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Original Article

Structural characteristics and physiological responses along the salinity gradients of *Ceriops tagal* (Perr.) C.B. Rob. dominated mangrove associations

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Abstract

Forest structure of Tagal mangrove (*Ceriops tagal* (Perr.) C.B. Rob.) and soil characteristics were examined at five different positions along the 1,800 m transect line perpendicular to the coast of Trat province, Thailand. Tree stands at the outermost station were highest and exhibited the decreasing trend from the coastal fringe landward. Average soil salinities were ranging from 22 to 37 ppt and increased with increasing distance from coastal to the inner zone. High organic matter contents (up to 44%) in soil from the inner stations indicated the peat formation in this mangrove landscape. Porewater nutrient concentrations including nitrite+nitrate, ammonia and phosphate at the inner zones were relatively low compared to other mangrove forests. Porewater sulfide was low and could not showed any negative effects on this mangrove vegetation. Responses of *C. tagal* to soil salinity gradient under field conditions were evaluated in term of chlorophyll *a* (chl-*a*), chlorophyll *b* (chl-*b*), carotenoids, sugar and starch. High salinity had no significant detrimental effects on photosynthetic pigments for both tree and seedling however, variation on plant responses pattern was achieved. This study indicated the physiological adaptation of *C. tagal* to survive an extensive variation of soil salinity could be varied depending on plant developmental stage.

Keywords: mangrove, *Ceriops tagal*, salinity, photosynthetic pigment, carbohydrate reserves

1. Introduction

Mangroves are halophytic vegetation, which successfully colonized in intertidal zone of tropical and subtropical regions worldwide. Various environmental setting along the intertidal zone can be resulted in variation of structural and functional characteristics geographically at global, regional and local scales (Sherman, Fahey, & Martinez, 2003). Soil salinity and persistent of tidal flooding are mentioned as the dominant stressors which can regulate development and productivity across the mangrove landscapes (Koch, 1997; Marchand, Baltzer, Lallier-Vergès, & Albéric, 2004; Perri, Viola, Noto & Molini, 2017). Mangrove plants generally grow within a certain range of salinity and out of the optimal salinity, reduction on growth is observed in various mangrove species (Khan & Aziz, 2001; Yan & Guizhu, 2007). Diverse mechanisms through physiological or biochemical adaptations are considered as the responses of mangroves to salinity stress. Mangroves may function with less efficient water transport which may be related to more conservative water use (Khan & Aziz; 2001). Furthermore, alteration in leaf structure, photosynthetic rates, photosynthetic pigment content, transpiration rate, stomatal conductance and enzymatic activity are also accounted in responses of mangroves to salinity stress (Asaeda, & Barnuevo, 2019; Biber, 2006; Das, Parida, Basak, & Das, 2002; Parida, Das, Sanada, & Mohanty, 2004; Perri, *et al.*, 2017; Qiu, Lin, & Guo, 2007). Biochemical mechanisms by which mangrove encounter the high osmolarity of salt have been reported with accumulation of compatible solutes (Krauss & Allen, 2003; Parida & Jha, 2010). Inhibition of photosynthesis in mangrove species have been reported for other stressors such as sulfide (Koch, 1997), heavy metals (MacFarlane & Burchett, 2001). In addition, the interplay between salinity and other

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environmental conditions e.g. drought, sulfide, high light levels may be of importance in accelerating the negative effects on mangrove responses (Koch, 1997; Krauss & Allen, 2003).

Tagal mangrove (*Ceriops tagal* (Perr.) C.B. Rob.) is usually distributed on well-drained soil, within the reach of occasional tides in the landward mangrove zone. It has salt grands in the leaves for secretion of excess salt and show tolerance to the changes in salinity gradients. The mangrove species of *C. tagal* at Pred Nai mangrove forest, Trat province, Thailand is distributed over a long range within the mangrove landscape from the coastal fringe up to 1,800 m landward. Mangrove communities can be varied within the environmental setting along the distance from shore to the inner locations. Consequently, responses of *C. tagal* to changing environmental conditions especially salinity can also be varied. The present study aimed to investigate abiotic factors including nutrients, salinity, soil redox potentials and other soil characteristics difference among the wide spread patch of *C. tagal* on the coastal of Trat province, Thailand. Plant physiological responses to such salinity gradients are determined in both tree and seedling to clarify the influence of salinity on *C. tagal* characteristics.

2. Materials and Methods

2.1 Study site description

Pred Nai mangrove forest is located in Trat, the easternmost province of Thailand (Figure 1). This mangrove forest covers the area of 1,920 ha and constitutes of various mangroves and mangrove associates diversity. Zonal distributions of major mangrove vegetation are generally clarified as *Avicennia alba*, *A. marina*, *Sonneratia alba* and *Rhizophora mucronata* distribute mainly as seaward zone mangroves whereas *R. apiculata*, *Ceriops tagal* and *Excoecaria agallocha* are growing interior as meso zone mangroves whilst *Lumnitzera racemosa* is exhibited as a landward zone mangrove (Wakushima, Kuraishi, Sakurai, Supappibul & Siripatanadilok, 1994). There are twelve canals run through the forest with six small branching creeks which are the way to support saline water to the inner mangrove zone. Although there are many canals connecting between inner and outer parts of the forest but mangrove vegetation in the inner part are occasionally flooded, only on a spring high tide. Mangrove vegetation in many parts of the area are secondary forest which regenerated and replanted after forest concession has been intervened since 1986 (per. com.). Most of the replanting mangrove species are *R. mucronata* and *R. apiculata* whereas *C. tagal* is left self-recolonization. The present study was undertaken between seventh and eighth canals where *C. tagal* was found naturally distributed from coast to 1,800 m mangrove edge in the inner zone.

2.2 Field sampling

Field sampling was performed in August 2010 during the rainy season where salinity gradients and salinity stress were expected to pronounce the least comparing to other seasons. The line transect was laid perpendicular to the coastal fringe further landward with the distance line up to 1,800 m. Following to the transect line, five zones of *C. tagal* vegetations were selected based on the distance which were clarified as 200 (A), 950 (B), 1,200 (C), 1,400 (D), and 1,550 (E) m from the sea. Plant characteristics observation was carried out within a 10x10 m plot representing each of *C. tagal* zones. To estimate density in each plot, all trees taller than 1.3 m were counted and stem diameter at breast height (DBH) was measured with DBH tape avoiding protrusions. All saplings (≥1.3 m tall and <4.5 cm in DBH) and seedlings (<1.3 m tall) were counted and identified. Twenty trees were chosen randomly in each plot to measure tree height using clinometer. Ten healthy from second leaf pairs of each top story tree canopy as well as ten samples of second leaf pairs from each seedling were randomly collected for determination of chlorophyll *a*, chlorophyll *b*, the derived parameters (total chlorophyll and chlorophyll *a/b* ratio) and carotenoids. Another portion from the same leaf pairs were harvest for further sugar and starch measurements.

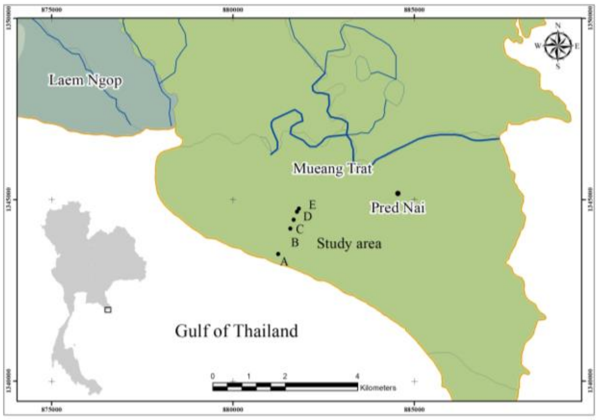

Figure 1. Five sampling stations lie up along the seventh canal at Pred Nai mangrove forest, Trat province, on the eastern coast of Thailand

2.3 Porewater sampling and analysis

Porewater was sampled in three replicate from each station using Plexiglas seeper technique (Koch, 1997) at a depth position of 5, 10, 20, and 30 cm. Porewater was slowly withdrawn from the sediment at depth, placed in polyethylene container and kept in cooler for further analysis. A 10 ml subsample for sulfide analysis was extracted first by immediately filtered through a 0.45 μm Millipore syringe filter into a centrifuge tube containing zinc acetate solution to trap sulfide. Dissolved sulfide was measured colorimetrically using the methylene blue method of Cline (1969) at a wavelength of 670 nm. Salinity and pH in porewater samples were measured in the field using multi-parameter measurement meter (YSI Model 650D). Other sample portions were filtered through a GF/C filter paper to polyethylene container for colorimetrically measurement of nitrite and nitrate (NO_2^-+NO_3^-), ammonium (NH_4^+) and phosphate (PO_4^3) concentrations using a Shimadzu Model UV-1601 apparatus.

2.4 Soil sampling and analysis

Triplicate plexiglass hand corers (5.4 cm inner diameter, 40 cm height) were extruded from each site to collect soil sample, then sectioned for 2 cm interval until the depth of 30 cm was achieved. Soil sample was placed in a polypropylene container and kept in cooler before transported back to laboratory for further analysis. 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. In the laboratory, soil samples were homogenized prior to ascertain for bulk density as weight of a known volume. Water content was determined as the proportional between fresh weight and dry weight at 60 °C for 48 hrs and calculated as a percentage of the original. Organic matter content was measured as loss on ignition in the muffle furnace for 3 hrs at 550 °C which reported in percentage of the original.

2.5 Photosynthetic pigments determination

Plant pigments were determined following the method of Inskeep and Bloom (1985) using *N,N*-dimethylformamide (DMF) as the extractant. The extract bottles were covered with aluminum foil and placed in a darkened container, to prevent light oxidation, prior to spectrophotometric determination in glass cuvettes (1 cm path length) on a spectrophotometer (Shimadzu Model UV-1601). Wavelengths chosen for analysis were 647 and 664 nm for the chlorophylls, and 480 nm for the carotenoids. Pigment contents were calculated in mg g DW^{-1} by applying the absorption coefficient equations described by Wellburn (1994).

2.6 Extraction and determination of soluble sugars and starch

Soluble sugars and starch were extracted following the procedure from Erskine and Koch (2000). A weight of 25-30 mg ground leaf tissue was extracted for soluble carbohydrates (glucose+fructose+sucrose) using 80% v/v ethanol solution in a centrifuge tube. The sequential extraction was repeated twice and the supernatants were pools. After final extraction, the tube was centrifuged at 3,800 x g for 15 min and the remaining supernatant added to the scintillation vial. The alcohol-sugar extract in the vials was dried under a fume hood with low heat (<40 ºC) and a direct air flow. The residue was then redistributed in 10-14 ml of warm (<40 ºC) distilled water and kept overnight in a dark refrigerator.

Insoluble carbohydrates (starch) were subsequently extracted from the alcohol-insoluble tissue in the centrifuge tube. The pellet was redistributed with 3 ml of 0.1 M NaOH and starch extracted overnight in the dark. Carbohydrate concentrations were quantified by an anthrone colorimetric reaction (Yemm & Willis, 1954). The reaction mixture absorbance was read on a spectrophotometer (Shimadzu Model UV-1601) at 600 nm against glucose standards.

2.7 Statistical analysis

Tests for significant differences in environmental characteristics among the forests were using analysis of variance (ANOVA) with sites as the main effect. The grouping and ranking of sites was done using the multiple range/post hoc test, Tukey's Honest Significant Difference (HSD) test. All statistical analyses were conducted with Minitab 14.

3. Results

3.1 Forest structure variation

Forest structure of *C. tagal* differed among five study stations in the area (Table 1). Tree density exhibited increasing trend from the coastal fringe landward with the lowest density of tree was found at station E (2,700 no ha^{-1}) which was the most landward station while the highest of 7,500 no ha^{-1} was recorded at station D. Sapling density varied between 600-2,700 no ha^{-1} while seedling had great variation from the lowest of 200 no ha^{-1} at station A and highest of 26,300 no ha^{-1} at station D with the increasing trend was pronounced from outer to inner zone as tree density. Tree DBH was ranging between 6.75±1.60 and 7.86±1.89 cm and showed an increase with increasing distance landward to reach the maximum at station C then reduced to the minimum at station D before increased again at station E (7.50±1.04 cm). Tree height showed similar pattern as DBH where maximum height of 13.42±4.12 m was recorded at the outermost station (A) whereas minimum tree height of 7.83±0.86 m was found at the innermost station (E).

3.2 Porewater and sediment qualities

The average salinity in porewater (21.50 to 36.71 ppt) varied significantly with depth and station ($p<0.01$). Vertical profile of porewater salinity was generally showed a low value on surface soil and exhibited an increasing trend with depth whilst spatial pattern indicated an increasing salinity value at the inner zone (Table 2). The average pH indicated an acidic condition at all studied sites and exhibited significant changes with depth and station ($p<0.01$). The closest station to the sea (A) had highest average pH value of 6.40 then decreased sharply with increasing distance to 5.76 at station B and 5.51 at station C before slightly increase to 5.58 at station D and 5.79 at the innermost station (E).

Table 1. Structural characteristics of Tagal mangrove (*Ceriops tagal*) recorded from five stations with variation of distance from sea coast landward (A to E) at Pred Nai mangrove forest, Trat province, Thailand. Values are means±S.D.

Station	Distance from sea (m)	Tree density (no ha^{-1})	DBH (cm)	Stand height (m)	Sapling density (no ha^{-1})	Seedling density (no ha^{-1})
A	200	4,700	7.57±3.88	13.42±4.12	900	200
B	950	5,700	7.79±2.43	10.60±1.12	600	700
C	1,200	5,600	7.86±1.89	8.85±0.82	1,500	1,300
D	1,400	7,500	6.75±1.60	8.82±0.62	1,300	26,300
E	1,550	2,700	7.50±1.94	7.83±0.86	2,700	6,400

Table 2. Depth distribution of porewater qualities within Tagal mangrove (*Ceriops tagal*) landscape at various distances from coastal fringe landward (A to E) at Pred Nai mangrove forest, Trat province, Thailand. Values are expressed as mean±S.D.

Station	Depth (cm)	Parameters					
		Salinity (‰)	pH	$NO_2^-+NO_3^-$ (µM)	NH_4^+ (µM)	PO_4^{3-} (µM)	H_2S (mM)
A	5	20.74±1.19	6.44±0.17	0.71±0.38	1.24±0.12	0.53±0.41	0.033±0.008
	10	20.48±0.28	6.40±0.11	1.07±0.39	1.29±0.10	2.17±3.43	0.026±0.021
	20	22.36±4.13	6.33±0.13	0.38±0.22	1.23±0.04	3.21±2.72	0.029±0.011
	30	23.02±5.34	6.43±0.11	0.22±0.06	1.95±1.47	1.39±1.13	0.032±0.010
Average		21.65±2.68	6.40±0.09	0.60±0.18	1.42±0.34	1.83±1.48	0.030±0.011
B	5	15.30±1.75	6.00±0.08	0.12±0.06	1.01±0.06	0.23±0.06	0.062±0.021
	10	18.53±5.16	5.72±0.17	0.29±0.28	1.02±0.13	0.28±0.11	0.064±0.040
	20	28.76±6.25	5.61±0.07	0.69±0.29	1.07±0.06	0.50±0.11	0.055±0.044
	30	35.91±3.60	5.72±0.14	0.34±0.06	1.08±0.04	1.10±1.02	0.098±0.012
Average		24.63±3.73	5.76±0.09	0.36±0.12	1.05±0.03	0.53±0.25	0.069±0.020
C	5	15.32±2.24	5.59±0.09	2.34±0.19	1.05±0.15	0.16±0.03	0.034±0.016
	10	18.22±1.60	5.47±0.03	1.39±1.65	0.95±0.04	0.21±0.12	0.042±0.013
	20	22.38±4.37	5.47±0.03	0.53±0.54	0.96±0.00	0.60±0.71	0.027±0.022
	30	30.09±5.85	5.52±0.02	0.16±0.01	0.96±0.03	3.64±2.96	0.043±0.018
Average		21.50±2.84	5.51±0.02	1.10±0.82	0.98±0.02	1.15±0.89	0.036±0.012
D	5	18.01±5.04	5.67±0.09	0.42±0.08	1.27±0.09	1.07±0.12	0.516±0.090
	10	22.85±5.44	5.54±0.02	0.46±0.28	1.14±0.03	1.25±0.15	0.341±0.091
	20	33.88±4.48	5.53±0.03	0.46±0.09	1.02±0.00	2.46±1.10	0.385±0.045
	30	43.09±1.28	5.59±0.08	0.36±0.11	1.01±0.03	3.65±1.46	0.330±0.093
Average		29.46±3.53	5.58±0.02	0.43±0.13	1.11±0.01	2.11±0.67	0.393±0.026
E	5	27.43±0.52	5.74±0.05	0.17±0.02	1.33±0.22	0.25±0.06	0.584±0.137
	10	38.69±8.53	5.76±0.14	0.98±0.44	1.36±0.37	0.30±0.16	0.693±0.059
	20	39.67±1.26	5.80±0.16	0.72±0.63	1.09±0.06	0.52±0.42	0.666±0.152
	30	41.60±5.44	5.87±0.19	0.48±0.16	1.22±0.10	0.77±0.54	0.647±0.044
Average		36.71±2.95	5.79±0.11	0.59±0.26	1.25±0.19	0.46±0.26	0.647±0.090
Mangrove inlet		17.84±2.20	6.66±0.22	1.30±0.17	12.52±0.32	0.89±0.08	-

All five stations contained low porewater nutrient concentrations (Table 2). Most of $NO_2^-+NO_3^-$ concentrations were <1 µM and fell within the range between 0.12±0.06 and 2.34±0.19 µM which can be accounted for 10-40% of inorganic nitrogen. Although, $NO_2^-+NO_3^-$ concentrations varied significantly among station and depth ($p<0.01$) but depth and spatial changing trends were not clear at all stations. NH_4^+ varied within the range from 0.95±0.04 to 1.95±1.47 µM which were low comparing to concentration found in the canal and significant change ($p<0.05$) was found only between stations. Concentration of NH_4^+ did not exhibited a clear changing trend with depth. Porewater PO_4^{3-} concentrations had greater variation especially variation with depth ($p<0.01$). Very low concentration was found in the upper soil (0.16-0.53 µM) at most of the sampling stations except high value of 1.07 µM at station D and increased with depth. Sulfide concentrations had a great variation among sampling stations ($p<0.01$) and exhibited less fluctuated with depth. Low sulfide concentrations ranged from 0.026±0.021 to 0.064±0.040 mM were detected at those three outermost stations (A, B and C) whereas high sulfide contents at approximately one order of magnitude (0.330±0.093 to 0.693±0.059 mM) were detected at both station D and E which located at the inner zone.

Higher redox potential (Eh) in soil was found in the inner comparing to outer station ($p<0.01$) and station A contained the lowest value (Figure 2). Organic matter content in soil was low as 15.27±1.19% at the coastal fringe zone (station A) and increased further landward as B (40.97±3.91%), C (37.17±4.03%) to reach the highest value of 43.49±6.53% at station D and organic matter content at station E was recorded as 34.63±8.93% with significantly variation ($p<0.01$) at both station and depth. It was noticed that organic matter contents in soil at station B to E were 2-3 times (up to 44%) higher compared to station A suggesting the peat formation in this mangrove landscape.

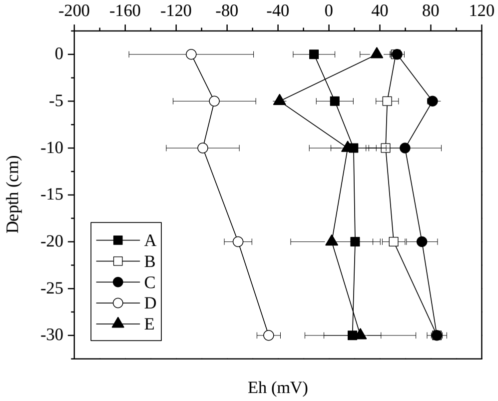

Figure 2. Soil redox potential (Eh) vertical depth profiles measured from five stations within the Tagal mangrove (*Ceriops tagal*) along the distance from sea coast through the inner zone at Pred Nai mangrove forest, Trat province, Thailand (A to E referred to sampling station at the distance of 200, 950, 1,200, 1,400, and 1,550 m from sea coast). Values are presented as mean±S.D.

3.3 Photosynthetic pigments

Photosynthetic pigments including Chl-*a*, *b* and carotenoid in tree leaves were showed in Table 3. The Chl-*a* varied between 1.46±0.25 and 1.87±0.73 mg g DW^{-1} with no significant change ($p=0.367$) among station. Less variation

Table 3. Pigment contents in leaves of trees of Tagal mangrove (*Ceriops tagal*) at various distances from coastal fringe landward (A to E) at Pred Nai mangrove forest, Trat province, Thailand. Values are expressed as mean±S.D.

Station	Distance (m)	Salinity (‰)	Chl *a* (mg g DW^{-1})	Chl *b* (mg g DW^{-1})	Total chlorophyll (mg g DW^{-1})	Chl *a*/*b*	Carotenoids (mg g DW^{-1})	Chl/Car
A	200	21.65	1.55±0.37	1.37±0.47	2.92±0.80	1.20±0.27	0.40±0.09	7.32±0.74
B	950	24.63	1.87±0.73	0.98±0.48	2.85±1.20	1.96±0.20	0.50±0.19	5.62±0.30
C	1,200	21.50	1.69±0.70	0.99±0.39	2.68±1.09	1.71±0.14	0.44±0.19	6.20±0.28
D	1,400	29.46	1.46±0.25	1.00±0.25	2.46±0.36	1.52±0.34	0.38±0.09	7.04±0.25
E	1,550	36.71	1.49±0.27	0.98±0.21	2.46±0.47	1.55±0.19	0.40±0.08	6.22±0.19

with no significant variation (p=0.108) between station was detected for Chl-*b* comparing to Chl-*a*. The Chl-*b* was found within the range from 0.98-1.00 mg g DW^{-1} with only exception for station A where high value of 1.37±0.47 mg g DW^{-1} was measured. Total chlorophyll accounted for 2.46±0.47 and 2.92±0.80 mg g DW^{-1} and exhibited the decreasing trend with distance landward although no significant variation (p=0.645) between stations. Carotenoid contents fluctuated within the narrow range between 0.38±0.09 and 0.50±0.19 mg g DW^{-1} without detected significant change (p=0.309) when comparison between stations.

Table 4 presented Chl-*a*, *b* and carotenoid contents in Tagal seedling. The Chl-*a* varied between 2.43±0.70 and 2.99±0.65 mg g DW^{-1} with no significant change (p=0.641) at all stations. The Chl-*b* had greater variation between 1.40±0.68 and 2.54±1.04 mg g DW^{-1} however, no significant change (p=0.140) among station was detected. The highest Chl-*b* value obtained at station A, followed by the lowest value at station B, before exhibited an increasing trend with distance landward. Total chlorophyll fluctuated within the range from 3.98±1.59 to 5.32±1.48 mg g DW^{-1} with changing pattern similar to Chl-*b* and no significant variation (p=0.382) was found between station. Carotenoid contents exhibited no significant change (p=0.568) between station and varied within the narrow range between 0.63±0.19 and 0.79±0.17 mg g DW^{-1} with minimum and maximum values were observed at station C and D, respectively. Although similar ration of Chl-*a*/Chl-*b* achieved from both tree and seedling but the amount of Chl-*a* and Chl-*b* in seedling were almost two times greater than tree suggesting that on the early growing stage of *C. tagal* required higher fixed carbon from photosynthetic processes compared to the older stage.

3.4 Carbohydrate reserves

Carbohydrate reserves in tree and seedling presented in the form of sugar and starch were summarized in Table 5. Sugar contents in tree varied between 17.20±3.39 and 23.83±2.55 mg g DW^{-1} with the highest value measured at station B and the lowest value was detected at station D. When salinity increased as increase distance landward, sugar level in tree decreased with the lowest value observed at station D however, no significant variation (p=0.315) between station was found. Most of starch content in tree leaves had small variation (p=0.559) within the value from 42.97 to 45.19 mg g DW^{-1} with only exception of low sugar content (37.28±10.86 mg g DW^{-1}) observed at station A.

Sugar contents measured from seedling differed from those found in tree (Table 5) with an increasing trend with distance as well as increasing salinity (p<0.01). Seedlings sugar contents varied between 11.97±1.71 and 30.97±6.79 mg g DW^{-1} with minimum value obtained at station A and the maximum value recorded at station E. The amount of starch content in seedling fell within the range from 15.46±3.04 to 24.85±7.03 mg g DW^{-1} with the highest value detected at station B whilst station A contained the lowest. Spatial change of starch content among stations was decreased with increasing distance or salinity landward (p<0.05).

4. Discussion

4.1 Forest structure, nutrient resources and stress factors

Since the field sampling was performed in rainy season where salinity gradients and salinity stress were expected to pronounce the least. Therefore, if this Tagal mangrove exhibits physiological responses to such salinity gradients, then more impacts of salinity stress on this mangrove plant species in cold-dry season and summer can be projected. Variation in *C. tagal* forest structure has been correlated with variation in porewater salinity along the transect line where hypersaline conditions prevailed in the interior zone. The interaction between physical factors e.g., evaporation, intensity of rain, tidal flooding and position in the mangrove and biological factors including transpiration potentially contributed to increasing salinity (Marchand *et al.*, 2004). High salinity resulted in increasing tree as well as sapling and seedling density up to salinity of 30 ppt which close to sea strength and beyond this limit high salinity showed effects with the reduction of plant density. Clear negative effect of high salinity on forest structure was tree height where decreasing tree height of *C. tagal* found at stand subjected to high salinity in the inner zone with the correlation (R^2) between salinity and tree height was 0.4389. Reduction of growth due to salinity stress has been reported for many mangrove species including *Bruguiera gymnorrhiza*, *B. parviflora* and *C. tagal* with vary degree of responses between different species (Basak, Gupta, Rautaray & Das, 2004). However, a number of studies mentioned that many factors may act in concert with salinity in mangrove growth limitation (Chen & Twilley, 1999; Koch, 1997; Lovelock, Feller, McKee & Thompson, 2005; McKee, 1993). Across variation in tree height, the porewaters nutrient concentrations varied widely. All nutrient forms including NO_2^-+NO_3^-, NH_4^+, and PO_4^{3-} fell within the range recorded in other mangrove forests (Chen & Twilley, 1999; Marchand *et al.*, 2004) however, porewater nutrient contents in the landward site were relatively low suggesting nutrient deficiency potentially acted in addition to

Table 4. Pigment contents in leaves of seedlings of Tagal mangrove (*Ceriops tagal*) at various distances from coastal fringe landward (A to E) at Pred Nai mangrove forest, Trat province, Thailand. Values are expressed as mean±S.D.

Station	Distance (m)	Salinity (‰)	Chl *a* (mg g DW^{-1})	Chl *b* (mg g DW^{-1})	Total chlorophyll (mg g DW^{-1})	Chl *a*/*b*	Carotenoids (mg g DW^{-1})	Chl/Car
A	200	21.65	2.77±0.50	2.54±1.04	5.32±1.48	1.35±0.76	0.72±0.12	7.29±1.48
B	950	24.63	2.59±1.00	1.40±0.68	3.98±1.59	2.07±0.60	0.67±0.26	5.95±0.47
C	1,200	21.50	2.43±0.70	1.96±1.04	4.39±1.67	1.45±0.50	0.63±0.19	6.89±0.95
D	1,400	29.46	2.99±0.65	2.22±0.89	5.21±1.47	1.44±0.37	0.79±0.17	6.58±0.46
E	1,550	36.71	2.69±1.06	2.01±1.18	4.70±2.18	1.61±0.60	0.72±0.29	6.44±1.04

Table 5. Soluble sugar and starch contents in leaves of trees and seedlings of Tagal mangrove (*Ceriops tagal*) at various distances from coastal fringe landward (A to E) at Pred Nai mangrove forest, Trat province, Thailand. Values are expressed as mean±S.D.

Station	Distance (m)	Salinity (‰)	Tree		Seedling	
			Soluble sugar (mg g DW^{-1})	Starch (mg g DW^{-1})	Soluble sugar (mg g DW^{-1})	Starch (mg g DW^{-1})
A	200	21.65	19.79±11.34	37.28±10.86	11.97±1.71	15.46±3.04
B	950	24.63	23.83±2.55	43.18±4.45	18.73±5.66	24.85±7.03
C	1,200	21.50	20.82±4.82	42.97±11.27	22.94±5.83	21.43±5.51
D	1,400	29.46	17.20±3.39	43.00±11.26	28.93±5.33	22.80±4.99
E	1,550	36.71	18.43±7.32	45.19±11.32	30.97±6.79	19.53±6.07

salinity stress on influencing the *C. tagal* forest structure in this mangrove landscape. Many studies suggested that reduced tidal flushing, reduced sediments and sulfide accumulation in sediment can affect the nutrient uptake, energy balance and growth of mangroves and other plant species (Erskine & Koch, 2000; Marchand *et al.*, 2004; McKee, 1993). Sediment Eh and sulfide concentrations were highly variable over variation in tree height. Sediments were moderately reducing at two stations in the innermost zone consistent with the observation of an infrequent tidal exchange resulting in accumulation of sulfide in porewater. Other three stations seaward were relatively oxidized in accordance with low sulfide detected suggesting that tidal exchange was strong enough to support the rhizosphere with oxygenated seawater. Moreover, the present study indicated low sulfide concentrations (0.03-0.70 mM) which fell within the lower end (Marchand *et al.*, 2004; McKee, 1993) and could not have a major reciprocal effects contributed to plant growth and development. These data demonstrated that forest structure and sediment characteristics could be varied widely within the wide distribution of one mangrove species. Although soil salinity seemed to be the major stressor affecting *C. tagal* forest structure in this area however, variation in tree height across the intertidal zone could not be linked to one single factor and patterns in forest structure development could be related to the complex interactions among diverse environmental factors.

4.2 Plant responses to stress conditions

The ability of higher plants to physiologically tolerate to stress conditions appears correlated with the maintenance of plant energy status. Major concerns of stressors in mangrove sedimentary environment are given to sulfide and NaCl in porewater. A number of studies have been carried out on physiological responses of mangrove to salinity stress (Basak *et al.*, 2004; Biber, 2006; Das *et al.*, 2002; Falqueto, Silva, & Fontes, 2008; Khan & Aziz, 2001; López-Portillo, Moctezuma, Bartlett, & Sack, 2016; Méndez-Alonzo, Parida *et al.*, 2004; Qiu *et al.*, 2007). Effects of salt stress on mangrove can be clarified into two categories either low salinity (down to 0 ppt) or high salinity. Although, mangroves are found growing within a wide range of salinities but responses of mangroves to salinity are varied among plant species and degree of stressors plant received (Falqueto *et al.*, 2008; Méndez-Alonzo *et al.*, 2016; Qiu *et al.*, 2007).

Slightly reduction in the levels of photosynthetic pigments, including chlorophyll *a* and *b* and accessory pigments such as carotenoids, on exposure to salinity stress has been observed both tree and seedling of *C. tagal*. Decreases in pigments suggesting that chlorophyll synthesizing system and chlorophyllase activity were affected at high salinity. Carotenoids are degraded to enhance the reception of ruminous energy for the reaction centers and protect chlorophyll against photooxidative damage (Behera & Choudhury, 2002). Thus, a decrease of photosynthetic pigments could directly reduce plant photosynthesis resulting in reduction of carbon fixation and energy transformation of the whole plant system. However, results from the present study showed no such a significant change in photosynthetic pigments for both tree and seedling of Tagal mangrove suggesting this plant species has high adaptability to salinity stress.

Mangroves develop diverse mechanisms associated with physiological or biochemical adaptive characteristics in response to stressors (Méndez-Alonzo *et al.*, 2016). Alterations in photosynthesis, photosynthetic pigment content, transpiration rate, and enzymatic activities were accounted to mangrove physiological adaptations (Parida & Jha, 2010). Carbohydrate reserves change in response to stress conditions have been documented in a number of plant species including seagrass and mangroves (Erskine & Koch, 2000; Parida *et al.*, 2004; Vichkovitten, Holmer, & Frederiksen, 2007; Yan & Guizhu, 2007). Change in soluble sugar and starch content in

C. tagal leaves with increasing salinity suggesting that salt induced sugar-starch conversion. The present study showed different in response between tree and seedling of *C. tagal* to salt stress. Soluble sugar contents in tree increased with salinity up to value of 25 ppt before a reduction was observed whilst starch content increased. The opposite trend was recorded for seedling with increment of soluble sugar content whereas starch content increased with salinity before decreasing at salinity beyond 25 ppt. A number of studies on carbohydrate reserves in response to salinity stress of mangrove provided a controversy results (Parida *et al.*, 2004; Yan & Guizhu, 2007). In general, mangroves can accumulate a type of low, compatible molecular compound which could be either inorganic ions or organic osmolytes to protect cell structure and water circulation (Parida *et al.*, 2004; Yan & Guizhu, 2007). Consequently, the osmotic potential decreases which in turn attracts water into the cell and enables to maintain pressure potential (Moghaieb, Saneoka, & Fujita, 2004). Thus, increase soluble sugars could improve the permeability and maintaining a balance of water metabolism. This mechanism may not important to salt secreting mangrove like *A. corniculatum* as well as *C. tagal* but it probably necessary for non-secreting mangrove such as *Sonneratia apetala* and *S. caseolaris* to overcome salt stress. Accumulation of sugar and starch in mangroves could be varied among species suggesting diverse mechanisms may act together in responses to salt stress. In addition, the present study indicated that the ability to cope with salinity stress by accumulation of sugar and starch in *C. tagal* may change over the course of development from seedling to tree and seedling seemed to have greater sensitivity to salinity stress than tree.

5. Conclusions

Tagal mangrove (*C. tagal* (Perr.) C.B. Rob.) forest structures and characteristics along the transect line at Pred Nai coastal area of Trat Province are varied dependent on the sedimentary environment and stress conditions. Reduction in tree height is an adaptability of *C. tagal* forest structures in responses to salt stress. From physiological aspects, high salinity stress could not have any harmful effects on photosynthetic pigments synthesis although slightly reduction in chlorophyll of *C. tagal* tree and seedling are detected. Accumulation of carbohydrate reserves in *C. tagal* represents a mechanism against salt stress. However, variation in soluble sugar and starch contents in both tree and seedling indicates the alteration of plant developmental stage in response to high salinity and seedling exhibits a greater sensitivity to salinity stress compare to tree. The present study suggesting that *C. tagal* has great ability to tolerate high salinity level which providing the beneficial for rehabilitation of mangrove forest in salty area e.g., abandon shrimp farm with less water circulation, regarding to coastal zone management effort.

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References

Asaeda, T., & Barnuevo, A. (2019). Oxidative stress as an indicator of niche-width preference of mangrove *Rhizophora stylosa*. *Forest Ecology and Management*, *432,* 73-82. doi:10.1016/j.foreco.2018.09.015

Basak, U. C., Gupta, N., Rautaray, S., & Das, P. (2004). Effects of salinity on growth of mangrove seedlings. *Journal of Tropical Forest Science*, *16*(4), 437-443.

Behera, R. K., & Choudhury, N. K. (2002). High irradiance induced pigment degradation and loss of photochemical activity of wheat chloroplasts. *Biologia. Plantarum*, *45*(1), 45-49.

Biber, P. D. (2006). Measuring the effects of salinity stress in the red mangrove, *Rhizophora mangle* L. *African Journal of Agricultural Research*, *1*(1), 1-4.

Chen, R., & Twilley, R. R. (1999). Patterns of mangrove forest structure and soil nutrient dynamics along the Shark river estuary, Florida. *Estuaries*, *22*(4), 955-970.

Cline, J. D. (1969). Spectrophotometric determination of hydrogen sulfide in natural waters. *Limnology and Oceanography*, *14,* 454-458.

Das, A. B., Parida, A., Basak, U. C., & Das, P. (2002). Studies on pigments, proteins and photosynthetic rates in some mangroves and mangrove associates from Bhitarkanika, Orissa. *Marine Biology*, *141,* 415-422. doi:10.1007/s00227-002-0847-0

Erskine, J. M., & Koch, M. S. (2000). Sulfide effects on *Thalassia testudinum* carbon balance and adenylate energy charge. *Aquatic Botany*, *67*(4), 275-285.

Falqueto, A. R., Silva, D. M., & Fontes, R. V. (2008). Photosynthetic performance of mangroves *Rhizophora mangle* and *Laguncularia racemosa* under field conditions. *Revista Árvore*, *32*(3), 577-582.

Inskeep, W. P., & Bloom, P. R. (1985). Extinction coefficients of chlorophyll *a* and *b* in *N,N*-Dimethylformamide and 80% acetone. *Plant Physiology*, *77*(2), 483-485.

Khan, M. A., & Aziz, I. (2001). Salinity tolerance in some mangrove species from Pakistan. *Wetlands Ecology and Management*, *9,* 219-223.

Koch, M. S. (1997). *Rhizophora mangle* L. seedling development into the sapling stage across resource and stress gradients in subtropical Florida. *Biotropica*, *29*(4), 427-439.

Krauss, K. W., & Allen, J. A. (2003). Influences of salinity and shade on seedling photosynthesis and growth of two mangrove species, *Rhizophora mangle* and *Bruguiera sexangula*, introduced to Hawaii. *Aquatic Botany*, *77,* 311-324. doi:10.1016/j.aquabot.2003.08.004

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*(3), 456-464.

MacFarlane, G. R., & Burchett, M. D. (2001). Photosynthetic pigments and peroxidase activity as indicators of heavy metal stress in the grey mangrove, *Avicennia marina* (Forsk.) Vierh. *Marine Pollution Bulletin, 42*(3), 233-240.

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. doi:10.1016/j.margeo.2004.04.015

McKee, K. L. (1993). Soil physicochemical patterns and mangrove species distribution – reciprocal effects? *Journal of Ecology*, *81*(3), 477-487.

Méndez-Alonzo, R., López-Portillo, J., Moctezuma, C., Bartlett, M. K., & Sack, L. (2016). Osmotic and hydraulic adjustment of mangrove saplings to extreme salinity. *Tree Physiology*, *36*, 1562-1572. doi:10.1093/treephys/tpw073

Moghaieb, R. E. A., Saneoka, H., & Fujita, K. (2004). Effect of salinity on osmotic adjustment, glycinebetaine accumulation and the betaine aldehyde dehydrogenase gene expression in two halophytic plants, *Salicornia europaea* and *Suaeda maritima*. *Plant Science*, *166*, 1345-1349. doi:10.1016/j.plantsci.2004.01.016

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. doi:10.1016/j.aquabot.2004.07.005

Parida, A. K., & Jha, B. (2010). Salt tolerance mechanisms in mangroves: A review. *Trees*, *24*, 199-217. doi:10.1007/s00468-010-0417-x

Perri, S., Viola, F., Noto, L. V., & Molini, A. (2017). Salinity and periodic inundation controls on the soil-plant-atmosphere continuum of gray mangroves. *Hydrological Processes*, *31*, 1271-1282. doi:10.1002/hyp.11095

Qiu, D.-L., Lin, P., & Guo, Z. (2007). Effects of salinity on leaf characteristics and CO_2/H_2O exchange of *Kandelia candel* (L.) Druce seedlings. *Journal of Forest Science*, *53*(1), 13-19.

Sherman, R. E., Fahey, T. J., & Martinez, P. (2003). Spatial patterns of biomass and aboveground net primary productivity in a mangrove ecosystem in the Dominican Republic. *Ecosystems*, *6*, 384-398. doi:10.1007/s10021-002-0191-8

Vichkovitten, T., Holmer, M., & Frederiksen, M.S. (2007). Spatial and temporal changes in non-structural carbohydrate reserves in eelgrass (*Zostera marina* L.) in Danish coastal waters. *Botanica Marina*, *50*, 75-87. doi:10.1515/BOT.2007.009

Wakushima, S., Kuraishi, S., Sakurai, N., Supappibul, K., & Siripatanadilok, S. (1994). Stable soil pH of Thai mangroves in dry and rainy seasons and its relation to zonal distribution of mangroves. *Journal of Plant Research*, *107*(1), 47-52.

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.

Yan, L., & Guizhu, C. (2007). Physiological adaptability of three mangrove species to salt stress. *Acta Ecologica Sinica*, *27*(6), 2208-2214.

Yemm, E. W., & Willis, A. J. (1954). The estimation of carbohydrates in plant extracts by anthrone. *Biochemical Journal*, *57*, 508-514.