

COMBINED EFFECTS OF WARMING AND SHADING ON GROWTH AND PHOTOSYNTHETIC PERFORMANCE OF SUBMERGED MACROPHYTES FROM SONGKHLA LAGOON, THAILAND

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(Received 23rd Feb 2021; accepted 14th May 2021)

Abstract. Macrophytes play an important role in maintaining high physical and biological diversity in freshwater ecosystems. However, during the past several centuries since the industrial revolution, human activities and climate change have caused significant changes in the structure and function of aquatic environments, for example via increased temperature or high sedimentation that reduces light penetration. This study investigated the combined effects of elevated temperature and low light on growth and photosynthetic performance of submerged macrophytes *Ceratophyllum demersum* and *Elodea canadensis* and identified temperature and light thresholds for these species. Photosynthetic performance, chlorophyll *a* and *b* concentrations, organic and carbon contents, and growth rates were estimated in these two dominant macrophytes sampled from the middle of Songkhla lagoon, subjected to 9 treatments (3 light intensities and 3 temperatures) for 9 weeks. The results show that photosynthetic performance according to the indicators EQY, α and $rETR_{max}$ was inhibited by low light in both species. *C. demersum* was more tolerant to temperature and light stresses. This study provides an understanding of physiological tolerance and response to light and temperature stresses, and improves the understanding of how aquatic macrophytes respond to future climatic and anthropogenic changes, supporting the development of sustainable lagoon management plans.

Keywords: *climate change, organic carbon, PAM fluorometry, chlorophyll, shading*

Introduction

During the past several centuries since the industrial revolution, human activities such as industrialization, urbanization and intensive agriculture activities have caused strong changes in the structure and function of nearby aquatic environments (Smith et al., 1999). The growth of human population has increased the pressure on both aquatic and terrestrial ecosystems causing land transformation and altering hydrological processes and geochemical cycles of carbon (C), nitrogen (N) and phosphorus (P) (Vitousek et al., 1997; Smith et al., 1999). Land transformation and altering hydrological process led to soil erosion and sedimentation in the waterways and in lakes (Pradit et al., 2010). High

turbidity from sediment load affects vertical light penetration, which leads to low-light conditions and disrupts ecosystem functions (Mi et al., 2019). Furthermore, the anthropogenic release of greenhouse gases into the atmosphere, predominantly carbon dioxide (CO₂), has led to increased global temperatures through the trapping of heat in the Greenhouse Effect. As a consequence, surface water temperature has increased and is predicted to increase in the future. Climate change is expected to have profound impacts to terrestrial and aquatic ecosystems and their resident organisms (Johnson et al., 2007).

Macrophytes play an important role in maintaining high physical and biological diversity and act as ecosystem engineers (Li et al., 2018) that provide nutrient cycling capacity, and also act as habitat structure and refugia for aquatic organisms (Wigand et al., 2000; Qiu et al., 2001; Cronk and Fennessy, 2016). Macrophytes are potentially used as powerful natural tools for water quality improvement in lakes and reservoirs due to their capacity in nutrient uptake and in preventing phytoplankton blooms (Liu et al., 2000; Lone et al., 2014). The growth and photosynthesis of submerged macrophytes can be affected by temperature (Chalanika De Silva and Asaeda, 2017), light (Chen et al., 2016), and high organic loads in sediments (Barko and Smart, 1983) due to several coupled biological, physical and chemical modifications of the benthic system (Sand-Jensen et al., 2005; Raun et al., 2010). Diurnal light changes affect photosynthetic activities, and Jiang et al. (2018) found that the Maximum Quantum Yield of photosystem II (MQY) of six common submerged macrophytes decreased at midday under ambient light, but there was no significant change under shade, and MQY was negatively correlated with photon radiance, except for *Ceratophyllum demersum*, which probably could support high light levels.

Light is a major environmental factor influencing photosynthetic organisms (Hanelt, 1992). Light penetration through a water column is influenced by several factors including depth, suspended particles, and dissolved compounds. A high load of suspended particles can reduce light transmission to photosynthetically active leaf surfaces (Reitsema et al., 2018) and alter gas and nutrient exchanges in submerged macrophytes (Korschgen et al., 1997). Chen et al. (2016) found that *Potamogeton maackianus* and *Vallisneria natans* increased their initial slope of RLC (α) and decreased their minimum saturating irradiance (E_k) and maximum relative electron transport rate (ETR_m) under low light stress, while higher Relative Growth Rate of *P. maackianus* than *V. natans* was seen with a stronger light intensity but it was decreased in a low light intensity. Shading caused a decrease in net photosynthesis in *Chara aspera* and *Chara canescens* within 24 hours, but their photosynthetic performances recovered within a short period, suggesting that these charophytes are able to adapt to low light conditions (Kovtun-Kante et al., 2014). In contrast, increasing irradiance in oligotrophic lake can lead to an increase in photosynthesis, oxygen production and growth rate of macrophytes (Eller et al., 2015). An increase in shoot density and biomass of *Vallisneria americana* was observed on increasing light intensity from 100 to 600 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ (Barko et al., 1984). However, exposure to a high level of light at a shallow depth can lead to a loss of photosynthetic activity through light-dependent down-regulation of photosynthesis, or a rise in photoinhibition and photodamage, which further inhibits growth (Jin et al., 2020).

Many studies have shown that an increase in global temperature influences the health and survivorship of aquatic organisms (Eissa and Zaki, 2011). Each species responds differently in terms of growth, photosynthesis, reproduction and survivorship to global warming (Gonzalez, 2010; Eissa and Zaki, 2011). Temperature influences the

physiological processes, including photosynthesis and biomass growth rate of macrophytes (Atta-Boateng et al., 2019). Thermal stress can reduce shoot elongation and increase hydrogen peroxide (H₂O₂) level, damaging photosynthetic pigments and cell membrane structures (Chalanika De Silva and Asaeda, 2018), and may result in shifts in distribution and abundance (Fernández et al., 2020; Miller et al., 2020). Barko and Smart (1981) found that aboveground biomass of submerged macrophytes increased with temperature. However, a recent study showed a decrease in biomass under increasing temperature alone, while an increase in temperature with elevated CO₂ increased photosynthetic performance and growth of *V. natans* (Cao and Ruan, 2015).

Songkhla Lagoon is a tropical estuarine lagoon system located on the eastern side of the southern Thai peninsula, and consists of four interconnected water bodies: Thale Noi, upper lagoon, middle lagoon, and lower lagoon (Pongpiachan et al., 2019). Songkhla Lagoon not only supports biodiversity, but also a large number of people whose livelihoods depend on that biodiversity via fishery, aquaculture and tourism (Community Development Department, 2009). Songkhla Lagoon is currently experiencing serious water pollution and sedimentation due to human activities (Pradit et al., 2010; Somboonsuke et al., 2018). This could lead to losing their valuable ecosystem services and functions such as carbon sequestration. The submerged macrophytes found in Songkhla Lagoon include *Ceratophyllum demersum*, *Cladophora* sp., *Najas malesiana*, *Najas marina*, *Najas graminea*, *Hydrilla verticillata*, and *Potamogeton malaianus* (Thongkao et al., 2001). Climate change is likely to affect each organism in each system differently due to interactions with other factors such as nutrient loading and light. Moreover, studies on effects of light and temperature on growth and photosynthesis of submerged macrophytes in a tropical estuarine lagoon system (like the Songkhla Lagoon) are still lacking. Hence, it is essential to consider the effects of climate change together with low light to successfully manage the eutrophic lagoon (Howarth et al., 2000; Yang et al., 2008).

This study aims to investigate the combined effects of elevated temperature and low light on growth and photosynthesis of submerged macrophytes *C. demersum* and *E. canadensis* and sought to identify temperature and light thresholds for these species. An understanding of physiological tolerance and response to light and temperature stresses is critical for identifying the main driver for growth photosynthesis and carbon capture potential of submerged macrophytes, and for predicting their performances under these stresses. Furthermore, this study could contribute to understanding how aquatic macrophytes will respond to future climatic and anthropogenic changes in temperature and light, and support the development of sustainable lagoon management plans.

Materials and Methods

Sample collection and experimental design

Samples of *Ceratophyllum demersum* and *Elodea canadensis* (Fig. 1) were randomly collected from the middle of Songkhla Lagoon (7° 28' 09.0" N, 100° 23' 45.0" E) (Fig. 2) in May 2018 and were maintained in an aquarium (50 L) at 30°C, 180 μmol photons m⁻² s⁻¹ on a 12 h: 12 h light: dark cycle for 2 weeks of acclimation. Then, samples (*n* = 4) were allocated to 9 controlled aquariums set to three light regimes: 180 (control), 90 (50% shading) and 45 (75% shading) μmol photons m⁻² s⁻¹ and three temperatures (30°C (control), 33°C (RCP4.5 Scenario at year 2046-2065), and 36°C (RCP8.5

Intergovernmental Panel on Climate Change, 2013)) for 9 weeks (*Table 1*). Temperature and light for each treatment were controlled with water heater (Eheim, Germany) and LED lights (Chihiros, China, 400-700 nm), respectively. Water change (20%) to each aquarium were done weekly with deionized water: Hoagland solution (9:1). Nitrate and phosphate concentration were tested with Nitrate test kit (API, USA) and phosphate test kit (API, USA). Other water quality parameters such as dissolved oxygen and pH were measured weekly by YSI Pro Plus multiparameter meter (YSI Inc. / Xylem Inc, USA). Pigment concentration, growth and organic and carbon contents were weekly assessed at initial time (Week 0) and at the end of the experiment (Week 9). Photosynthetic performances were assessed every week from the start to the end of the experiment.

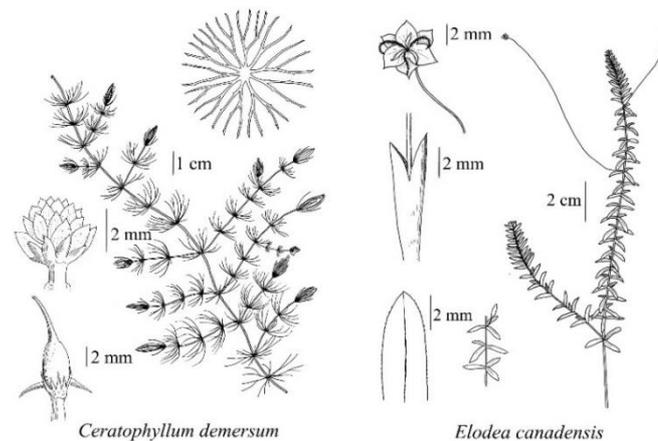


Figure 1. Drawings of *Ceratophyllum demersum* (left) and *Elodea canadensis* (right)

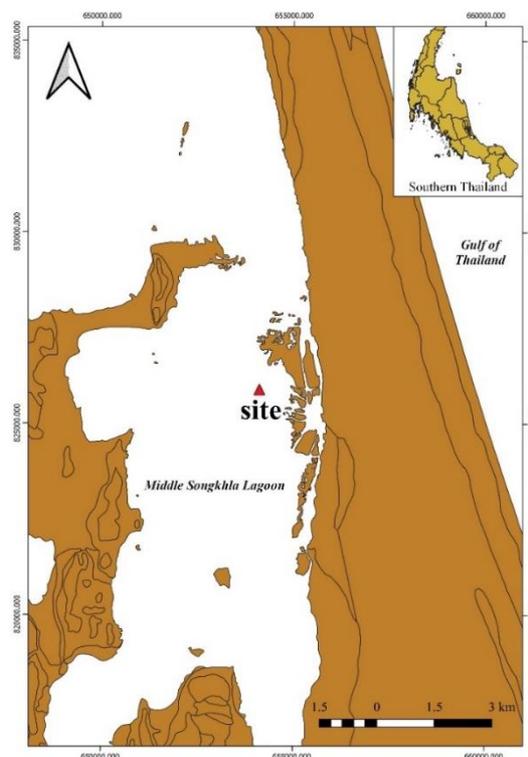


Figure 2. The study site at the middle of Songkhla Lagoon in peninsular Thailand

Table 1. Experimental design for each treatment and abbreviations

		Light intensity ($\mu\text{mol photons m}^{-2} \text{s}^{-1}$)		
		180	90	45
Temperature ($^{\circ}\text{C}$)	30	T30L180	T30L90	T30L45
	33	T33L180	T33L90	T33L45
	36	T36L180	T36L90	T36L45

Photosynthetic activity

Photosynthetic activities were observed weekly through a measure of chlorophyll *a* fluorescence using Junior Pulse Amplitude Modulated (Junior-PAM) fluorometer (Walz, Germany). Dark-adapted photosystem II (PSII) photochemical efficiency was measured as maximum quantum yield (MQY) before lights were on ($n = 4$). Rapid Light Curves (RLCs) were determined ($n = 4$) with 9 increasing actinic light intensities (0, 66, 90, 125, 190, 285, 420, 625 and 920 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$), with 0.8 s saturating pulse ($> 4500 \mu\text{mol photons m}^{-2} \text{s}^{-1}$) between each actinic light intensity every 10 s. Effective quantum yield (EQY), maximum relative electron transport rate ($r\text{ETR}_{\text{max}}$), minimum saturating irradiance (I_k) and initial slope (Alpha (α)) of each RLC were calculated using curve fitting protocols following Ralph and Gademann (2005).

Chlorophyll *a* and *b* concentrations

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

Growth rate

Growth rates of *C. demersum* and *E. canadensis* were determined ($n = 4$) as changes in total length per day, using equation (Eq.1) that is modified from Knauer et al. (2006).

$$\text{Growth rate} = (\text{final length} - \text{initial length})/\text{day} \quad (\text{Eq.1})$$

Organic and carbon contents

Macrophyte samples were oven dried at 105°C and ground to less than 1 mm particle sizes. A 1.0 g ground sample was ashed in a muffle furnace (FHX, DAIHAN, China) at 550°C for 8 h (Armecin and Gabon, 2008). Organic matter in the macrophytes was determined using data from the ashed samples ($n = 4$), and mineral matter (MM; Eq.2), organic matter (OM; Eq.3) and organic carbon (OC; Eq.4) contents were computed as follows:

$$\% \text{MM} = \left(\frac{\text{AW}}{\text{DW}} \right) \times 100 \quad (\text{Eq.2})$$

$$\% \text{OM} = 100 \times (\text{DW} - \text{AW})/\text{DW} \quad (\text{Eq.3})$$

$$\%OC = \%OM/1.724 \quad (\text{Eq.4})$$

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

Statistical analyses

Three-way mixed ANOVA tests were used to test for significant differences among treatments over time, in the chlorophyll fluorescence parameters. Two-way ANOVA was used to test for significant differences among treatments and species in leaf pigments, growth rate, and organic content. All tests were performed with a significance level of 95%, and Tukey's honestly significant difference *post hoc* tests were used to verify statistical significances. If the data did not meet the assumptions of normality (Kolmogorov-Smirnov test) and constant variance (Levene's test), they were transformed using square root or \log_{10} . If the transformed data did not meet the assumptions, then non-parametric tests were used.

Results

Photosynthetic activity

Responses of photosynthetic activity were measured under ambient temperature (30°C), or elevated temperature (33 and 36°C) with ambient light (180 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$) or low light (90 and 45 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$). Results showed differences in photosynthetic activity for each macrophyte species.

Maximum quantum yield (MQY)

At week 0, MQY of *Ceratophyllum demersum* and *Elodea canadensis* was 0.77 ± 0.01 and 0.76 ± 0.03 , respectively. A difference between the species showed up at elevated temperature (36°C) where the lowest MQY of *C. demersum* (0.61) occurred in T36L180 (Fig. 3a). On the other hand, *E. canadensis* in T36L180 treatment significantly decreased at week 1 ($p < 0.05$) then followed by T36L90 at week 3 and by T36L45 at week 4 (Fig. 3b). At the end of experiment, there were significant differences in MQY among the treatments in both species ($p < 0.05$). The data indicate that only temperature affected MQY of *C. demersum* ($p < 0.05$) while MQY of *E. canadensis* was affected by both light and temperature ($p < 0.05$).

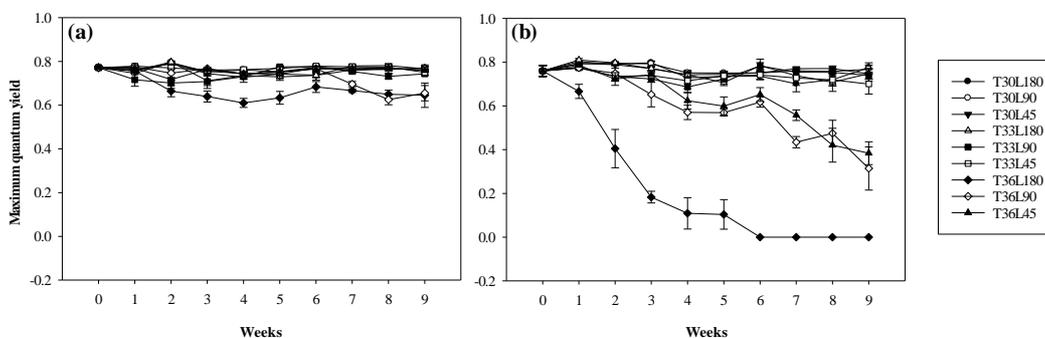


Figure 3. Maximum quantum yields of *C. demersum* (a), and *E. canadensis* (b) from Week 0 to Week 9 in each treatment. Data are shown as Mean \pm SE

Effective quantum yield (EQY)

At week 0, EQY of *C. demersum* and *E. canadensis* was 0.68 ± 0.01 and 0.73 ± 0.01 , respectively. EQY showed similar trends to MQY for both species, and at the end of experiment there were significant differences in EQY among the treatments ($p < 0.05$). T36L180 treatment gave the lowest of EQY in both species (Figs. 4a and b) but it instantly decreased in *E. canadensis*. EQY of *C. demersum* and *E. canadensis* depended on both light and temperature ($p < 0.05$) and there was significant difference between the species ($p < 0.05$).

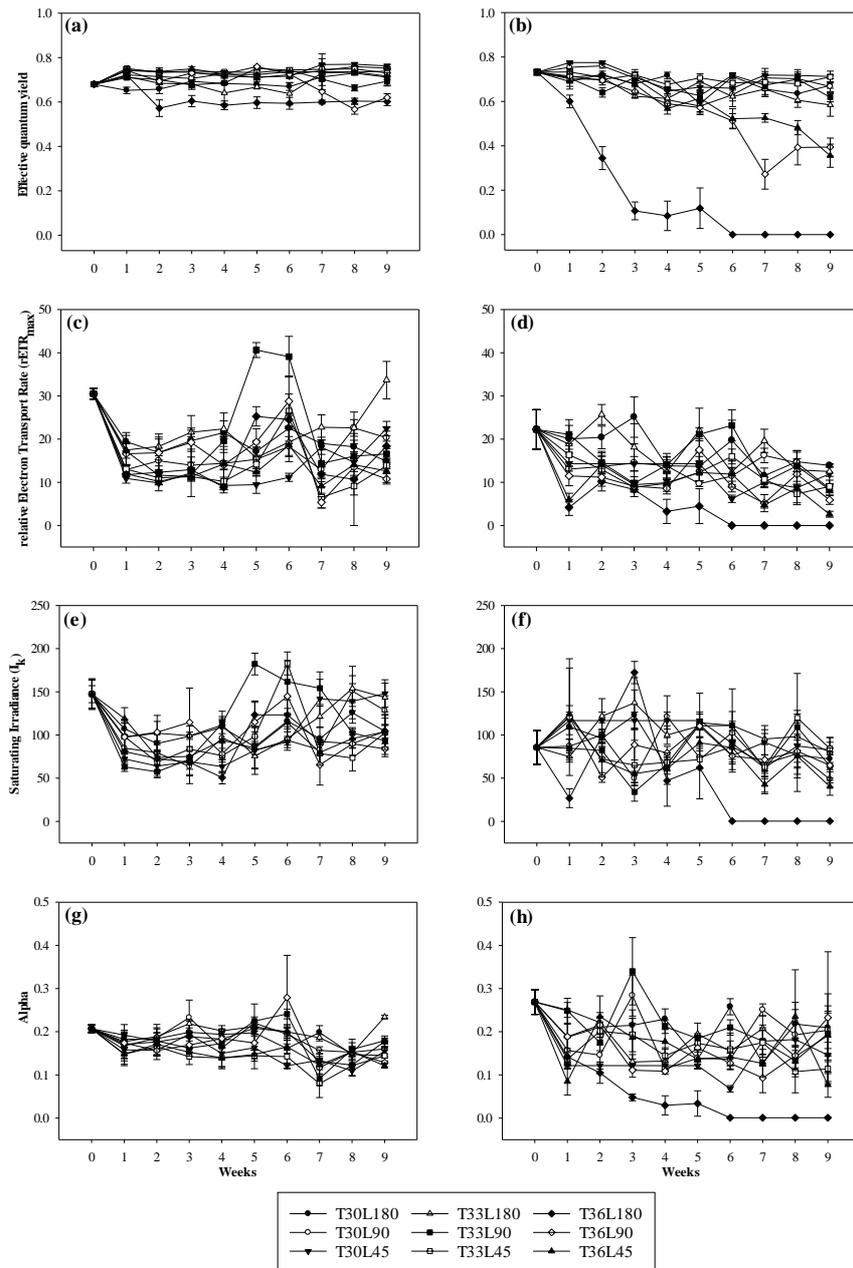


Figure 4. Effective Quantum Yield (EQY; a,b), maximum relative Electron Transport Rate (rETR_m; c,d), Saturating Irradiance (I_k; e,f) and Alpha (α; g,h) from Week 0 to Week 9 for *C. demersum* (a, c, d) and *E. canadensis* (b, d, f) in each treatment. Data are shown as Mean±SE

Maximum relative electron transport rate (rETR_{max})

At week 0, rETR_{max} of *C. demersum* and *E. canadensis* were 30.49±1.21 and 22.25±4.54 μmol electrons m⁻² s⁻¹, respectively. rETR_{max} of *C. demersum* did not significantly change from week 1 to week 9 (13.56 to 18.82 μmol electrons m⁻² s⁻¹; Fig. 4c) while high rETR_{max} was mostly found in T33L180 treatment. However, rETR_{max} of *E. canadensis* slightly decreased from week 0 to week 9 and ranged between 8.07 to 15.22 μmol electrons m⁻² s⁻¹ (Fig. 4d), with high rETR_{max} mostly found in T33L180 and T33L90 and low found in T36L180. At week 9, rETR_{max} significantly differed by treatment in both species (p<0.05). rETR_{max} of both species depended on light and temperature (p<0.05) and was significantly different by species (p<0.05).

Saturating irradiance (I_k)

At week 0, I_k of *C. demersum* and *E. canadensis* was 147.32±16.36 and 85.57±19.50 μmol photons m⁻² s⁻¹, respectively. I_k in *C. demersum* significantly increased from week 2 to end of the experiment (Fig. 4e) continually. On the other hand, *E. canadensis* showed quite stable trend in the range from 59.70 to 96.18 μmol photons m⁻² s⁻¹ (Fig. 4f). I_k was not significantly different between treatments at the end of experiment for *C. demersum* (p>0.05) and there was no significant dependence on light or temperature (p>0.05). In contrast, *E. canadensis* showed significant differences between treatments at the end of experiment (p<0.05) and also by temperature (p<0.05), and there were significant differences by species (p<0.05). I_k for each treatment and species significantly differed by week (p<0.05). I_k of *C. demersum* showed acclimation in the last two weeks in 33 and 36°C treatments, while *E. canadensis* showed acclimation in the last four weeks to 45 and 90 μmol photons m⁻² s⁻¹ treatments.

Alpha (α)

At week 0, α of *C. demersum* and *E. canadensis* was 0.21±0.01 and 0.27±0.03, respectively (Figs. 4g and 4h). At the end of experiment, there were significant differences in α by treatment for *C. demersum* (p<0.05) but not for *E. canadensis*. High α was mostly found in 180 and 90 μmol photons m⁻² s⁻¹ treatments for *C. demersum*, while *E. canadensis* showed various trends. It was found that only light affected α of *C. demersum* but *E. canadensis* was significantly affected by both light and temperature (p<0.05) and the difference between species was not significant (p>0.05).

Chlorophyll a and b concentrations

Chlorophyll a (Chl a)

Chl a concentration of *C. demersum* and *E. canadensis* at week 0 was 1,953.27±301.05 and 2,131.66±324.50 μg g⁻¹ fw, respectively. Decreasing Chl a concentration with time was observed in both species and in all treatments (Figs. 5a and 5b). At week 8, Chl a concentration of both species was significantly different by treatment (p<0.05) and highest in T30L180 and T33L90 for *C. demersum* and *E. canadensis*. T30L180 gave the highest Chl a concentration for *C. demersum* while the lowest was observed with T33L180, T33L90 and T33L45 treatments of *E. canadensis*. It was found that Chl a significantly depended on temperature (p<0.05) and Chl a of *C. demersum* at 30°C was higher than at other tested temperatures, while Chl a of *E. canadensis* in 36°C treatment was lower than at other temperatures.

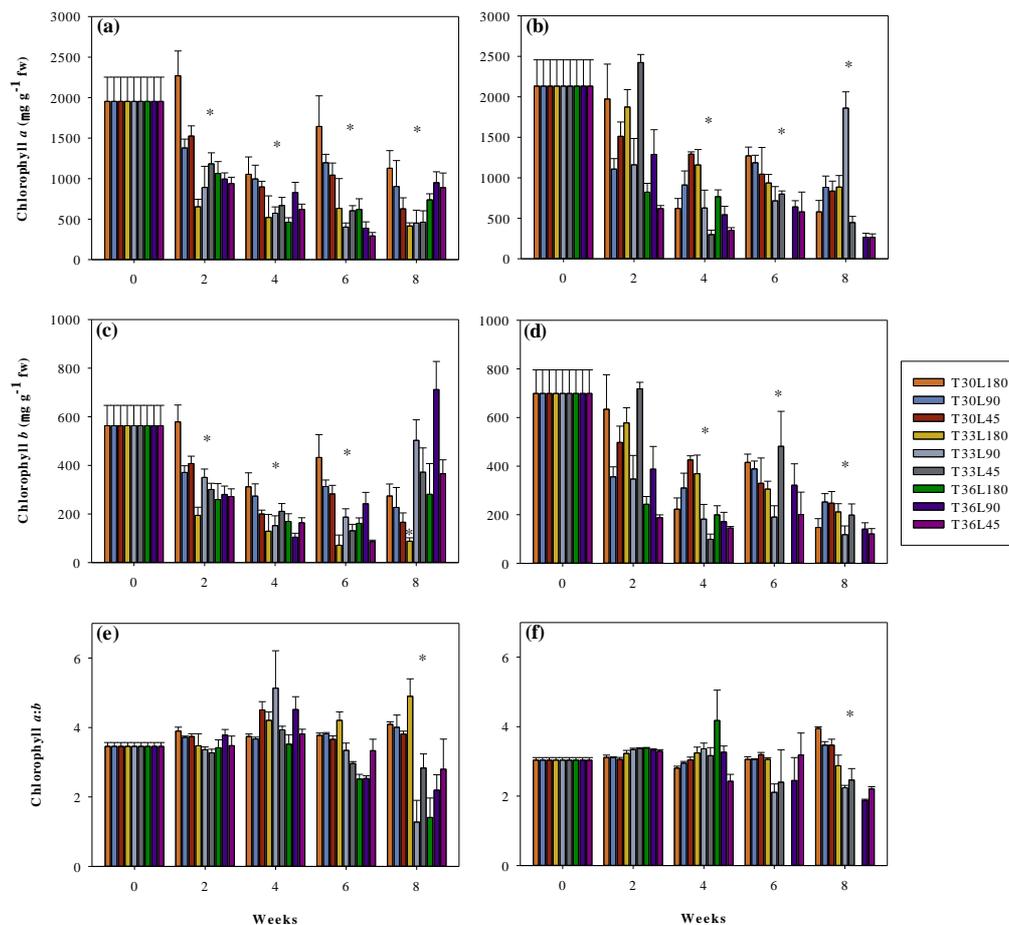


Figure 5. Chlorophyll a (a,b) and b (c,d) concentrations and chlorophyll a:b ratio (e,f) at Week 0 and Week 9 for *C. demersum* (left) and *E. canadensis* (right) in each treatment. Data are shown as Mean±SE and * represent significant difference

Chlorophyll b (Chl b)

Chl b concentration of *C. demersum* and *E. canadensis* at week 0 was 563.88 ± 83.47 and $699.50 \pm 96.80 \mu\text{g g}^{-1} \text{fw}$, respectively. Chl b of *C. demersum* decreased from week 2 to week 6, then increased at week 8 with an elevated temperature treatment (T33 or T36). Chl b of *E. canadensis* tended to dramatically decrease until the end of experiment (Figs. 5c and 5d). At week 8, Chl b was significantly different between the treatments ($p < 0.05$) in both species being highest in T36L90 for *C. demersum* and in T33L90 for *E. canadensis*. Chl b of *C. demersum* did not significantly depend on temperature or light ($p > 0.05$) but for *E. canadensis* it significantly depended on temperature ($p < 0.05$) and was significantly different between the species ($p < 0.05$).

Chlorophyll a:b ratio

Chl a:b ratio of *C. demersum* and *E. canadensis* at week 0 was 3.46 ± 0.11 and 3.04 ± 0.07 , respectively. Response mostly showed in week 4 and was higher for *C. demersum*. 30°C treatments showed more stable trends of Chl a:b ratio than the 33 and 36°C treatments that gave slight decreases over time (Figs. 5e and 5f). There was a

significant difference between the species and both species' responses significantly depended on temperature ($p < 0.05$). At week 8, there were significant differences by treatment in both species ($p < 0.05$).

Growth rates

Growth of *C. demersum* and *E. canadensis* was measured from week 0 to week 8. The highest growth rate of *C. demersum* and *E. canadensis* was in T30L180 treatment, namely 0.45 ± 0.06 and 1.67 ± 0.18 cm day^{-1} , respectively ($p < 0.05$) (Figs. 6a and 6b); and the lowest was in T36L180 treatment at -0.04 ± 0.01 and -0.05 ± 0.00 cm day^{-1} , respectively ($p < 0.05$). *E. canadensis* had significant faster growth than *C. demersum* in all treatments ($p < 0.05$). Both species' growth significantly depended on temperature and light ($p < 0.05$).

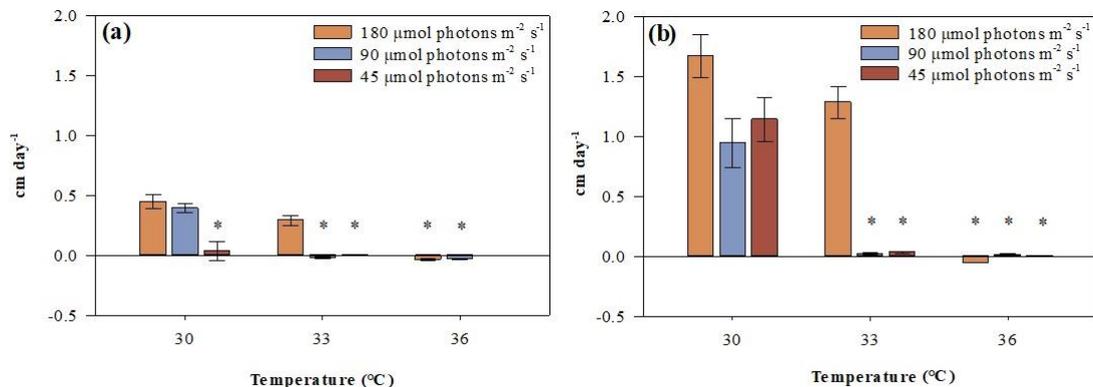


Figure 6. Growth rate (cm day^{-1}) from Week 0 to Week 9 for *C. demersum* (a) and *E. canadensis* (b) in each treatment. Data are shown as Mean \pm SE and * represent significant difference

Organic matter (OM) and organic carbon (OC) contents

OM of *C. demersum* and *E. canadensis* at week 0 was $89.58 \pm 1.24\%$ and $89.94 \pm 0.92\%$, respectively. OM of *C. demersum* significantly decreased in week 8 in all treatments except for T33L180, but *E. canadensis* showed dramatic decrease from week 0 to week 8 (Figs. 7a and 7b). There was a significant difference between treatments, with OM of *C. demersum* the lowest in T36L90 and the highest in T30L180, while OM of *E. canadensis* was the lowest in T36L180 and the highest in T36L45 treatment. However, there was no significant difference between the species, but at week 8 the OM of both species significantly differed by treatment ($p < 0.05$). Light and temperature did not significantly affect OM of *C. demersum* ($p > 0.05$) but significantly affected OM of *E. canadensis* ($p < 0.05$).

OC of *C. demersum* and *E. canadensis* at week 0 was $51.96 \pm 0.72\%$ and $52.17 \pm 0.53\%$, respectively. OC of both species showed similar trends to OM (Figs. 7c and 7d) and there were significant differences by treatment. OC of *C. demersum* was the lowest in T36L90 and the highest in T30L180, while OC of *E. canadensis* was the lowest in T36L180 and the highest in T36L45 treatment. OC of both species significantly differed by treatment ($p < 0.05$) at the end of experiment. Light and temperature did not significantly affect OC of *C. demersum* ($p > 0.05$) but both significantly affected OC of *E. canadensis* ($p < 0.05$).

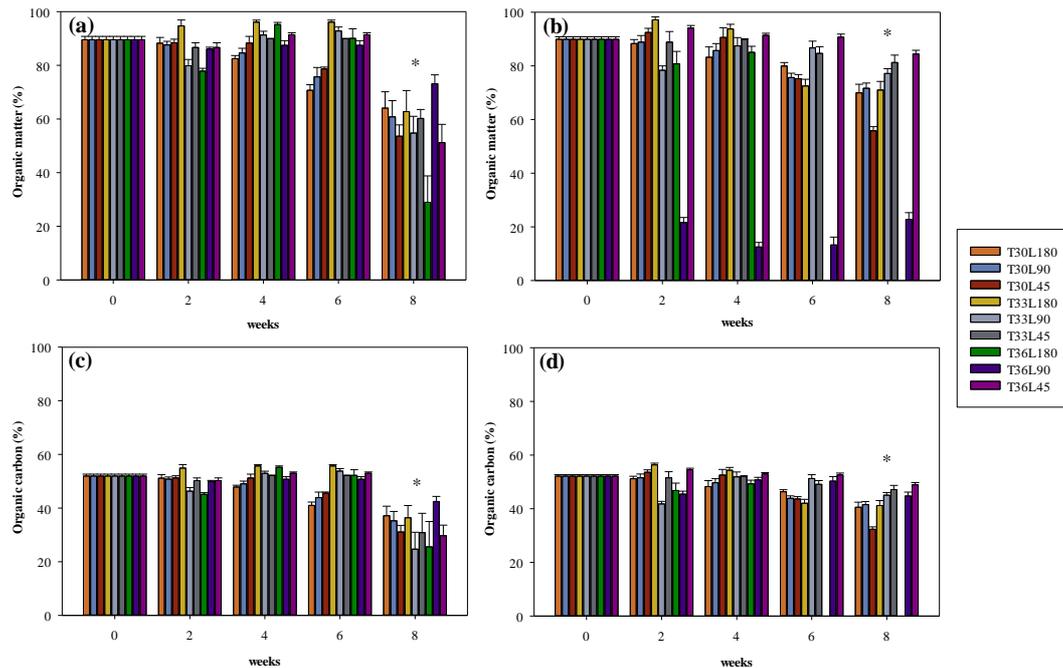


Figure 7. Organic matter (a,b) and organic carbon contents (c,d) at Week 0 to Week 8 for *C. demersum* (a,c) and *E. canadensis* (b,d) in each treatment. Data are shown as Mean±SE and * represent significant difference

Discussion

The combined effects of elevated temperature and low light were investigated in *C. demersum* and *E. Canadensis*, which are the dominant species in the middle of Songkhla lagoon, for 9 weeks. Photosynthetic performance of both species was affected by temperature and/or low light, as seen in the maximum quantum yield (MQY). Elevated temperature and ambient light (36°C and 180 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$) showed faster down-regulation of *C. demersum* photosynthesis at week 2, while elevated temperature with 50% shading (36°C and 90 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ treatment) caused down-regulation at weeks 2 and 7. On the other hand, other light shading at a lower temperature (30 or 33°C) did not induce changes in MQY. This indicates that the temperature had stronger effects on photosynthesis performance of *C. demersum* than light shading. This result is consistent with Jiang et al. (2018) who found no difference in MQY of *C. demersum* between shade and no shade. On the other hand, *E. canadensis* was more sensitive to temperature and light stress, showing response to 36°C treatment at weeks 1, 3 and 4 with 180, 90, and 45 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$, respectively. This is consistent with Chalanika De Silva and Asaeda (2017) reporting that the PSII activity of *E. nuttallii* was significantly reduced under elevated temperatures. The present study showed that a combination of ambient light and elevated temperature induced the greatest impact in photosynthetic activities of both tested species, especially *E. canadensis*. Netten et al. (2013) showed that the effects of elevated temperature and low light on *E. canadensis* are most likely caused by increased metabolic activity and reduced photosynthesis, to respectively adjust photo-physiology and to maintain a net positive carbon balance (Chartrand et al., 2018).

Climate change scenario and human activities could change many environment factors (Gallardo et al., 2017) especially light and temperature, which are among the main factors

for growth of aquatic plants (Carr et al., 1997). Thus, to maintain positive carbon balance and cope with light and temperature conditions, macrophytes had strategies, such as adjustments of light harvesting capacity and light use efficiency and modifying rates of growth (Chartrand et al., 2018). Moreover, light harvesting capacity (threshold) of each species can specify the species composition in the future, which faces climate and anthropogenic changes.

Light threshold for photosynthesis was shown by saturating irradiance (I_k). Our results indicate that *E. canadensis* was not affected by low light (high turbidity of water) and there was faster adaptation (I_k close to the light intensity) in the last 4 weeks in 90 and 45 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ treatments, while *C. demersum* showed response in the last two weeks. *C. demersum* was more tolerant to ambient light (180 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$), consistent with Jiang et al. (2018) stating that different light regimes did not show different photosynthetic activities in *C. demersum*; while the growth rate of *C. demersum* was lower in the light limited treatments than the rate of *E. canadensis* that was not affected.

E. canadensis was more sensitive to elevated temperature than *C. demersum* as shown by all indicators measured. *C. demersum* had more tolerance of a wide range of temperatures, and temperature did not much affect photosynthetic activities as *C. demersum* achieved homeostasis in photosynthesis and respiration rates, and the temperature optimum for photosynthesis changed according to its acclimation temperature (Hyldgaard et al., 2014). Elevated temperature, in contrast, did affect photosynthetic activities, chlorophyll concentration and carbon contents of *E. canadensis*.

Changes of environment by changing light intensity and temperature affect species composition (Li et al., 2017). Macrophytes capable of adaptation will survive and dominate in the lagoon. Decreasing light in a water column induced changes in photosynthetic activities, shown in the α for both tested species. Changes of α revealed the light responses clearly in *C. demersum*. Although *C. demersum* was able to adapt to a low light, due to the lower energy available the low light regime slowed down growth of *C. demersum*. *E. canadensis* showed various response in α , induced by combinations of light and temperature.

Only T33L90 treatment had increasing Chl *a* and *b*, revealing that only optimal temperature and light intensity allowed *E. canadensis* to thrive. Similar results were shown in *E. nuttallii* which Chl *a* and Chl *b* significantly increasing in a 30°C heat shock treatment and decreasing in a 35°C heat shock treatment (Chalanika De Silva and Asaeda, 2017). *C. demersum* showed increasing Chl *a* and *b* in T33L45, T36L90 and T36L45 to maintain photosynthetic activities. This reveals a wider range of temperature and light to which *C. demersum* can adapt, by more light harvesting in a low light regime, consistent with Dar et al. (2013) that found that the pigment in *C. demersum* was positively correlated with water temperature.

Macrophytes are fast growing plants that can on their death make a large amount of carbon settle to the bottom. Climate change and anthropogenic changes will affect growth (Zhang et al., 2018), species compositions (Li et al., 2017) and the carbon sink function as well. Carbon content of these 2 species did not differ, but only *E. canadensis* showed response to low light and elevated temperature that affected its photosynthetic activities. Degraded photosynthesis affected carbon capture by the macrophyte and reduced organic matter and organic carbon. Thus, reducing a macrophyte's carbon capture might reduce carbon sink efficiency in a lagoon, and might affect other species around the macrophyte.

Mal et al. (2002) found that *E. canadensis* growth (in control) was about 1.4 cm per day. Comparing *C. demersum* and *E. canadensis* for growth in similar conditions, Pinowska (2002) found that *E. canadensis* (final weight increased by about 17% of initial fresh weight) grew faster than *C. demersum* (final weight increased by about 7% of initial fresh weight) which is consistent with this current study.

Growth rates showed that 30°C was a near optimal temperature for growth of both species. At this temperature, *E. canadensis* had 2-3 times higher growth rates than *C. demersum* because the habitats of these species differ in position in the water column. *C. demersum* is a free-floating aquatic plant (Huxley et al., 1992) mostly found at the water surface where it can get full force of the sunlight, while *E. canadensis* is a submergent macrophyte with roots growing in the muddy bottom (Huxley et al., 1992) where it could be shaded by other plants and/or sediments. Thus, fast expansion is a strategy to get more sunlight. Previous research on competition of *E. nuttallii* with *Myriophyllum verticillatum*, *Vallisneria spiralis* and *C. demersum* found that *E. nuttallii* grew the fastest and its expansion ability was the strongest in autumn-winter and spring, but degenerated in the summer (Duan et al., 2011). In terms of species composition, there are spatial and temporal dynamics in species composition among these 2 species, dependent on environmental factors. However, climate change and anthropogenic activities that change the environment will affect species compositions in the future.

Anthropogenic activities that induce eutrophication (Nwankwegu et al., 2019) and algal blooms or high turbidity, and decrease light penetration in a water column, might affect growth of *C. demersum*. The IPCC Representative Concentration Pathways (RCPs) 4.5 and 8.5 scenarios predict that average temperatures would increase by about 1 to 3°C in 2020-2050 (Science Framework Climate Working Group, 2016) and this might affect photosynthesis and carbon content of *E. Canadensis*, which can grow in narrow light intensity and temperature ranges.

Low light and elevated temperature will change species composition so that the scale of *E. canadensis* will decrease at an elevated temperature, while *C. demersum* might not decrease in scale but in growth. However, since *C. demersum* is a free-floating macrophyte on water surface, eutrophication might affect the light harvesting by *C. demersum* very little. Thus, in species composition *C. demersum* might increase and dominate in the lagoon. Due to different points in the water column for these 2 macrophytes species, the loss of *E. canadensis* might affect middle - bottom water column microhabitat and related ecosystem.

C. demersum can improve water quality, specifically turbidity and nutrients, but its overgrowth will have disadvantages, such as increased sediment accumulation, reduced light penetration, and dissolved oxygen. Dai et al. (2012) found that water quality measures, such as turbidity, chlorophyll *a*, and nutrient concentrations, improved significantly in the presence of *C. demersum*, but there was a negative correlation between these reductions and the coverage of *C. demersum*. Therefore, 20% is probably the optimal restoration coverage area for *C. demersum* in the lagoon.

These results indicate that *C. demersum* prefers ambient light intensity (180 and 90 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$) while *E. canadensis* prefers ambient light with a comparatively low (30°C) temperature. This study provided data related to species composition in a lagoon, associated to scenarios of climate change and expected anthropogenic activities in the future.

Conclusions

To understand responses of macrophytes to climate change (RCP4.5 and RCP8.5) and to anthropogenic stresses, in terms of photosynthesis and carbon content, two dominant species from the middle of Songkhla lagoon in Thailand were subjected to experimental treatments in the lagoon. We found that photosynthetic activity indicators EQY, α and $rETR_{max}$ in both species were induced by light. Then, pigmentation in both species depended also on temperature, while the carbon content of *C. demersum* was unaffected by temperature or light, and *E. canadensis* was affected by both. *C. demersum* was more tolerant to temperature and light stresses but had slower growth of the two species. As regards species composition, the limiting factor for *C. demersum* vegetation is light shading, while for *E. canadensis* elevated temperature may be limiting. This study should study more about biochemical and physiological stress responses such as protein content, catalase activity, lipid peroxidation, and cellular membrane permeability as well as *in situ* measurement to confirm the results of this study.

Acknowledgements. This work was supported by the Development and Promotion of Science and Technology Grant for New Scholar, The Institute for the Promotion of Teaching Science and Technology [Grant number: 026/2559]. Authors would like to thank Associate Professor Seppo Karrila and the Research and Development Office, PSU, for proofreading the English language.

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