J. Fish. Soc. Taiwan, **33**(3): 253-263

Effects of Temperature on the Oxygen- and Fluorescence-Based Estimates of Photosynthetic Parameters in the Reef Coral *Stylophora pistillata*

Tai-Ying Wu[1], Chang-Feng Dai[1] and Tung-Yung Fan[2,3]*

(Received, August 25, 2006; Accepted, September 5, 2006)

ABSTRACT

The effect of temperature on the O_2-based and chlorophyll fluorescence of Photosystem II (PSII)-based parameters of photosynthesis in the reef coral *Stylophora pistillata* was investigated. Coral nubbins were maintained in coral reef mesocosms at three temperature levels (20, 25 and 28 ℃) for ten days. The maximum PSII quantum efficiency (F_v/F_m) and electron transport rates (ETR) were measured by diving pulse amplitude modulate (PAM) fluorometry and the rate of O_2 evolution was carried out by oxygen respirometry. The tissue composition, maximum rate of gross photosynthesis (P^g_{max}) and sub-saturation irradiance (I_k) measured by respirometry, photosynthetic efficiency (α) measured both by respirometry and PAM, as well as F_v/F_m were similar among different temperature treatments. However, the maximum electron transport rate of photosynthesis (ETR_{max}) of corals at 25 and 28℃ was two times higher than that of corals at 20℃. In addition, the sub-saturation irradiance ($I_{k\text{-}ETR}$) was significantly higher at 28 and 25℃ than that at 20℃. It suggests that the photosynthetic process of PSII electron transport rate is rather sensitive to temperature and ETR_{max} and $I_{k\text{-}ETR}$ increased with increasing temperature. Furthermore, a similar linear relationship between gross photosynthesis rate (GP) and ETR was found under irradiances below 400 μE $m^{-2}s^{-1}$ or GP less than 14 μmol O_2 $m^{-2}s^{-1}$ at the three temperature treatments. This suggests that diving-PAM may provide a quick and non-invasive way to estimate primary productivity of corals under moderate irradiances.

***Key words**: Fluorescence, Photosynthesis, Reef coral, Stylophora pistillata, Temperature.*

INTRODUCTION

Photosynthesis of symbiotic algae is important to reef function and primary production by providing reef corals with a large fraction of organic carbon that is required for metabolism, growth and calcification (Barnes and Chalker, 1990). The photosynthetically fixed carbon of zooxanthellae is not only the major energy source of reef corals, but also can be transported to other organisms through mucus-releasing of corals (Wild *et al*., 2004). This is the main reason that supports coral reefs with high primary production in oligotrophic environment.

Some factors, such as temperature, light and nutrient, appear to regulate the photosynthetic rate of corals (Barnes and Chalker, 1990). Temperature and light not only change on seasonal, daily and hourly time scales but also co-vary, thus confounding their individual effects in field situations. In order to accurately modeling rates of primary production on coral reefs, it is necessary to identify the relationships between temperature and photosynthesis (Morris and Kromkamp, 2003).

Various methods have been used to

[1] Institute of Oceanography, National Taiwan University, Taipei, Taiwan 106, R.O.C.
[2] National Museum of Marine Biology and Aquarium, Pingtung, Taiwan 944, R.O.C.
[3] Institute of Marine Biodiversity and Evolution, National Dong Hwa University, Hualien, Taiwan 974, R.O.C.
* Corresponding author. E-mail: tyfan@nmmba.gov.tw

measure photosynthetic parameters and primary production. PAM (pulse amplitude modulate) chlorophyll fluorescence methods offer an alternative to traditional gas exchange techniques for the non-intrusive analysis of photosynthetic activity (Beer *et al*., 1998; Ralph *et al*., 1999). There is a growing interest in using PAM techniques for making qualitative comparisons of photosynthetic performance under different conditions and for quantifying aquatic productivity. Comparisons of photosynthetic rates estimated from PAM fluorometry and oxygen evolution have been made in a number of marine organisms and linear correlations between these two measurements have been reported (e.g. Figueroa *et al*., 2003; Morris and Kromkamp, 2003). However, few attempts have been made by using electron transport rate (ETR) for quantitative calculations of photosynthetic rates in reef corals (Beer *et al*., 2000; Yakovleva and Hidaka, 2004).

Mesocosms are increasingly being used for coral and coral reef experiments (Atkinson *et al*., 1995; Marubini *et al*., 2001). They provide powerful tools for experimental studies that can not be carried out in natural systems, such as the evaluation of the effects of environmental parameters (e.g. temperature or light intensity) on coral physiology.

In this study, we investigate the effects of temperature on tissue parameters and photosynthesis-irradiance (P-I) curve parameters in the reef coral *Stylophora pistillata* (Esper, 1797) cultured in coral reef mesocosms under controlled temperatures (20, 25 and 28 ℃) for 10 days. Both oxygen evolution and PAM fluorescence methods were applied and the relationship between ETR and gross photosynthesis was examined by comparing the values obtained from these methods.

MATERIALS AND METHODS

Biological materials

Six colonies of the branching zooxanthellate reef coral *Stylophora pistillata* were collected from 6-8 m depth at Nanwan Bay, southern Taiwan (21°56'29"N, 120°44'70"E). Fifteen coral nubbins were removed from each of the 6 colonies (n = 90) and then randomly suspended with nylon lines in 6 mesocosms under the same conditions. After 1 month, coral nubbins were entirely covered with new tissue and were used in temperature experiments.

Maintenance of mesocosms

Temperature experiments were conducted using 6 oval-shaped fiberglass tanks, each with dimensions of 3 m length × 2 m width × 1 m depth. The tanks were located indoors and shaded from direct sunlight. The tanks were filled with seawater pumped from an inshore reef at 5 m depth and filtered through sand filters (50 μm). Approximately 10% of the water was replaced daily with fresh seawater to keep the stability of the mesocosms. Water circulation in each mesocosm was facilitated independently by a 4500 l h^{-1} centrifugal pump. Seawater temperatures were controlled (±1℃) using an automated microcomputer and were recorded by HOBO electronic temperature loggers (Onset Computer Co., MA, USA). Three 400-W metal halide lamps (HQI-BT 400W/D, Osram) provided a constant irradiance of 200 μmol photons $m^{-2}s^{-1}$ (photoperiod 12 : 12 h = light : dark). The lamps could be moved up or down to control the irradiance as required. Light was measured using a LI-COR 193SA spherical quantum sensor attached to a data logger.

Prior to the experimental treatments, the biotic communities in the mesocosms have been established for 4 years. The substratum was a live sand system with a carbonate sand layer separating the main seawater from a layer of confined, stagnant water (Jaubert 1989). Living organisms in the mesocosms were collected from reefs in southern Taiwan. They include scleractinians, alcyonaceans, and coralline algae, as well as surgeonfishes (*Zebrasoma* sp., *Acanthurus* sp.), rabbitfishes (*Siganus* sp.), sea urchins (*Tripneustes gratilla*, *Echinometra mathaei*), sea cucumbers (*Holothuria* (*Mertensionthuria*) *leucospilota*), gastropods (*Trochus* sp.), crustaceans and polychaetes.

Temperature of the 6 mesocosms was originally maintained at 25℃. After experi-

mental nubbins recovered from tissue damage, temperatures of 4 mesocosms were changed gradually, with 2 mesocosms were elevated by 1℃ per 3 days until they reached 28℃ and 2 mesocosms were lowered by 1℃ per 2 days until they reached 20℃. The 2 mesocosms maintained at 25℃ served as the control group. After maintaining at temperature treatments for 10 days, 3 nubbins from each mesocosm were used to measure their photosynthesis parameters by the fluorescence and O_2 evolution methods. Tissue composition of the nubbins was also measured.

Chlorophyll a fluorescence measurements

Fluorescence of coral nubbins was measured using the diving PAM (Walz, Germany). The ratio of variable (F_v) to maximum fluorescence (F_m), F_v/F_m, was used as an indicator of maximum potential quantum yield. Measurements of F_v/F_m were taken following a dark-adaptation period for 30 min (Jones and Hoegh-Guldberg, 1999). Electron transport rates (ETR) were measured under different irradiances (0, 50, 100, 200, 400, 600, 800, 1200 and 1600 μmol photons m^{-2} s^{-1}) based on the function:

$$ETR = Y \times PPFD \times FA \times 0.5,$$

where Y is quantum yields of photosystem II (PSII), PPFD is photosynthetic photon flux density, FA is the estimated fraction of light absorbed by coral (we used 0.84 as the default value), and 0.5 is the estimated value indicates that half of the light is used in PSII (Beer *et al*., 1998; Ralph *et al*., 1999).

The P-I curve parameters were estimated by fitting the model (Jassby and Platt, 1976):

$$ETR = ETR_{max}(1-\exp(-I/I_{k\text{-}ETR})),$$

where ETR_{max} is the maximum electron transport rates, I is the irradiance, $I_{k\text{-}ETR}$ is the sub-saturation irradiance. The α value, the slope of the P-I curve, was obtained from the following relationship: $\alpha = ETR_{max} / I_{k\text{-}ETR}$.

O_2 evolution measurements

Nubbins were placed in a respirometric chamber (390 ml) containing a WTW Cellox 325 oxygen electrode and immersed in a thermostat water bath (20, 25 or 28℃, respectively). The oxygen sensor was calibrated using air-saturated seawater and a saturated solution of sodium sulfite (zero oxygen). The chamber was filled with filtered seawater (0.45 μm) and the incubation medium was continuously stirred with a stirring bar. Nubbins were incubated for 20 min under their corresponding culture irradiance (0, 50, 100, 200, 400, 600, 800, 1200, 1600 and 0 μ mol photons m^{-2} s^{-1}). Light was attenuated to the desired intensity by changing the elevation between the lamp and the chamber. Oxygen was recorded every 60 s. Rates of photosynthesis and respiration were estimated using a linear regression of oxygen data against time.

Descriptive parameters of the P-I curves were estimated by fitting the data to an exponential function using a non-linear regression technique (Romaine *et al*., 1997):

$$P_n = P^g_{max}〔1-\exp(-I/I_k)〕 + R,$$

where P_n is net photosynthetic rate, P^g_{max} is gross maximum photosynthetic rate, I is irradiance, I_k is irradiance at which initial slope (α) intersects light-saturation rate (P^g_{max}; μmol $m^{-2}s^{-1}$), and R is respiration rate. The α value, the slope of the P-I curve, was obtained using the following function: $\alpha = P^g_{max}/I_k$.

Finally, the nubbins were frozen at -20℃ over night, then the zooxanthellae density, chlorophyll a concentration, protein concentration and surface area were measured.

Determination of zooxanthellae density, chlorophyll a content and protein

A jet of filtered seawater (0.45 μm) was used to collect the nubbin tissue and homogenized to 70 ml (Johannes and Wiebe, 1970). Ten ml of the tissue was used to determine the density of zooxanthellae by using a hemocytometer, 30 ml was used to quantify chlorophyll *a* and *c* concentrations, and 30 ml was used for protein analysis. For

chlorophyll a and c concentrations, the tissue was filtered by GF/C filter and 100% acetone was used to extract chlorophyll at 4℃ for 24 h, then calculated using the equations of Jeffrey and Humphrey (1975). For protein analysis, 30 ml was filtered by GF/C filter and solublized using 1*N* NaOH at 90℃ for 30 min. Total protein content was measured with a Coomassie Brilliant Blue assay (Bradford, 1976).

Determination of surface area

Surface area of nubbins was determined using melted wax maintained at 65°C in a water bath (Stimson and Kinzie, 1991). Nubbins were dipped in the melted wax for 5 s, weighed, and then dipped in the wax and weighed again. The difference between the first and the second weight allows the surface area to be calculated by comparing with standardized cubes of known surface area (Stimson and Kinzie, 1991).

Statistical analyses

Data from the same temperature treatment were pooled since most parameters of nubbins from 2 mesocosms of the same temperature treatment were not statistically different (Mann Whitney test, most $p > 0.05$, with few $p = 0.05$). The effect of temperature was examined using the Kruskal-Wallis test. Statistical analysis was performed using StatView 5.01. Data are reported as mean ± standard error.

RESULTS

After coral nubbins of *Stylophora pistillata* grew at different temperature treatments for 10 d, tissue parameters including protein concentration (0.389 - 0.491 mg cm^{-2}), chlorophyll *a* concentration (12.519 - 17.878 μg cm^{-2}), zooxanthellae concentration (3.171 - 4.087 10^6 cells cm^{-2}), ratio of chlorophyll *a* to protein (32.427 - 40.402 μg mg^{-1}), chlorophyll *a* per zooxanthellae (4.108 - 4.413 pg $cell^{-1}$), zooxanthellae per unit protein (7.463 - 9.349 10^6 cells mg^{-1}) and the ratio of chlorophyll a to c (2.926 - 3.172) were not statistically different among different temperature treatments (Table 1).

The 3 P-I curves of gross photosynthetic rates versus irradiance under different temperature treatments display a similar pattern (Fig. 1A, B, C). All parameters of photosynthesis were not significantly different among temperature treatments (Table 2). The sub-saturation irradiance (I_k) and the photosynthesis to respiration ratio ranged from 245.5 to 283.7 μmol quanta m^{-2} s^{-1} and from 3.2 to 3.6, respectively. F_v/F_m (0.681 - 0.717) and photosynthetic efficiency (α, 0.167 - 0.205 μmol electrons μmol $quanta^{-1}$) measured by PAM were not significantly different under all treatments (Table 3).

The P-I curve of relative ETR versus irradiance at 25 and 28℃ (Fig. 1D, E) shows different pattern from that at 20℃ (Fig. 1F). ETR_{max} at 25 and 28℃ (Table 3, 63.037 and 66.546 μmol electrons m^{-2} s^{-1}, respectively) were two times higher than that at 20℃ (33.091 μmol electrons m^{-2} s^{-1}). In addition, the sub-saturation irradiance ($I_{k\text{-}ETR}$) at 25 and 28℃ (330.4 and 439.9 μmol quanta m^{-2} s^{-1}, respectively) was significantly higher than that at 20℃ (192.4 μmol quanta m^{-2} s^{-1}).

Linear relationships between gross photosynthesis rate (GP) and ETR were found under light intensity lower than 400 μmol photons m^{-2} s^{-1} or GP smaller than 14 μmol O_2 m^{-2} s^{-1} (Fig. 2). The slopes (2.91-3.33) of these regression lines were similar among different temperature treatments (Kruskal-Wallis test, $H = 0.813$, $p > 0.05$). However, deviations from linearity occurred at light intensity higher than 400 μmol photons m^{-2} s^{-1} or GP higher than 14 μmol O_2 m^{-2} s^{-1}.

DISCUSSION

The F_v/F_m, tissue composition and photosynthetic parameters based on O_2 evolution of *Stylophora pistillata* were not significantly different among three temperature treatments for 10 days. These results indicate that the physiological condition of the organisms assessed is healthy.

The P : R ratios obtained for *S. pistillata* in this study (3.2-3.6) were higher than those measured in other studies using this species

Table 1. Coral tissue parameters of reef coral *Stylophora pistillata* after temperature treatment for 10 days and the results of Kruskal-Wallis analysis.

	20°C			25°C			28°C					
Response parameter	Mean	SE	n	Mean	SE	n	Mean	SE	n	H	P	
Tissue composition												
Protein (mg cm^{-2})	0.389	0.090	6	0.491	0.130	6	0.445	0.080	6	3.61	0.16	ns
Chlorophyll a (µg cm^{-2})	12.519	2.380	6	16.466	6.764	6	17.878	5.274	6	4.26	0.12	ns
Zooxanthella concentration (10^6 cells cm^{-2})	3.171	0.717	6	3.714	1.237	6	4.087	0.694	6	2.47	0.29	ns
Ratio of chlorophyll a to protein (µg mg^{-1})	32.693	5.333	6	32.427	6.415	6	40.402	10.406	6	3.19	0.20	ns
Chlorophyll a per zooxanthella (pg $cell^{-1}$)	4.108	1.047	6	4.336	0.525	6	4.413	1.127	6	0.33	0.85	ns
Zooxanthellae per unit protein (10^6 cells mg^{-1})	8.264	1.721	6	7.463	1.051	6	9.349	1.999	6	2.82	0.24	ns
Ratio of chlorophyll a to *c*	2.970	0.215	6	2.926	0.094	6	3.172	0.389	6	0.88	0.64	ns

ns: not significant

Table 2. The oxygen-based estimates of photosynthetic parameters of reef coral *Stylophora pistillata* using different normalized methods after temperature treatment for 10 days and the results of Kruskal-Wallis analysis.

	20°C			25°C			28°C					
Response parameter	Mean	SE	n	Mean	SE	n	Mean	SE	n	H	P	
Photosynthetic parameters (from respirometer)												
P^g_{max} (μmol O_2 h^{-1}) per cm^2	4.972	0.872	6	6.129	1.714	6	6.629	0.470	6	5.24	0.07	ns
P^g_{max} (μmol O_2 h^{-1}) per mg protein	13.022	2.310	6	12.845	3.778	6	15.283	2.956	6	3.61	0.16	ns
P^g_{max} (μmol O_2 h^{-1}) per mg chlorophyll a	410.561	121.432	6	414.466	172.926	6	392.510	92.269	6	0.43	0.81	ns
P^g_{max} (μmol O_2 h^{-1}) per 10^6 cells	1.599	0.261	6	1.728	0.499	6	1.653	0.250	6	0.08	0.96	ns
α (nmol O_2 h^{-1} (μmol quanta m^{-2} $s^{-1})^{-1}$) per cm^2	20.571	3.425	6	21.633	6.109	6	24.720	2.977	6	2.82	0.24	ns
α (nmol O_2 h^{-1} (μmol quanta m^{-2} $s^{-1})^{-1}$) per mg protein	54.763	13.305	6	45.573	14.655	6	56.579	9.799	6	2.33	0.31	ns
α (μmol O_2 h^{-1} (μmol quanta m^{-2} $s^{-1})^{-1}$) per mg chlorophyll a	1.720	0.576	6	1.481	0.678	6	1.451	0.313	6	2.11	0.35	ns
α (nmol O_2 h^{-1} (μmol quanta m^{-2} $s^{-1})^{-1}$) per 10^6 cells	6.783	1.978	6	6.153	2.021	6	6.217	1.432	6	0.61	0.74	ns
R (-μmol O_2 h^{-1}) per cm^2	0.808	0.206	6	0.919	0.307	6	1.040	0.230	6	2.82	0.24	ns
R (-μmol O_2 h^{-1}) per mg protein	2.090	0.338	6	1.982	0.867	6	2.407	0.704	6	0.85	0.65	ns
R (-μmol O_2 h^{-1}) per mg chlorophyll a	64.536	8.986	6	66.403	39.004	6	61.770	21.353	6	0.57	0.75	ns
R (-μmol O_2 h^{-1}) per 10^6 cells	0.267	0.087	6	0.272	0.129	6	0.256	0.050	6	0.01	0.99	ns
I_k (μmol quanta m^{-2} s^{-1})	245.465	46.753	6	283.764	16.077	6	270.576	29.564	6	2.71	0.26	ns
I_c (μmol quanta m^{-2} s^{-1})	97.754	30.450	6	101.591	28.052	6	102.538	27.808	6	0.22	0.89	ns
Ratio of photosynthesis to respiration	3.218	0.803	6	3.619	1.101	6	3.270	0.705	6	0.36	0.83	ns

ns: not significant

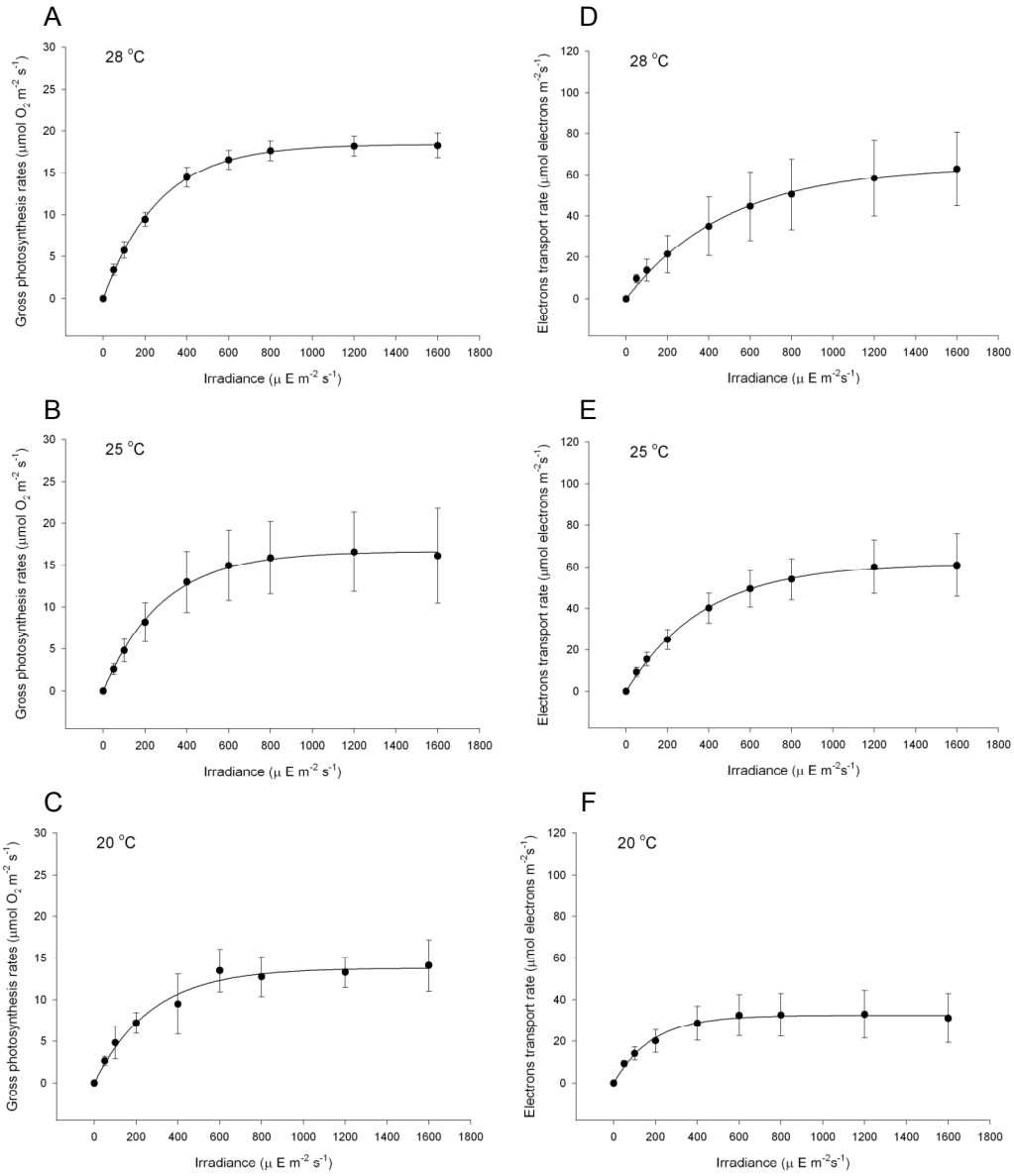

Fig. 1. Gross photosynthetic rate and electron transport rate as a function of the irradiance measured for reef coral, *Stylophora pistillata*, cultured at different temperatures for 10 days. (A) 28℃, (B) 25℃, (C) 20℃, (D) 28℃, (E) 25℃, (F) 20℃. (mean ± SE, n = 6)

(1.10-1.76 in Porter *et al*., 1984; 0.9-1.5 in Ferrier-Pages *et al*., 1999). The high P : R ratios suggest that the amount of carbon fixed by photosynthesis highly exceeds the basal metabolic demands.

The effect of temperature on ETR_{max} and $I_{k\text{-}ETR}$ was significantly different between treatments. It suggests that the photosynthetic process of PSII electron transport rate is more sensitive to temperatures compared with the rate of oxygen evolution. The most prominent effect of temperature on photosynthesis in *S. pistillata* occurred between 20 and 25-28℃, where the ETR_{max} and $I_{k\text{-}ETR}$ increase with increasing temperatures. A possible explanation is that the corals in this

Table 3. The fluorescence-based estimates of photosynthetic parameters of reef coral *Stylophora pistillata* after temperature treatment for 10 days and the results of Kruskal-Wallis analysis.

	20℃			25℃			28℃				
Response parameter	Mean	SE	n	Mean	SE	n	Mean	SE	n	H	P
Photosynthetic parameters (from PAM)											
F_v/F_m	0.681	0.039	6	0.681	0.042	6	0.717	0.027	6	3.28	0.19 ns
ETR_{max} (μmol electrons m^{-2} s^{-1})	33.091[a]	11.157	6	63.037[b]	17.044	6	66.546[b]	18.256	6	8.67	<0.05 *
α_{-ETR} (μmol electrons μmol quanta^{-1})	0.205	0.031	6	0.168	0.038	6	0.167	0.044	6	3.19	0.20 ns
$I_{k\text{-}ETR}$ (μmol quanta m^{-2} s^{-1})	192.402[a]	76.831	6	330.400[b]	24.029	6	439.912[b]	75.775	6	12.98	<0.01 **

ns: not significant, *p < 0.05, **p < 0.01, [abc]means with different letters are significantly different at $p < 0.05$

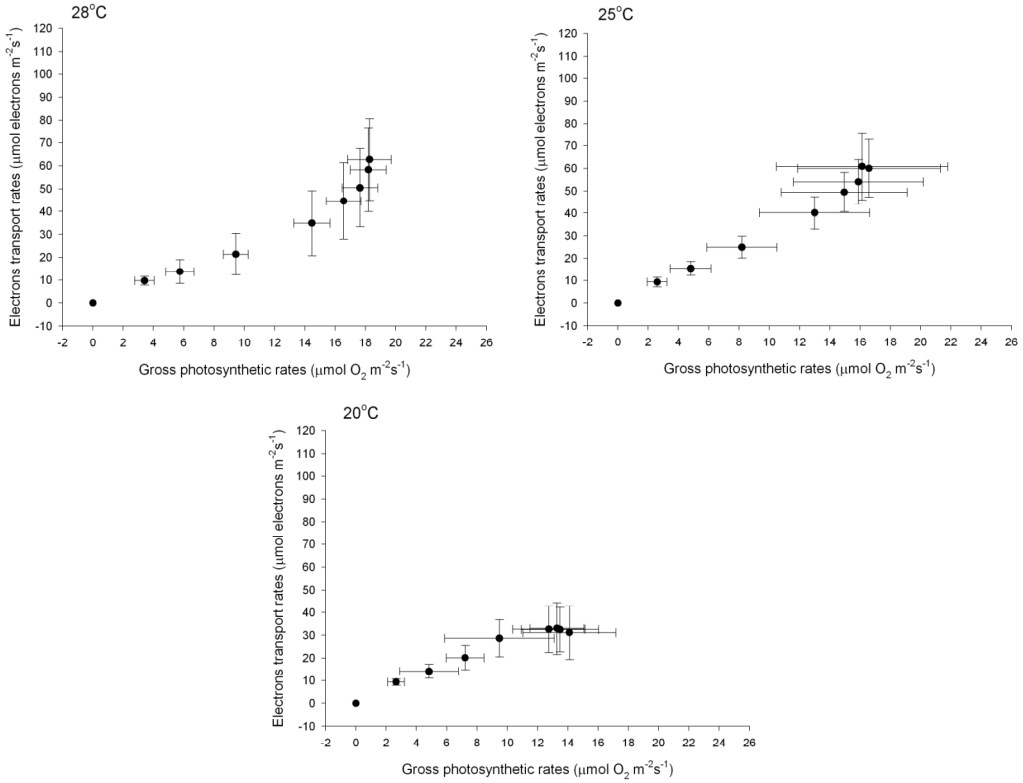

Fig. 2. The relationship between electron transport rates (ETR) and gross photosynthetic rates (GP) of reef coral *Stylophora pistillata*. (mean ± SE, n = 6)

study had been adapted to the temperatures in the field (mean temperatures ranged 23-28℃).

ETR_{max} of *S. pistillata* in this study were low (33-66μmol electrons $m^{-2}s^{-1}$) as comparing with those of other species (e.g. ETR_{max} of *Acropora aspera*, *Goniastrea* sp. and *Porites* sp. measured in the field were 180 to 270 μmol electrons $m^{-2}s^{-1}$, Ralph *et al.*, 1999). The low photosynthetic capacity of *S. pistillata* is possibly due to its adaptation to the low-light conditions at 200 μmol quanta $m^{-2}s^{-1}$ in the mesocosms.

ETR_{max} of *S. pistillata* at 25 and 28℃ was two times higher than that at 20℃. Morris and Kromkamp (2003) suggested that, within favorable temperatures, the ETR_{max} increases with increasing temperature and this response may be modulated by photorespiration.

The sub-saturation irradiance ($I_{k\text{-}ETR}$) of

S. pistillata was higher at 28 and 25℃ than that at 20℃, suggesting that low temperature may reduce the sub-saturation irradiance.

A similar linear relationship between gross photosynthesis rate (GP) and ETR was found under irradiances below 400 μE $m^{-2}s^{-1}$ or GP less than 14 μmol O_2 $m^{-2}s^{-1}$ within the temperatures ranged from 20 to 28℃. It suggests that the seasonal variation of seawater temperatures in the field, as *S. pistillata* experienced in Nanwan Bay, southern Taiwan, is not likely to affect the relationship between GP and ETR. Yakovleva and Hidaka (2004) reported that a significant linear correlation between rETR and O_2 evolution was found at irradiance up to 500-550 μmol photons m^{-2} s^{-1} in the reef corals, *Montipora digitata* and *Pavona divaricata*. These evidences suggest that diving-PAM provides a quick and reliable way to estimate primary productivity of some coral species at least under moderate irradiances.

Above the saturating irradiance for photosynthesis, the relationship between GP and ETR was curvilinear. This may be because the ETR was saturated at higher light intensity than GP, due to the possible alternative electron sinks in the photosynthetic processes (Franklin and Badger, 2001; Figueroa *et al*., 2003; Morris and Kromkamp, 2003). Such a deviation was more evident at 28℃ treatment possibly because the differences in enzyme activities under various temperature conditions (Saxby *et al*., 2003). Morris and Kromkamp (2003) proposed that this non-linearity is more apparent at irradiances exceeding the saturating irradiance for photosynthesis, and could be due to alternative electron sinks such as the Mehler ascorbate-peroxidase reaction and photorespiration, or to changes in the optical cross-section.

ACKNOWLEDGEMENTS

This study was supported by a grant from the National Science Council, R. O. C. (NSC 92-2311-B-291-006).

REFERENCES

Atkinson, M. J., B. Carlson and G. L. Crow (1995). Coral growth in high-nutrient, low-pH seawater: a case study of corals cultured at the Waikiki Aquarium, Honolulu, Hawaii. *Coral Reefs*, **14**: 215-223.

Barnes, D. J. and B. E. Chalker (1990). Calcification and photosynthesis in reef-building corals and algae. In Ecosystems of the world 25: Coral reefs (Z. Dubinsky, ed.). Elsevier, Amsterdam, 109-131.

Beer, S., M. Ilan, A. Eshel, A. Weil and I. Brickner (1998). Use of pulse amplitude modulated (PAM) fluorometry for in situ measurements of photosynthesis in two Red Sea faviid corals. *Mar. Biol.*, **131**: 607-612.

Beer, S., C. Larsson, O. Poryan and L. Axelsson (2000). Photosynthetic rates of *Ulva* (Chlorophyta) measured by pulse amplitude modulated (PAM) fluorometry. *Eur. J. Phycol.*, **35**: 69-74.

Bradford, M. (1976). A rapid and sensitive method for the quantitation of microgram quantities of protein utilizing the principle of protein dye binding. *Anal. Biochem.*, **72**: 248-254.

Ferrier-Pages, C., J. P. Gattuso and J. Jaubert (1999). Effect of small variations in salinity on the rates of photosynthesis and respiration of the zooxanthellate coral *Stylophora pistillata*. *Mar. Ecol. Prog. Ser.*, **181**: 309-314.

Figueroa, F. L., R. Conde-Álvarez and I. Gómez (2003). Relations between electron transport rates determined by pulse amplitude modulated chlorophyll fluorescence and oxygen evolution in macroalgae under different light conditions. *Photosynth. Res.*, **75**: 259-275.

Franklin, L. A. and M. R. Badger (2001). A comparison of photosynthetic electron transport rates in macroalgae measured by pulse amplitude modulated chlorophyll fluorometry and mass spectrometry. *J. Phycol.*, **37**: 756-767.

Jassby, A. D. and T. Platt (1976). Mathematical formulation of the relationship between photosynthesis and light for phytoplankton. *Limnol. Oceanogr.*, **21**: 540-547.

Jaubert, J. (1989). An integrated nitrifying-denitrifying biological system capable of purifying sea water in a closed circuit aquarium. *Bull. Inst. Océanogr. Monaco*, **5** (special): 101-106.

Jeffrey, S. W. and G. P. Humphrey (1975). New spectrophotometric equations for determining chlorophylls a, b, c1 and c in higher plants,

algae and natural phytoplankton. *Biochem. Physiol. Pflanzen*, **167**: 191-194.

Johannes, R. E. and W. J. Wiebe (1970). Method for determination of coral tissue biomass and composition. *Limnol. Oceanogr.*, **15**: 822-824.

Jones, R. J. and O. Hoegh-Guldberg (1999). Effects of cyanide on coral photosynthesis: implications for identifying the cause of coral bleaching and for assessing the environmental effects of cyanide fishing. *Mar. Ecol. Prog. Ser.*, **177**: 83-91.

Marubini, F., H. Barnett, C. Langdon and M. J. Atkinson (2001). Dependence of calcification on light and carbonate ion concentration for the hermatypic coral *Porites compressa*. *Mar. Ecol. Prog. Ser.*, **220**: 153-162.

Morris, E. P. and J. C. Kromkamp (2003). Influence of temperature on the relationship between oxygen- and fluorescence-based estimates of photosynthetic parameters in a marine benthic diatom (*Cylindrotheca closterium*). *Eur. J. Phycol.*, **38**: 133-142.

Porter, J. W., L. Muscatine, Z. Dubinsky and P. G. Falkowski (1984). Primary production and photoadaptation in light- and shade-adapted colonies of the symbiotic coral, *Stylophora pistillata*. *Proc. R. Soc. London B*, **222**: 161-180.

Ralph, P. J., R. Gademann, A. W. D. Larkum and U. Schreiber (1999). In situ underwater measurements of photosynthetic activity of coral zooxanthellae and other reef-dwelling dinoflagellate endosymbionts. *Mar. Ecol. Prog. Ser.*, **180**: 139-147.

Romaine, S., E. Tambutte, D. Allemand and J. P. Gattuso (1997). Photosynthesis, respiration and calcification of a zooxanthellate scleractinian coral under submerged and exposed conditions. *Mar. Biol.*, **129**: 175-182.

Saxby, T., W. C. Dennison and O. Hoegh-Guldberg (2003). Photosynthetic responses of the coral *Montipora digitata* to cold temperature stress. *Mar. Ecol. Prog. Ser.*, **248**: 85-97.

Stimson, J. and R. A. Kinize III (1991). The temporal pattern and rate of release of zooxanthellae from the reef coral *Pocillopora damicornis* (Linnaeus) under nitrogen-enrichment and control conditions. *J. Exp. Mar. Biol. Ecol.*, **153**: 63-74.

Wild, C., M. Huettel, A. Klueter, S. G. Kremb, M. Y. M. Rasheed and B. B. Jorgensen (2004). Coral mucus functions as an energy carrier and particle trap in reef ecosystem. *Nature*, **428**: 66-70.

Wu, T. Y. (2004). The effects of temperature and light intensity on the photosynthesis in reef coral *Stylophora pistillata*. M. Sc. theses, Institute of Oceanography, National Taiwan University, Taipei. 47pp.

Yakovleva, I. and M. Hidaka (2004). Differential recovery of PSII function and electron transport rate in symbiotic dinoflagellates as a possible determinant of bleaching susceptibility of corals. *Mar. Ecol. Prog. Ser.*, **268**: 43-53.

溫度對萼柱珊瑚光合作用的影響：溶氧法與螢光法的比較

吳岱穎[1]・戴昌鳳[1]・樊同雲[2,3]*

(2006 年 8 月 25 日收件；2006 年 9 月 5 日接受)

本研究利用呼吸儀和水下螢光儀(diving pulse amplitude modulate, Diving PAM)以及測量珊瑚組織參數，包括蛋白質濃度、葉綠素 *a* 濃度和共生藻密度等方法，探討萼柱珊瑚(*Stylophora pistillata*)在不同溫度(20、25、28℃)珊瑚礁中型生態箱養殖 10 天對其光合作用的影響。結果發現各項組織參數、呼吸儀測得的最大總光合作用速率(P^g_{max})、光合作用效率(α)和半飽和光照(I_k)，以及水下螢光儀測得的光合作用效率(α)及光系統 II 的光化學效率(F_v/F_m)等都無顯著差異。然而，25 和 28℃ 下珊瑚的最大電子傳遞速率(ETR_{max})和半飽和光照($I_{k\text{-}ETR}$)皆顯著高於 20℃ 的珊瑚，顯示光系統 II 的電子傳遞速率對溫度的反應較敏感，並且最大電子傳遞速率和半飽和光照隨溫度上升而增加。此外，在 3 種溫度下，當光照強度低於 400 μE $m^{-2}s^{-1}$，或是總光合作用速率(gross photosynthesis rate, GP)低於 14 μmol O_2 $m^{-2}s^{-1}$ 時，GP 與 ETR 都呈現直線關係，顯示在中等強度的光照環境下，水下螢光儀可能具有以非破壞方式快速估計珊瑚初級生產力的潛力。

關鍵詞：螢光法，光合作用，造礁珊瑚，*Stylophora pistillata*，溫度。

[1] 國立台灣大學海洋研究所
[2] 國立海洋生物博物館
[3] 國立東華大學海洋生物多樣性及演化研究所
* 通訊作者