



Seasonal Variation on Photosynthetic Pigment, Soluble Sugars and Starch Contents of Mangrove (*Avicennia alba* Bl.)

Tidarat Ponpiboon, and Tritep Vichkovitten*

Abstract— Field samplings of photosynthetic pigment, soluble sugars and starch contents of mangrove (*Avicennia alba* Bl.) located at Chonburi province, in the eastern part of Thailand were performed in three occasions in 2016 from cold-dry (January), summer (May) and the rainy season (September). Three study sites were selected based on the distance from the shore. Environmental parameters including light intensity and air temperature were recorded at each time of the field visits. The average daily light intensity in summer (24.64 klux) was similar to the rainy season (23.98 klux) and were higher than the cold-dry season (5.35 klux). The highest average temperature of 34.0 °C was observed in summer, the rainy season had an average of 30.2 °C, whereas cold-dry had the lowest of 25.7 °C. The Chl-a contents varied between 1.04 to 1.69 mg g⁻¹, where low Chl-a contents were observed in the morning and late afternoon and the highest amounts of Chl-a were generally found between 10 a.m. to 2 p.m. with detected high light intensities. The quantities of Chl-b were lower than Chl-a with a varied range of 0.29-0.43 mg g⁻¹. Amount of carotenoids were close to Chl-b with the value ranging from 0.25 to 0.30 mg g⁻¹. The sugar contents varied between 15.02 and 42.70 mg g DW⁻¹ with the highest values were observed in the rainy season, the intermediate values were found in summer, whereas, the lowest values were detected in cold-dry season. The starch contents also exhibited the same seasonal pattern like sugars but less quantitative amounts with the value of 6.80-27.96 mg g DW⁻¹. There were less different in sedimentary environments including redox potential (Eh) and organic matter content. The present study suggesting that photosynthetic pigments, as well as photosynthetic products of mangrove (*A. alba*), was influenced by light intensity throughout the study period. High photosynthetic activity accelerated the growth of mangrove during the growing period in the rainy season. Variation of plant characteristics and responses were also attributable to benthic environmental conditions particularly sulfide across the mangrove landscape. Plant vulnerability to sulfide stressor was pronounced during the rainy season especially in the area with high sediment organic matter accumulation.

Keywords— *Avicennia alba* Bl., chlorophyll, mangrove, starch, sugar.

1. INTRODUCTION

Mangroves are a kind of halophytic woody vegetations which have been successfully developed in tropical and subtropical regions worldwide. They provide important resources of foods, woods for construction and fuel to support human livelihood in coastal areas [1]-[2]. Mangroves also provide a large number of ecological services including nutrients generation which is an importance supply for marine food web [3]-[4]. They help to accumulate and stabilize sediment therefore, reduce coastal erosion and flooding [4]-[5]. Mangroves generally grow across complex environmental gradients of the coastal areas resulting in the variation on forest community structure and growth responses [6]-[7]. Mangrove plants distribution, development and productivity are regulated by biotic influences, such as herbivory, seed predation and competition and abiotic factors, such as light, tidal inundation, salinity, sulfide concentrations, pH and redox potential [8]-[9]. Abiotic stress may limit plant characteristic and growth and to some extent, may even cause to death [10]. Mangrove

plants are generally established well in the coastal zone across the tropical regions and thus, prefer the exposed habitats with high light intensity. Photosynthesis in plants is a function of light where chlorophylls serve as antenna molecules capture light energy for the photosynthetic processes. Thus, chlorophyll contents can be applied in mangrove ecosystem for determining the way in which mangrove plants response to changing environmental parameters. There are considerable difference in light requirement among mangrove plant species resulting in variation in plants zonation and succession [11]. In addition to light, two other stressors of coastal wetlands are salinity and soil inundation [9]-[10], [12]. A large salinity variation occurred in both spatial and temporal is characteristics of mangrove habitats. Mangrove species often show growth stimulation at low salinity and growth decline with further increases in salinity. Exposure to high soil salinity can directly affect photosynthesis as well as indirectly limit carbon fixation by restricting stomatal opening [13]-[14]. Persistent soil flooding also inhibits plant development by restricting root oxygen availability [7]. This lack of root oxygen minimizes aerobic root respiration and metabolic energy for growth. Mangrove possesses a variety of adaptations to extreme environmental stresses. Plants adaptability may reflect to physiology and characteristics by developing the salt exclusion by root ultrafiltration and salt secretion via glands [15]. In addition, mangrove species can also accumulate ion in leaf and some may change their leaf physiology into succulent leaf. Responses of mangrove to environmental stressors reflect alterations in

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photosynthesis, photosynthetic pigment content, transpiration rate and enzyme activities [13], [16]-[17].

The *Avicennia alba* Bl. is a species of mangrove plant that commonly exists and forms the patch on the coastal fringe of Thailand. This particular species is known to be a pioneer species, generally colonized newly-formed mud banks on seaward side. Its widespread root system with large numbers of pneumatophores helps to stabilize new deposits of sediment. *Avicennia* species are known to be able to thrive in habitats with high salinity and silt. The *A. alba* has special adaptability to survive in areas that have highly fluctuated salinity, waterlogged muddy sediment. This mangrove plant has specialized salt-secreting glands which are small slit-like openings found on the upper surface of the leaves [15], [18]. It is interesting to know in addition to salt excretion glands, that how *A. alba* has physiological adaptability in relation to the maintenance of metabolic cost to survive and grow in such severe environments. The purpose of this study is to examine environmental characteristics change and plant physiological responses to changing environments.

2. MATERIALS AND METHODS

2.1 Studies sites

The study area of *A. alba* was located at the preserved mangrove forest in Chonburi province, on the eastern part of Thailand (13°20'31" N and 100°56'33" E), which covered a total area of 80 ha (Fig. 1).

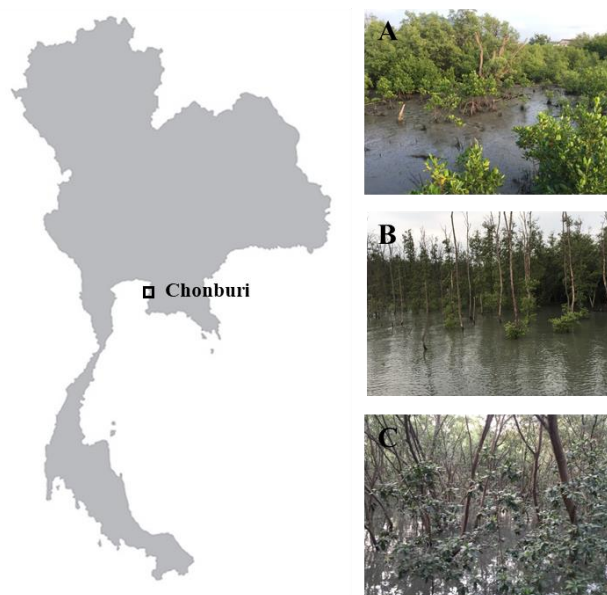


Fig. 1. Sampling sites of mangrove *Avicennia alba* Bl. at Chonburi province on the eastern coast of Thailand. The letters A, B and C refers to three sampling sites clarified by the distance of 50, 100 and 150 m from the shore, respectively.

The majority of plant species in this mangrove fringe system is *Avicennia alba* Bl., and it generally grows in association with *Rhizophora mucronata* Lam. Field samplings were performed in three occasions with

seasonal variation in 2016 from cold-dry (January), summer (May) and rainy season (September). Three study sites were selected based on the distance from the shore, site A located in the innermost part of the estuary (50 m from shore). Site B stood in the middle (100 m from shore) whereas site C was located in the outermost seaward part (150 m from shore). Forest structure in the area was previously described as reduction of tree size and developmental stage were presented in a decreasing order from site A, representing mature stage categories to site C, which representing the young tree categories [19]. However, mangrove die-off event occurred since 2010 caused a lot of mangrove plants died from site A and some was detected at site B. Re-colonization of mangrove plants was existing at site A during the last 4-years, therefore sampling site of the present study is mainly focused on the distance from the shore, which could contributable to degree of inundation and variation of sedimentary environment.

2.2 Sampling and analysis

Six healthy from the third leaf pairs were randomly collected every two hours from 6 a.m. to 6 p.m. for determination of chlorophyll *a* (Chl-*a*), chlorophyll *b* (Chl-*b*), and carotenoids. After collection, leaves were immediately wrapped in a paper towel, kept in a zip-lock bag and stored in a cooling box prior to transportation to laboratory. One portion of fresh leaf tissues were extracted for measurement of pigment content, using *N,N*-dimethylformamide (DMF) prior to spectrophotometric determination following the method of Inskeep and Bloom [20]. Pigment contents were calculated based on dry weight basis in mg g⁻¹ by applying the absorption coefficient equations described by Wellburn [21]. Another portion from the same leaf pairs were harvested for sugar and starch measurements. Soluble carbohydrates (glucose+fructose +sucrose) were extracted using 80% v/v ethanol solution, whereas insoluble carbohydrates (starch) were subsequently extracted from the alcohol-insoluble tissue [22]. Carbohydrate concentrations were quantified by an anthrone colorimetric reaction and the absorbance was read on a spectrophotometer against glucose standards [23].

Environmental parameters including light intensity and air temperature were recorded at each time of the field visits. Porewater was collected once on January 2017 using peeper technique (peeper-type diffusive devices modified from Gonçalves et al. [24] and Johnston et al. [25]) for sulfide and nutrients determination. Briefly, the peeper sampling device contained an array of eight cylindrical PVC capsules with diameter ~5 cm. Two open-end of each capsule was sealed with 0.45 μm membranes. The capsule was filled with de-ionized water through a hole on the capsule wall then sealed with silicone prior to install in the field. Each peeper was placed in the sediment for 7 d for chemical equilibrium by ionic diffusion. After retrieval, porewater samples were withdrawn from the PVC capsule using 10-ml syringe, one sample portion was precipitated with zinc acetate solution for sulfide determination. The other sample portions were then kept in polyethylene container

for further measurement of nutrients. Sediment sampling was carried out at low tide within a plot of three plant categories. Sediment samples were collected in triplicate using plexiglass hand corers (50 mm i.d. and 50 cm in length). Cores were cut into 2 cm interval until the depth of 20 cm was reached then placed in 50 ml polypropylene bottles, kept in cooler and transported back to laboratory. In the laboratory, the redox potentials (Eh) were measured in the field at 5, 10, 20 and 30 cm depth, using an oxidation-reduction potential (ORP) Pt electrode and after equilibrating the electrode for a few minutes. Sediment samples were dried and homogenized prior to determine for organic matter content as loss on ignition in the muffle furnace for 3 h at 550 °C which reported in percentage of the original.

2.3 Statistical analysis

The differences between sampling sites and seasons were statistically compared using the analysis of variance (ANOVA). Significant differences were identified using Tukey's post-hoc test with pair-wised comparison among source of variations. All statistical analyses were conducted with Minitab 14.

3. RESULTS

3.1 Environmental conditions

The daily illumination change was similar among those three seasons, cold-dry, summer and rainy season, following the classical pattern where light intensity increased from morning to reach the maximum value around noon before decreased through the afternoon with slightly different of day-light period was detected (Fig. 2).

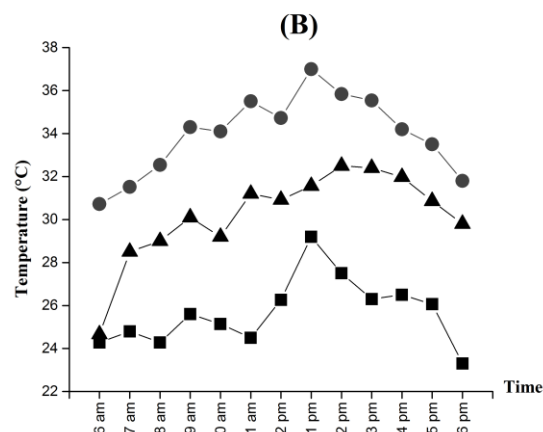
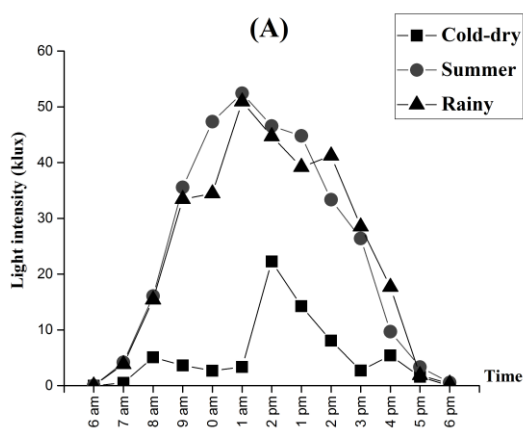


Fig. 2. Variation of daily light intensity (A) and air temperature (B) among three seasons; cold-dry, summer and rainy season in the mangrove (*Avicennia alba* Bl.) forest.

The highest maxima daily light intensity of 52.44 klux was detected in summer, the second went to rainy season with the value of 50.94 klux and cold-dry season had the lowest of 22.28 klux. The average daily light intensity in summer (24.64 klux) was similar to rainy season (23.98 klux) and was higher than cold-dry season (5.35 klux). The daily temperature changes among those three seasons were following the same pattern as light intensity where temperature increased with increasing light from morning to reach the highest value in the early afternoon before decreased till evening. In summer, the daily temperature fluctuated between 30.7 and 37.0 °C with the average value of 34.0 °C. The daily temperature in rainy season was found within the range of 24.7-32.5 °C with the average value of 30.2 °C. The temperature in cold-dry season varied between 24.3 and 29.2 °C with the lowest average value of 25.7 °C compared to the others (Fig. 2).

3.2 Plant pigments and carbohydrate reserves

Photosynthetic pigments including Chl-*a*, *b* and carotenoid in *A. alba* leaves from three different sites were showed in Table 1. The daily patterns of all photosynthetic pigments were generally related to light intensity where all photosynthetic pigments especially Chl-*a* increased with increasing light intensity with high values were almost found between 10 a.m. to 2 p.m. and low values were observed in the early morning and late afternoon. However, comparison to Chl-*a* contents, we found less influences of light intensity on Chl-*b* and carotenoid. The amount of Chl-*a* varied between 1.04 and 1.69 mg g⁻¹ and site B generally had the highest value followed by site C whereas site A contained the lowest value in all three seasons. Statistical analysis indicated no significant change ($p=0.224$) among sampling sites however, Chl-*a* contents varied significantly ($p<0.05$) among seasons where collected leaves in summer period contained the highest Chl-*a* whereas rainy season had the lowest values. The variation of Chl-*b* among sampling sites followed the same pattern as for Chl-*a* but the amount was ~4 times lesser than Chl-*a* content. Chl-*b* was quantitatively found

within the range from 0.29 to 0.43 mg g⁻¹ and it was noticed that variation of Chl-*b* contents was significantly different among sampling sites and also among seasons ($p < 0.05$).

Table 1. Seasonal variation in photosynthetic pigments including Chl-*a*, Chl-*b* and carotenoids of *Avicennia alba* Bl. leaves. The values are expressed as mean±S.D.

Variables	Sites	Pigment contents (mg g ⁻¹)		
		Cold-dry	Summer	Rainy
Chl- <i>a</i>	A	1.27±0.06	1.32±0.60	1.04±0.10
	B	1.41±0.11	1.69±0.84	1.17±0.07
	C	1.36±0.23	1.35±0.56	1.15±0.26
Chl- <i>b</i>	A	0.37±0.03	0.29±0.07	0.31±0.07
	B	0.43±0.04	0.38±0.11	0.35±0.03
	C	0.39±0.07	0.31±0.10	0.34±0.08
Carotenoid	A	0.29±0.02	0.27±0.05	0.25±0.02
	B	0.30±0.02	0.29±0.06	0.26±0.01
	C	0.29±0.04	0.26±0.04	0.25±0.04

Plants from site B had the highest Chl-*b* contents and site A possessed the lowest values. The cold-dry season influenced Chl-*b* contents to reach the maximum value whereas the minimum value was measured in summer. Carotenoid contents exhibited no significant change ($p=0.101$) among sampling sites and varied within the narrow range between 0.25 and 0.30 mg g⁻¹ however, carotenoid contents were significantly different when comparison between seasons was made and the highest value of carotenoid was found in cold-dry season and the lowest value was measured in rainy season.

Table 2. Seasonal variation in carbohydrate reserves expressed as sugar and starch of *Avicennia alba* Bl. leaves. The values are expressed as mean±S.D.

Variables	Sites	Carbohydrate (mg g DW ⁻¹)		
		Cold-dry	Summer	Rainy
Sugar	A	16.20±2.62	23.91±9.20	42.70±4.89
	B	16.14±2.97	21.91±8.16	39.48±7.23
	C	15.02±2.99	21.30±7.91	38.59±5.99
Starch	A	6.98±3.79	16.11±9.65	27.63±2.89
	B	6.80±3.36	16.83±9.70	27.96±4.89
	C	7.33±2.90	15.86±9.89	16.65±5.02

Carbohydrate reserves in *A. alba* presented in the form of sugar and starch were summarized in Table 3. Sugar contents in plant leaves varied between 15.02 and 42.70 mg g DW⁻¹. There was significantly different ($p < 0.05$) of sugar contents among seasons where plant accumulate high amount of sugars in rainy season (38.59-42.70 mg g DW⁻¹), summer had the intermediate of 21.30-23.91 mg g DW⁻¹) and cold-dry contained the lowest values of 15.02-16.20 mg g DW⁻¹. Plant sugar contents were arranged in decreasing order as site A>B>C for all seasons (Table 2) although no significant variation was calculated ($P=0.363$). Starch contents varied from 6.80 to 27.96 mg g DW⁻¹ but were lesser compared to sugar contents for all sampling sites and changing patterns

followed the same trend as of sugars. Plants at site A had similar starch content to site B and generally higher than site C except for the cold-dry season which were lower with no significantly different ($P=0.961$) among sampling sites was observed. However, significantly different of starch contents ($P < 0.05$) was measured when comparison among seasons was made. Plants in rainy season had the highest amount of starch (16.65-27.96 mg g DW⁻¹) up to 4 times compared to the amount measured in cold-dry season (6.80-7.33 mg g DW⁻¹) and plants in summer had the intermediate value of 15.86-16.83 mg g DW⁻¹.

3.3 Sediment and porewater qualities

High organic matter contents were recorded from all three sites and varied between 14.39 and 18.21%. The highest organic matter content values are presented on the surface layer followed by decreasing values with depth. Site A and site C had similar values of organic matter content at each depth layer and were higher compared to site B (Table 3). The pH values showed less fluctuation among sites (7.18-7.63) and exhibited increasing trend with depth. The Eh values were all presented with the negative sign, ranging between -116.1 and -258.9 mV indicated the reducing condition was pronounced for all three sites. The vertical profile of Eh values exhibited a decreasing trend for all three sampling sites. Sulfide concentrations from all three sampling sites varied between 0.06 and 4.76 mM with similar vertical profiles where low concentration of H₂S detected at surface layers and exhibited increasing trend with depth. It is noticed that sulfide concentrations from 20-cm layer were much higher than sediment surface layer (> 2 times) especially at site A (Table 3). High phosphate concentrations were measured at all sites with the values varied from 36.73 to 89.13 μM. There were not clear trends in phosphate concentrations vertical profiles for site A and site C but the decreasing trend was recorded for site B. Ammonium concentrations were fluctuated between 12.04 and 76.81 μM and exhibited increasing values with depth for all sampling sites. The highest value was recorded at site B and site A had the lowest. The concentration of nitrite+nitrate varied from 0.87 to 5.32 μM and exhibited increasing trend with depth for site A and site B whereas decreasing value of nitrite + nitrate was recorded with depth at site C (Table 3).

Table 3. Depth distribution of sediment and porewater qualities from three sampling sites of mangrove (*Avicennia alba* Bl.) collected in January 2017 of Chonburi coastal area, Thailand. Site A, B and C is subjected to the distance of 50, 100 and 150 m from the shore, respectively. All values are expressed as mean from three replicates.

Sites	Depth (cm)	Parameters						
		OM (%)	pH	Eh (mV)	H ₂ S (mM)	PO ₄ ³⁻ (μM)	NH ₄ ⁺ (μM)	NO ₂ ⁻ +NO ₃ ⁻ (μM)
A	5	18.21	7.40	-116.1	0.06	44.23	12.04	0.87
	10	17.32	7.31	-164.9	0.35	44.48	32.53	3.33
	20	15.70	7.40	-190.4	1.51	36.73	60.95	2.56
	30	n.d.	7.48	-207.0	4.53	89.13	66.77	1.71
B	5	16.97	7.18	-151.0	1.98	74.97	55.64	1.21
	10	15.79	7.25	-156.7	3.65	72.80	56.96	1.37
	20	14.39	7.56	-242.5	4.54	51.72	71.38	2.46
	30	n.d.	7.45	-231.8	4.24	44.54	76.81	2.31
C	5	18.09	7.32	-123.5	1.57	82.79	32.27	5.32
	10	17.15	7.45	-223.7	2.27	79.14	42.11	4.46
	20	15.56	7.55	-258.9	3.29	83.04	51.32	2.21
	30	n.d.	7.63	-232.0	4.76	49.48	47.67	2.03

n.d. = No data

4. DISCUSSION

The geographical structure of the embayment, the influences of climate, in accordance to mangrove vegetation structures could contribute to sedimentary characteristics [9]-[10], [12]. High organic matter contents recorded from all sites, especially for site A and C reached up to 18% suggesting high accumulation potential occurred in this mangrove wetland. The high organic matter contents at site A, which is located in the innermost part could be attributable to high sedimentation resulted from low current velocity in the area. Although, site C is located in the outermost part, but well developed with more complex forest structure could contribute to high sediment accumulation. The *A. alba* forest structure in the area exhibited decreasing order from more complex at the landward site to less complex at the seaward site [19]. Less influence of forest structure found on sedimentary organic matter in this study could be due to intervention of previous die-off event occurred at site A in 2010. The organic matter contents of 14-18% were higher compared to 9-11% from the previous study [19] and thus could accelerate decomposition processes in this mangrove wetland.

Mangrove root system can influence sedimentary environment through the supplement of oxygen to rhizosphere or provide carbon source to sediment microorganisms via root exudates. Forest structure is generally contributed to variation in Eh values however, no such a clear picture is recorded in this study suggesting the influence of mangrove plant succession and forest development must be considered in accordance to forest structure background. Major concerns of stressors in mangrove sedimentary environments are given to salinity and sulfide in porewater. Salinity is believed to be one of the important factors limiting mangrove forest structure and growth [9]-[10], [12], [26]. Salinity stress could reduce growth with vary degree of responses between different mangrove plant species [27]. Previous recorded of salinity in the area was less than the upper range of sea

water (<35 ppt) [19]. In addition, porewater salinity varied between 22-28 ppt (data not show) and exhibited less variation across the mangrove landscape, indicating that salinity was of minor importance contributed to forest structure and responses. The present study revealed high amount of NH₄⁺ and PO₄³⁻ concentrations suggesting that nutrients did not limit plant growth and development in the areas [19]. High sulfide concentrations in this study were similar to those found in other mangrove sediments [10], [28], which could be harmed to mangrove vegetation therefore, responses of *A. alba* to environmental stressors could be attributed to sulfide.

The *A. alba* responses to increasing sulfide concentrations by increasing photosynthetic pigments including Chl-*a* and Chl-*b* but less clearly change in carotenoid contents is observed. Increment of photosynthetic pigments could induce plant photosynthesis in order to accelerate carbon fixation rate and plant energy transformation which can be resulted in variation of carbohydrate reserves. Many studies indicate a variety of plant species response to stress conditions by changing amount of carbohydrate reserves [13], [22], [29]-[30]. Change in soluble sugar and starch contents in *A. alba* leaves suggesting the induction of sugar-starch conversion. Both sugar and starch contents seem to be fairly related to sulfide concentrations where high sulfide induce accumulation of soluble sugar and starch contents in *A. alba* leaves for all three seasons. However, plant accumulates the highest amounts of soluble sugar and starch in rainy season whereas less accumulation of carbohydrate reserves was evaluated in cold-dry season. In addition, low light intensity could also be resulted in low photosynthetic pigments as well as carbohydrate reserves in cold-dry season compared to summer period. Although light intensity in rainy season was similar to value obtained in summer but less Chl-*a* was pronounced. Carbohydrate reserves turned to the other way around where the highest value recorded in rainy season compared to summer and this could be due in part to the growing season of this mangrove vegetation. Therefore, diverse environmental factors may act

together contributing to variation in *A. alba* carbohydrate reserves.

Plants are generally stored photosynthates in the insoluble forms like starch and on the other hand they need to convert insoluble forms of carbohydrate reserves into soluble forms prior to utilize in the production of new cell during growth processes [31]. Plant can allocate a considerable amount of carbohydrate to the roots in preparation for re-sprouting as well as fuel supporting for root respiration. It is known that plants store large amount of starch which, under normal condition, are mobilized only partially [31]. Under stress condition, mangrove plants can accumulate a type of low, compatible molecular compound to protect cell structure and water circulation [13], [30], [32]. Therefore, high sugar/starch ratio in cold-dry season suggesting high transformation rate of starch to sugar and it could be related to high sulfide concentrations. The sugar/starch ratios measured in summer were low and exhibited similar values to those achieved in rainy season with high amount of sugar and starch contents. The explanation could be due to either the availability of high photosynthates achieved from photosynthetic activity during the growing season or the mechanism of carbohydrate allocation to support root respiration.

5. CONCLUSION

The mangrove (*A. alba*) plant which is generally occupied coastal wetlands of Thailand has the adaptability to survive in the harsh environments. This study indicated that photosynthetic pigments of *A. alba* especially Chl-a is a function to light intensity. Seasonal variation in temperature may also act in concert to light intensity influencing the photosynthetic pigments. Variation of soluble sugars and starch contents could be due to the mechanism in responses to changing environments. In addition to soil waterlogging, sulfide concentrations may also contribute to detrimental effects to this mangrove species. Therefore, a variety of environmental factors may act in concert contributing to the variation of mangrove plant responses. The results would be useful for the predicted changes due to global warming condition involving of increases in light, temperature, salinity and tidal inundation, which consequently may alter and affect the structure, function, and distribution of mangrove vegetations and their responses to such changing environments.

REFERENCES

- [1] Alongi, D.M., 2002. Present state and future of the world's mangrove forests. *Environmental Conservation* 29: 331-349.
- [2] Walters, B.B., Rönnbäck, P., Kovacs, J.M., Crona, B., Hussain, S.A., Badola, R., Primavera, J.H., Barbier, E., Dahdouh-Guebas, F., 2008. Ethnobiology, socio-economics and management of mangrove forests: a review. *Aquatic Botany* 89: 220-236.
- [3] Rivera-Monroy, V.H., Madden, C.J., Day, J.W., Jr., Twilley, R.R., Vera-Herrera, F., Alvarez-Guillén, H., 1998. Seasonal coupling of a tropical mangrove forest and an estuarine water column: enhancement of aquatic primary productivity. *Hydrobiologia* 379: 41-53.
- [4] Kathiresan, K., 2012. Importance of mangrove ecosystem. *International Journal of Marine Science* 2: 70-89.
- [5] Lee, S.Y., Primavera, J.H., Dahdouh-Guebas, F., McKee, K., Bosire, J.O., Cannicci, S., Diele, K., Fromard, F., Koedam, N., Marchand, C., Mendelsshohn, I., Mukherjee, N., Record, S., 2014. Ecological role and services of tropical mangrove ecosystems: a reassessment. *Global Ecology and Biogeography* 23: 726-743.
- [6] Chen, R., Twilley, R.R., 1999. Patterns of mangrove forest structure and soil nutrient dynamics along the Shark River Estuary, Florida. *Estuaries* 22: 955-970.
- [7] Lovelock, C.E., Feller, I.C., McKee, K.L., Thompson, R., 2005. Variation in mangrove forest structure and sediment characteristics in Bocas del Toro, Panama. *Caribbean Journal of Science* 41: 456-464.
- [8] Sherman, R.E., Fahey, T.J., Howarth, R.W., 1998. Soil-plant interactions in a neotropical mangrove forest: iron, phosphorus and sulfur dynamics. *Oecologia* 115: 553-563.
- [9] Marchand, C., Baltzer, F., Lallier-Vergès, E., Albéric, P., 2004. Pore-water chemistry in mangrove sediments: relationship with species composition and developmental stages (French Guiana). *Marine Geology* 208: 361-381.
- [10] McKee, K.L., 1993. Soil physicochemical patterns and mangrove species distribution – reciprocal effects? *Journal of Ecology* 81: 477-487.
- [11] Kitao, M., Utsugi, H., Kuramoto, S., Tabuchi, R., Fujimoto, K., Lihpai, S., 2003. Light-dependent photosynthetics indicated by chlorophyll fluorescence in five mangrove species native to Pohnpei Island, Micronesia. *Physiologia Plantarum* 117: 379-382.
- [12] McKee, K.L., Mendelsshohn, I.A., Hester, M.W., 1988. Reexamination of pore water sulfide concentrations and redox potentials near the aerial roots of *Rhizophora mangle* and *Avicennia germinans*. *American Journal of Botany* 75: 1352-1359.
- [13] Parida, A.K., Das, A.B., Sanada, Y., Mohanty, P., 2004. Effects of salinity on biochemical components of the mangrove, *Aegiceras corniculatum*. *Aquatic Botany* 80: 77-87.
- [14] Parvaiz, A., Satyawati, S., 2008. Salt stress and phyto-biochemical responses of plant. *Plant, Soil and Environment* 54: 89-99.
- [15] Parida, A.K., Jha, B., 2010. Salt tolerance mechanisms in mangroves: a review. *Trees* 24: 199-217.
- [16] Takemura, T., Hanagata, N., Sugihara, K., Baba, S., Karube, I., Dubinsky, Z., 2000. Physiological and biochemical responses to salt stress in the mangrove, *Bruguiera gymnorrhiza*. *Aquatic Botany* 68: 15-28.
- [17] Biber, P.D., 2006. Measuring the effects of salinity stress in the red mangrove, *Rhizophora mangle* L. *African Journal of Agricultural Research* 1: 1-4.

- [18] Yuan, F., Leng, B., Wang, B., 2016. Progress in studying salt secretion from the salt glands in recretohalophytes: how do plants secret salt? *Frontiers in Plant Science* 7: Article 977. doi: 10.3389/fpls.2016.00977.
- [19] Vichkovitten, T., Kiratipayoon, S., 2017. Litter production, sediment organic matter and nutrient dynamics among different size classes of mangrove (*Avicennia alba* Bl.) stands. In *GMSARN International Conference on Energy Connectivity, Environment, and Development in GMS*. Danang, Vietnam, 28-30 November.
- [20] Inskeep, W.P., Bloom, P.R., 1985. Extinction coefficients of chlorophyll *a* and *b* in *N,N*-Dimethylformamide and 80% acetone. *Plant Physiology* 77: 483-485.
- [21] Wellburn, A.R., 1994. The spectral determination of chlorophylls *a* and *b*, as well as total carotenoids, using various solvents with spectrophotometers of different resolution. *Journal of Plant Physiology* 144: 307-313.
- [22] Erskine, J.M., Koch, M.S., 2000. Sulfide effects on *Thalassia testudinum* carbon balance and adenylate energy charge. *Aquatic Botany* 67: 275-285.
- [23] Yemm, E.W., Willis, A.J., 1954. The estimation of carbohydrates in plant extracts by anthrone. *Biochemical Journal* 57: 508-514.
- [24] Gonçalves, W.F.O., Luiz-Silva, W., Machado, W., Nizoli, E.C., Santelli, R.E., 2012. Geochemistry of intertidal sediment pore waters from the industrialized Santos-Cuatão estuarine system, SE Brazil. *Anais da Academia Brasileira de Ciências* 84: 427-441.
- [25] Johnston, S.G., Burton, E.D., Keene, A.F., Bush, R.T., Sullivan, L.A., Isaacson, L., 2009. Pore water sampling in acid sulfate soil: a new peeper method. *Journal of Environmental Quality* 38: 2474-2477.
- [26] Otero, X.L., Ferreira, T.O., Vidal-Torrado, P., Macías, F., 2006. Spatial variation in pore water geochemistry in a mangrove system (Pai Matos island, Cananeia-Brazil). *Applied Geochemistry* 21: 2171-2186.
- [27] Basak, U.C., Gupta, N., Rautaray, S., Das, P., 2004. Effects of salinity on growth of mangrove seedlings. *Journal of Tropical Forest Science* 16: 437-443.
- [28] McKee, K.L., 1995. Interspecific variation in growth, biomass partitioning, and defensive characteristics of neotropical mangrove seedlings: response to light and nutrient availability. *American Journal of Botany* 82: 299-307.
- [29] Vichkovitten, T., Holmer, M., Frederiksen, M.S., 2007. Spatial and temporal changes in non-structural carbohydrates in eelgrass (*Zostera marina* L.) in Danish coastal waters. *Botanica Marina* 50: 75-87.
- [30] Yan, L., Guizhu, C., 2007. Physiological adaptability of three mangrove species to salt stress. *Acta Ecologica Sinica* 27: 2208-2214.
- [31] Regier, N., Streb, S., Zeeman, S.C., Frey, B., 2010. Seasonal changes in starch and sugar content of poplar (*Populus deltoides* × *nigra* cv. Dorskamp) and the impact of stem girdling on carbohydrate allocation to roots. *Tree Physiology* 30: 979-987.
- [32] Liang, S., Zhou, R.C., Dong, S.S., Shi, S.H., 2008. Adaptation to salinity in mangroves: implication on the evolution of salt-tolerance. *Chinese Science Bulletin* 53: 1708-1715.