EFFECT OF *IN SITU* EXPERIMENTAL SHADING ON THE PHOTOSYNTHESIS OF CANADIAN WATERWEED (*ELODEA CANADENSIS*) FROM SONGKHLA LAGOON, THAILAND

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Abstract. Macrophytes play an important role in providing habitat structure, nutrient cycling and improvement of water quality in freshwater ecosystems. However, increasing human population and the industrial revolution during past several centuries have increased the utilization of natural resources and have caused strong changes in the structure and function of the environment, such as high sedimentation that decreases light penetration. This study investigated the effects of *in situ* experimental shading on photosynthetic performance of submerged *Elodea canadensis* macrophytes and identified the level of light that is critical for growth and photosynthesis of this species. Photosynthetic performance, chlorophyll *a* and *b* concentrations, organic and carbon contents, percentage cover, and morphology were estimated in *E. canadensis* from middle of Songkhla lagoon under 4 treatments (25, 50, 75, and 100% of natural light) for 10 weeks. The results show that there were no differences in growth and photosynthesis among the treatments, but low light led to changes in chlorophyll concentration, F_v/F_m, and I_k, suggesting adaptations to a low light regime. This study provides an understanding of physiological tolerance and response to shading and shows how species of aquatic macrophytes respond to future climatic and anthropogenic changes, thereby supporting development of sustainable lagoon management plans.
Keywords: *low light, submerged macrophyte, PAM fluorometry, ecophysiology, carbon content*

Introduction

Increasing human population and the industrial revolution during the past several centuries have led to increased utilization of natural resources of both aquatic and terrestrial types. Anthropogenic activities have direct and indirect effects on ecosystems, such as land transformation and altering hydrological processes. Agriculture causes soil erosion and large inputs of N and P into water bodies that can lead to eutrophication in a lake. Eutrophication is a condition of increased nutrient supply caused by human activities and/or natural processes, as lakes age and get filled with sediments, and this may become a major problem for aquatic systems globally (Wurtsbaugh et al., 2019). Sediment runoff and eutrophication have been the main causes of water quality management problems in lakes globally, including the Songkhla Lagoon in Southern part of Thailand (Sompongchaiyakul et al., 2004; Sompongchaiyakul and Sirinawin, 2007;

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Chesoh and Lim, 2008). Nutrient enrichment induces excessive growth of algae and aquatic plants and results in the disturbance of ecosystem functions, such as insufficient oxygen concentration for aquatic life, and a reduction in light penetration to the lake bottom (Wurtsbaugh et al., 2019). Sediment loads reduce light penetration and affect photosynthetic organisms.

Macrophytes play an important role in maintaining high physical and biological diversity and act as ecosystem engineers that provide nutrient cycling, habitat structure and refugia for aquatic organisms (Wigand et al., 2000; Qiu et al., 2001; Cronk and Fennessy, 2016). Macrophytes are potential biological tools to improve water quality in lakes and reservoirs due to their abilities in nutrient uptake, preventing phytoplankton blooms (Lone et al., 2014; Song et al., 2019) by producing allelochemicals to inhibit phytoplankton and epiphytic growth (Mohamed, 2017), and could prevent eutrophication in a lake.

E. canadensis is a submergent macrophyte with roots growing in mud at the bottom of the water (Huxley et al., 1992). This species originates from North America and has been introduced to Europe and nowadays *E. canadensis* are common in many water bodies and are invasive species in some areas. There are many factors that affect growth and photosynthesis of macrophytes, and consequently their species composition, such as temperature, light intensity, nutrients, and pH (Netten et al., 2013), and responses to these depend on the macrophyte species. Netten et al. (2013) showed that high levels of NH_x and temperature together with low pH and low light cause the strongest toxic effects to relative growth rate and leaf tissue mortality. Moreover, high temperature and low light had negative effects on *E. canadensis* via increased metabolic activity and reduced photosynthesis, respectively. Shading experiments were performed by Ellawala Kankanamge et al. (2019) revealing that *E. canadensis* at week 4 increased biomass under all shading conditions (35%, 63%, 79%, 90%, and 95%) except 35%, then after 8 weeks, *E. canadensis* had the highest biomass at lowest shade level.

Songkhla Lagoon is a tropical estuarine lagoon system located on the eastern side of the southern peninsular Thailand and consists of four interconnected water bodies: Thale Noi, upper, middle, and lower parts (Pongpiachan et al., 2019). Songkhla Lagoon not only supports biodiversity, but also a large number of people whose livelihoods depend on that biodiversity. Over 1.4 million people are living in Songkhla Lagoon Basin area (Community Development Department, 2009). *E. canadensis* is one of the dominant species in Songkhla Lagoon (Thongkao et al., 2001). Nowadays, Songkhla Lagoon is facing low water quality and sediment overloading due to human activities (Pradit et al., 2010; Somboonsuke et al., 2018). This could lead to loss of valuable ecosystem services and functions.

This study investigated the effects of *in situ* experimental shading (low light) on growth and photosynthesis of submerged *E. canadensis* macrophytes. An understanding of response to different light regimes is necessary for identifying which level of light is critical for growth, photosynthesis, and carbon capture potential of submerged macrophytes and for predicting their performance under shading. Furthermore, the findings could give a better understanding regarding how *E. canadensis* will respond to anthropogenic changes in light, and support the development of sustainable lagoon management plans.

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Materials and Methods

Study site and experimental design

This study was carried out from October to January 2018 (10 weeks) in the middle of Songkhla Lagoon (7° 28’ 09.0’’ N, 100° 23’ 45.0” E), Thailand to investigate the effects of low light on growth and photosynthesis *in situ*. Shading net (XH-SNN, Hebei Tuosite Plastic Net) were used to manipulate light conditions to 25%, 50%, 75%, and 100% (no shade, control) of the natural irradiance in the experiment plots (n=3), which were randomly placed within a macrophytes patch. The experiment plots consist of shading net with PVC frame (1 m x 1 m) and 4 PVC poles (1.5 m height above ground) (*Fig. 1*). The experiment plots height was deployed at the median of tide level to stimulate shading at water surface. Light can penetrate through shading net approximately 25%, 50%, and 75% as experimental design and shading net was not change the wavelength composition (Kotilainen et al., 2018). Photosynthetic activity (maxiumum quantum yield (F_v/F_m), effective quantum yield ($\Delta F/F_{m'}$), relative Maximum Electron Transport Rate ($rETR_{max}$), initial slope (alpha, α), saturating irradiance (I_k)), pigment concentration, morphology, percentage cover, and organic matter and carbon contents of the macrophytes were estimated biweekly from the start to the end of the experiment.

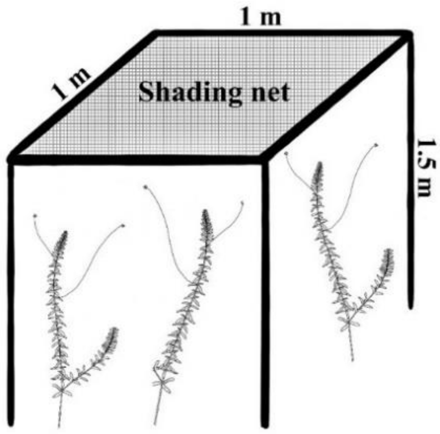

Figure 1. *The experiment plots*

Photosynthetic activity

Photosynthetic activities were observed biweekly by estimating chlorophyll *a* fluorescence using a Pulse Amplitude Modulated (Diving-PAM) fluorometer (Walz, Germany). Dark-adapted photosystem II (PSII) photochemical efficiency was measured as maximum quantum yield (F_v/F_m) after using dark-adapted leaf clip for 15 min (n=3). Rapid Light Curves (RLCs) were performed with 9 increasing actinic light intensities (0, 66, 90, 125, 190, 285, 420, 625 and 920 μmol photons m^{-2} s^{-1}), with 0.8 s saturating pulse (> 4500 μmol photons m^{-2} s^{-1}) between each actinic light intensity every 10 s. Effective quantum yield ($\Delta F/F_{m'}$), maximum relative electron transport rate ($rETR_{max}$), minimum saturating irradiance (I_k) and initial slope (alpha, α) of RLCs were calculated using the curve fitting protocols following Ralph and Gademann (2005).

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Chlorophyll a and b concentrations

Photosynthetic pigment concentrations (chlorophylls Chl *a* and Chl *b*) were determined using the standard spectrophotometric method of Ritchie (2006). Chl *a* and *b* (µg g^{-1} fw) were extracted by homogenizing samples in 4 ml of 90% acetone at 4°C for 24 h then centrifuging at 1500 g for 10 min; and the supernatant was placed into a quartz cuvette in a spectrophotometer (Metertech, SP8001, 190-1100 nm), with absorbance measured at 647, 664 and 750 nm.

Organic matter (OM) and organic carbon (OC)

20 g *E. canadensis* samples for each time were collected and oven dried at 105°C and ground to particle sizes less than 1 mm. A 1.0 g subsample of a ground sample was ashed in a muffle furnace (FHX, DAIHAN, China) at 550°C for 8 h (Armecin and Gabon, 2008). Organic matters of macrophytes were determined using data obtained from the ashed samples, and mineral matter (MM; *Eq.1*), organic matter (OM; *Eq.2*) and organic carbon (OC; *Eq.3*) contents were computed using the following equations:

$$\%\mathrm{MM} = \left(\frac{\mathrm{AW}}{\mathrm{DW}}\right) \times 100 \quad \text{(Eq.1)}$$

$$\%\mathrm{OM} = 100 \times (\mathrm{DW} - \mathrm{AW})/\mathrm{DW} \quad \text{(Eq.2)}$$

$$\%\mathrm{OC} = \%\mathrm{OM}/1.724 \quad \text{(Eq.3)}$$

where AW and DW are ash weight of the sample and dry weight of the sample, respectively (Armecin and Gabon, 2008).

Statistical analyses

Two-way mixed ANOVA tests were used to test for significant differences among treatments over time in chlorophyll fluorescence parameters, pigment content, organic matter and carbon content, and percentage cover of *E. canadensis*. One-way ANOVA was used to test for significant differences among treatments in chlorophyll fluorescence parameters, pigment content, organic matter and carbon content, and percentage cover of *E. canadensis* at the end of experiment. All tests employed a significance level of 95%, and Tukey's honestly significant difference *post hoc* tests were used to confirm the statistical significances. If data did not meet the assumptions of normality (Kolmogorov-Smirnov test) and equal variance (Levene's test), they were transformed using square root or $\log_{10}$. If transformed data did not meet the assumptions, non-parametric tests were used.

Results

Macrophyte percentage cover

In the middle of Songkhla lagoon *E. canadensis* was the dominant species with 56.67±15.90%, 56.67±16.67%, 56.67±12.02%, and 53.33±18.56% (*Fig. 2a*), followed by *Cladophora* sp. with 28.33±15.90%, 40.00±15.28%, 43.33±12.02%, and 36.67±17.64% (*Fig. 2b*) percentage cover at the start of experiment (October) in control, 25%, 50%, and 75% treatments, respectively. There were significant increases with time ($p<0.05$) but no

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differences between the treatments (p>0.05). Percentage cover of *E. canadensis* decreased at week 2 in all treatments except for the 75% treatment, and tended to increase through time in all treatments (*Fig. 2*). At the end of the experiment, percentage cover of *E. canadensis* showed no differences among the treatments (p>0.05).

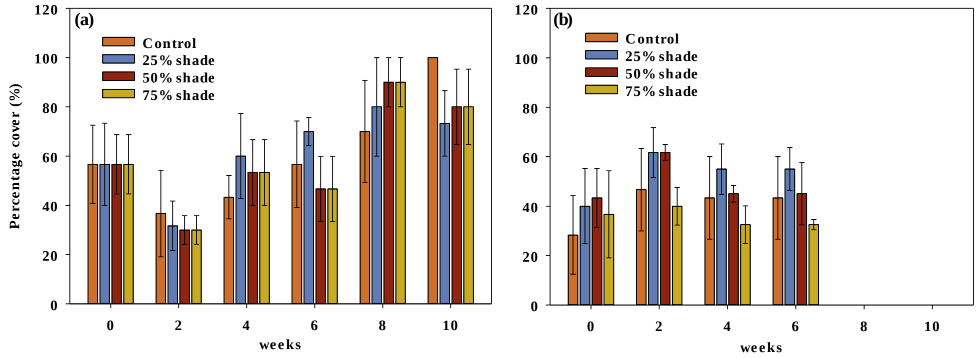

Figure 2. *Percentage cover of E. canadensis at Songkhla Lagoon from week 0 to week 10 for each treatment. Data are given as Mean±SE*

Morphology

Leaf length of *E. canadensis* at the start of the experiment was 0.78±0.07 cm. After 10 weeks, leaf lengths in control, 25%, 50%, and 75% were in the ranges 1.12±0.04, 0.96±0.03, 0.94±0.08, and 1.05±0.05 cm, respectively (*Fig. 3a*). Leaf width of *E. canadensis* at the start of experiment was 0.20±0.01 cm then after 10 weeks, leaf widths in control, 25%, 50%, and 75% were in the ranges 0.20±0.01, 0.19±0.01, 0.20±0.01 and 0.20±0.02 cm, respectively (*Fig. 3b*). At the end of the experiment, leaf length and width were not significantly different between the treatments (p>0.05).

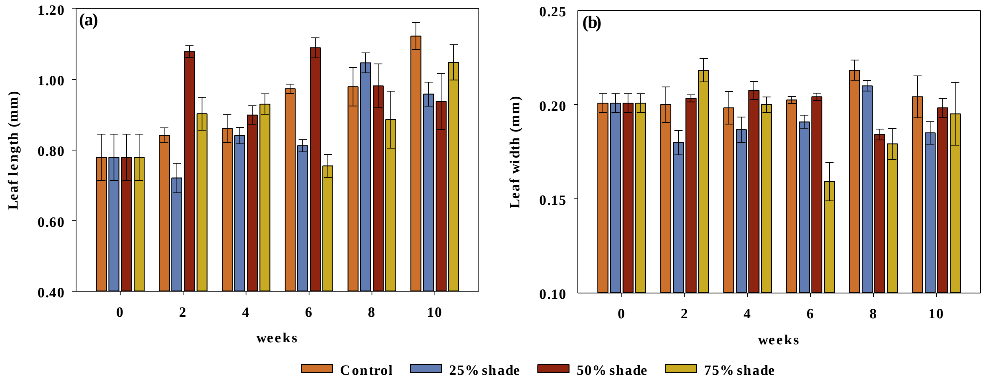

Figure 3. *Leaf length (a) and width (b) of E. canadensis at Songkhla Lagoon from week 0 to week 10 in each treatment. Data are given as Mean±SE*

Photosynthetic activities

Maximum quantum yield (F_v/F_m) and effective quantum yield ($\Delta F/F_{m'}$)

At the start of experiment, F_v/F_m of *E. canadensis* was 0.76±0.02. There was a significant increase through time in all treatments (p<0.05; *Fig. 4*). At the end of

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experiment (week 10), F_v/F_m of *E. canadensis* was not significantly different (p>0.05) among the treatments.

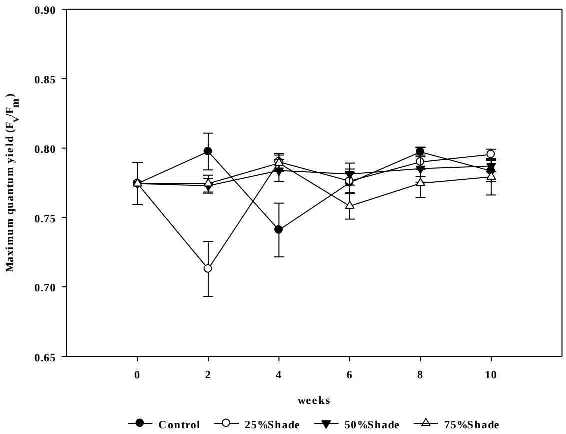

Figure 4. *F_v/F_m of E. canadensis at Songkhla Lagoon from week 0 to week 10 in each treatment. Data are given as Mean±SE*

At the start of experiment, $\Delta F/F_{m'}$ of *E. canadensis* was 0.74±0.01. There was significant increase through time in all treatments (p<0.05; *Fig. 5a*). At the end of experiment (week 10), $\Delta F/F_{m'}$ of *E. canadensis* was not significantly different (p>0.05) among the treatments.

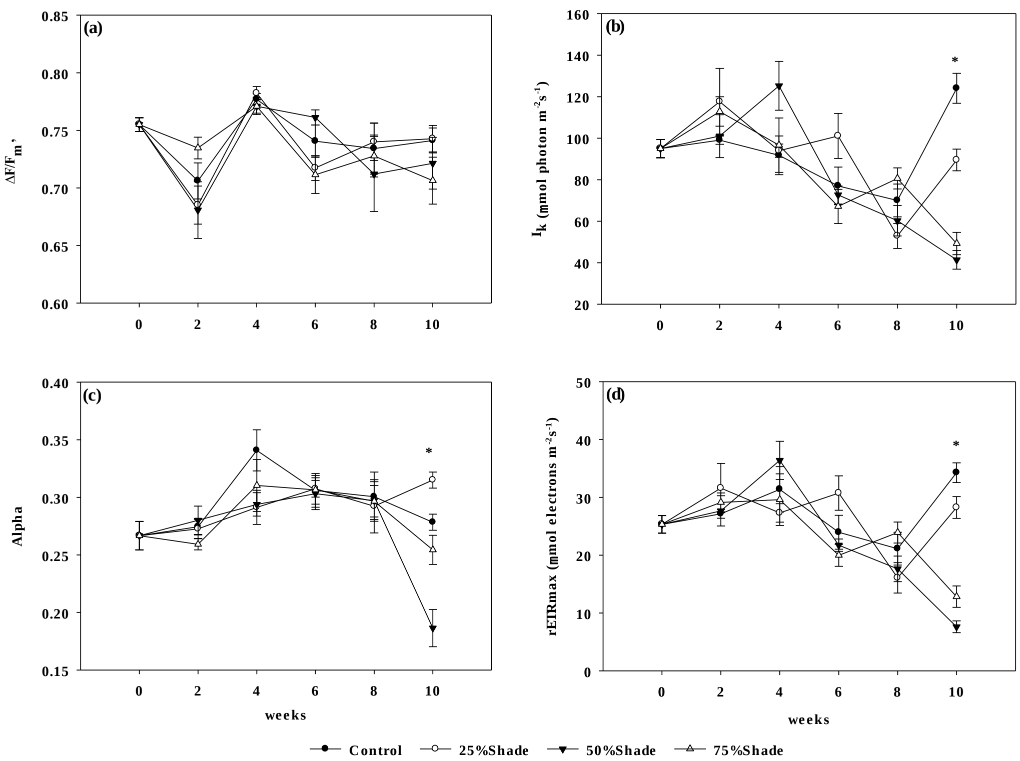

Figure 5. *$\Delta F/F_{m'}$ (a), I_k (b), Alpha (c) and $rETR_{max}$ (d) of E. canadensis at Songkhla Lagoon from week 0 to week 10 in each treatment. Data are given as Mean±SE and * represents significant difference*

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Rapid light curves (RLCs)

Rapid light curves (RLCs) with 25%, 50% and 75% shading changed through duration of the experiment. At the end of the experiment (week 10), RLCs of 50 and 75% shading treatments were significantly lower than those of control and 25% treatments (*Fig. 6*).

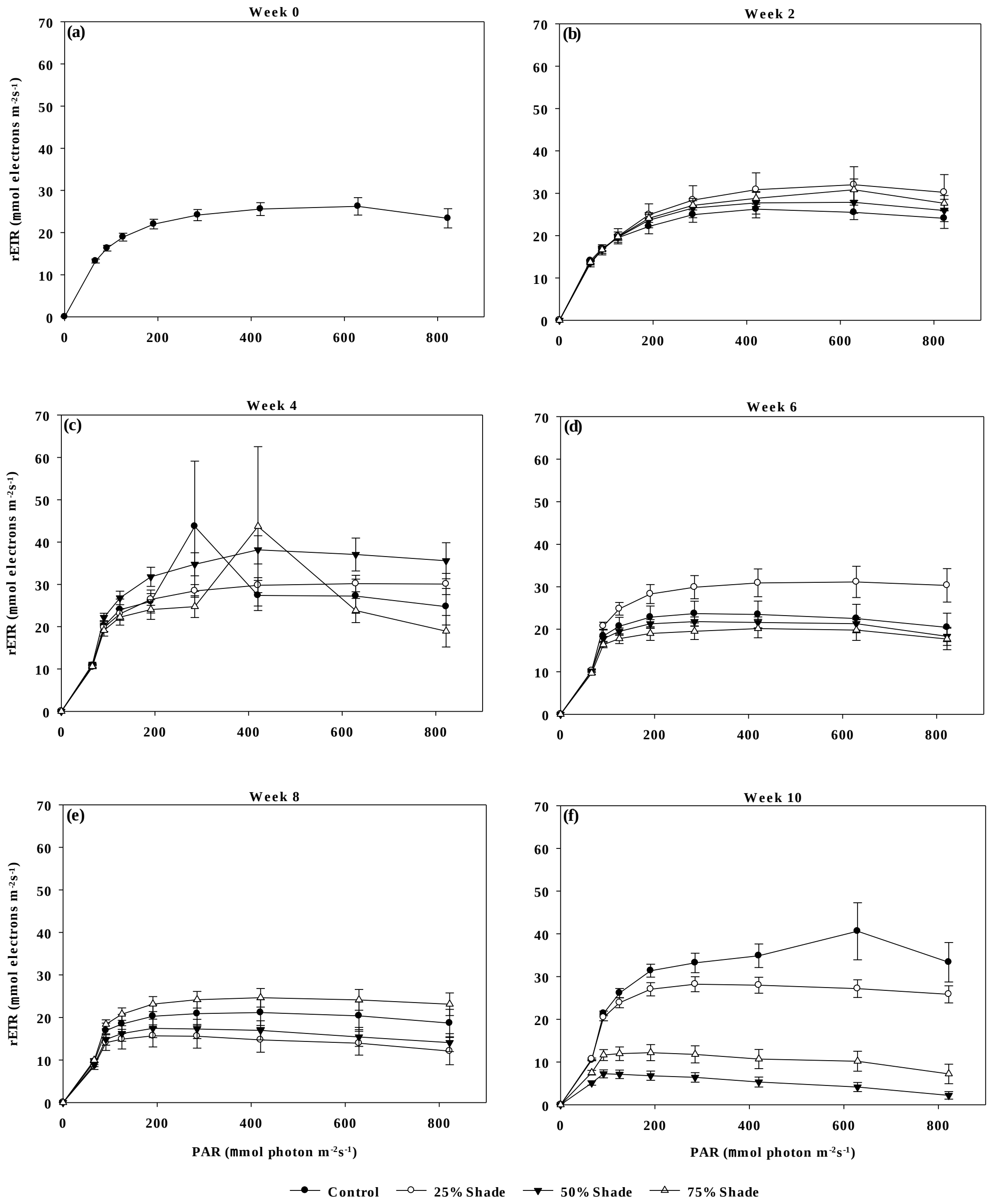

Figure 6. *rETR vs PAR of E. canadensis at Songkhla Lagoon from week 0 to week 10 (a,b,c,d, and f) in each treatment. Data are given as Mean±SE*

Saturating irradiance (I_k)

At the start of experiment, I_k of *E. canadensis* was 95.02±4.39 μmol photons m^{-2} s^{-1}. There was no significant difference among treatments or by time (p>0.05). At the end of

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experiment (week 10), I_k of *E. canadensis* was significantly different between the treatments ($p<0.05$). I_k at 50% treatment was significantly lower than those for 75%, 25%, and control, respectively (*Figure 5b*).

Initial slope (Alpha, α)

At the start of experiment, alpha of *E. canadensis* was 0.27±0.01. Increasing of alpha only occurred in 25% treatment. There was significant difference by time in all treatments ($p<0.05$; *Fig. 5c*). At the end of experiment (week 10), alpha of *E. canadensis* was different among the treatments ($p<0.05$) with 50% treatment significantly the lowest while the control had similar alpha as the 25% and 75% treatments.

Maximum relative electron transport rate ($rETR_{max}$)

At the start of experiment, $rETR_{max}$ of *E. canadensis* was 25.34±1.53 μmol electrons m^{-2} s^{-1}. $rETR_{max}$ of *E. canadensis* showed similar trend as the I_k (*Fig. 5d*). There was significant difference between treatments and by time ($p<0.05$). At the end of experiment (week 10), $rETR_{max}$ was different among the treatments ($p<0.05$). $rETR_{max}$ of 50% and 75% treatments were significantly lower than those of control and 25% treatments.

Chlorophyll a and b (Chl a and b) and chlorophyll a:b ratio (Chl a:b)

At the start of the experiment, Chl *a* and Chl *b* in control of *E. canadensis* were in the ranges 571.65±95.82 and 188.33±22.61 μg g^{-1} fresh weight (fw), respectively. Chl *a* and Chl *b* in all treatments tended to increase with time, except for the control treatment which decreased at week 10. The final Chl *a* and *b* concentrations in 25%, 50%, and 75% treatments were about 2.5 to 3-fold those from the start of experiment, in the ranges 1842.21±77.09, 1684.60±106.92, 1433.17±256.52, 734.85±102.05, 583.38±42.22, and 474.34±93.92 μg g^{-1} fw, respectively (*Fig. 7a,b*). There were significant changes with time ($p<0.05$). At week 10, there was a significant difference in Chl *a* and Chl *b* among the treatments ($p<0.05$) with 25% having the highest Chl *a* and *b* concentrations and control treatment the lowest concentrations.

At the start of experiment, Chl *a:b* ratio of *E. canadensis* was in the range 3.00±0.17. There was significant difference by time ($p<0.05$) but no differences among the treatments, even on week 10 ($p>0.05$).

Organic matter (OM) and organic carbon (OC)

At the start of experiment, OM of *E. canadensis* was in the range 91.37±0.79%. OM of *E. canadensis* was not significantly different among the treatments at week 10 ($p>0.05$) with control, 25%, 50% and 75% treatments in the ranges 82.37±0.27%, 86.68±1.02%, 80.84±2.65%, and 85.70±3.60%, respectively (*Fig. 8a*). However, there were significant decreases in OM with time ($p<0.05$).

OC of *E. canadensis* was in the range 53.00±0.46% at the start of experiment. OC showed similar trend as OM. The OC of *E. canadensis* was not significantly different among the treatments at week 10 ($p>0.05$) and the control, 25%, 50% and 75% treatments were in the ranges 47.78±0.15%, 50.28±0.59%, 46.89±1.54%, and 49.71±2.09%, respectively (*Fig. 8b*). However, there were significant decreases with time ($p<0.05$).

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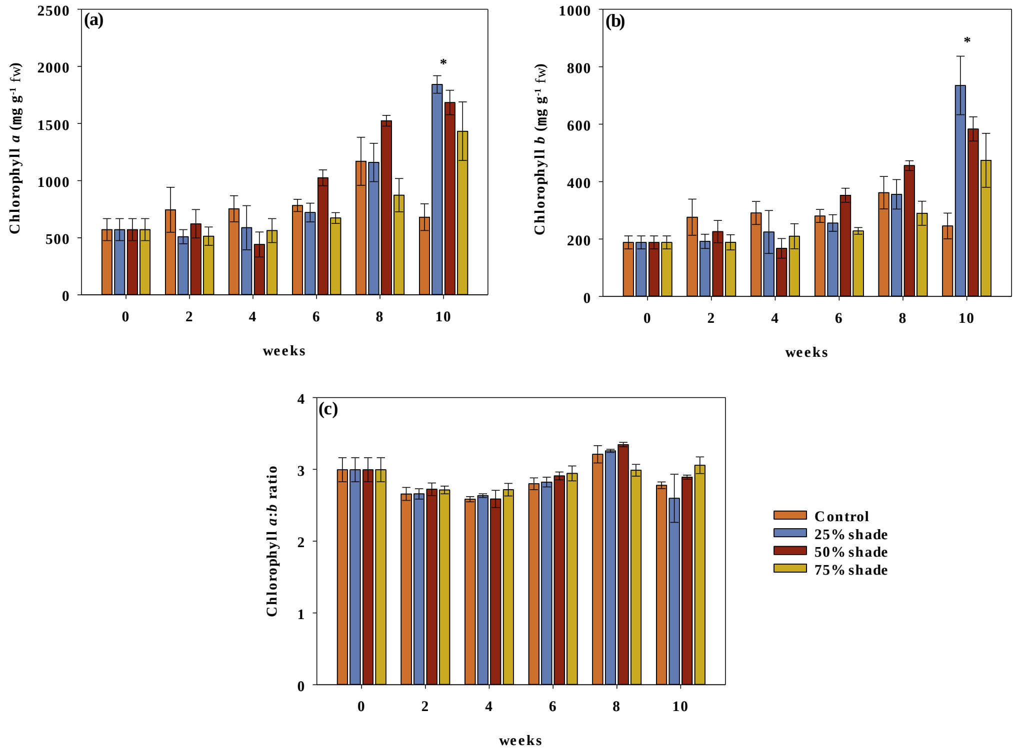

Figure 7. *Chlorophyll a (a) and b (b) concentrations and Chlorophyll a:b (c) ratio of E. canadensis at Songkhla Lagoon from week 0 to week 10 in each treatment. Data are given as Mean±SE and * represent significant difference*

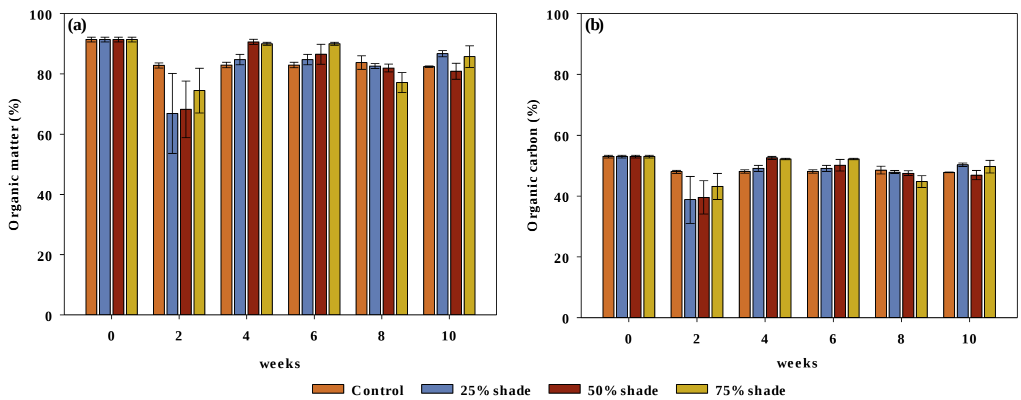

Figure 8. *Organic Matter (OM) (a) and Organic Carbon (OC) (b) of E. canadensis at Songkhla Lake from week 0 to week 10 in each treatment. Data are given as Mean±SE*

Discussion

Shading experiments (Control (100%), 25%, 50%, and 75% of ambient light) were set *in situ* to estimate effects of low light on photosynthetic activities and growth of *E. canadensis* in Songkhla lagoon, Thailand. This study found that the photosynthetic efficiency of *E. canadensis* significantly changed during the experimental period. Decrease of Effective Quantum Yield ($\Delta F/F_{m'}$) occurred on week 2 due to light reduction,

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which affected light harvesting. After week 2, *E. canadensis* showed adaptive capacity by increasing Chl *a* and *b* in order to maintain photosynthesis and a net positive carbon balance (Chartrand et al., 2018). Increasing chlorophyll led to improved efficiency in light harvesting to get more light in low light situation, which showed in increasing Maximum Quantum Yield (F_v/F_m) after week 2.

Saturating irradiant (I_k) revealed adaptation of *E. canadensis* to cope with light situation in this study. Light reduction led to decreased I_k (Ralph and Gademann, 2005) especially in 50% and 75% treatments in the final week, which was consistent with Chen et al. (2016) where *Potamogeton maackianus* and *Vallisneria natans* under low light (2.8%, 7.1%, 17.1%, and 39.5% ambient light) increased their initial slopes of RLCs (α) and decreased their minimum saturating irradiances (I_k). On the other hand, F_v/F_m increased revealing that *E. canadensis* was able to maintain its photosynthesis. The percentage cover of *E. canadensis* increased through duration of the experiment, which is consistent with F_v/F_m and chlorophyll concentrations, hence, no significant change in morphology of *E. canadensis* was seen in the experiment.

There are many factors that can negatively affect *E. Canadensis,* such as nutrient enrichment, low pH, elevated temperature, and low light (Netten et al., 2013) in combination, but low light by itself did not show clear effects on *E. canadensis* in this study. Different light intensities from shading did not affect photosynthesis and growth of *E. canadensis* due to its ability to adapt to a low light situation by chlorophyll adjustment. *E. canadensis* is a submergent macrophyte with roots in the mud at the bottom of the water (Huxley et al., 1992) where it could be shaded by other floating plants or sediment. Further, Ellawala Kankanamge et al. (2019) revealed that *Elodea* species are adapted to relatively low light conditions by gradual increasing in total chlorophyll content and act as pioneer macrophytes in eutrophic freshwater habitats in the transition from the phytoplankton-dominated to the macrophyte-dominated state, and they can tolerate moderate shading by periphyton and other submerged macrophytes.

Changes of environment as regards light intensity and temperature affect species composition (Li et al., 2017) especially in combination with other environmental factors. However, changes in light only did not affect population of this species in this study. At the end of the experiment, percentage cover by *E. canadensis* was not significantly different among the treatments, which is consistent with the photosynthetic activities, pigment content, and organic content that are factors supporting macrophyte growth (Kirschbaum, 2011) and percentage cover (Feng et al., 2008). Moreover, morphology (leaf length and width) of *E. canadensis* did not change by time or by treatment. However, it is suggested that the shoot length increased due to shading.

There are advantages that *E. canadensis* possesses in terms of materials cycling and energy flow and including phytoplankton and epiphytic growth inhibition with allelochemicals (Mohamed, 2017) that could prevent eutrophication in a lake. Exhibiting high growth rates with a high tolerance to wide ranges of environmental conditions, low vulnerability to grazing and other stress factors, high distribution, and reproduction potential of *E. canadensis* (Zehnsdorf et al., 2015) make it an invasive species that dominates in many lakes. This study found that the photosynthesis and growth of *E. canadensis* in Songkhla lagoon are affected by low light regime for a short period (2 weeks), while in the long run *E. canadensis* adapted by chlorophyll concentration adjustment to cope with a low light regime.

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Conclusions

E. canadensis was the dominant species and continuously increased during the experiment but there were no differences by shading treatment, while the leaf length and width did not show clear patterns in response to a low light. Photosynthetic activities showed changes due to shading in some parameters such as I_k and $rETR_{max}$ in 50% and 75% shading treatments, but there were no changes in photosynthetic efficiency of this species. This study suggests that this species is able to cope well with shading. Under future anthropogenic changes in turbidity, this species could be able to grow well and might flourish under eutrophic conditions (e.g. high nutrient loading), which might be a problem for Songkhla lagoon management. Therefore, management of this species should take an integrated approach recognizing these benefits and disadvantages. Future study should estimate about shading on other species for prediction the species composition of Songkhla lagoon which face to eutrophication in the future.

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