Photosynthetic Response of Filamentous Green Algae (*Oedogonium*) to Irradiance and Temperature Variations

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ABSTRACT

Oedogonium is a fast-growing filamentous green macroalgae. It has been used for the bioremediation of wastewater, for fertilizer and soil conditioners, and as a tool for carbon sequestration in some countries. In Thailand, this alga is widely distributed in shallow freshwater but is very rare in brackish waters. Recently, this alga has been targeted for biomass applications. However, the different strains of the alga and their physiological responses have not yet been examined. Therefore, the aim of this work was to determine the effects of irradiance and temperature on the photosynthesis of *Oedogonium* strains ABRC001, ABRC002 and ABRC003. Samples were tested at light intensities of 30, 60, 100, 150, 200, 250 and 500 μmol photons·m⁻²·s⁻¹ and at temperatures of 15, 20, 25, 30, 35 and 40 °C in the laboratory. The results showed differences in the photosynthetic responses among the algal strains. The net photosynthetic rates (Pnet) of strains ABRC001, ABRC002, and ABRC003 increased as light intensity increased up to 60, 200 and 100 µmol photons·m⁻²·s⁻¹, respectively, and decreased at higher light intensity (up to 500 µmol photons m⁻²·s⁻¹). Likewise, the P_{net} increased with temperature from 20-30 °C and decreased when the temperature increased from 35-40 °C. This study indicated good adaptation of the algal strain ABRC001 to low light intensity ($E_k = 30 \mu mol photons \cdot m^{-2} \cdot s^{-1}$), while strains ABRC002 and ABRC003 tolerated higher light intensity levels at Ek values of 100 and 60 µmol photons·m⁻²·s⁻¹, respectively.

Keywords: Green algae, PAM, Photosynthesis

INTRODUCTION

The genus *Oedogonium* is comprised of species of unbranched filamentous green macroalgae. This alga has a worldwide distribution and is a common taxon of natural ecosystems. The alga grows either attached to stones or epiphytic on other aquatic plants or free-floating objects (Wehr and Sheath, 2015). In Thailand, this alga is commonly encountered in shallow standing waters (ponds, ditches) and freshwater habitats (Chonudomkul *et al.*, 1998; Moonsin, 2016), but is very rare in

brackish waters. Recently, there have been several reports on diverse applications of the *Oedogonium* species (Cole *et al.*, 2013; Ellison *et al.*, 2014; Verawaty *et al.*, 2017; Adegoke *et al.*, 2018; Connell and Wilkie, 2018). The production of *Oedogonium* has been used for wastewater treatment (Cole *et al.*, 2014; Ellison *et al.*, 2014) and as an economical way of producing algal biomass (Verawaty *et al.*, 2017). It has also been reported as a tool for carbon sequestration, and its biomass has been used for bioenergy applications (Cole *et al.*, 2013; Adegoke *et al.*, 2018; Connell and Wilkie, 2018). The

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filament of Oedogonium has fast growth capability, which is related to its response to environmental factors (Verawaty et al., 2017). In general, abiotic factors, such as light and temperature, are the main contributors to the growth and distribution of the algae (Singhn and Singh, 2015; Wehr and Sheath, 2015). Those factors influence photosynthetic responses and respiration (Lobban and Harrison, 1994). The algal growth and productivity depend on light absorption for photosynthesis; however, excess light can result in photoinhibition and limit growth (Takahashi and Badger, 2011). Cultivation of the tropical strain of Oedogonium intermedium under different light intensities showed the highest productivity at 224 μmol photons·m⁻²·s⁻¹ (Cole et al., 2018). The amount of light required to balance absorbed light energy with energy consumed by metabolic pathways depends on the algal strain. Likewise, the optimal temperature for growth depends on the species of the algae. Some Oedogonium species have been reported to have maximum growth rates at temperatures between 24-28 °C (Lawton et al., 2014), while Oedogonium intermedium has a wider range of 20-35 °C (Cole et al., 2018).

Several studies have reported on the taxonomic diversity, cultivation and biomass application of the genus Oedogonium (Cole et al., 2013; Ellison et al., 2014; Verawaty et al., 2017; Adegoke et al., 2018; Halder, 2018). However, there are few studies on physiological responses in tropical species of this alga (Cole et al., 2018). A few studies have reported on diversity of this taxon in Thailand (Heckman, 1979; Poniewozik et al., 2020), whereas research concerning cultivation and biomass application, as well as physiological aspects of this algae is lacking. Thus, the aim of this study was to examine the physiological responses of three strains of Oedogonium-ABRC 001, ABRC002 and ABRC003-to different levels of irradiance and temperature. We focused the analysis on the effects of these factors on the photosynthetic activity of the algal filament. This study will provide information that can be used to improve future cultivation of the genus Oedogonium in Thailand.

MATERIALS AND METHODS

Sample preparation

Samples of the *Oedogonium* strains were originally collected from naturally occurring ponds at different locations in Nonthaburi Province (Latitude: 13.84°N; Longitude: 100.51°E) and in Bangkok (Latitude: 13.84° N to 13.85°N; Longitude: 100.57°E), Thailand, in November 2018. The general characteristics of the algal collecting sites are shown in Table 1. The collected samples were isolated and cultured in flasks using Bold's Basal Medium to acclimate them to laboratory conditions of 25 °C and light intensity of 100 μ mol photons·m²-s¹ for one month; then, healthy filaments (2 g fw each) were selected for further experiments.

Rapid light curves

The relative electron transport rate of the alga (2 g fw each, n=10), from specimens described above, was examined under laboratory conditions. Rapid light curves (RLCs) were generated by running the standard algorithm of a pulse amplitudemodulated (PAM) fluorometer (JuniorPAM, Walz/ Germany) using an incremental sequence of actinic illumination periods, with photosynthetic active radiation (PAR) intensity increasing in ten steps from 0 to 1500 µmol photons·m⁻²·s⁻¹. The relative electron transport rate (rETR) was calculated using the following equation: rETR=0.5*Y*PAR*AF, where Y is the effective quantum yield of photosystem II (PSII), the factor 0.5 assumes that half of the photons are absorbed by PSII, and AF is the fraction of incident light assumed to be absorbed by the sample (i.e., 0.84) (Khreauthong *et al.*, 2018).

Effect of irradiance on photosynthesis

The algal samples were examined (2 g fw each, n=3) after acclimation for one month in laboratory conditions (as described above). Photosynthesis rates were determined at different levels of light intensity (0, 30, 60, 100, 150, 200, 250 and 500 µmol photons·m-2·s-1) at 25 °C (three

Algal strains	Location	General environment		
ABRC001	Nonthaburi Province	Thalli were grown with lotus plants and		
	(Lat 13.84°N, Long 100.51°E)	sailfin molly (Poecilia reticulata) in a basin		
		of 30 cm depth, surrounded by large trees		
		providing shade all day. Thalli were exposed		
		to light intensity of 100-150 μmol photons·m ² ·s ⁻¹		
		and water temperature of 26–27 °C.		
ABRC002	Kasetsart University, Bangkok	Thalli were grown with lotus plants and		
	(Lat 13.84°N; Long 100.57°E)	sailfin molly in a basin of 30 cm depth,		
		surrounded by large trees, with shade during		
		morning but exposed to light during		
		afternoon. Light intensity was 300 µmol		
		photons·m ² ·s ⁻¹ when shaded, and 1,500		
		μmol photons·m ² ·s ⁻¹ during sunshine, with		
		temperature of 32 °C.		
ABRC003	Kasetsart University, Bangkok	Thalli were grown with lotus plants in a basin;		
	(Lat 13.85°N; Long 100.57°E)	mostly exposed to light intensity of 290 µmol		
		photons·m ² ·s ⁻¹ , but up to 1,500 μ mol		
		photons·m ² ·s ⁻¹ during sunshine, with		
		temperature of 32 °C.		

Table 1. Collection location and general environment of green alga *Oedogonium* strains.

replicates per level). The net photosynthetic rates (P_{net}) and the dark respiration were determined by measuring the dissolved oxygen concentration (mg·L⁻¹) every 5 min for 30 min. After these measurements, a 30-min period per incubation was used to allow the sample to acclimate to each set of experimental conditions. The slope of the linear regression was determined from the data from 30-min measurements of the estimated rates. Dissolved oxygen (DO) was measured using a DO meter (YSI 5000). The light saturation point was considered to be the optimal density and was used in experiments to determine the effects of temperature on photosynthesis.

Effect of temperature on photosynthesis and dark respiration

Photosynthetic rates were determined at different levels of temperature (15, 20, 25, 30 and 40 °C) (three replicates per level). Samples were incubated under the light saturation point (from the data described above), and the Pnet and dark respiration were determined as described above.

Statistical analysis

The data are presented as mean±standard deviation (SD). Statistical analyses were performed using one-way analysis of variance (ANOVA). Means were compared by two-tailed *t* test at a confidence level of 95 %.

RESULTS

Three strains of the *Oedogonium* species, ABRC001, ABRC002 and ABRC003, were isolated based on morphological characteristics. Figure 1 shows the habits of vegetative filaments and zoospores of the strains. The vegetative cells of the strain ABRC001 were cylindrical, at 50–57 $\mu m \times 168–170~\mu m$. The vegetative cells of strains ABRC002 and ABRC003 were cylindrical and slightly capitellate, at 40–45 $\mu m \times 130–170~\mu m$ for strain ABRC002 and 30–35 $\mu m \times 90–150~\mu m$ for strain ABRC003.

The experiments showed that the three *Oedogonium* strains had different responses to irradiance and temperature (Figures 2–6). The algal strains all showed an increase in the rapid light curve (measured as relative electron transport (rETR)) until reaching an asymptote and photoinhibition. The ETR of strains ABRC001 and ABRC003 increased until the PAR reached 400 and 800 μmol photons·m⁻²·s⁻¹, respectively, while an asymptote in the curve for strain ABRC002 was not apparent until the PAR reached 1,150 μmol photons·m⁻²·s⁻¹ (Figure 2).

The response of the photosynthetic rate of the *Oedogonium* strains to different levels of irradiance was measured at a temperature of 25 °C.

The photosynthesis rates were found to be different among strains (Figure 3). The net photosynthetic rate (P_{net}) of strain ABRC001 steadily increased from 0 to 60 µmol photons·m-2·s-1 and then gradually decreased with increasing light intensity from 60 to 500 µmol photons·m-2·s-1. The average P_{net} of the ABRC001 strain was 9.84 µg O_2 ·g-1 ww·min-1 at the light saturation point (E_k) of 30 µmol photons·m-2·s-1 (Figure 3a). Under the same conditions, the P_{net} of strain ABRC002 steadily increased when the light intensity increased from 0 to 200 µmol photons·m-2·s-1 and gradually decreased with increasing light intensity from 200 to 500 µmol photons·m-2·s-1. This algal strain had an average P_{net} (15.87 µg O_2 ·g-1 ww·min-1) at the light saturation point of 100 µmol photons·m-2·s-1

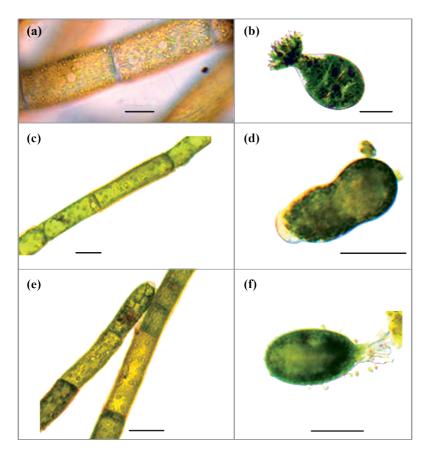
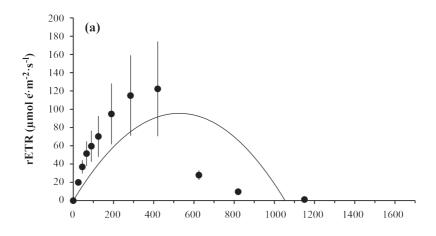
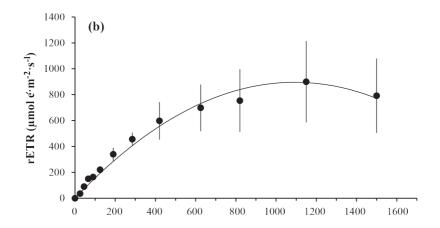


Figure 1. Morphological characteristics of three *Oedogonium* strains: habit of filament (a) and zoospore (b) of strain ABRC001; habit of filament (c) and zoospore (d) of strain ABRC002; habit of filament (e), zoospore (f) of strain ABRC003; scale bar=50 µm.





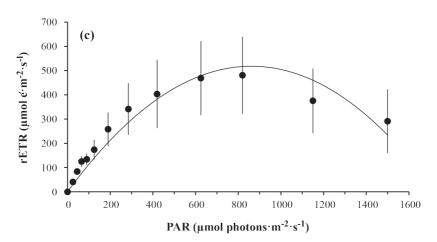


Figure 2. Influence of exposure to irradiance between 0–1,500 μmol photons·m⁻²·s⁻¹ on the relative electron transport rate (rETR) (mean±SD) of Chlorophyll *a* fluorescence of *Oedogonium* strains ABRC001 (a), ABRC002 (b) and ABRC003 (c).

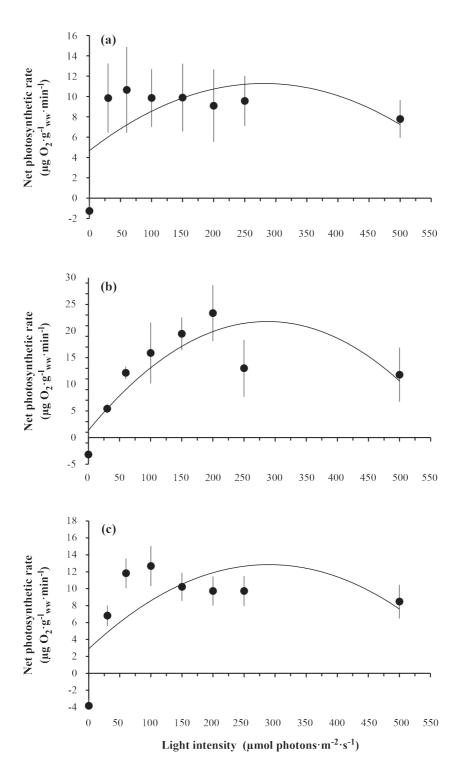


Figure 3. Response in photosynthetic rates (mean±SD) of *Oedogonium* strains ABRC001 (a), ABRC002 (b) and ABRC003 (c) at light intensity of 0, 30, 60, 100, 150, 200, 250 and 500 μmol photons·m⁻²·s⁻¹.

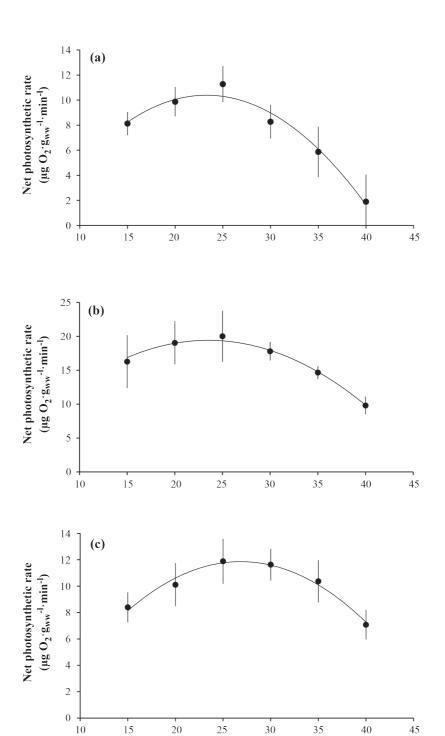
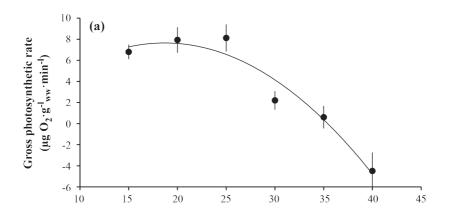
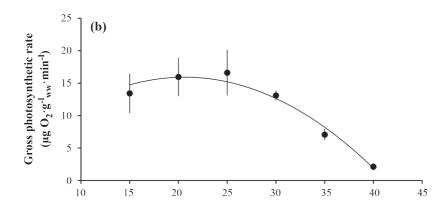


Figure 4. Response in photosynthetic rates (mean±SD) of *Oedogonium* strains ABRC001 (a), ABRC002 (b) and ABRC003 (c) at temperatures of 15, 20, 25, 30, 35 and 40 °C, measured at the light saturation level of each strain.

Temperature (°C)





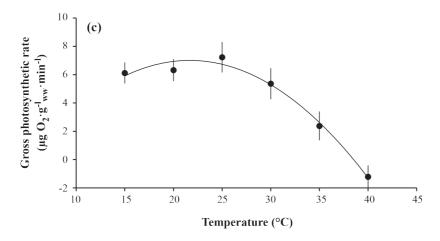


Figure 5. Response in gross photosynthetic rate (mean±SD) of *Oedogonium* strains ABRC001 (a), ABRC002 (b) and ABRC003 (c) at different temperatures of 15, 20, 25, 30, 35 and 40 °C.

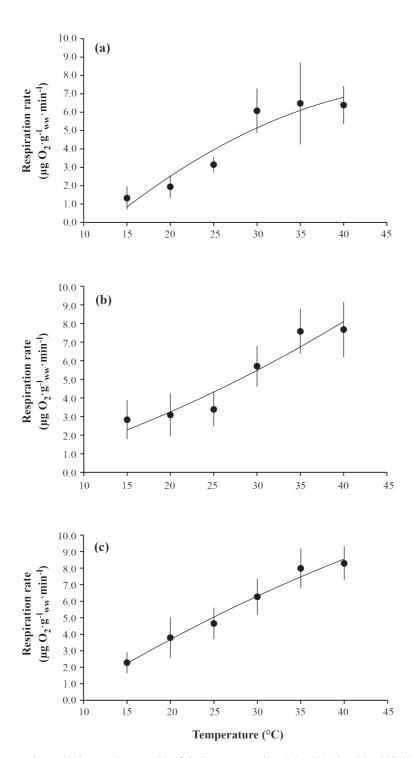


Figure 6. Response in respiration rate (mean±SD) of *Oedogonium* strains ABRC001 (a), ABRC002 (b) and ABRC003 (c) at temperatures of 15, 20, 25, 30, 35 and 40 °C.

(Figure 3b). The P_{net} of strain ABRC003 steadily increased from 0 to 100 μ mol photons·m⁻²·s⁻¹ and gradually decreased from 100 to 500 μ mol photons·m⁻²·s⁻¹, with average P_{net} (11.81 μ g O_2 ·g⁻¹_{ww}·min⁻¹) at the light saturation point of 60 μ mol photons·m⁻²·s⁻¹ (Figure 3c). The P_{net} was significantly different among the algae strains (p<0.05) at the light saturation points (Table 2).

Figure 4 shows responses of the *Oedogonium* strains ABRC001, ABRC002, and ABRC003 to different temperatures at light saturation points of 30, 100, and 60 μmol photons·m⁻²·s⁻¹, respectively. The highest P_{net} was observed at different points within the range of 20 to 30 °C, depending on the algal strain, and decreased at temperatures above and below this range (Figure 4).

Table 2. Results of analysis of variance on effects of light intensity and temperature (at light saturation point) on photosynthesis of *Oedogonium* strains ABRC001, ABRC002, and ABRC003 (P_{net}=net photosynthesis; GPP=gross photosynthesis; R=dark respiration).

Factors			SS	df	MS	F	p-value
Light intensity	ABRC001-P _{net}	Between Groups	392.089	7	56.013	11.144	0.000
		Within Groups	201.044	40	5.026		
		Total	593.132	47			
	ABRC002-P _{net}	Between Groups	1667.161	7	238.166	22.940	0.000
		Within Groups	415.284	40	10.382		
		Total	2082.445	47			
	ABRC003-P _{net}	Between Groups	323.038	7	46.148	46.635	0.000
		Within Groups	39.583	40	0.990		
		Total	362.621	47			
Temperature	ABRC001-P _{net}	Between Groups	289.599	5	57.920	74.728	0.000
		Within Groups	23.252	30	0.775		
		Total	312.851	35			
	ABRC002-P _{net}	Between Groups	400.591	5	80.118	65.170	0.000
		Within Groups	36.881	30	1.229		
		Total	437.472	35			
	ABRC003-P _{net}	Between Groups	104.430	5	20.886	21.058	0.000
		Within Groups	29.755	30	0.992		
		Total	134.185	35			
	ABRC001-GPP	Between Groups	805.132	5	161.026	375.297	0.000
		Within Groups	12.872	30	0.429		
		Total	818.004	35			
	ABRC002-GPP	Between Groups	957.034	5	191.407	290.886	0.000
		Within Groups	19.740	30	0.658		
		Total	976.774	35			
	ABRC003-GPP	Between Groups	307.145	5	61.429	248.702	0.000
		Within Groups	7.410	30	0.247		
		Total	314.555	35			
	ABRC001-R	Between Groups	185.439	5	37.088	121.675	0.000
		Within Groups	9.144	30	0.305		
		Total	194.583	35			
	ABRC002-R	Between Groups	151.789	5	30.358	37.723	0.000
		Within Groups	24.142	30	0.805		
		Total	175.932	35			
	ABRC003-R	Between Groups	171.802	5	34.360	59.977	0.000
		Within Groups	17.187	30	0.573		
		Total	188.989	35			

The highest P_{net} for the ABRC001 strain (11.27 $\mu g \ O_2 \cdot g^{-1}_{ww} \cdot min^{-1}$) occurred at 25 °C (Figure 4a), while highest P_{net} values for ABRC002 were 19.04 and 20.00 $\mu g \ O_2 \cdot g^{-1}_{ww} \cdot min^{-1}$ at 20 °C and 25 °C, respectively (Figure 4b). The highest P_{net} values for the ABRC003 strain were at 25 °C (11.88 $\mu g \ O_2 \cdot g^{-1}_{ww} \cdot min^{-1}$) and 30 °C (11.63 $\mu g \ O_2 \cdot g^{-1}_{ww} \cdot min^{-1}$) (Figure 4c). The average P_{net} was significantly different among the algal strains (p<0.05) (Table 2).

Similar trends were found for gross photosynthesis. The algal strains ABRC001, ABRC002, and ABRC003 had the highest rates of gross photosynthesis of 8.13, 16.62, and 7.23 μg $O_2 \cdot g^{-1}_{ww} \cdot min^{-1}$, respectively (Figure 5). The gross photosynthesis rate gradually increased with increasing temperature and showed a maximum value at 25 °C, but markedly decreased with higher temperature. This study also showed that the dark respiration rate increased with temperature for all three strains from 15 °C to 35 °C (Figure 6). The highest respiration rates varied from 6.48 μg $O_2 \cdot g^{-1}_{ww} \cdot min^{-1}$ at 35 °C for strain ABRC001 to 8.29 μg $O_2 \cdot g^{-1}_{ww} \cdot min^{-1}$ at a higher temperature of 40 °C for strain ABRC003.

DISCUSSION

Photosynthesis and respiration are important processes in photosynthetic organisms and help determine the overall growth rate of algae (Mettler et al., 2014). The growth rate and productivity of algae can also be influenced by a wide range of environmental conditions (Lobban and Harrison, 1994), and their physiological responses vary as a function of light regime, temperature and nutrient status (Sakshaug et al., 1997). In the present study, the photosynthesis of *Oedogonium* strains was influenced by the level of light intensity and temperature treatments. The photosynthesis of the three algal strains clearly responded to the controlled conditions of the treatments. The Oedogonium strains were considered typical shade-loving plants, and similar to those grown in local habitats. The algal strain ABRC001 exhibited good adaptation to low light intensity and temperature. This strain usually grows in shaded habitats at a low water temperature (see Table 1) and is susceptible to high light intensity and temperature. In contrast, the strains ABRC002 and ABRC003 tolerated higher light intensity and temperature levels. The photosynthetic response of the *Oedogonium* strains was similar to those of the freshwater green algae *Cladophora glomerata* (Dodds and Gudder, 1992; Higgins *et al.*, 2008) and the red algae *Batrachospermum delicatulum* (Necchi and Alves, 2005), which were reported as shade-adapted plants.

In the current study, the P_{net} was significantly different among the strains ABRC001, ABRC002 and ABRC003 at light saturation levels of 30, 100 and 60 µmol photons·m⁻²·s⁻¹, respectively. The strain ABRC001 has saturating light intensity at a lower level than strains ABRC002 and ABRC003, which corresponds with the rapid light curves (ETR) for these algal strains. The former strain was more shade-adapted, while the latter two strains were more sun-adapted. This result was similar to the green algae Ulva procera and Cladophora glomerata grown in the northern Baltic Sea (Choo et al., 2005). Photosynthetic characteristics of strains ABRC002 and ABRC003 included a wide range of response to irradiance, reflecting their wide tolerance to this variable. Several works have been published on adaptation to low irradiance, as indicated by parameters derived from photosynthesis-irradiance (PI) curves, in freshwater red algae (Karsten *et al.*, 1993; Leukart and Hanelt, 1995; Necchi and Zucchi, 2001). Another study reported that the red algae Bostrychia radicans had a low light-compensation point at 3-4 µE·m⁻²·s⁻¹ and correlated with a low photon flux density of 70–100 μE·m⁻²·s⁻¹ for saturation of photosynthesis (Karsten and Kirst, 1989).

Moreover, our study showed that the algae strains grown at low light intensity may increase chlorophyll synthesis and growth rate. It has similarly been reported that microalgae cultured at low light intensity reduced the duration of lag phase, and then increased chlorophyll synthesis and growth rate of the algae (Shugarman and Appleman, 1966). In the current study, the P_{net} of the algae declined when exposed to high intensity of light (ABRC001>60 μmol photons·m⁻²·s⁻¹, ABRC002> 200 μmol photons·m⁻²·s⁻¹, and ABRC003>100 μmol photons·m⁻²·s⁻¹), which was thought to be

caused by damage to the chlorophyll pigment. This result corresponds to findings of another study, in which growth of algae declined at high light intensity due to damage of light pigments (Janssen *et al.*, 1999). Converti *et al.* (2009) likewise reported that algal growth was inhibited at high light intensity and that sunlight harmed algal cells.

The photosynthesis of algae is known to be sensitive to changes in temperature (Major and Davison, 1998). The photosynthesis of freshwater macroalgae has been shown at various optimal temperatures; in both individual species and groups of algae (Davison, 1991). Growths of algae that tolerate temperature changes are typically correlated with the temperature in the local habitat of the algae (Eggert, 2012). Similarly, in our study, we observed significant adverse effects of low and high temperature on the Oedogonium strains. Photosynthesis and growth rates of macroalgae are generally increased when temperature increases up to an optimal point, and then rapidly decline near an upper critical point of temperature (Davison, 1991; Eggert, 2012). The temperature responses of algal species are often correlated with local thermal environments (Lobban and Harrison, 1994). In this study, the response of oxygen evolution (net and gross photosynthetic rate) showed a characteristic dome-like shape, with the highest P_{net} and gross photosynthetic rate ranging from 20–30 °C. This result was similar to a recent study that reported an optimal temperature range for growing Oedogonium intermedium between 20 and 35 °C; also, its productivity increased with increasing photon flux within this temperature range (Cole et al., 2018). Photosynthesis of the three algae also appeared to be affected at temperatures above the range of 25-30 °C. This agrees with a previous study, which reported best growth of Oedogonium sp. at 24 °C, but with a decrease at 32 °C (Munir *et al.*, 2015).

The responses in photosynthesis of the algae to light and temperature relate to the thallus morphology. Johansson and Snoeijs (2002) stated that differences in morphology were reflected by the light-saturated net photosynthetic rate (P_{max}) and the rate of respiration in darkness (R_d): high

P_{max} and R_d for algae with high surface-to-volume ratios (sheets and filamentous), and lower Pmax and R_d for algae with low surface-to-volume ratios (coarsely branched and thick-leathery). The photosynthetic properties were highly dependent on thallus morphology; a thinner and more filamentous species reflected a higher O₂ production rate, while a coarser and thicker species had a lower rate (Johansson and Snoeijs, 2002). There has been a report on the relationship between surface area/ volume ratio (SA/V) and maximum productivity (P_{max}) of Caulerpa; productivity decreased with an increase in morphological complexity of the thallus (Gacia et al., 1996). They reported that the surface area/volume ratio of the Caribbean Caulerpa had high correlation to net photosynthetic rate. In the current study, the strains ABRC002 and ABRC003 were thinner forms of filamentous algae, while the strain ABRC001 was a thicker form. The higher rates of photosynthesis in the strains ABRC002 and ABRC003 may be correlated to the ratio of surface area and volume of the algae; however, this study did not measure these parameters. Further investigation is needed to clarify the relationship of photosynthesis and thallus morphology in these algal strains.

CONCLUSION

The *Oedogonium* strains examined in this study exhibited wide ranges of photosynthetic responses to irradiance and temperature, which reflected their susceptibility to variation in these environmental variables. The information obtained is of fundamental importance in identifying the geographical limitation for growing this alga in Thailand. The results indicated that the photosynthetic rates of these algal strains were influenced by the temperature and light environments to which they were exposed, and that each of the algal strains required a different set of growth conditions when cultured under controlled conditions in the laboratory. This is the first work to report on photosynthesis in Thai species of *Oedogonium*. Further studies are needed to examine factors influencing algal growth and production for optimal utilization of the Oedogonium strains.

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