.9 ± 11.0 <sup>b</sup>	18.7 ± 5.0 <sup>b</sup>	8.4 ± 0.9 <sup>b</sup>
	U	0.3 ± 0.0 <sup>a</sup>	4.8 ± 2.3 <sup>a</sup>	39.3 ± 13.5 <sup>a</sup>	19.3 ± 3.0 <sup>a</sup>	170.6 ± 58.5 <sup>a</sup>	4.9 ± 2.4 <sup>a</sup>
	Ca <sup>2+</sup>	I	3.5 ± 1.8 <sup>b</sup>	6.0 ± 3.0 <sup>a</sup>	43.8 ± 13.0 <sup>a</sup>	31.8 ± 5.8 <sup>a</sup>	15.5 ± 8.5 <sup>b</sup>
D		4.0 ± 0.5 <sup>b</sup>	10.0 ± 1.0 <sup>b</sup>	41.5 ± 9.5 <sup>a</sup>	35.8 ± 9.3 <sup>a</sup>	10.4 ± 1.7 <sup>b</sup>	3.5 ± 0.7 <sup>a</sup>

Note: Enrichment ratios = ion concentrations of leaf sap / ion concentrations of soil interstitial water. Abbreviations: *D* downstream, *I* intermediate, *U* upstream. Data are mean values ± SE, *n* = 3. Different letters within the same column indicate significant differences (*P* < 0.05)

## Discussion

Both field investigations and controlled experiments with seedlings under constant salinities have demonstrated that *A. corniculatum* has limited salt tolerance (Ye et al. 2005; Ball 1988). *Aegiceras corniculatum* growth performance is best under fresh water (Ye et al. 2005) or low salinity (50 mM NaCl, or 10–25% seawater) conditions (Ball 1988; Ball and Farquhar 1984b; Burchett et al. 1989; Clarke and Hannon 1970). In this study, the growth and photosynthetic performance of *A. corniculatum* were best at the intermediate site, which is characterized by moderate interstitial water salinity (14–54% seawater) (Table 1).

At the downstream site, both the soil interstitial water salinity (> 17‰) and water salinity (> 20‰) were higher than the optimum salinity for *A. corniculatum* growth (0–14‰) (Burchett et al. 1989; Clarke and Hannon 1970; Ye et al. 2005). *Aegiceras corniculatum* here thus suffers from strong salt stress. At the upstream site, both the soil interstitial water salinity (0.5‰) and river water salinity (1.2‰) were close to that of fresh water in the wet season, indicating that *A. corniculatum* at this site has to tolerate long-term (up to 310 h) freshwater conditions.

Many field reports have demonstrated that changes in leaf  $\delta^{13}\text{C}$  values are independent of N or P levels (McKee et al. 2002), but are affected by changes in salinity (Lin and Sternberg 1993; McKee et al. 2002; Medina and Francisco 1997). Although the N and P concentrations of the soils from the upstream and intermediate sites were significantly higher than that of the downstream site, there were no significant differences in N or P concentrations in the mature leaves among the three sites (Table 2). This implied that nutrition was not the key factor accounting for the significant differences in growth conditions. In the wet season, the increase in leaf  $\delta^{13}\text{C}$  values from the upstream to intermediate to downstream sites was parallel to the increase in soil water salinity (from 0.5 to 20.2‰) (Fig. 5, Table 1). However, this trend was not observed in the dry season. In the dry season, although water salinity increased from the upstream (2.3‰) to intermediate (8.3‰) to downstream (24.3‰) sites, the lowest leaf  $\delta^{13}\text{C}$  value occurred at the intermediate sites rather than the upstream site. In a southern mangrove region in China, Wei et al. (2008) found that an increase in salinity (from 14.1 to 19.8‰) was associated with an increase in  $\delta^{13}\text{C}$  values in the mature leaves of *K. obovata*, but a decrease in the leaves of *A. corniculatum*. *Rhizophora mangle* in south Florida and Twin Cays in Belize demonstrated a pattern of increasing  $\delta^{13}\text{C}$  values with decreasing tree height from fringe to draft stands (Lin and Sternberg 1992; McKee et al. 2002). McKee et al. (2002) suggested that leaf  $\delta^{13}\text{C}$  values simply reflect the variation in environmental conditions caused by changes in tree height and canopy development. A similar result was also found in the dry season in the present study. From the intermediate to upstream to downstream sites, the mean heights of *A. corniculatum* trees decreased from 4.9 m to 2.5 m to 1.1 m, while the  $\delta^{13}\text{C}$  values increased from -29.83 to -29.19 to -27.07‰ (Fig. 5, Table 1). However, this pattern was not observed in the wet season. The relationship between salinity and leaf  $\delta^{13}\text{C}$  value in the natural environment is thus more complex than previously thought.

Changes in PSII activity can be rapidly diagnosed by measuring chlorophyll fluorescence (Ball et al. 1994; Maxwell and Johnson 2000; Papageorgiou and Govindjee 2004). The actual PSII efficiency and electron transport rate were significantly lower at the downstream site than the other two sites in both seasons, suggesting that the high salinity of the downstream site adversely modified the PSII photochemistry in light-adapted leaves. Our results also showed that  $1 - qP$  and NPQ were higher at the downstream site in both seasons (Fig. 4d, e).  $1 - qP$ , the proportion of PSII reaction centers that were closed, is also termed the 'excitation pressure' on PSII (Maxwell et al. 1994). The higher  $1 - qP$  suggested that the excitation pressure on PSII, which has been recognized as a

determining factor for photodamage to PSII (Demmig-Adams and Adams 1992), was higher at the downstream site. As high salinity resulted in a significant decrease in actual PSII efficiency and an increase in  $1 - qP$  at the downstream site, the high NPQ at this site may be a mechanism for dissipating excess excitation energy and down-regulating photosynthetic electron transport, thus protecting PSII from photodamage. However, a depression in  $F_v/F_m$  in *A. marina* seedlings was previously observed at high salinities (Björkman et al. 1988; Naidoo 2006). Similarly,  $F_v/F_m$  at the downstream site was significantly lower than the other two sites in both seasons (Fig. 3a), indicating that the photoprotection was insufficient and *A. corniculatum* at this site suffered a higher degree of photoinhibition than at the other sites.

In the dry season, the water salinity at the upstream site recovered to a moderate levels suitable for *A. corniculatum* growth (Table 1). The  $\Phi_{PSII}$  and ETR at the upstream site were higher, whereas  $1 - qP$  and NPQ were lower than those at the downstream sites. There was also no difference in these parameters between the upstream and intermediate sites. Thus, in the dry season, *A. corniculatum* at the upstream site had a relatively high photochemistry efficiency and suffered no salt stress. In the wet season, *A. corniculatum* at the intermediate site had the highest  $\Phi_{PSII}$  and ETR and the lowest  $1 - qP$  and NPQ, indicating that the water salinity here (mean value 4.9‰) was optimal for *A. corniculatum*. This suggests that *A. corniculatum* has limited salt tolerance. Our result is consistent with previous results obtained under greenhouse culture (Burchett et al. 1989; Clarke and Hannon 1970).

In the wet season, the water salinity was very low (0–6.8‰) at the upstream site.  $\Phi_{PSII}$  and ETR were significantly lower, while  $1 - qP$  and NPQ were significant higher, at this site than at the intermediate site where the soil salinity was moderate. These results indicated that low salinity adversely modified the PSII photochemistry of *A. corniculatum* and that there may be a higher degree of photoinhibition/photoprotection in the leaves at the upstream site. Many studies have demonstrated that many mangrove species, including *A. corniculatum*, grow poorly under extremely low salinities (Ball 2002; Ball and Pidsley 1995; Clarke and Hannon 1970; Clough 1984; Downton 1982; Tuffers et al. 2001; Werner and Stelzer 1990; Yan et al. 2007). In the present study, although the average tree height of *A. corniculatum* at the upstream site was lower than that of the intermediate site, they still exhibited normal growth. The relatively high  $F_v/F_m$  suggested that there was no photodamage at this site (Fig. 3a), but rather simply down-regulated photoprotection. In comparison to the downstream site, the lower water salinity at the intermediate site was associated with increased photosynthesis and tree height. This was consistent with the conclusion that a reduction in salinity led to an increase in primary production (Gabler et al. 2017; Osland et al. 2018).

Although the  $Na^+$  and  $Cl^-$  concentrations of the soil interstitial water were higher in the dry season than in the wet season, the concentrations of these two elements in the leaves in the dry season were similar to those of the wet season. From upstream through to the intermediate to downstream sites, the  $Na^+$  and  $Cl^-$  concentrations of the soil interstitial water increased significantly. The  $Na^+$  and  $Cl^-$  concentrations of the leaves also increased, but not to the same extent. In the wet season, the  $Na^+$  concentration of the soil interstitial water increased 33.8 times from the upstream site to the downstream sites; however, the  $Na^+$  concentrations of the leaves only increased by 0.6 times, and  $Cl^-$  showed similar results (Table 4). There were no significant differences in leaf osmolality between the upstream and downstream sites in both seasons (Fig. 2). These results suggested that despite the significant seasonal and spatial variations in water salinity and  $Na^+$  and  $Cl^-$  concentrations of the soil interstitial water, *A. corniculatum* can maintain relatively constant concentrations of  $Na^+$ ,  $K^+$ ,  $Ca^{2+}$  and  $Cl^-$  on a bulk-leaf water basis in its body.

Mangroves show higher  $Na^+$  and  $Cl^-$  accumulation ability under low salinity or freshwater (Downton 1982; Mallery and Teas 1984; Patel and Pandey 2009). Though only traces of NaCl were present in the growth medium, the tissue  $Na^+$  and  $Cl^-$  concentrations in mangrove organs were comparatively high (Aziz and Khan 2001; Clough 1984; Patel and Pandey 2009; Werner and Stelzer 1990). Kura-Hotta et al. (2001) discovered that high-salt treatment induced  $Na^+$  extrusion and low-salt treatment induced  $Na^+$  accumulation in suspension-cultured cells of the mangrove *Bruguiera sexangula* (Lour.) Poir. Energy-dispersive X-ray microprobe analyses showed that the root vacuoles of *R. mangle* under freshwater had a  $Na^+$  preference, while those of salt-treated plants revealed a strong  $Na^+$  exclusion (Werner and Stelzer 1990). In the wet season, *A. corniculatum* showed very high  $Na^+$  and  $Cl^-$  enrichment ratios of 45.7 and 25.2, respectively, at the upstream site where the water salinity was very low. Even at the intermediate site, the enrichment ratios of  $Na^+$  and  $Cl^-$  were higher than 1. However, in the dry season, none of the enrichment ratios of these two elements were higher than 1. These results suggest that preferentially taking up  $Na^+$  and  $Cl^-$  is a strategy for *A. corniculatum* dealing with freshwater or low salinity.

The surprisingly higher  $Na^+$  and  $Cl^-$  enrichment ratios in the wet season can be explained in the way: *A. corniculatum* has a very strong enrichment capacity for  $Na^+$  and  $Cl^-$  under low salinity. However, many greenhouse studies under constant salinity have indicated that the  $Na^+$  and  $Cl^-$  concentrations of mangrove seedlings living under freshwater were much lower than the salinity-treated groups (Paliyavuth et al. 2004; Parida et al. 2004; Yan et al. 2007). According to the above findings, the  $Na^+$  and  $Cl^-$  concentrations of the leaves of *A. corniculatum* at the upstream site should be lower in the wet season than the dry season. However, our data showed that the  $Na^+$  and  $Cl^-$  concentrations of *A. corniculatum* at the upstream site remained at a high level in the wet season and did not differ significantly from the dry season. Under constant salinity, the concentrations of  $Na^+$  and  $Cl^-$  in the leaves of *A. corniculatum* seedlings grown in a solution containing 250 mmol NaCl were significantly higher than those grown in 50 mmol NaCl (Ball and Farquhar 1984a). These two salt levels are similar to the mean salt levels of soil interstitial water at the downstream site (20.2) and intermediate site (4.9) in the wet season in the present study (Table 1). However, there were no significant differences in the leaf  $Na^+$  and  $Cl^-$  concentrations between the two sites in the wet season (Table 4). We thus assumed that *A. corniculatum* at the upstream site was unable to take up much  $Na^+$  and  $Cl^-$  from the soil during the wet season. Munns (2002) and Tattini et al. (1995) revealed that soil leaching will rapidly restore the water relations of plants but will not affect salt levels in the leaves. This means that plants can store certain salts in their leaves. Thus, some of the salt in the leaves of *A. corniculatum* at the upstream site in the wet season is accumulated during the dry season when water salinity is relatively high. Our results confirm the suggestion that mangroves grown under fluctuating salinity behave differently from those grown under constant salinity (Beckett et al. 1995; Lin and Sternberg 1993; Wang et al. 2020).

Stored water in the leaves plays an important role in salt tolerance in mangroves (Lechthaler et al. 2016; Nguyen et al. 2017). By storing water in the leaves, mangroves can buffer rapid increases in rhizosphere salinity (Lechthaler et al. 2016). Our results indicated that under long-term freshwater, *A. corniculatum*

can actively accumulate a certain level of salts in its body in order to maintain low water potentials. This helps to maintain water uptake in response to a sudden increase in salinity (Reef et al. 2015). Under fluctuating salinity, stored salts (mainly Na<sup>+</sup> and Cl<sup>-</sup>) in the leaves are also important for osmotic adjustment.

## Conclusions

The present study revealed that the photosynthetic performance of *A. corniculatum* was adversely affected by very low (1.4‰) and high salinity (19.6‰). At the upstream site in the wet season, *A. corniculatum* experiencing long-term freshwater conditions showed lower photosynthetic ability. However, photodamage did not occur; this may be because higher Na<sup>+</sup> and Cl<sup>-</sup> concentrations were maintained in the leaves. The Na<sup>+</sup> and Cl<sup>-</sup> were accumulated to maintain a “salt bank” when the roots experienced moderate salinity (12.0‰). The better photosynthetic performance of *A. corniculatum* at the intermediate site than at the upstream and downstream sites was consistent with its estuarine distribution pattern. These results confirmed earlier reports that *A. corniculatum* has limited salt tolerance ability. We conclude that *A. corniculatum* grown under fluctuating salinities behaved differently from those grown under constant salinity. Our findings suggest that mangrove can tolerate freshwater well enough to survive, corroborating the results of Krauss and Ball (2013).

## Declarations

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## Authors' contributions

Wenqing Wang and Changpeng Xin designed research, Li Xu and Chao Liu performed research, collected and analyzed data; all authors discussed the results and revised the manuscript. The authors read and approved the final manuscript.

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## Availability of data and materials

All data are available from the corresponding author on request.

## Ethics approval and consent to participate

Not applicable.

## Consent for publication

Not applicable.

## Competing interests

All authors have no conflict of interest.

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## Figures

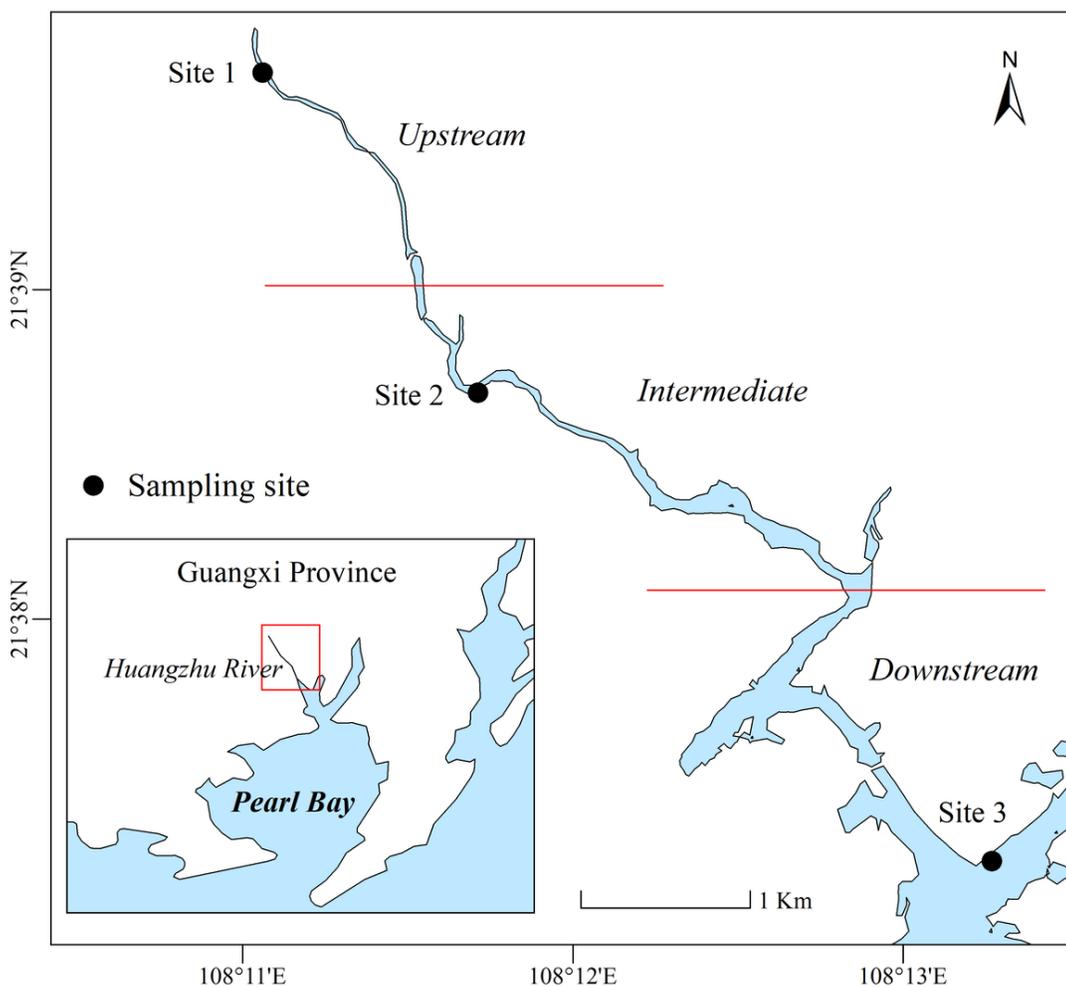
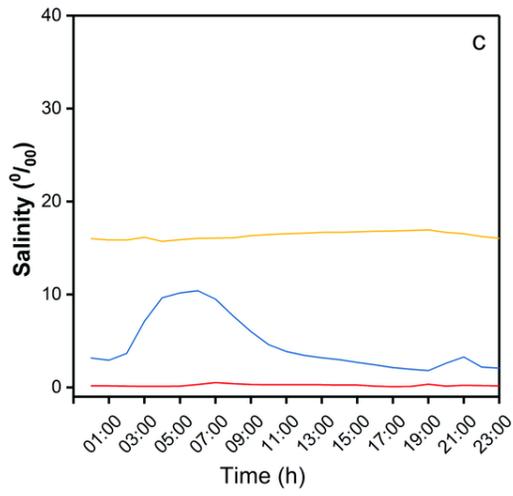
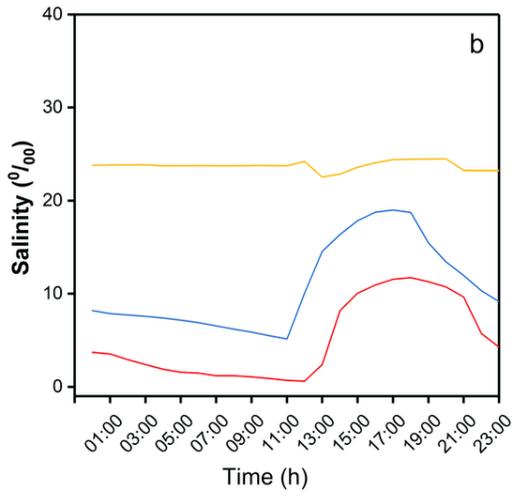
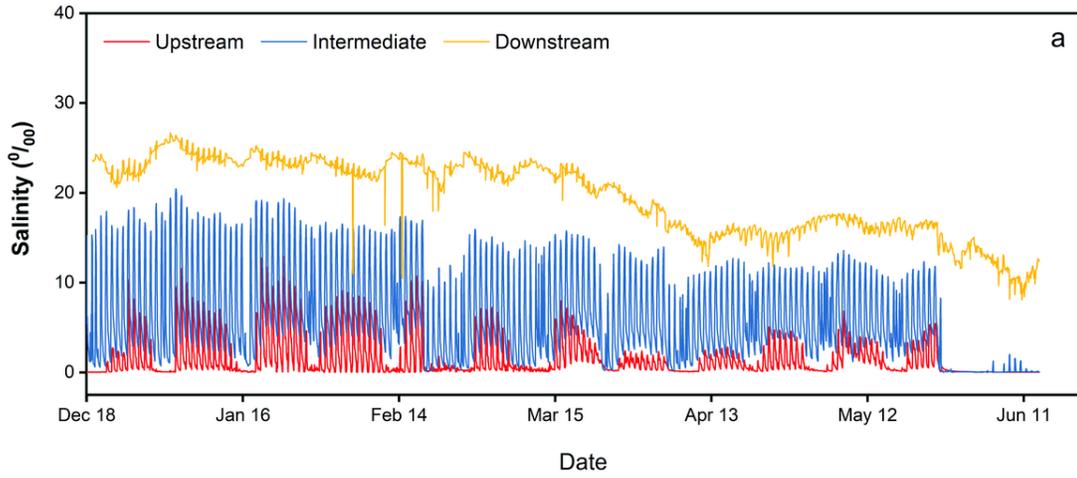
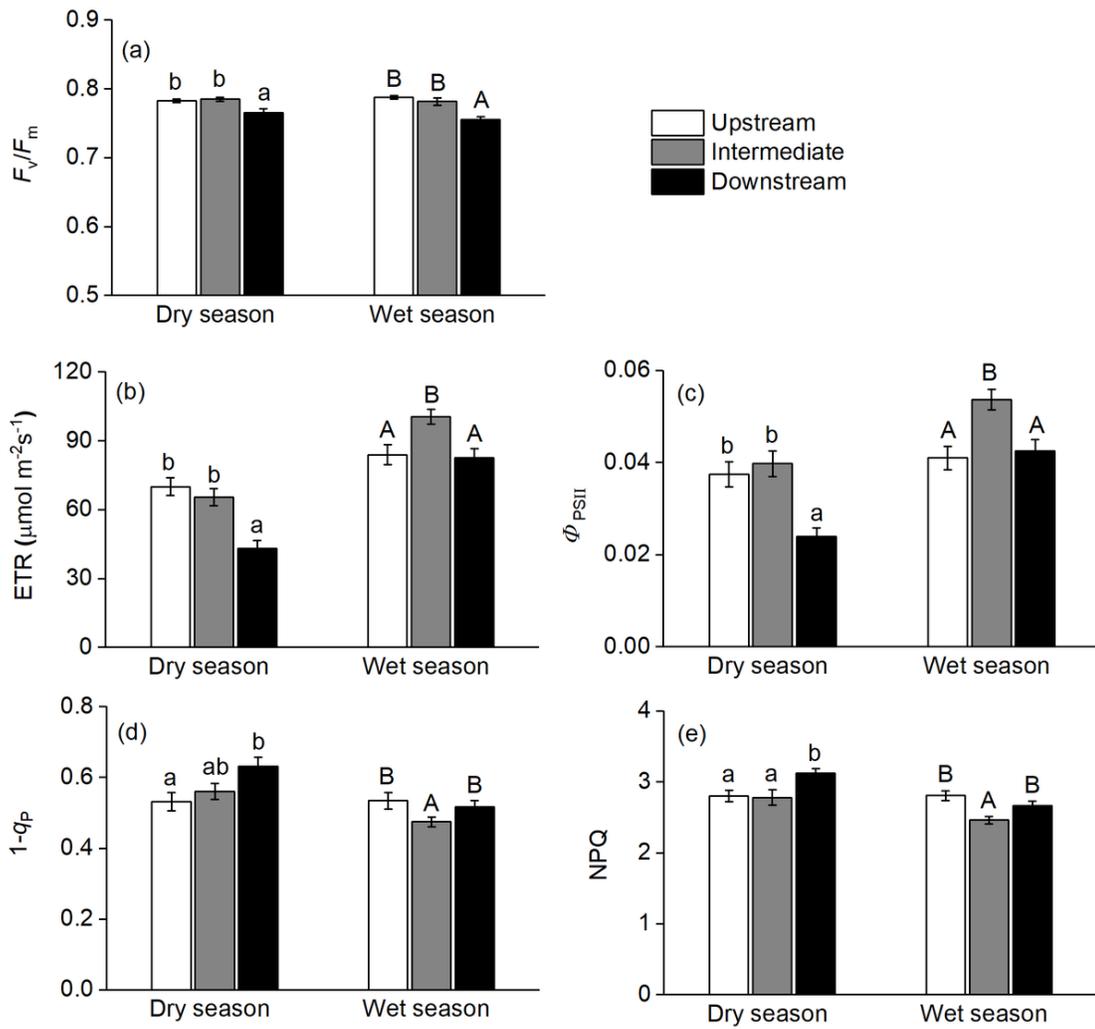


Figure 1

Map of the Huangzhu River showing the study area and sample sites used in this study



**Figure 2**  
 The surface water salinity at the three sample sites in the dry season and wet season. a: salinity from 18th December to 18th June. b, c: the diurnal change in water salinity in a typical day in the dry season and wet season



**Figure 3**  
 Chlorophyll fluorescence of *Aegiceras corniculatum* at the three sampling sites along the Huangzhu River during the dry and wet seasons. D downstream, I intermediate, U upstream. Different letters within columns indicate significant differences ( $P < 0.05$ ). Values are mean  $\pm$  SE, wet season,  $n = 32$ ; dry season,  $n = 20$

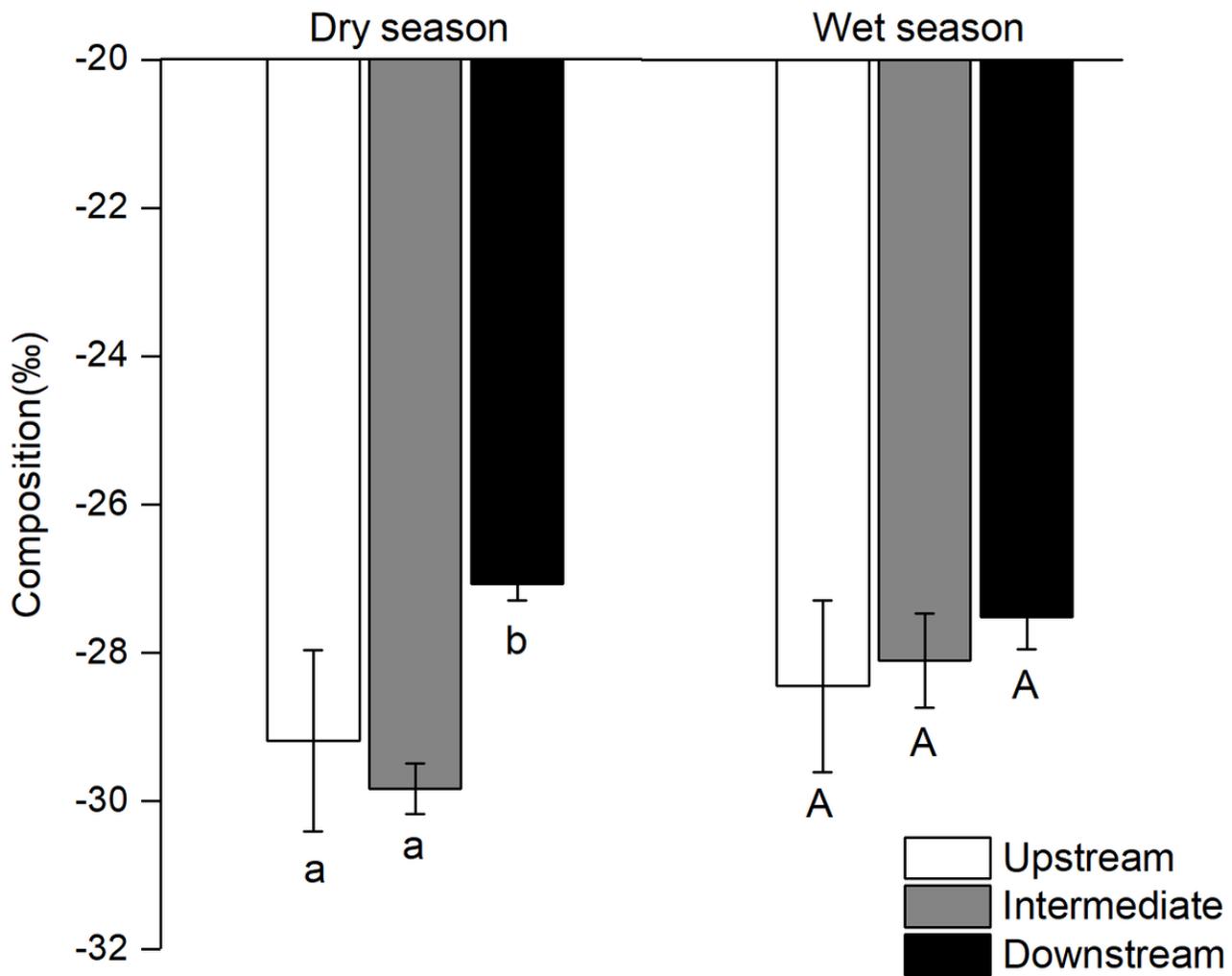


Figure 4  
 Carbon stable isotope composition ( $\delta^{13}C$ ) of *Aegiceras corniculatum* leaves along the Huangzhu River during the dry and wet seasons. Different letters within columns indicate significant differences ( $P < 0.05$ ). Values are mean  $\pm$  SE,  $n = 3$

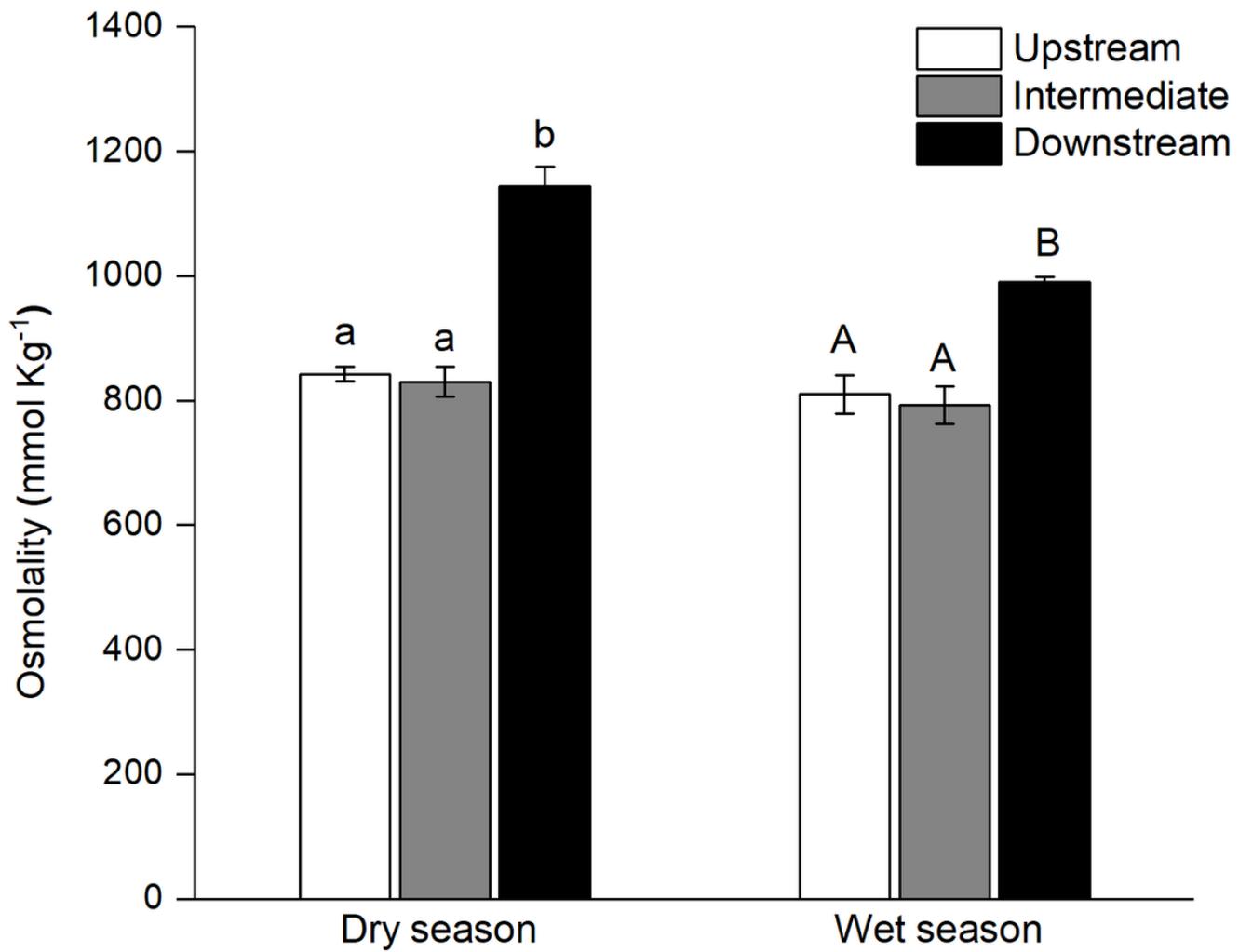


Figure 5  
 Osmolality of *Aegiceras corniculatum* leaf sap at different sites along the Huangzhu River during the dry and wet seasons. Different letters within columns indicate significant differences ( $P < 0.05$ ). Values are mean  $\pm$  SE,  $n = 9$