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Combined effects of irradiance and temperature on the *PSII* photochemical efficiency in the heteromorphic life history stages of cultivated *Pyropia* (Bangiales): *P. yezoensis* f. *narawaensis* and *P. tenera* from Japan

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Abstract

The combined effects of irradiance and temperature on photosystem II (*PSII*) photochemical efficiency were investigated in the microscopic sporophyte and macroscopic gametophyte stages of the cultivated red algae *Pyropia yezoensis* f. *narawaensis* and *Pyropia tenera* (Bangiales) from Kyushu Island, Japan. Continuous 12-h exposures to 10, 100, and 1000 μmol photons m^{-2} s^{-1} at 8, 20, and 28 °C revealed that sporophyte and gametophyte stages of both species have different tolerance characteristics to irradiance and temperature. Effective quantum yields (Φ_{PSII}) of sporophytes declined at 100 and 1000 μmol photons m^{-2} s^{-1}, and their maximum quantum yields (F_v/F_m) did not fully recover even after 12 h of dark acclimation, indicating photodamage. Furthermore, this depression was greatest at 8 °C, suggesting low temperature-enhanced photoinhibition. Larger declines of Φ_{PSII} and subsequent failure of F_v/F_m recovery in the gametophyte were observed only at 1000 μmol photons m^{-2} s^{-1}, suggesting that the macroscopic stage is more tolerant to relatively higher irradiance than the sporophyte. Farming protocols, including the timing of conchospore seeding, as well as depth range and duration for Nori-net cultivation need to be optimized to ensure sustainable production of these high-valued seaweed cultivars.

Keywords Algae · Nori · Photochemical efficiency of *PSII* · Pulse amplitude-modulation (PAM)-chlorophyll fluorometry · *Pyropia*

Introduction

Species of *Pyropia* (Bangiales) are an important edible resource in east Asian countries, particularly in Japan. The country's annual production of Nori (*Pyropia* in Japanese) has been reported to be approximately 60,000 t dry weight (=340,000 t wet weight), with a value of 80 billion JPY (Ohno and Largo 1998; Zemke-White and Ohno 1999; Thomas 2002; Kikuchi 2012). Nori cultivation has been widely practiced in the temperate regions of Kyushu, Honshu, and Shikoku islands, Japan; Kyushu Island is the main production area of Nori, supporting more than 50% of the annual production.

After the discovery of its heteromorphic life history that features the alternation between microscopic sporophyte (known as the *conchocelis*-phase) and macroscopic gametophyte (Drew 1949, 1954), modern techniques for Nori cultivation were highly improved in the 1960–1980s, including the

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development of artificial seeding and Nori-net frozen storage technique (Watanabe et al. 2017) to store gametophytes. Typically, tank cultures of the sporophyte are carried out during early summer through autumn under controlled conditions (e.g., irradiance, photoperiod, and temperature) in land-based facilities. Subsequent conchospore seeding and Nori-net (gametophyte) cultivation is conducted during autumn through winter in the sea surface of the cultivation field (Oohbusa 1993). These cultivation methods made it possible to maintain relatively high and stable harvests of Nori (Iwasaki 1961; Migita 1964, 1966; Terumoto 1965; Tajiri and Aruga 1984; Miura 1988; Oohbusa 1993).

Recent studies of *Pyropia*, which employ methods based on pulse amplitude-modulation (PAM)-chlorophyll fluorometry and/or dissolved oxygen evolution, have revealed its physiological response to various environmental states during Nori cultivation (Wang et al. 2011; Zhang et al. 2012, 2014; Watanabe et al. 2014, 2016, 2017). For instance, temperature optima for photosynthesis were found to vary between the two life history stages of *Pyropia yezoensis* (Ueda) Hwang and Choi, and *Pyropia tenera* (Kjellman) Kikuchi et al.; the differences were most likely related to their respective seasonal occurrences (Watanabe et al. 2014, 2016). However, in these previous studies, we focused only on the effect of a single environmental factor (i.e., temperature or irradiance); their combined effect remained to be elucidated. In many cases, the impact of any particular stressor on the photosynthetic performance and growth of macroalgae will depend upon the presence and magnitude of additional limiting or disruptive stressors (Borlongan et al. 2016, 2018; Terada et al. 2018).

The present study was conducted to examine the response of the photosystem II (*PSII*) photochemical efficiency of the two life history stages of cultivated *Pyropia*, *P. yezoensis* f. *narawaensis*, and *P. tenera* when exposed to different combinations of irradiance and temperature. It is the continuation of our earlier studies (Watanabe et al. 2014, 2016, 2017) to provide a complete and modern perspective regarding the response of photosynthetic activity during commercial Nori cultivation by using PAM fluorometry.

Materials and methods

Sample collection

The samples of *Pyropia yezoensis* f. *narawaensis* (*PYEZO*; Saga #5 Strain, Kawamura et al. 1991; Watanabe et al. 2016) and *P. tenera* (*PTENE*; Noguchi Strain, Watanabe et al. 2014) examined in the present study were obtained from cultivar strains developed by the Saga Prefectural Ariake Fisheries Research and Development Center (SAFREDEC), Saga Prefecture, Japan, and by the Kagoshima Prefectural Fisheries Technology and Development Center (KPFTDC), Kagoshima Prefecture, Japan, respectively.

The sporophytes of these two species were originally from the in vitro stock culture strains of each institution. To seed the sporophytes onto the dead oyster shells, roughly separated free-living sporophytes were distributed on the shells in an indoor aquarium tank (ca. 20–1000 L) at each institution on 17 April (SAFREDEC) and 24 May (KPFTDC) 2017, respectively. The sporophytes that attached to the shells were then cultured in the aquarium tank containing sterile enriched seawater (Noriseed, Daiichi Seimo Co. Ltd., Kumamoto, Japan), at ambient water temperature (i.e., 14–28 °C) and irradiance of around 10–40 μmol photons m^{-2} s^{-1} (Watanabe et al. 2014, 2016). The photoperiod was identical with the natural photoperiod from spring to autumn (12L:12D–14L:10D). Culture medium was changed almost every 4 weeks during the 5-month culture period.

Oyster shells (10 shells for *PYEZO*; 5 shells for *PTENE*) with attached sporophytes were randomly selected, placed into separate plastic bottles (1000 mL), and then transported to Kagoshima University on 25 (*PYEZO*; Saga) and 29 (*PTENE*; Kagoshima) September 2017. Upon arrival in the laboratory, each shell was placed in 500 mL flasks containing modified 1/2 SWM-III medium (Ogata 1970; Fujiyoshi and Kikuchi 2006). They were maintained for a few days in an incubator with irradiance and temperature conditions similar during tank cultivation.

The macroscopic gametophytes of *PYEZO* and *PTENE* were collected from the "autumn batch" of Nori-nets (Watanabe et al. 2017) at SAFREDEC farm site in Ariake Bay (33° 11 ′47″ N, 130° 12′ 31 ″ E) on 29 November 2017, and at Fukunoe in Yatsushiro Bay (32° 6′ 40″ N, 130° 18′ 20″ E) on 7 January 2018, respectively. These germlings come from conchospores that were derived from the tank-cultured sporophytes, and seeded onto nets in October 2017. In this sense, the sporophytes and gametophytes used in our experiments were from the same strain (Watanabe et al. 2014, 2016). The collected gametophytes were stored in plastic bags, and were transported directly to the laboratory of Kagoshima University in a cooler at approximately 12 °C. The samples were maintained for 1 to 4 days before examination in flasks (500 mL) containing modified 1/2 SWM-III medium. The flasks were placed in an incubator set at 12 °C, and irradiance of 90 μmol photons m^{-2} s^{-1} (12:12 h light: dark cycle). (Note: difference in the gametophyte collection period was due to the difference in the duration of cultivation at the two sites. Given the different collection periods of the gametophytes for each species, temperature and light stress experiments on *PTENE* were carried out later than *PYEZO*.)

Temperature and light stress experiments

The combined effects of irradiance and temperature on quantum yields of *PYEZO* and *PTENE* were determined at 18 treatments, based on the combinations of two life-history stages, three irradiances (10, 100, and 1000 μmol photons m^{-2} s^{-1}) and three temperatures (8, 20, and 28 °C). Mini Imaging-PAM (Heinz Walz GmbH, Germany) measurements followed the procedures from our previous studies (Watanabe et al. 2014, 2016, 2017; Borlongan et al. 2018; Terada et al. 2018).

Randomly selected gametophytes (on the dead oyster shells) and sporophytes were prepared to provide 10 replicates for each irradiance-temperature treatment group. Samples were initially incubated at each temperature condition (8 °C, 20 °C, and 28 °C) overnight (12 h) in the dark; and their maximum quantum yields of *PSII* ($F_v/F_m = [F_m - F_o] / F_m$) were measured to provide initial values ($n = 10$ per treatment). Specimens were then placed in separate beakers (500 mL) containing sterile natural seawater maintained at a specific temperature in a water bath, and were exposed to either 10, 100 or 1000 μmol photons m^{-2} s^{-1} (metal-halide lamp; MHN-150D-S, Nichido Ind. Co. Ltd., Osaka, Japan) for 12 h. Water in the beakers was continuously stirred throughout the exposure. Effective quantum yields ($\Phi_{PSII} = [F_m' - F] / F_m'$) were measured every 1 or 2 h of continuous exposure to each irradiance/temperature treatment ($n = 10$ per treatment). Following the experiment, specimens were once more dark-acclimated overnight (i.e., 12 h, corresponding to the night period under natural conditions) at their respective temperatures; and their final F_v/F_m were measured to confirm the possibility of recovery.

In quantum yield (F_v/F_m; Φ_{PSII}) measurements, each specimen was placed in a stainless-steel tray (12 × 10 × 3 cm) containing sterilized natural seawater. The tray was then placed on top of a block incubator (BI-536T, Astec, Japan) for temperature control. A thermocouple (testo 925, Testo AG, Germany) was used to confirm the water temperature.

Statistical analyses

Statistical analyses were done using R version 3.3.3 (R Development Core Team 2017). A one-way ANOVA was used to examine if continuous irradiance exposures affected Φ_{PSII} for each irradiance and temperature treatment. Time was considered a factor with levels: 0, 12, and 24 h after the start of the experiment (i.e., initial F_v/F_m, Φ_{PSII} after 12 h, and the final F_v/F_m after 12 h of darkness).

Results

Responses of the *PSII* photochemical efficiency over 12 h of continuous exposures to 10, 100 and 1000 μmol photons m^{-2} s^{-1} at 8, 20, and 28 °C, and recovery after a 12-h dark acclimation period varied in the two life history stages of *PYEZO* and *PTENE* (Figs. 1 and 2).

***P. yezoensis* (PYEZO)** Quantum yields of *PYEZO* sporophyte throughout the 10 μmol photons m^{-2} s^{-1} irradiance exposure and after dark acclimation were stable at 0.43–0.49 on all temperature treatments (Fig. 1a). Responses of *PYEZO* gametophyte to such irradiance were likewise steady at 0.42–0.51 at 8 °C, 0.41–0.45 at 20 °C, and 0.38–0.43 at 28 °C, respectively (Fig. 1b).

Under 100 μmol photons m^{-2} s^{-1}, quantum yields of the sporophyte significantly decreased ($P < 0.0001$) from initial F_v/F_m of 0.46 ± 0.005 to Φ_{PSII} of 0.19 ± 0.012 at 8 °C, from 0.49 ± 0.007 to 0.27 ± 0.024 at 20 °C, and from 0.44 ± 0.011 to 0.28 ± 0.025 at 28 °C (Fig. 1c). Despite the rise in their respective post-dark acclimation F_v/F_m, values were still significantly different ($P < 0.0001$) from initial on all temperature treatments. As for the gametophyte, only their quantum yields at 28 °C decreased from 0.39 ± 0.017 to 0.31 ± 0.060 (Fig. 1d); those at 8 and 20 °C increased from 0.46 ± 0.011 to 0.52 ± 0.032, and 0.32 ± 0.005 to 0.40 ± 0.022, respectively. Final F_v/F_m after 12 h of dark acclimation was restored to initial values on all temperature treatments.

Significant declines in quantum yields ($P < 0.0001$) were observed for both sporophyte and gametophyte stages of *PYEZO* exposed to 1000 μmol photons m^{-2} s^{-1} on all temperature treatments (Fig. 1e, f). Their post-dark acclimation F_v/F_m also remained significantly low ($P < 0.0001$).

***P. tenera* (PTENE)** Photoinhibition-recovery responses of *PTENE* sporophyte and gametophyte were similar to those of *PYEZO*, with relatively uniform quantum yields throughout the 10 μmol photons m^{-2} s^{-1} irradiance exposure on all temperature treatments (Fig. 2a, b).

Under 100 μmol photons m^{-2} s^{-1}, quantum yields of the sporophyte significantly declined ($P < 0.0001$) from initial F_v/F_m of 0.39 ± 0.008 to Φ_{PSII} of 0.13 ± 0.007 at 8 °C, from 0.41 ± 0.006 to 0.23 ± 0.011 at 20 °C, and from 0.37 ± 0.017 to 0.23 ± 0.015 at 28 °C (Fig. 2c). Although their final F_v/F_m increased, values were still significantly different ($P < 0.0001$) from initial on all temperature treatments. As for the gametophyte, quantum yields at 8 and 20 °C remained the same as their initial values (Fig. 2d), while those at 28 °C significantly dropped ($P < 0.0001$) from 0.35 ± 0.015 to 0.19 ± 0.009. F_v/F_m after 12 h dark acclimation (0.34 ± 0.023) almost recovered to initial.

Quantum yields of *PTENE* sporophyte and gametophyte exposed to 1000 μmol photons m^{-2} s^{-1} decreased ($P < 0.0001$) on all temperature treatments. Final F_v/F_m of the sporophyte remained low ($P < 0.0001$) at 0.01–0.13 (Fig. 2e, f). Despite the rise in post-dark acclimation F_v/F_m of the gametophyte at 8 °C (0.34 ± 0.014) and 20 °C (0.33 ±

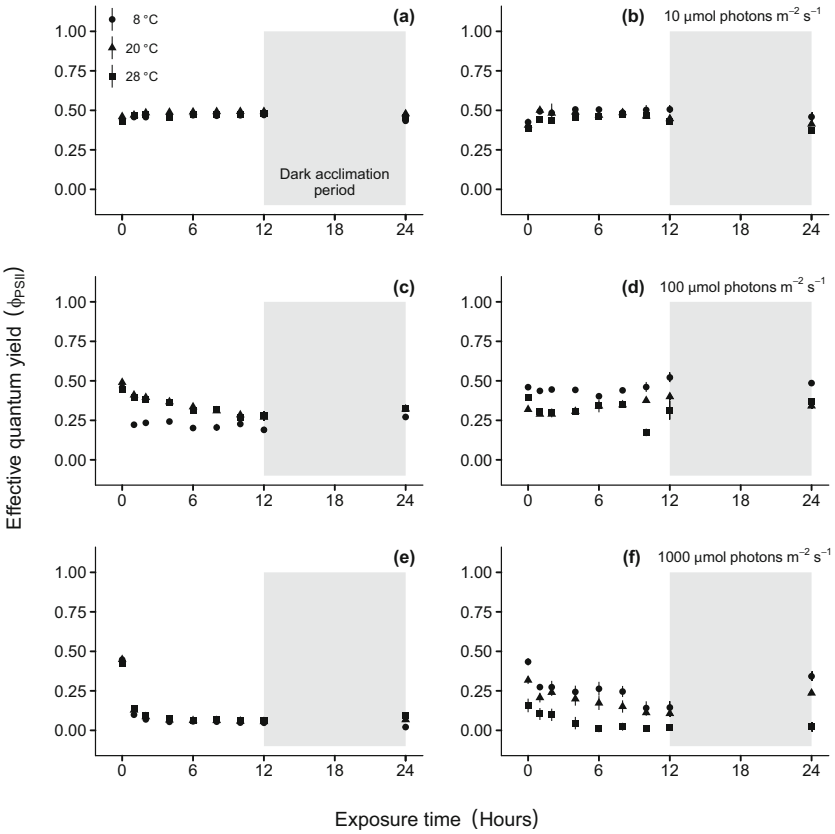

Fig. 1 The hourly response of effective quantum yield (Φ_{PSII}) in microscopic sporophyte (SPO; **a**, **c**, **e**) and macroscopic gametophyte (GAM; **b**, **d**, **f**) of cultivated *Pyropia yezoensis* f. *narawaensis* (PYEZO) to irradiance at 10 μmol photons m^{-2} s^{-1} (**a**, **b**), 100 μmol photons m^{-2} s^{-1} (**c**, **d**), and 1000 μmol photons m^{-2} s^{-1} (**e**, **f**), under 8 °C (circle), 20 °C (triangle), and 28 °C (square). The symbols indicate the average of actual values measured ($n = 10$), and bars indicate standard deviation. Shaded areas indicate the 12-h dark acclimation period after 12-h light exposure. Initial values and the values after 12-h dark acclimation were measured as the maximum quantum yield (F_v/F_m).

0.009), values were still significantly different ($P < 0.0001$) from their initial (0.51 ± 0.006 at 8 °C; 0.40 ± 0.010 at 20 °C).

Discussion

In the annual heteromorphic life history of *Pyropia*, the microscopic sporophyte stage occurs on the dead oyster shells during early summer to autumn; whereas the macroscopic gametophyte occurs on intertidal rocks or mariculture nets during early winter through spring (Oohbusa 1993; Watanabe et al. 2016). In our previous studies, temperature response of photosynthesis was completely different in the two life history stages; this difference was related to their respective adaptations to the temperature environment during their occurrence period (Watanabe et al. 2014, 2016). In the present study, continuous 12-h exposures to 10, 100, and 1000 μmol m^{-2} s^{-1} at 8, 20, and 28 °C revealed that the sporophyte and gametophyte also have different tolerance characteristics, in response to both irradiance and temperature. The two cultivars had similar light stress-recovery responses, suggesting that the response was a common characteristic in the species of *Pyropia*.

PSII photochemical efficiencies of the sporophyte and gametophyte were unaffected at 10 μmol photons m^{-2} s^{-1}, as shown by their stable quantum yields throughout the light stress experiments on all temperature treatments. Indeed, the PAR level to which the samples were continuously exposed was lower than their estimated saturation irradiances (e.g., E_k = 35–64 μmol photons m^{-2} s^{-1} for *P. tenera* gametophyte, Watanabe et al. 2014; 70–88 and 154–225 μmol photons m^{-2} s^{-1} for *P. yezoensis* f. *narawaensis* sporophyte and gametophyte, Watanabe et al. 2016). In contrast, exposure to 1000 μmol photons m^{-2} s^{-1} caused a sharp decline in their Φ_{PSII}, with no indication of recovery even after 12 h of dark acclimation. This irradiance level was apparently high for the species to suffer from photodamage, especially for gametophytes during Nori-net cultivation. It is relative to note that the incident irradiance on the sea surface at noon, under fine clear sky ranges from 1235 (January) to 2165 μmol photons m^{-2} s^{-1} (June) in Kagoshima Bay, Kyushu Island (Terada et al. 2018). Young gametophytes on Nori-nets during the early period of nursery rearing (late October and November) were most likely affected by these intense levels and relatively high temperature (around 26–30 °C), as they were periodically emersed during the day due to tidal fluctuation (Note: Fisherman in Ariake Bay generally arrange the height of the Nori-nets so that they are emersed for about 2 h (during the nursery rearing period) and for 2 to 3 h (during the harvesting period) during the low tide). The combined effects of emersion, intense light, and high temperature exposure may have stressed the seaweeds, causing them to decline (Mine unpublished). Gametophytes during the "second season" of cultivation

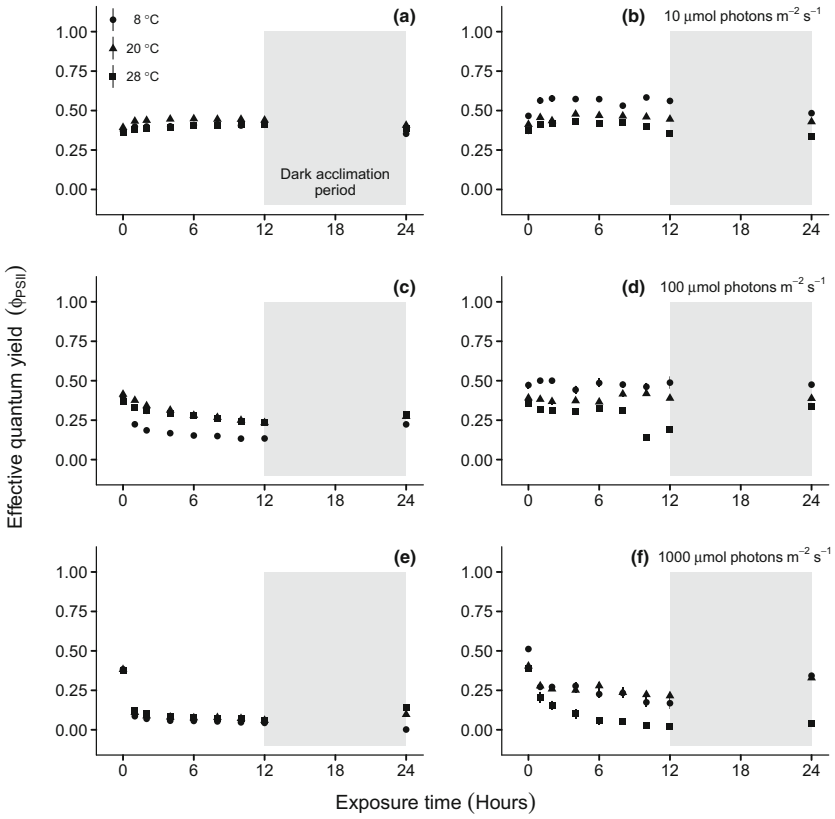

Fig. 2 The hourly response of effective quantum yield (Φ_{PSII}) in microscopic sporophyte (SPO; **a**, **c**, **e**) and macroscopic gametophyte (GAM; **b**, **d**, **f**) of cultivated *Pyropia tenera* (*PTENE*) to irradiance under 10 µmol photons m^{-2} s^{-1} (**a**, **b**), 100 µmol photons m^{-2} s^{-1} (**c**, **d**), and 1000 µmol photons m^{-2} s^{-1} (**e**, **f**), at 8 °C (circle), 20 °C (triangle), and 28 °C (square). The symbols indicate the average of actual values measured ($n = 10$), and bars indicate standard deviation. Shaded areas indicate the 12-h dark acclimation period after 12-h light exposure. Initial values and the values after 12-h dark acclimation were measured as the maximum quantum yield (F_v/F_m).

(January to March; Watanabe et al. 2017) may likewise be affected by such stressors (i.e., when low tide occurs during the day, and gametophytes are aerially exposed). Indeed, the failure of conchospore seeding has been reported by local fisherman to occur during emersion and when there are little clouds in the sky, which may be attributed to photodamage. The complex interactions between the timing of extreme spring tides and the abiotic factors define the occurrence of the hardest abiotic conditions encountered by macroalgae throughout the year (Delebecq et al. 2011). Hence, timing of conchospore seeding and proper depth range of Nori-nets is critical to minimize stress during cultivation. Field measurements are required to confirm these insights.

A difference in light stress-recovery response between the two life stages of *Pyropia* was evident at 100 µmol photons m^{-2} s^{-1}. The extent of depression in Φ_{PSII} of the sporophyte increased with decreasing temperature, with more pronounced declines at 8 °C (59–67%) than at 20 °C (44–45%) and 28 °C (36–38%). Despite the increase in their post-dark acclimation F_v/F_m (14–42% for *PYEZO*; 17–69% for *PTENE*), values were still significantly different from their initial, signifying chronic photoinhibition in the microscopic stage. Its partial or delayed recovery from photoinhibition can be attributed to low temperature that must have slowed down the repair process of *PSII*, as protein synthesis decreases with declining temperatures (Takahashi and Murata 2008). Alternatively, full recovery may have occurred if the samples were acclimated under dim-light conditions (< 30 µmol photons m^{-2} s^{-1}). *PSII* repair activity progresses during recovery under dim light, and is suppressed under excessive light (Schubert et al. 2015); a diversity of photoacclimation and photoprotection mechanisms occurs in red algae, and is related to the kinds of carotenoids present (Schubert and García-Mendoza 2008; Schubert et al. 2011). Nevertheless, sensitivity to light stress differed between the two life history stages, where the gametophyte expressed a reduction in Φ_{PSII} at 28 °C only; and yet their final F_v/F_m was restored to initial.

Given the occurrence of chronic photoinhibition only at 1000 µmol photons m^{-2} s^{-1} in the gametophyte, the macroscopic stage seemed to be more tolerant to high irradiance than the sporophyte. Such observations correspond well with their respective adaptations to irradiance and temperature in their habitat, and during their occurrence / cultivation period (Oohbusa 1993). The sporophytes are cultured under controlled irradiance (i.e., less than 60 µmol photons m^{-2} s^{-1}) in tanks; their growth is depressed under high irradiance environment (80 µmol photons m^{-2} s^{-1}; Mine unpublished). Whereas artificially-seeded conchospores and gametophytes in Nori-nets are often exposed to "supersaturating" irradiances that may cause damage to *PSII*, especially at autumn (October and November) and early spring (March) when temperatures become close to their thermal inhibition (14–22 °C; Watanabe et al. 2014, 2016).

Overall, the results of this study provide additional evidences of the difference in photosynthetic characteristics of the two life history stages of *Pyropia*. Variations in photosynthetic performance of the sporophyte and gametophyte (Watanabe et al. 2014, 2016) may have been due to the susceptibility to low temperature-enhanced light stress of the sporophyte, and to high temperature-enhanced light stress of the gametophyte. Further research on physiological responses of the species to other environmental stress factors (e.g., nutrient limitation, desiccation) is recommended. Photoprotective mechanisms as well as photosynthetic performances change through seasonal acclimation processes in relation to the ambient light conditions, but also to other environmental conditions such as temperature and nutrients (Gévaert et al. 2002; Fairhead and Cheshire 2004; Delebecq et al. 2011). Examining the non-photochemical quenching patterns of the alga may likewise be necessary to further predict its response to rapid environmental changes during field cultivation. Along with our earlier studies (Watanabe et al. 2014, 2016, 2017), the present study somehow brought a complete description of the photosynthetic pattern of *Pyropia* throughout its cultivation. Such pattern of response is closely linked to the rapid environmental changes and their ability to cope with it.

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