

## Photosynthetic characteristics of the economic brown seaweed *Hizikia fusiforme* (Sargassaceae, Phaeophyta), with special reference to its “leaf” and receptacle

Dinghui Zou<sup>1,\*</sup> and Kunshan Gao<sup>1,2</sup>

<sup>1</sup>Marine Biology Institute, Science Center, Shantou University, Shantou, Guangdong 515063, China; <sup>2</sup>Institute of Hydrobiology, The Chinese Academy of Sciences, Wuhan, Hubei 430072, China

\*Author for correspondence: e-mail: dhzhou@stu.edu.cn

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### Abstract

Photosynthetic responses to irradiance and temperature of “leaves” and receptacles were compared in February (vegetative stage) and May (reproductive stage) in the seaweed, *Hizikia fusiforme* (Harvey) Okamura (Sargassaceae, Phaeophyta) from Nanao Island, Shantou, China. Irradiance-saturated photosynthesis ( $P_{\max}$ ) was significantly higher in receptacles than in “leaves” on a fresh weight basis, and that of “leaves” was greater in May than in February at ambient seawater temperatures. The optimum temperature for  $P_{\max}$  was 30 °C for both “leaves” and receptacles, being 5–10 °C higher than the ambient seawater temperature. The apparent photosynthetic efficiencies were greater in receptacles than in “leaves” within the tested temperature range of 10–40 °C. The irradiance for saturating photosynthesis for both “leaves” and receptacles was temperature-dependent, with the highest values (about 200  $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ ) at 30 °C.

### Introduction

Seaweeds often experience large fluctuations in irradiance and temperature, both on a daily and a seasonal scale. They adapt such environmental fluctuations with a high, genetically fixed potential for photosynthetic acclimation, enabling them to tune their metabolism in harmony with the changes in temperature and/or irradiance (e.g. Davison, 1991; Falkowski & LaRoche, 1991; Terrados & Ros, 1992; Dring & Lüning, 1994; Stengel & Dring, 1998). Photosynthetic performances also correlate with developmental stages or life cycles (Oh & Koh, 1996; Brenchley et al., 1997; Campbell et al., 1999). Additionally, it is known that differentiation in the seaweeds results in different photosynthetic capacities (Gao & Umezaki, 1988; Gao, 1991). For example, the maximum photosynthetic rate of the receptacle tissue of *Fucus serratus*, was about 50% lower compared to vegetative tissue, whereas the receptacles of *Himantalia elongata* were capable of

maintaining photosynthetic rates three times higher than the vegetative tissues (Brenchley et al., 1997).

*Hizikia fusiforme* (Harvey) Okamura (Sargassaceae, Phaeophyta) is one of the most common brown seaweeds endemic to northwest coasts of the Pacific Ocean, growing on lower intertidal rocks (Tseng, 1983, 2000). In China, the natural resources of this species has been being endangered by over exploitation for the last decade. Due to high economic value and market demand, aquaculture of *H. fusiforme* is now being considered in China for larger scale production. A number of studies have been carried out on its reproductive biology and seedling and cultivation techniques (reviewed by Zhang et al., 2002). However, the ecophysiology of this alga is not yet fully understood. A typical *Hizikia* plant consists of a holdfast, a “stem” from which main “branches” (or main axes) are formed and which, in turn, give rise to “leaves” which are the main photosynthetic tissues, lateral branches and vesicles (Tseng, 1983, 2000). During the fertile season,

the receptacles (reproductive tissue) develop mainly on the lateral branches. The relative photosynthetic performance of the reproductive and vegetative tissues of *H. fusiforme* is of interest. We have previously found that the “leaves” of *H. fusiforme* were capable of using  $\text{HCO}_3^-$  as a source of inorganic carbon for photosynthesis via the mediation of an external carbonic anhydrase, and that  $\text{CO}_2$  concentrations in the culture media affected photosynthesis (Zou et al., 2003). In the present study we examine the photosynthetic characteristics of *H. fusiforme* “leaves” and receptacles with respect to irradiance and temperature.

### Materials and methods

*Hizikia fusiforme* (Harvey) Okamura plants were collected from the low intertidal zone in February and May 2003 at Yunao Bay, Nanao Island, Shantou, China ( $23^\circ 20' \text{N}$ ,  $116^\circ 55' \text{E}$ ). Average seawater temperature in February and May was about 15 and 25 °C, respectively. The plants were non-fertile from January to March, and began to show signs of receptacles in the middle of April, fully reaching the sexual reproductive phase in May, with receptacles being 5–10 cm in length. The reproductive phase ended in late June.

The collected plants, cleaned of epiphytes and rinsed of sediments, were placed in a plastic barrel with seawater and transported to the laboratory within 3 h. They were maintained in vigorously aerated filtered seawater at 15 °C (in February) or 25 °C (in May) at about  $120 \mu\text{mol photons m}^{-2} \text{s}^{-1}$  (fluorescent illumination, 12 h:12 h LD cycle), an intermediary irradiance in relation to light saturation of photosynthesis at 10–25 °C as determined in preliminary experiments. Experiments were carried out immediately after the algal samples were returned to laboratory or within two days of collection, a period during which the photosynthetic characteristics were not affected. “Leaves” (February and May) and receptacles (May) were cut from the middle part of the plants with a sharp razor blade and used for photosynthetic measurements. To minimize the possible effects of cutting, the leaves and receptacles were maintained under the same conditions as above for about 2 h before photosynthetic measurements.

Photosynthetic  $\text{O}_2$  evolution was measured by using a Clark-type oxygen electrode (YSI Model 5300, USA), with a water jacket connected to a cooling circulator for temperature control. Illumination was provided by a halogen lamp and photon irradiance was

measured with a quantum sensor (SKP 200, ELE International) at the surface of the chamber. Irradiance was varied by altering the distance between the electrode chamber and the light source. Filtered seawater (pH 8.2, total dissolved inorganic carbon concentration 2.2 mM) was used as the medium for photosynthetic measurements. A 0.1–0.3 g fresh weight sample was introduced into the chamber containing 8 mL of seawater, which was magnetically stirred. After 15 min acclimatization at each combination of light and temperature, the medium was renewed and the photosynthetic rate was determined over 5 min, during which period a linear change in oxygen concentration in the chamber was obtained. Preliminary experiments showed that slight changes of pH and dissolved inorganic carbon within the seawater did not affect photosynthesis over this period. Dark respiration ( $R_d$ ) was measured by completely blacking out the electrode chamber. Irradiance-saturated maximum net photosynthetic rate ( $P_{\text{max}}$ ) was calculated as the mean of values in the asymptote region of the photosynthesis versus irradiance ( $P$  vs  $I$ ) curve. Apparent photosynthetic efficiency ( $\alpha$ ) was estimated as the irradiance-limited slope of the  $P$  vs  $I$  curve, and the irradiance saturation point ( $I_k$ ) was estimated by  $(P_{\text{max}} + R_d)/\alpha$ , according to Henley (1993). All data plotted on graphs are mean values with standard deviations ( $n \geq 3$ ).

### Results

The photosynthesis versus irradiance curves (Figure 1) of *H. fusiforme* measured at ambient temperature showed distinct differences (ANOVA,  $p < 0.01$ ) in the irradiance-saturated net photosynthesis rate ( $P_{\text{max}}$ ) between the “leaves” and receptacles.  $P_{\text{max}}$  of leaves was 74.3% higher on a fresh weight basis and 35.6% higher on a chlorophyll-*a* basis during May (25 °C) compared to February (15 °C). During May,  $P_{\text{max}}$  was 76.8% higher in terms of fresh weight and 56.6% higher on a chlorophyll-*a* basis, in the receptacles compared to the “leaves”. Photoinhibition of photosynthesis was not observed in either the “leaves” or the receptacles over the range of irradiances tested. Dark respiration ( $R_d$ ) of the “leaves” was not significantly (ANOVA,  $p > 0.05$ ) different between February and May, but was about twice as high in the receptacles than in the “leaves”. The apparent photosynthetic efficiency ( $\alpha$ ), based on either fresh weight or chlorophyll-*a*, and  $I_k$  were higher in the receptacles compared to the “leaves” (ANOVA,  $p < 0.01$  &  $p < 0.05$  respectively).

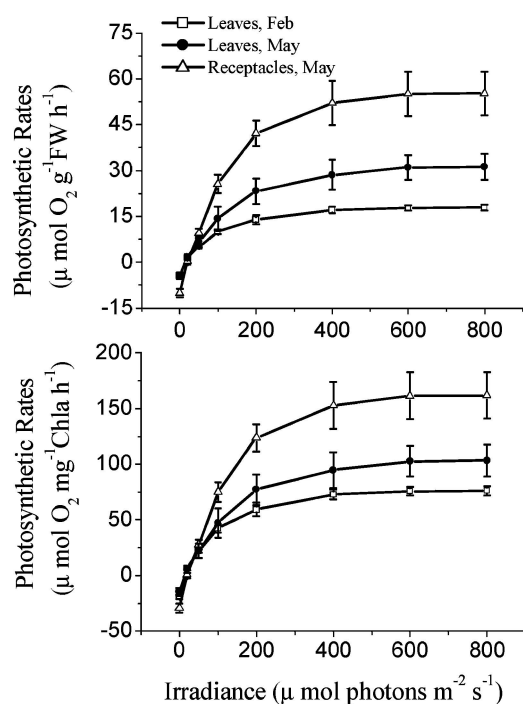


Figure 1. Photosynthesis vs irradiance curves of “leaves” and receptacles of *Hizikia fusiforme* measured at ambient seawater temperatures in February (ca. 15 °C) and May (ca. 25 °C). Error bars = standard deviations.

Figure 2 shows the relationship between photosynthesis and temperature of “leaves” and receptacles at different irradiances. The net photosynthetic rates ( $P_n$ ) at irradiances  $\geq 200 \mu\text{mol photons m}^{-2} \text{s}^{-1}$  of both “leaves” and receptacles increased with increasing of temperature from 10 °C reaching a maximum at 30 °C (the apparent temperature optimum) and then decreased dramatically with further increases of temperature.  $P_n$  was less temperature sensitive at lower irradiances. The optimum temperature for photosynthesis of both “leaves” and receptacles decreased with decreasing irradiance to 20–30 °C at 50 and 100  $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ , and to 10–20 °C at 20  $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ . The low-temperature compensation of  $P_n$  at high irradiance was not reached in either receptacles or “leaves” at the lowest temperature (10 °C) tested. However, by extrapolation it was estimated to be about 3 °C for receptacles and 5 °C for “leaves”. The high-temperature compensation points were about 40 °C for both receptacles and “leaves”.

Temperature had little effect on the  $R_d$  of “leaves” between 10 to 35 °C. However,  $R_d$  increased at 40 °C, with a  $Q_{10}$  of about 1.4 from 30 to 40 °C. In contrast, temperature had a pronounced effect on the  $R_d$  of receptacles, increasing from 10 to 40 °C, with a  $Q_{10}$  of 1.4 from 10 to 20 °C, 1.3 from 20 to 30 °C and 2.0 from

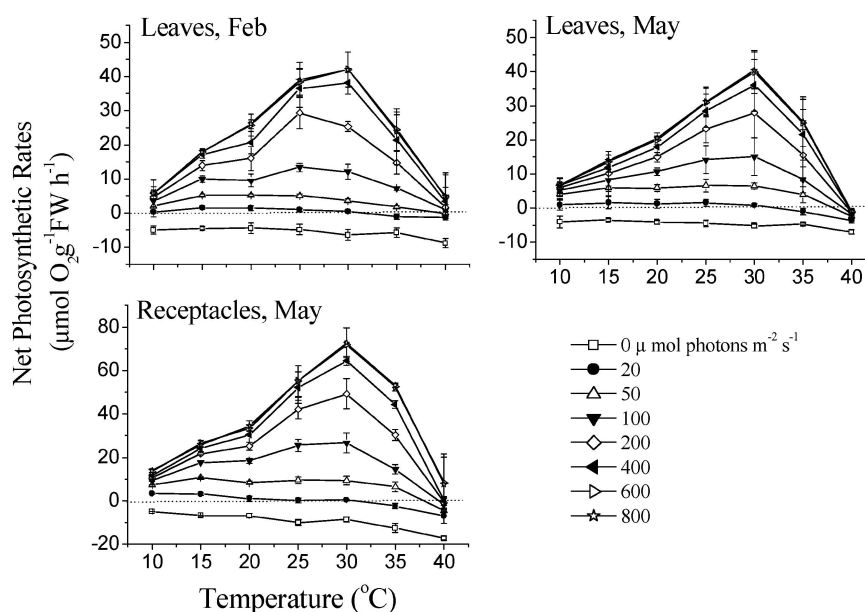


Figure 2. Photosynthesis versus temperature curves at different irradiance in “leaves” and receptacles of *Hizikia fusiforme* determined in February and May. Error bars = standard deviations.

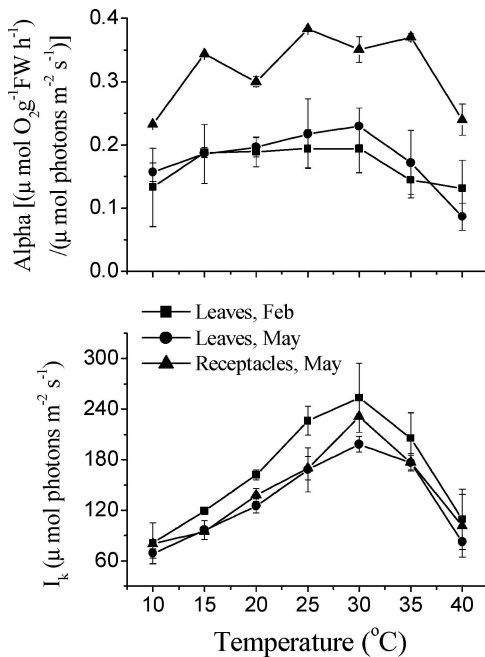


Figure 3. Variation with temperature in apparent photosynthetic efficiency (alpha) and irradiance saturation point ( $I_k$ ) of  $P$  vs  $I$  curves of "leaves" and receptacles with temperature in *Hizikia fusiforme* determined in February and May. Error bars = standard deviations.

30 to 40 °C.  $R_d$  was significantly higher ( $p < 0.05$ ) in the receptacles than in the "leaves" at all temperatures tested (Figure 2).

The apparent photosynthetic efficiency ( $\alpha$ ) was higher ( $p < 0.01$ ) in the receptacles than in the "leaves", but differed little ( $p > 0.05$ ) between February and May for the "leaves" (Figure 3).  $\alpha$  hardly changed over the temperature range of 10–35 °C, but declined at higher temperatures. The saturating irradiance for photosynthesis ( $I_k$ ) of both "leaves" and receptacles increased with increasing temperature from 10 to 30 °C, and then decreased with further rises in temperature. The  $I_k$  of "leaves" was slightly higher in February than in May between 15–30 °C, but there were no differences in  $I_k$  between "leaves" and receptacles for the fertile plants (in May) at all temperatures.

## Discussion

The present study showed that receptacles of *Hizikia* were photosynthetically more active than the vegetative "leaves", with higher rates of irradiance-saturated photosynthesis, dark respiration and photosynthetic

efficiency. In contrast, the photosynthetic capacity of the receptacles of *Fucus serratus* has been reported to be much lower compared to that of vegetative tissue (Brenchley et al., 1997). Brenchley et al. (1997) assumed that the receptacles of *F. serratus* act as a resource drain on the vegetative tissue in fertile plants. In the present study, the higher photosynthetic capacity of the receptacles might still not be high enough to meet the photoassimilate requirements of the receptacles of *H. fusiforme*, since photosynthetic activity in the "leaves" of fertile plants was enhanced by elevated *in situ* seawater temperatures during the reproductive season; this would increase the photoassimilate available to supply the requirements of receptacles. This is further supported by the remarkable reduction in the growth rate of fertile plants compared to non-fertile plants (data not shown). At the same time, receptacle development did not appear to affect the photosynthetic activity of the "leaves" in fertile *H. fusiforme*.

Irradiance-saturated photosynthetic rate in "leaves" of *H. fusiforme* was higher in May than in February when measured at *in situ* temperatures, reflecting a seasonal fluctuation of photosynthetic activity. However, photosynthesis versus temperature curves indicated that the photosynthetic capacities in "leaves" of *H. fusiforme* in February were similar to those in May when measured at the same temperature, indicating that the difference in photosynthetic capacity in "leaves" between February and May was due to differences in ambient seawater temperature. In some brown algae seasonal variance in photosynthetic capacity has been demonstrated even when measured at a constant temperature (e.g. Levitt & Bolton, 1991). Brenchley et al. (1997) have shown that the photosynthetic capacities of non-fertile plants of *F. serratus* and *Himantalia elongata* remained fairly constant throughout the year, despite being measured at temperatures between 4 to 16 °C, reflecting the high ability of these two species to acclimate their photosynthetic capacity to seasonally varying temperatures.

The photosynthetic temperature optima of *H. fusiforme* "leaves" showed no appreciable changes between February and May. The temperature optima for irradiance-saturated photosynthesis of both "leaves" and receptacles were higher than the *in situ* seawater temperature, suggesting that photosynthesis in the field might be limited by low temperature. Other authors also have shown that the temperature optima of seaweeds were higher than the highest mean monthly seawater temperature (Zupan & West, 1990; Sakanishi & Iizumi, 1998). However, the range of temperature

optima for photosynthesis in *H. fusiforme* became broader and lower with a reduction in irradiance as has also been shown for several other species of brown algae (Kurashima et al., 1996; Sakanishi & Iizumi, 1998). Under *in situ* conditions, such low irradiances could occur on cloudy days as well as a result of overshadowing by the algal community itself, and attenuation within the water column. Consequently, the photosynthesis of *H. fusiforme* might not be temperature-limited under such low irradiance conditions.

The present results show that the apparent photosynthetic efficiency ( $\alpha$ ) of *H. fusiforme* remained nearly constant over a wide temperature range in both "leaves" and receptacles. However,  $\alpha$  was reduced at 40 °C, suggesting a reduction in the efficiency of light-harvesting and energy conversion. The saturating irradiance for photosynthesis ( $I_k$ ) of *H. fusiforme* for both "leaves" and receptacles were temperature-dependent, with the maximal irradiance requirement at 30 °C. It appeared that  $I_k$  correlated better with irradiance-saturated photosynthesis than with  $\alpha$  in *H. fusiforme*, as also reported for *Ulva rotundata* (Henley, 1992). It has been suggested that a low value of  $I_k$  usually indicates the inefficient use of high irradiance rather efficient use of low irradiance (Henley, 1993). Therefore, the patterns of  $\alpha$  and  $I_k$  with temperature suggest that over the temperature range of 10–30 °C, *H. fusiforme* (both "leaves" and receptacles) maintained a relative constant efficiency at low irradiances, but an increasingly efficient use of high irradiances with increasing temperature up to about 40 °C.

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