

Physiological Responses of *Avicennia marina* var. *acutissima* and *Bruguiera parviflora* under Simulated Rise in Sea Level

(Respon Fisiologi *Avicennia marina* var. *acutissima* dan *Bruguiera parviflora* di Bawah Simulasi Kenaikan Aras Air Laut)

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ABSTRACT

Climate change components such as increased in atmospheric carbon dioxide (CO_2) and rising sea levels are likely to affect mangrove ecosystems. Healthy mature propagules of *A. marina* var. *acutissima* and *B. parviflora* were subjected to two tidal treatments; shallow and deep; for six months. Shallow treatment mimicked the current tidal fluctuations and deep treatment simulated future tidal conditions under rise in sea level. Deep treatment decreased A_{400} of both species and significant two way interactions between tidal treatments and species were observed. A_{400} was significantly reduced in the deep treatment in *B. parviflora* but not in *A. marina*. Carbon dioxide compensation point was not affected by the tidal treatments but varied significantly between both species. The ratio A_{400}/A_{max} was significantly lower in the shallow treatment in *B. parviflora* indicating higher carbon sink potential at moderate tidal flooding whereas A_{400}/A_{max} of *A. marina* was less variable between tidal treatments. Chlorophyll conductance was insensitive to tidal flooding but was significantly higher in *B. parviflora* than in *A. marina*. Carbon sequestration of *B. parviflora* was substantially reduced in the deep treatment while the difference between tidal treatments was much less in *A. marina*. These results indicated that these two species responded differently under tidal flooding where *A. marina* was less sensitive to tidal. Thus, *A. marina* is better adapted to the projected climate change than *B. parviflora*.

Keywords: Climate change; inundation; mangroves; seedling growth; water logging

ABSTRAK

Unsur-unsur perubahan iklim seperti kenaikan karbon dioksida atmosfera dan aras air laut sememangnya mempengaruhi ekosistem hutan paya bakau. Dalam kajian ini, propagul *Avicennia marina* var. *acutissima* dan *Bruguiera parviflora* didedahkan kepada 2 perlakuan air pasang; dalam dan cetek; selama 6 bulan. Perlakuan cetek mewakili keadaan semasa sementara perlakuan dalam mewakili keadaan kenaikan aras air laut pada masa hadapan. Perlakuan dalam mengurangkan nilai A_{400} untuk kedua-dua spesies. Nilai A_{400} menurun dengan bererti bagi *B. parviflora* tetapi tidak *A. marina* untuk perlakuan dalam. Titik imbangan karbon dioksida tidak dipengaruhi oleh perlakuan air pasang tetapi menunjukkan perbezaan bererti antara kedua-dua spesies. Nisbah A_{400}/A_{max} adalah rendah pada perlakuan cetek *B. parviflora* yang menandakan potensi sinki karbon yang lebih tinggi manakala nisbah A_{400}/A_{max} bagi *A. marina* kurang menunjukkan variasi. Konduktans klorofil tidak sensitif terhadap air pasang namun *B. parviflora* menunjukkan nilai lebih tinggi berbanding *A. marina*. Sekuestrasi karbon *B. parviflora* menurun pada perlakuan dalam tetapi tidak begitu ketara pada *A. marina*. Kesemua keputusan menunjukkan *A. marina* lebih toleren terhadap kenaikan aras air laut berbanding *B. parviflora*.

Kata kunci: Kebanjiran; kegenangan air; paya bakau; pertumbuhan biji benih; perubahan iklim

INTRODUCTION

Two major climate change components that are likely to affect mangrove communities are the increased in atmospheric carbon dioxide (CO_2) and rising sea levels (Krauss et al. 2008). Increased in atmospheric CO_2 could enhanced the growth rates via increased net assimilation rates and increased leaf area ratio and through increased water use efficiency (Ball et al. 1997). Likewise increased in atmospheric CO_2 concentrations determine the stomatal regulation of water loss (Morison 1998). However, the extent to which individual species respond to increased CO_2 depends on other growth limiting factors such as

nutrient availability and the presence of stress factors such as salinity and flooding (Ball et al. 1997; McKee & Rooth 2008).

Mangroves are exposed to various levels of tidal inundations depending on the geomorphological characteristics of the shoreline (Woodroffe & Grindrod 1991). Rise in sea level is likely to prolong tidal inundation and cause intense soil anoxia (Pezeshki 2001). Under experimental cultures, soil flooding can reduce oxygen concentrations of the soil by as much as 28% after 6 h of flooding and as much as 72% after 20 h (Skelton & Allaway 1996). Intense soil anoxia triggers various physiological

responses in mangroves (Pezeshki 2001). Soil flooding reduced light saturation levels and photosynthesis of *Kandelia candel* seedlings (Chen et al. 2005), decreased stomatal conductance and leaf xylem water potential of *A. marina* (Sayed 1995), while tidal flooding enhanced biomass of *Xylocarpus granatum* (Allen et al. 2003). Thus mangrove plants exhibit variations in the physiological responses to tidal inundations.

The combined effects of increased CO₂ and rise in sea level on mangroves are poorly understood. The aim of the current study was to evaluate the physiological response of *A. marina* var. *acutissima* and *Bruguiera parviflora* under simulated rise in sea level and to determine the carbon sequestration of these species when subjected to different tidal treatments. It is hypothesized that; firstly, physiological responses of *A. marina* var. *acutissima* Stapf and Moldenke and *B. parviflora* Wight and Arnold ex Griffith will vary between tidal treatments; secondly, carbon sequestration of both species will be affected by the tidal treatments and thirdly, the effects of tidal flooding will affect *A. marina* to a lesser extent than that of *B. parviflora* because *A. marina* predominates the lower intertidal zones of the mangrove forests.

MATERIALS AND METHODS

Healthy, mature propagules of *A. marina* var. *acutissima* and *B. parviflora* were collected and planted individually in polybags (10 cm × 20 cm) using soil from the mangrove forest as a potting medium. The seedlings were nurtured in a nursery adjacent to the mangrove forest in the Klang River under natural tidal conditions for a period of three months. The average initial height of the seedlings of *A. marina* and *B. parviflora* ranged between 39 ± 2.7 and 19.5 ± 3.5 cm (mean ± standard deviation), respectively. The seedlings were acclimatized in the greenhouse for five days before subjecting to the treatments.

Two identical fibreglass tanks measuring 226 cm long × 122 cm wide × 76 cm deep were used to set up artificial tidal tanks simulating daily semidiurnal tides with two 'high' and 'low' tide periods. The artificial seawater was prepared by dissolving commercial sea salt. Salinity was maintained at 30‰ throughout the study period either by adding water or salt whenever needed. In each tidal tank, four subplots were established using small aquarium tanks. Two treatments, shallow and deep were specified and each fibreglass tank represented one treatment. The shallow treatment mimicked the current tidal fluctuations with daily 12 h of high and low tides. Seawater was pumped into the shallow tanks at 'high tide' at 00:00 h and 12:00 h and ebbed at 'low tide' at 06:00 and 18:00 h. During high tide the water level was 20 cm and at low tide water level was 5 cm.

The deep treatment tank simulated the tidal fluctuations under rise in sea level with 16 and 8 of daily high and low tide periods, respectively. In this tank, sea water was pumped into the tanks at 'high tide' from 01:00 to 09:00 and 13:00 to 21:00 and ebbed at 'low tide' from 09:00 to

13:00 and 21:00 to 01:00. The water level of high and low tide was 50 and 20 cm, respectively. All the seedlings in the deep treatment were fully submerged at high tide at the beginning of the experiment.

PHYSIOLOGY AND CARBON SEQUESTRATION

The physiological data collection was carried out at the end of sixth months after subjecting the seedlings to the treatments. Six seedlings from each treatment of each species were randomly selected to study physiological variations between the tidal treatments. A portable photosynthesis system (PPSystem, CIRAS-1, USA) was used to obtain both physiological and carbon sequestration data both test species by clipping 2.5 cm² of sample from the youngest fully expanded leaves to a microclimate chamber of the photosynthesis system.

Curve fitting of assimilation-carbon dioxide response curves was done for individual plants using a non-linear regression to hyperbolic equation. The maximum photosynthetic rates (A_{max}), photosynthetic rates at ambience (A_{400}) and CO₂ compensation point were determined from the CO₂ response curves. The ratio A_{400}/A_{max} was obtained to determine the deviation of the current photosynthetic rate from the maximum value that the species can reach under elevated atmospheric CO₂. The lower the ratio A_{400}/A_{max} , the higher the carbon sink potential of that species; which indicates that the species can increase its photosynthetic rate with further increasing atmospheric CO₂ in the future. Chlorophyll conductance of the seedlings was recorded using a portable chlorophyll meter (SPAD-502, Minolta, Japan) to determine if the variations in the physiological responses were related to chlorophyll conductance of the plants which could be altered as a result of the tidal treatments.

Analysis of Variance (ANOVA) was performed to determine any variations in the physiological parameters and chlorophyll conductance between two predictor variables; treatment and species. Likewise ANOVA was used to determine the differences in the rate of assimilation between treatment, species and carbon dioxide concentrations. Post-hoc statistical groupings were observed with a Turkey's test at $\alpha = 0.05$. All the analyses were performed with SPSS version 16.0 software.

RESULTS

The variations in the tidal treatment affected physiological parameters of *A. marina* and *B. parviflora* (Table 1; Figure 1). Prolonged inundation in the deep treatment decreased A_{400} of *B. parviflora* but no significant difference in A_{400} was observed in *A. marina*. Carbon dioxide compensation point (Γ CO₂) was not affected by the tidal treatment but varied significantly between *A. marina* and *B. parviflora*. In both species, A_{max} was significantly lower in the deep treatment and A_{max} of *B. parviflora* was significantly lower than that of *A. marina*. Significant two-way interactions between tidal treatment and species on A_{max} were observed.

The ratio between A_{400} and A_{\max} of both species was lower in the shallow treatment than in the deep treatment. In *A.*

marina, the difference in A_{400}/A_{\max} was less between tidal treatments compared to *B. parviflora*.

TABLE 1. Two-way ANOVA results of the physiological parameters between treatments and species

Parameter (Source of Variation)	df	MS	F	p
$A_{(\max)}$				
Species	1	578.104	37.8	<0.0001
Treatment	1	1382.443	90.5	<0.0001
Species x Treatment	1	82.993	5.4	0.030
$A_{(400)}$				
Species	1	366.914	11.6	0.003
Treatment	1	693.805	21.9	<0.0001
Species x Treatment	1	52.570	1.7	0.212
Γ_{CO_2}				
Species	1	95.600	5.7	0.027
Treatment	1	29.560	1.7	0.202
Species x Treatment	1	0.570	0.03	0.856
$A_{(400)}/A_{(\max)}$				
Species	1	0.005	0.5	0.476
Treatment	1	0.023	2.5	0.129
Species x Treatment	1	0.002	0.3	0.613
Chlorophyll conductance				
Species	1	5185.81	164.5	<0.0001
Treatment	1	73.153	2.3	0.132
Species x Treatment	1	8.646	0.274	0.602

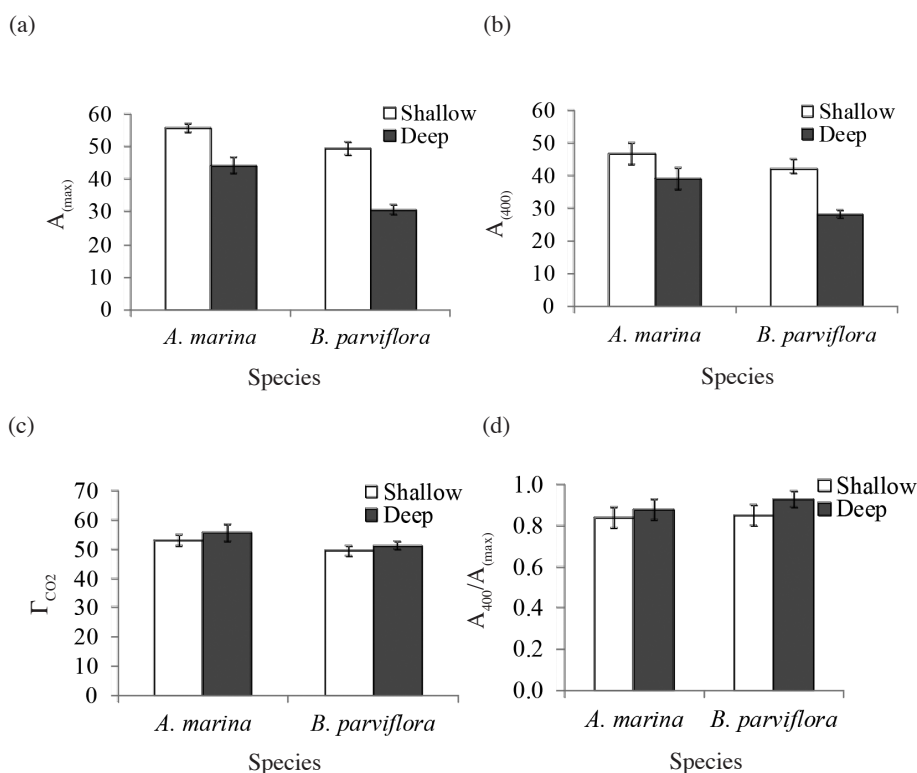


FIGURE 1. Variations in (a) A_{\max} , (b) A_{400} , (c) Γ_{CO_2} and (d) A_{400}/A_{\max} of *A. marina* and *B. parviflora* in tidal treatment

Chlorophyll conductance of *A. marina* and *B. parviflora* was not affected by the tidal treatments (Table 1; Figure 2). However, chlorophyll conductance of *B. parviflora* was significantly higher compared to *A. marina*.

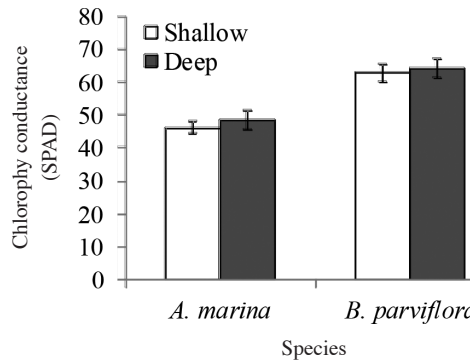


FIGURE 2. Chlorophyll conductance of *A. marina* and *B. parviflora* in tidal treatments

In *A. marina*, increased assimilation was observed with increased CO_2 in both tidal treatments, but this increase was much rapid in the shallow treatment compared to the deep treatment (Figure 3). Assimilation rate of *B. parviflora* increased with increasing CO_2 in the shallow treatment but increased CO_2 did not increase assimilation in the deep treatment and CO_2 saturation was observed below ambience. The assimilation rates varied significantly between species, treatments and CO_2 concentrations. However, the three-way interaction between species, treatment and CO_2 concentration was not significant (Table 2).

DISCUSSION

Prolonged inundation decreased both A_{max} and A_{400} of *B. parviflora* while it only affected A_{max} of *A. marina* indicating that assimilation rate of *A. marina* was unaffected at ambient CO_2 concentration by the tidal

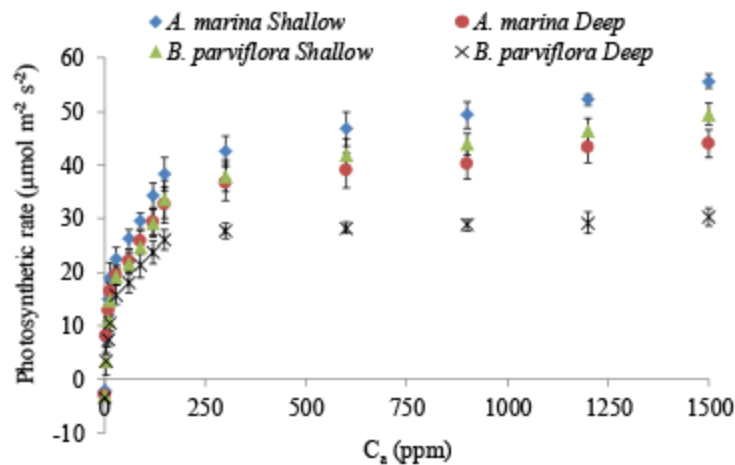


FIGURE 3. CO_2 response curves for *A. marina* and *B. parviflora* in tidal treatments at PAR $1800 \mu\text{mol m}^{-2} \text{s}^{-1}$

TABLE 2. Three-way ANOVA results of assimilation between species, treatments and CO_2 concentrations

Parameter (Source of Variation)	df	MS	F	p
Assimilation ($\mu\text{mol m}^{-2} \text{s}^{-1}$)				
Species	1	2882.652	145.4	<0.0001
Treatment	1	3364.522	169.7	<0.0001
CO_2	13	5159.369	262.1	<0.0001
Species \times Treatment	1	145.676	7.3	0.007
Species \times CO_2	13	38.18	1.9	0.027
Treatment \times CO_2	13	138.807	7	<0.0001
Species \times Treatment \times CO_2	13	15.054	0.759	0.703

flooding. Similarly, A_{\max} and A_{400} were much higher in *A. marina* at a given treatment than *B. parviflora*, which explains, to some extent, the variations in the growth forms of these two species. The lower A_{400}/A_{\max} in both species in the shallow treatment suggests that these two species can withstand increased CO_2 concentrations under moderate tidal flooding. In *A. marina*, the ratio of A_{400}/A_{\max} was less variable between tidal treatments. In contrast, A_{400}/A_{\max} of *B. parviflora* was significantly lower in the shallow treatment indicating that this species can only maximize photosynthesis with increasing CO_2 concentrations under moderate tidal inundation. Reduced assimilation under tidal flooding has been reported in *K. candel* (Chen et al. 2005) and *R. mangle* (Ellison & Farnsworth 1997). Similarly, short term flooding decreased leaf-level carbon assimilation in *A. germinans*, *L. racemosa* and *R. mangle* while long term flooding had slight effects on the leaf gas exchange parameters of these species (Krauss et al. 2006).

Chlorophyll conductance of *B. parviflora* was much higher compared to *A. marina* in both tidal treatments. Reduced chlorophyll conductance have been observed in some wetland plants grown in flooded soils (McKevlin et al. 1995; Ye et al. 2004) while no significant differences were observed in others (Pezeshki et al. 1996). The increased chlorophyll conductance of *B. parviflora* in this study did not increase the assimilation rates of this species.

Carbon sequestration of *B. parviflora* was substantially reduced in the deep treatment while the difference between tidal treatments was much lesser in *A. marina*. Decreased assimilation under prolonged tidal inundation is often associated with stomatal closure. Stomatal closure resulting from changes in the guard cell turgor has been reported in mangroves (Naidoo et al. 1997). Decreased stomatal conductance under prolonged tidal inundation has been reported in *A. marina* (Sayed 1995), *B. gymnorhiza* (Naidoo 1983) and *K. candel* (Ye et al. 2004). Similarly, increased CO_2 induced stomatal closure to enhance photosynthetic water use efficiency (Urban 2003). The results of carbon sequestration, therefore, suggest that *A. marina* is likely to benefit from increased atmospheric carbon dioxide even under prolonged tidal inundation. In contrast, the benefits of increased CO_2 are likely to be compensated for in *B. parviflora* by reduced growth in response to longer hydroperiods under rise in sea level. In addition to stomatal closure, another potential mechanism that reduces photosynthesis under tidal flooding could be hormone-mediated physiological variations. For instance, the amount of ethylene has been associated with decreased photosynthesis resulting from lack of mesophyll photosynthetic capacity (Taylor & Gunderson 1988). Alternatively, reduced photosynthesis could arise from altered enzymatic activity such as reduced rubisco activity induced by the decreased leaf water potential (Pezeshki 1994).

CONCLUSION

The physiological responses of *A. marina* and *B. parviflora* under tidal treatments indicated that these two species responded differently. In *A. marina*, the only physiological parameter that varied between tidal treatments was A_{\max} while in *B. parviflora* A_{\max} and A_{400} was significantly reduced when exposed to tidal flooding. Hence the first hypothesis which states that physiological responses of *A. marina* var. *acutissima* and *B. parviflora* will vary between tidal treatments is accepted. However, the difference in A_{\max} and A_{400} was not limited by the chlorophyll conductance of both species as chlorophyll conductance was insensitive to tidal treatments. Similarly, carbon sequestration of *A. marina* and *B. parviflora* was reduced in the deep treatment but the reduction was much prominent in *B. parviflora*. Thus, the second hypothesis which states that carbon sequestration of both species will be affected by the tidal treatments is accepted. Overall, *A. marina* showed fewer responses to tidal flooding than *B. parviflora*. Thus, the third hypothesis which states that tidal flooding will affect *A. marina* to a lesser extent than that of *B. parviflora* is accepted. These results indicated that *A. marina* is better adapted for the projected climate change than *B. parviflora*.

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