



Foliar Carbon Isotope Discrimination and Water Sources of Mangrove Forests Along Natural Soil Salinity Gradients and Implications for Their Distribution Pattern

Minshen Huang*, Qing Li**, Tongchao Le***† and Fanglin Tan***

*Key Laboratory of the Ministry of Education for Coastal and Wetland Ecosystems, College of the Environment and Ecology, Xiamen University, Xiamen, Fujian 361005, China

**Center for Earth System Science, Ministry of Education Key Laboratory for Earth System Modeling, Tsinghua University, Beijing 100084, China

***Fujian Academy of Forestry, Fuzhou, Fujian 350012, China

†Corresponding author: Tongchao Le

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ABSTRACT

Field species composition investigation showed an obvious zonation pattern of three main species of mangrove forests along Zhangjiang estuary. *Aegiceras corniculata* was mostly found in upstream and *Avicennia marina* mainly distributed in intermediate and downstream, while *Kandelia obovata* grows across the estuary and a majority in upstream and intermediate. Foliar carbon isotope discrimination of the three species, decreased from both upstream to downstream and wet to dry season, indicated their increased water use efficiency to increased soil salinity and decreased availability of freshwater. Increased ocean water uptake ratio (increased $\delta^{18}\text{O}$ values) of all the three species from upstream to downstream further indicated their adaptations to decreased availability of freshwater. Decreased responses of water use efficiency in response to ocean water uptake ratio were also observed in all the three species. Significant relations observed in *Avicennia marina* and *Kandelia obovata* may indicate their higher adaptations to increased ocean water uptake than *Aegiceras corniculata* with no significant relationships, which may explain why the distribution of *Aegiceras corniculata* was confined to the low salinity area. All the results above, implicated that the zonation pattern of mangrove forests were linked to their physiological process on how water use efficiency responded to change of ocean water uptake ratio.

INTRODUCTION

As the most productive and biologically important ecosystem in the world, mangrove forests provide an important and unique ecosystem service such as stabilizing shorelines and reducing devastating impact of natural disasters (Giri et al. 2011). However, sea level rise resulted from climate change, in the future, may threaten the survival of mangrove ecosystem (Krauss et al. 2014). Responses of mangrove forests carbon and water cycle and especially its community structure to frequently flooded and highly saline environment, will provide important information on their capacity to climate change mitigation and adaptation, thus becoming an important issue (Krauss et al. 2014, Duarte et al. 2013, Li et al. 2014). Mangrove forests exhibited strong zonation of species, which was largely attributed to the responses of individual species to the variation of abiotic factors, including tidal inundation and salinity across intertidal (Ellison et al. 2000). Notwithstanding, the mechanisms resulted in a zonation pattern of mangrove were still under investigation and an analysis of data from 17 riverine estuaries of man-

grove forests showed that the species distribution of mangrove across intertidal was variable and unpredictable (Bunt 1996).

Water availability was regarded as the key determinant of zonation patterns in estuarine vegetation (Wei 2013). Previous investigation showed that the coastal vegetation change was determined by responses of each species to saline ocean water and especially whether it can use ocean water or not (Sternberg & Swart 1987). Vegetation nearest to the sea demonstrated a plastic response to ocean water deposition, including elevated integrated water use efficiency and uptake ratio of ocean water (Greaver & Sternberg 2007). Mangrove forests evolved highly specialized adaptations, including morphological, anatomical, physiological, biochemical and molecular features, which allowed them to cope up with tidal inundation and saline water (Duke et al. 1998, Parida & Jha 2010). But no evidence was obtained to relate zonation pattern of mangrove forests to their individual capacity of ocean water uptake until recently, due to the high complexity of water sources. Research in a

perennial forb *Carex korshinskyi* revealed that $\delta^{13}\text{C}$ values increased with decreased water availability and those populations with higher $\delta^{13}\text{C}$ values have the higher occurrence in the plant community and contributed more to the total aboveground biomass and community productivity, which indicated increased water use efficiency of the plant may relate to their increased competence ability and adaptation strategy to the stressful environment (Chen et al. 2004). Thus, the hypothesis in the present study was, interspecific differences in salt tolerance among mangroves may have resulted in their different responses of water use efficiency to increased soil salinity and ocean water uptake ratio, which would reflect their different competencies within the community and finally being used to explain the occurrence of zonation pattern.

Water sources of mangrove forest were complex and composed of groundwater, rainwater, seawater and mixtures, which are usually characterized by different oxygen isotopic signatures, and stem water indicated the isotopic composition of the water sources. Additionally, water use efficiency can be assessed with leaf carbon isotope discrimination (Δ). Thus the aim of the present study was to combine carbon, hydrogen and oxygen stable isotope technique with community survey result, so as to explore the responses of water use pattern and water use efficiency of different species of mangroves to natural salinity gradients along Zhangjiang estuary, and how such responses relate to the local distribution pattern.

MATERIALS AND METHODS

Site description: The mangrove forests studied were in Zhangjiangkou Mangrove National Nature Reserve (23°55'N, 117°23'E) along Zhangjiang estuary of China, and the local main species including *Kandelia obovata*, *Avicennia marina* and *Aegiceras corniculata* (Lin 2001). The study sites for leaf and stem sampling and soil salinity test were located in the upstream (S1), intermediate (S5) and downstream (S9) along Zhangjiang estuary respectively (Figs. 1 & 2). The soil salinity (ppt) was converted from electrical conductivity (EC) multiplied by 0.64, which was determined on a 1:5 soil-water paste, extracted by shaking for 30min using a bench top conductivity/TDS-pH/mV-temperature meter (labCHEM-CP;TPS,). In the sampling year of 2011, the average minimum and maximum temperature were 18.6-19.9°C and 28.2-28.9°C respectively. The local annual precipitation was about 1169 mm with 80% occurring during May to September. The data were obtained from a local installed meteorological instrument station.

Species composition analysis: Nine sampling sites of mangrove forests located in high tides (S1-S3), mid-tides (S4-

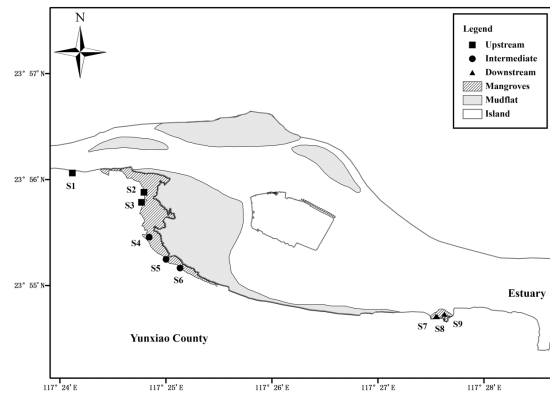


Fig. 1: Maps of mangroves distribution along Zhangjiang estuary and locations for leaf and stem samplings and community structure investigation.

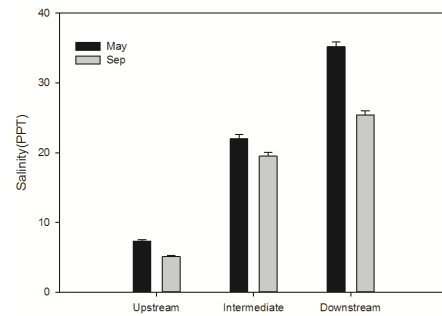


Fig. 2: Soil salinity of the three sampling sites.

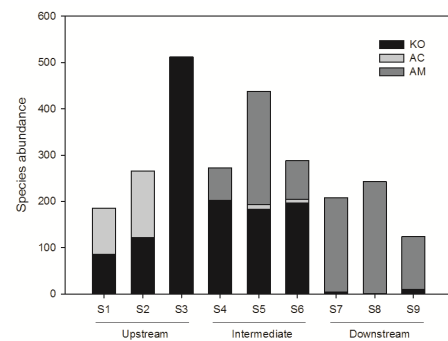


Fig. 3: The species proportion of mangrove forests along increased soil salinity.

S6) and low tides (S7-S9) areas along Zhangjiang estuary were chosen in order to perform species composition analysis (Figs. 1 & 3). The quadrat areas were all set in 20m×20m, and the species, height, diameter at breast height and crown of each tree in each quadrat were recorded.

Stem and source water collection and $\delta^2\text{H}$, $\delta^{18}\text{O}$ analysis: All stem and source water samples (oceanwater and groundwater) were collected in May 2011 (dry) and September 2011 (wet) respectively. Five replicates of the stem samples of the three species were collected in May from each

of the three areas (S2, S5, and S8). The stem samples were then placed in pyrex tubes and sealed with threaded caps that were secured with parafilms for transporting to the lab where the samples were frozen until analysis. To prevent water loss from the stem by evaporation/transpiration, the case was taken to collect well-suberized stems. Water was distilled from stem samples by vacuum distillation (Sternberg 1986) for isotopic analysis. The water samples were pyrolyzed to form H₂ and CO, and then analysed for δ²H and δ¹⁸O. Gases were transported in a continuous-flow fashion by using a He carrier gas from the point of the pyrolysis reaction through a GC separation column to the ionization source of the isotope ratio mass spectrometer, and the international reference standard was used in the stable isotope analysis for SMOW for δ²H and δ¹⁸O, respectively. According to the repeated measurements of specific laboratory working standards, the 2σ precisions of δ²H and δ¹⁸O analyses of water samples were 1‰ and 0.2‰, respectively.

Leaf collection and δ¹³C analysis: Leaves were collected from five different individuals of each species for which stems were collected. The leaves were collected from terminal internode positions because those were most likely borne during the season in which they were collected. Back to the laboratory, the leaf samples were oven dried under 60°C for 48 hrs and then grounded to a fine powder for carbon isotope analysis. 0.2-5 mg dried samples of leaf were weighed into tin capsules for carbon isotope ratio measurements. Carbon isotope ratios were measured by flash combustion of the samples on the elemental analyser coupled to the mass spectrometer (Delta V Advantage, Thermo). The international reference standard used in the stable isotope analysis for δ¹³C was PDB. According to the repeated measurements of specific laboratory working standards, the 2σ precision for δ¹³C measurements of organic matter samples was 0.1‰. Carbon isotope discrimination was finally calculated following the convention (1) (Farquhar & Richards 1984):

$$\Delta = (\delta_{air} - \delta_{plant}) / (1 + \delta_{plant}) \quad \dots(1)$$

where δ_{plant} is δ¹³C of leaf material and δ_{air} is assumed to be constant (-8‰) for experiments in the open air.

Calculation and statistical analysis: One-way ANOVA was used to analyse the variances of soil salinity and Δ values of each species among the three sampling locations. The Paired T test was used to analyse the Δ values between dry and wet season for each species within the same location. All statistical analyses were performed using the SPSS software (SPSS 15.0 for Windows, SPSS Inc.).

RESULTS

The species composition of mangrove forests from high

tides to low tide areas: The soil salinity increased from upstream to downstream in both wet (Sep) and dry (May) season (Fig. 2), and significant sites and seasonal differences were observed. The community composition investigation indicated that the *A. corniculatum* was mainly distributed in the upstream areas, and seldom was found in intermediate areas (Fig. 3), although several individuals for leaf and stem sampling in downstream, out of the sampling plots for species composition investigation, were also observed. The distribution of *K. obovata* was mostly in upstream and intermediate and seldom was found in the low intertidal areas (Fig. 3). In contrast to *K. obovata* and *A. corniculatum*, *A. marina* was in majority distributed in middle and low intertidal areas with higher soil salinity (Fig. 3), while seldom individuals were also found in leaf and stem sampling in upstream, out of our sampling plots for species composition investigation.

The carbon isotope discrimination of mangrove: Along with the increased soil salinity from upstream to downstream areas, decreased carbon isotope discrimination of *K. obovata* was observed in both dry and wet season, while significant difference was only observed in dry season. Significant seasonal difference was also observed in the downstream areas (Fig. 4). Significant decreased carbon isotope discrimination was also observed in *A. marina* between upstream and intermediate or downstream areas in the dry season, and from intermediate to downstream areas in wet season (Fig. 4). However, decreased carbon isotope discrimination from high to low intertidal area was not observed in *A. corniculatum* in either wet or dry season. And significant decreased carbon isotope discrimination was only found in the intermediate area compared to an upstream area in dry season (Fig. 4).

The water sources of mangrove: Values of oxygen stable isotopes of stem water were lower than the ocean water and higher than the groundwater. The data indicated that oxygen stable isotopes of stem water, of all the three species of mangroves, increased from upstream to downstream area in both wet and dry season (Table 1). Contributions of ocean water and groundwater to stem were then calculated by using the two-sources mixing model. The results indicated that mangroves can use as much as 79.9% of ocean water (*A. corniculatum* in low intertidal area in May) and can also use 92.7% of ground water in the wet season (*K. obovata* in upstream in September, Table 1). And more ocean water, as compared to ground water, was utilized by all the three species in dry season, than in wet season (Table 1). Inter-specific difference of groundwater uptake ratio was also observed. *K. obovata* and *A. corniculatum* obviously decreased the groundwater uptake ratio from 67.6% in wet season to

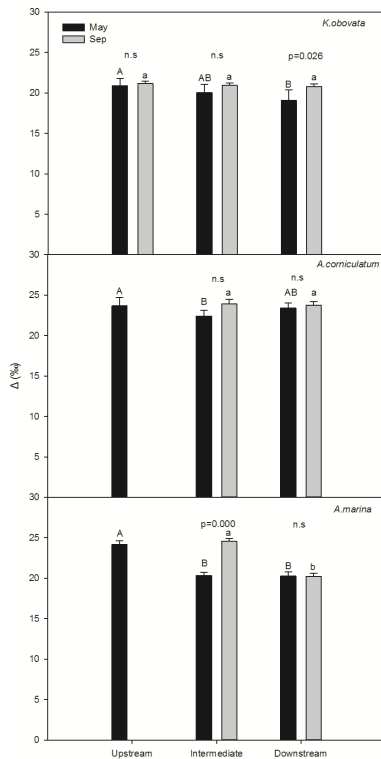


Fig. 4: The stable carbon isotope discrimination values of leaf.

29% and 20.1%, respectively, in dry season in the downstream areas. While the groundwater uptake ratio of *A. marina* in a low downstream area slightly decreased from 54.4% in wet season to 46.4% in dry season (Table 1).

The relations of carbon isotope discrimination and oxygen stable isotopes of mangrove: Relations of carbon isotope discrimination and oxygen stable isotopes were further analysed for each species of mangrove forest. The results showed that the carbon isotope discrimination values of mangrove forests decreased along with the increased oxygen stable isotopes. However, significant linear relations were obtained in *K. obovata* ($\Delta=18.75-0.4366 \delta^{18}\text{O}$, $R^2=0.3564$, $P=0.0005$) and *A. marina* ($\Delta=16.72-1.27 \delta^{18}\text{O}$, $R^2=0.59$, $P<0.0001$) but not in *A. corniculatum* ($\Delta=23.16-0.08 \delta^{18}\text{O}$, $R^2=0.0190$, $P=0.5111$) (Fig. 5). And the absolute value of the slopes in regression line obtained from *A. marina* was higher than *K. obovata* (Fig. 5).

DISCUSSION

Distribution pattern of mangrove forests: The species composition investigation in our research indicated that *A. corniculatum* were confined to the upstream area with lower soil salinity, while *A. marina* adapted well to the higher salinity environment and numerically dominated in the middle and low intertidal area. *K. obovata* distributed from high

Table 1: The contributions of ocean and groundwater sources to plant stem water.

		Ocean (%)		Ground (%)	
		May	Sep	May	Sep
KO	Upstream	16.8	7.3	83.2	92.7
	Intermediate	40.6	29.3	59.4	70.7
	Downstream	71.0	32.4	29.0	67.6
AC	Upstream	9.4	NA	91.6	NA
	Intermediate	32.1	29.7	67.9	70.3
	Downstream	79.9	32.4	20.1	67.6
AM	Upstream	10.9	NA	89.1	NA
	Intermediate	27.4	8.3	72.6	91.7
	Downstream	53.6	45.6	46.4	54.4

to low intertidal area, indicating tolerance to wide salinity levels. The results obtained here, were in well accordance to the investigations in India, where *A. marina* dominated the low intertidal zone and occurrence of *A. corniculatum* was limited to the low salinity areas (Sukardjo et al. 2014). There was also a greenhouse experiment in China which showed that *A. marina* was more tolerant to the tidal environment than *A. corniculatum* (He et al. 2007).

Zonation in mangrove forests was regarded to be the result of the responses of individual species to gradients of tidal inundation, salinity and other predictable co-vary variables across intertidal (Ellison et al. 2000). Previous research indicated that mangrove (*K. obovata*) inundation tolerance is found to be inversely dependent on salinity concentration (Yang et al. 2013), and interspecific difference in salt tolerance of mangrove was correlated to their distribution pattern along natural gradients (Ball & Pidsley 1995). However, intertidal distributions were also regarded to be variable and essentially unpredictable (Bunt 1996). The distribution patterns along a natural salinity gradient of the three species of mangrove forests obtained in the present study, reflected their different tolerance to increased soil salinity, although more investigation should be performed in order to figure out the change of the physiological variables of mangrove forests to natural gradients of environmental drivers.

Water-use efficiency and water use pattern and its response to salinity gradients of different species of mangrove: Since salinity was considered to be the principle abiotic factor affecting the growth of mangrove, thus, how their physiological process responded to increased soil salinity was an important issue (Ball & Farquhar 1984, Clough 1984). Foliar carbon isotope discrimination were proved to reflect the integrated response of plant physiological processes to the environment factors (Ehleringer 1989, Brugnoli & Lauter 1991, Wei et al. 2008), especially as the index of water-use efficiency of plant (Farquhar et al. 1989, Pate 2001). High salinity environment resulted in so called “physiological

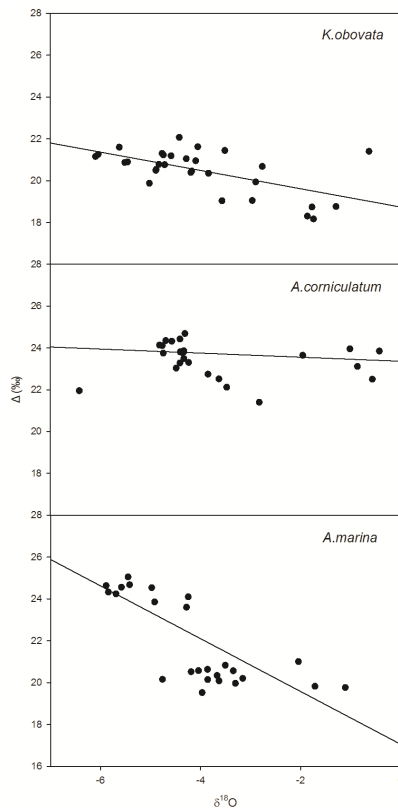


Fig. 5: The relations between Δ values and stable oxygen isotope values. KO ($\Delta = 18.75 - 0.4366 \delta^{18}\text{O}$, $R^2 = 0.3564$, $P = 0.0005$), AC ($\Delta = 23.16 - 0.08 \delta^{18}\text{O}$, $R^2 = 0.0190$, $P = 0.5111$), AM ($\Delta = 16.72 - 1.27 \delta^{18}\text{O}$, $R^2 = 0.59$, $P < 0.0001$)

dry” of mangrove forest (Paliyavuth et al. 2004), thus many species evolved with high water-use efficiency characteristics compared to other terrestrial vegetation (Clough et al. 1982, Ball 1988, Clough & Sim 1989). Previous studies in Zhangjiang estuary found that $\delta^{13}\text{C}$ of mangrove was positively related to salinity in *K. obovata* and *A. marina*, and the reverse was observed in *A. corniculatum* (Wei et al. 2008). Direct calculations also showed that an intrinsic water use efficiency of mangrove increased in response to increased natural soil salinity (Clough & Sim 1989, Parida & Jha 2010).

The decreased carbon isotope discrimination (increased $\delta^{13}\text{C}$) from upstream to downstream area with increased soil salinity in *K. obovata* and *A. marina* in both dry and wet season, in the present study, was corresponding to the previous study. A non-significant difference of carbon isotope discrimination between intermediate and downstream areas in *A. marina* and increased carbon isotope discrimination of *A. corniculatum* from intermediate to downstream area in dry season added more insights and reflect the inter-species variance of water-use efficiency of mangrove forests and their different responses to increased soil salinity. Besides, although significant seasonal differences of carbon isotope

discrimination were observed only in *K. obovata* of downstream area and in *A. marina* of intermediate area, the decreased averages of carbon isotope discrimination values of all the species in dry season compared to wet season, provide information on the responses of mangrove water-use efficiency to water stress. Changes of carbon isotope discrimination which was index of water-use efficiency in response to increasing salinity and seasonal dry of mangroves were similar to those reported for terrestrial plants experiencing drought (Schulze 1986).

Generally speaking, mangrove toward the interior of the coasts were using freshwater while those toward the edge were using ocean water. The increased ocean water uptake ratio from upstream to downstream area of all the three species of mangrove, without exceptions, were observed in accordance with the previous conclusions. And more groundwater use ratio in wet seasons than dry season also indicated the dependency of mangrove on ocean water and its adaptations to less available of freshwater environment in dry season. More groundwater uptake ratio of *A. marina* than *K. obovata* and *A. corniculatum* in dry season in low intertidal may reflect the competitive advantage of *A. marina* and corresponding to their distribution pattern.

Relations between water-use efficiency and water uptake ratio and the implications: Previous studies regarded vegetation changes in the coastal area were determined by both, changes of boundary between the freshwater table and ocean water and each species particular physiological response to saline ocean water. Differential flood tolerance was hypothesized to be a factor controlling zonation pattern of mangrove forests, but it has not been investigated thoroughly (McKee 1993). The water-use efficiency of all the three species of mangrove forests was increased with increased ocean water uptake ratio, however, the non-significant regression line of *A. corniculatum* may mean that it was unable to increase the water use efficiency in response to increased ocean water uptake ratio in intermediate and downstream areas where the soil salinity might exceed their tolerance threshold. And all of these were the reasons why *A. corniculatum* was mainly distributed in high upstream areas and only seldom individuals can be found in middle and lower intertidal sites. Besides, the significant regression line indicated that *K. obovata* and *A. marina* could increase their water-use efficiency in response to increased ocean water uptake ratio. And the more steeper regression line of *A. marina* demonstrated their higher tolerance to saline environment than *K. obovata* and the conclusion may provide explanations why the distribution of *A. marina* was mostly in the downstream area with higher soil salinity while *K. obovata* was in majority distributed in upstream and intermediates. All the results presented here from the physiological viewpoint, provide ex-

planations to the distribution pattern of the local mangrove forests of Zhangjiang estuary.

CONCLUSION

Zonation pattern and inter-species and seasonal variation of water use efficiency and water sources of mangrove forest along salinity gradients in Zhangjiang estuary were observed. Different relationships between water use efficiency and water sources of mangrove forest indicated their different tolerance to saline water and decreased availability of freshwater, which could be further used to explain the emergence of local distribution pattern of mangrove forest. Thus the physiological process of mangrove forests may result in their distribution pattern through changing of water use efficiency in response to increased soil salinity and oceanwater uptake ratio.

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REFERENCES

- Ball, M.C. 1988. Ecophysiology of mangroves. *Trees*, 2(3): 129-142.
- Ball, M.C. and Farquhar, G. D. 1984. Photosynthetic and stomatal responses of two mangrove species, *Aegiceras corniculatum* and *Avicennia marina*, to long term salinity and humidity conditions. *Plant Physiology*, 74(1): 1-6.
- Ball, M.C. and Pidsley, S. M. 1995. Growth responses to salinity in relation to distribution of 2 mangrove species, *Sonneratia alba* and *S. lanceolata*, in northern Australia. *Funct. Ecol.*, 9(1): 77-85.
- Brugnoli, E. and Lauteri, M. 1991. Effects of salinity on stomatal conductance, photosynthetic capacity, and carbon isotope discrimination of salt-tolerant (*Gossypium hirsutum* L.) and salt-sensitive (*Phaseolus vulgaris* L.) C3 non-halophytes. *Plant Physiology*, 95(2): 628-635.
- Bunt, J. S. 1996. Mangrove zonation: an examination of data from seventeen riverine estuaries in tropical Australia. *Annals of Botany*, 78(3): 333-341.
- Chen, S.P., Bai, Y.F., Han, X.G., An, J.L. and Guo, F.C. 2004. Variations in foliar carbon isotope composition and adaptive strategies of *Carex korshinskyi* along a soil moisture gradient. *Acta Phytocologica Sinica*, 28(4): 515-522.
- Clough, B. F. 1984. Growth and salt balance of the mangroves *Avicennia marina* (Forsk.) Vierh. and *Rhizophora stylosa* Griff. in relation to salinity. *Functional Plant Biology*, 11(5): 419-430.
- Clough, B. F., Andrews, T. and Cowan, I. 1982. Physiological processes in mangroves. In: *Mangrove Ecosystems in Australia: Structure, Function and Management*, Australian National University Press, pp.193-210.
- Clough, B. F. and Sim, R. 1989. Changes in gas exchange characteristics and water use efficiency of mangroves in response to salinity and vapour pressure deficit. *Oecologia*, 79(1): 38-44.
- Duarte, C. M., Losada, I. J., Hendriks, I. E., Mazarrasa, I. and Marba, N. 2013. The role of coastal plant communities for climate change mitigation and adaptation. *Nature Climate Change*, 3(11): 961-968.
- Duke, N., Ball, M. and Ellison, J. 1998. Factors influencing biodiversity and distributional gradients in mangroves. *Global Ecology & Biogeography Letters*, 7(1): 27-47.
- Ehleringer, J. R. 1989. Carbon isotope ratios and physiological processes in aridland plants. In: *Stable Isotopes in Ecological Research*, Springer, Berlin, pp. 41-54.
- Ellison, A.M., Mukherjee, B.B. and Karim, A. 2000. Testing patterns of zonation in mangroves: scale dependence and environmental correlates in the Sundarbans of Bangladesh. *Journal of Ecology*, 88(5): 813-824.
- Farquhar, G. D., Hubick, K. T., Condon, A. G. and Richards, R. A. 1989. Carbon isotope fractionation and plant water-use efficiency. In: *Stable Isotopes in Ecological Research*. Springer, New York, pp. 21-40.
- Farquhar, G. and Richards, R. 1984. Isotopic composition of plant carbon correlates with water-use efficiency of wheat genotypes. *Functional Plant Biology*, 11(6): 539-552.
- Giri, C., Ochieng, E., Tieszen, L. L., Zhu, Z., Singh, A., Loveland, T., Masek, J. and Duke, N. 2011. Status and distribution of mangrove forests of the world using earth observation satellite data. *Global Ecology and Biogeography*, 20(1): 154-159.
- Greaver, T. L. and Sternberg, L. S. L. 2007. Fluctuating deposition of ocean water drives plant function on coastal sand dunes. *Global Change Biology*, 13(1): 216-223.
- He, B., Lai, T., Chen, J., and Qiu, G. 2007. Studies of the tolerance of *Avicennia marina* and *Aegiceras corniculatum* to seawater immersion in Guangxi, China. *Acta Ecologica Sinica*, 27(3): 1130-1138.
- Krauss, K. W., McKee, K. L., Lovelock, C. E., Cahoon, D. R., Saintilan, N., Reef, R. and Chen, L. 2014. How mangrove forests adjust to rising sea level. *New Phytologist*, 202(1): 19-34.
- Li, Q., Lu, W., Chen, H., Luo, Y. and Lin, G. 2014. Differential responses of net ecosystem exchange of carbon dioxide to light and temperature between spring and neap tides in subtropical mangrove forests. *The Scientific World Journal*, 2014: 11.
- Lin, P. 2001. The synthetically scientific investigation of Zhangjiangkou mangrove wetland natural reserve in Fujian. Xiamen, Xiamen University Press.
- McKee, K. L. 1993. Soil physicochemical patterns and mangrove species distribution-reciprocal effects. *Journal of Ecology*, 81: 477-487.
- Paliyavuth, C., Clough, B. and Patanaponpaiboon, P. 2004. Salt uptake and shoot water relations in mangroves. *Aquatic Botany*, 78(4): 349-360.
- Parida, A. K. and Jha, B. 2010. Salt tolerance mechanisms in mangroves: a review. *Trees*, 24(2): 199-217.
- Pate, J. 2001. Carbon isotope discrimination and plant water-use efficiency. In: *Unkovich, M., Pate, J., McNeill, A. and Gibbs, D. J. (eds.) Stable Isotope Techniques in the Study of Biological Processes and Functioning of Ecosystems*, Springer, Netherlands, pp. 19-36.
- Schulze, E. D. 1986. Whole-plant responses to drought. *Functional Plant Biology*, 13(1): 127-141.
- Sternberg, L.D.S., Deniro, M.J., and Johnson, H.B. 1986. Oxygen and hydrogen isotope ratios of water from photosynthetic tissues of CAM and C3 plants. *Plant Physiology*, 8(2): 428-431.
- Sternberg, L.S. L. and Swart, P. K. 1987. Utilization of freshwater and ocean water by coastal plants of southern Florida. *Ecology*, 68(6): 1898-1905.
- Sukardjo, S., Alongi, D. M. and Ulumuddin, Y. I. 2014. Mangrove community structure and regeneration potential on a rapidly expanding, river delta in Java. *Trees*, 28(4): 1105-1113.
- Wei, L., Lockington, D. A., Poh, S. C., Gasparon, M. and Lovelock, C. E. 2013. Water use patterns of estuarine vegetation in a tidal creek system. *Oecologia*, 172(2): 485-494.
- Wei, L., Yan, C., Guo, X. and Ye, B. 2008. Variation in the $\delta^{13}\text{C}$ of two mangrove plants is correlated with stomatal response to salinity. *J. Plant Growth Regul.*, 27(3): 263-269.
- Wei, L., Yan, C., Ye, B. and Guo, X. 2008. Effects of salinity on leaf $\delta^{13}\text{C}$ in three dominant mangrove species along salinity gradients in an estuarine wetland, southeast China. *Journal of Coastal Research*, 24(1): 267-272.
- Yang, S. C., Shih, S. S., Hwang, G. W., Adams, J. B., Lee, H. Y. and Chen, C.P. 2013. The salinity gradient influences on the inundation tolerance thresholds of mangrove forests. *Ecological Engineering*, 51: 59-65.