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ORIGINAL ARTICLE

Photosynthetic parameters of sexually different parts of *Porphyra katadai* var. *hemiphylla* (Bangiales, Rhodophyta) during dehydration and re-hydration

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Abstract Physiological data from extreme habitat organisms during stresses are vital information for comprehending their survival. The intertidal seaweeds are exposed to a combination of environmental stresses, the most influential one being regular dehydration and re-hydration. *Porphyra katadai* var. *hemiphylla* is a unique intertidal macroalga species with two longitudinally separated, color distinct, sexually different parts. In this study, the photosynthetic performance of both PSI and PSII of the two sexually different parts of *P. katadai* thalli during dehydration and re-hydration was investigated. Under low-grade dehydration the variation of photosystems of male and female parts of *P. katadai* were similar. However, after the absolute water content reached 42%, the PSI of the female parts was nearly shut down while that of the male parts still coordinated well and worked properly with PSII. Furthermore, after re-hydration with a better conditioned PSI, the dehydrated male parts were able to restore photosynthesis within 1 h, while the female parts did not. It is concluded that in *P. katadai* the susceptibility of photosynthesis to dehydration depends on the accommodative ability of PSI. The relatively lower content of phycobiliprotein in male parts may be the cause for a stronger PSI after severe dehydration.

Keywords Chlorophyll fluorescence · Desiccation-tolerant · Effective quantum yield · Electron transport rate · $P700^+$ absorbance · *Porphyra*

Abbreviations

AWC	The absolute water content of the thalli
ETRI	Relative rates of photosynthetic electron transport of PSI
ETRII	Relative rates of photosynthetic electron transport of PSII
F_0	The minimal fluorescence yield
F_m	The maximum fluorescence yield
$F_{m'}$	The maximum fluorescence yield in illuminated samples
FR	Far red light
F_v/F_m	Optimum quantum yield
P700	The reaction center of PSI
PAR	Photosynthetic active radiation
PPF	Photosynthetic photon flux
PSI	Photosystem I
PSII	Photosystem II
qL	Photochemical quenching
RLC	Rapid light curve
SP	Saturation pulse
W_0	Wet weight of the thalli
W_d	Dry weight of the thalli
W_t	Weight of the thalli after a particular time of dehydration
YI	Effective PSI quantum yield
YII	Effective PSII quantum yield

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Y(NA)	Nonphotochemical quantum yield of PSI caused by acceptor side limitation
Y(ND)	Nonphotochemical quantum yield of PSI caused by donor side limitation

Introduction

Porphyra katadai var. *hemiphylla* C. K. Tseng and T. J. Chang is a unique *porphyra* species marked by a distinctively separated spermatangial (male) region and carposporangial (female) region, with the female parts usually taking a much larger area within the thalli (see Fig. 1). *P. katadai* is endemic to China and can be found in the western Huanghai sea region from Qingdao (35°35′N, 119°30′E) to Dalian (39°04′N, 121°49′E) (Tseng et al. 1983). The life history of *P. katadai* typically corresponds to that of *Porphyra* sp.: a biphasic life history composed of a macroscopic laminar gametophytic phase and a microscopic sporophytic filamentous phase, known as conchocelis. In Qingdao, the species is strictly seasonal. The silken blades appear on the intertidal rocky substratum, on oyster shells, or as epiphytes on seaweeds such as *Ulva* sp. in the mid-tidal zone in the beginning of January. The blades normally start deteriorating from the end of March, and they completely disappear by the end of April.

Many factors restrict the development of photosynthetic organisms, but the most important one of them is water deficiency (Bukhov et al. 2004c). Consequently, of all marine seaweeds, those living in the intertidal zones are the species most severely challenged by their environment. *P. katadai* regularly experiences emersion and submersion with the tides both daily and monthly. When emerged in the air, the alga cannot protect its thalli from over-drying. Thus, the water content of the thalli is strongly dependent on environmental conditions. Furthermore, in the *Porphyra* cultivation industry there is a technique known as ‘drying out’, which means artificially exposing the cultivated *Porphyra* sp. to air or prolonging emersion time. It is used by the experienced cultivators to get rid of harmful seaweeds and strengthen the disease resistance of the cultivated *Porphyra* sp. Therefore, regular dehydration and re-hydration of the thalli is one of the most influential and significant events in the life cycle of *P. katadai*.

Fig. 1 An intact thallus of *P. katadai* with clearly separated female part (*A*) and male part (*B*). *Arrow* indicates the line that separates the female and male parts. *Bar* 1 cm

Physiological data from extreme habitat organisms provides vital information for the understanding of how certain life forms survive the hostile environment where others cannot. Since photosynthetic electron transport is highly sensitive to environmental conditions, marine seaweeds in shallow coastal waters need mechanisms for acclimation to the fast changes in their environment (Kaiser 1987; Andersson et al. 2006). To date, some information has been published regarding the influences of dehydration and re-hydration on the photosynthetic performance of *Porphyra* sp (Satoh et al. 1983; Smith et al. 1986; Zou and Gao 2002). It was reported that different *Porphyra* species may react differently under the same water-deficient conditions: some species being extremely resistant to dehydration, while others are not (Smith et al. 1986). However, the mechanisms behind this phenomenon remain unknown. Some research has reported that the anti-dehydration capabilities of intertidal and subtidal algal species are well coordinated with the distribution of their habitat (Smith et al. 1986). Up to now, however, it is hard to determine whether these differences among different species are caused by innate factors or merely by acquired adaptations to their hostile environment.

Porphyra katadai possesses two distinctively color-separated, sexually different parts in the same individual. This color difference suggests that the pigments that directly affect the photosynthetic performance of the alga *P. katadai* may differ in each sexually different part. It can be deduced that there might be differences between the two regions regarding photosynthetic responses to desiccation. Since both parts are in the same thallus, no distributional differences can exist between them. Therefore, if there exists a significant difference between them in their anti-dehydration ability, we can conclude that there are innate reasons behind the phenomenon. As a sensitive and non-destructive technology, chlorophyll fluorescence measurement has proven a fascinating method for in vivo photosynthetic investigations (Schreiber et al. 1994; Beer and Ilan 1998; Bischof et al. 1998; Roháček and Barták 1999; Mercado et al. 1999). Nonetheless, these investigations have yielded no direct information about PSI. The aim of the present study is to simultaneously investigate the photosynthetic performance of the PSI and PSII of the sexually different parts of *P. katadai* during dehydration and re-hydration, using a Dual-PAM-100 fluorometer.

Materials and methods

Sample collection

Wild *Porphyra. katadai* var. *hemiphylla* were sampled from the rocky coast of Huiquan Bay (36°.0′3″N, 120. 2′0″E), Qingdao, China. Experiments were performed immediately after sampling. Healthy blades with distinctively separated female and male regions were chosen and cleaned with brushes in sterilized seawater to remove epiphytes and other contaminants.

Pigment extraction and light absorption analysis

Before extraction, the same weights of sexually different segments of the algae were cut in to small pieces and used in each group of experiments, respectively. Liposoluble pigments were extracted by means of an 80% acetone/water (v/v) buffered solution to avoid chlorophyll conversion to pheophytin. Water-soluble pigments were extracted by the repeated freeze thawing method in distilled water. The extractions were then analyzed with a spectrophotometer (DU650, Beckman, Fullerton, CA, USA).

Water content determination

The absolute water content (AWC) of the thalli was determined according to the formula: $\mathrm{AWC} = (W_t - W_d)/(W_0 - W_d) \times 100\%$, where W_0 is wet weight (the weight of the fresh thalli immediately after the gentle removal of water from the surface), W_d is dry weight (the weight of the thalli after the treatment of 80°C 24 h in a dry box), W_t is the weight of thalli after a set time of dehydration. To dehydrate the thalli, the blades were spread thoroughly on a piece of black plastic foil; and two layers of tissue paper were put on the blades with a culture dish weighting 50 g on the top to accelerate dehydration. After dehydration, the thalli were put back into seawater to re-hydrate. During the whole process of dehydration and re-hydration, the photosynthetic performance of the thalli was measured discontinuously.

Photosynthetic measurements

The in vivo chlorophyll fluorescence of PSII and the absorbent changes of PSI were determined by means of the Dual-PAM-100 (Heinz Walz, Effeltrich, Germany) connected to a PC with WinControl software, using the pulse–amplitude modulated method. Experiments were carried out using the automated induction and recovery curve routine provided by the Dual PAM software, with repetitive application of saturation pulses (SP) for assessment of fluorescence and P700 parameters. The intrinsic fluorescence (F_0) was determined after keeping the tissue in darkness for 15 min. Saturating actinic light pulses (SP) were applied to obtain maximum fluorescence (F_m) in the dark-adapted samples. The maximum fluorescence yields in the illuminated samples were recorded as $F_{m'}$. The effective PSII quantum yield, YII, was calculated according to the formula

$$\mathrm{YII} = (\mathrm{F_{m'}} - \mathrm{F})/\mathrm{F_{m'}} \tag{1}$$

Relative rates of the photosynthetic electron transport of PSII (ETRII) were calculated as the effective quantum yield (*Y*) multiplied with the photosynthetic active radiation (PAR) received by PSII.

$$\mathrm{rETR} = Y \times \mathrm{PAR} \times 0.5 \tag{2}$$

Saturation pulses, which were introduced primarily for PAM fluorescence measurement, were applied for assessment of P700 parameters as well. The P700 signals may vary between a minimal level (P700 fully reduced) and a maximal level (P700 fully oxidized). The latter level, which in analogy to F_m is called P_m, can be determined by application of a SP in the presence of Far red light (FR). The P700 parameter P_m is defined in analogy to the Fluo parameter F_m. It was determined after Far-Red preillumination through application of a saturation pulse. $P_{m'}$ was also defined in analogy to the Fluo parameter $F_{m'}$. P700 red., which was determined in a given state with the help of a saturation pulse, represents the fraction of overall P700 that is reduced in a given state. The nonphotochemical quantum yields of PSI caused by donor side limitation and acceptor side limitation, *Y*(ND) and *Y*(NA) were calculated respectively according to the formulae

$$Y(\mathrm{ND}) = 1 - \mathrm{P700\ red.} \tag{3}$$

$$Y(\mathrm{NA}) = (P_m - P_{m'})/P_m \tag{4}$$

The photochemical quantum yields of PSI, *Y*(*I*) were calculated according to the formula

$$Y(I) = 1 - Y(\mathrm{ND}) - Y(\mathrm{NA}) \tag{5}$$

The relative rates of photosynthetic electron transport of PSI (ETRI) were also calculated according to Eq. 2.

The photosynthesis versus irradiance (*P*–*I*) curves of both PSI and PSII were also generated by Dual-PAM-100. Rapid light curves (RLCs) of both the male and female parts of *P. katadai*, all of which were light adapted for 5 min before measurement, were measured during both dehydration and re-hydration. The RLC consists of the fluorescence responses to ten different and increasingly actinic irradiances (PAR 0, 14, 21, 30, 61, 103, 134, 224, 347 and 539 µmol m^{-2} s^{-1}) of 30 s duration.

Statistics

The results are expressed as mean values ± SD. The experiments were repeatedly performed, and the most precise experiments (i.e., where both, female and male parts, were dehydrated exactly to the desired content) were used for statistics. Data were analyzed with the statistical software STATISTICA 7.0 via ANOVA repeated measurements. When ANOVA indicated treatment effects, Newman–Keuls post hoc tests were used to discover the main effect of the means.

Results

Light absorption analysis

The absorption spectrum of *P. katadai* reached its maximum at 430, 500, 550, 620, and 650 nm (Fig. 2). The components in the sexually different parts of the alga were the same, but the contents of phycoerythrins (peaks at 498 and 564 nm) in male parts were significantly lower than that in female parts (Fig. 2). No significant difference in the chlorophyll content (peak at 430, 475 and 665 nm) was found between the two parts.

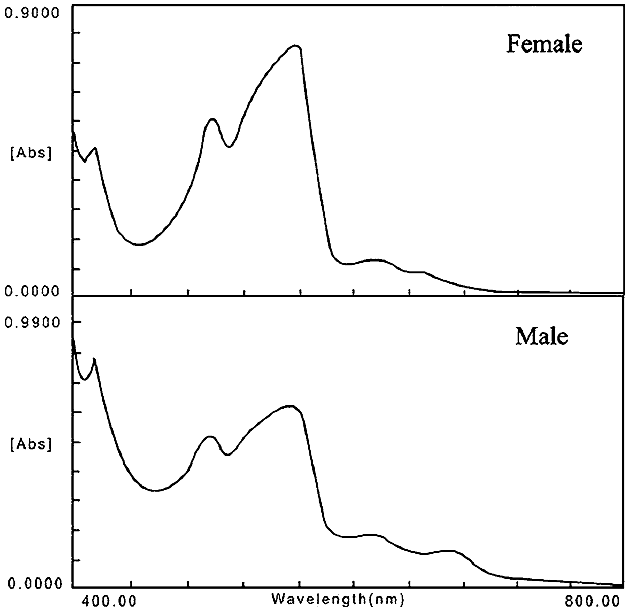

Fig. 2 Light absorption analysis of water-soluble pigments of female and male parts of *P. katadai*

Effective quantum yield of PSI (YI) and PSII (YII) of the male and female part of *P. katadai* during dehydration and re-hydration

The variance of YII of the female and male parts showed a similar pattern during dehydration. The YII values dropped steadily with dehydration. They both reached their lowest level (around 0.15) when AWC reached 42% and remained at this level. During re-hydration, however, they showed very different patterns ($P < 0.05$). When re-wetted, the YII of the male parts bounced back to the initial level, while the YII of the female parts showed little response. On the other hand, the YI of the female and male parts showed a similar pattern, except that the YI of the female parts fluctuated much more than that of the male parts (Fig. 3).

Optimum quantum yield, F_v/F_m and photochemical quenching (qL)

During dehydration the F_v/F_m of both the female and male parts dropped steadily along with dehydration (Fig. 4). No

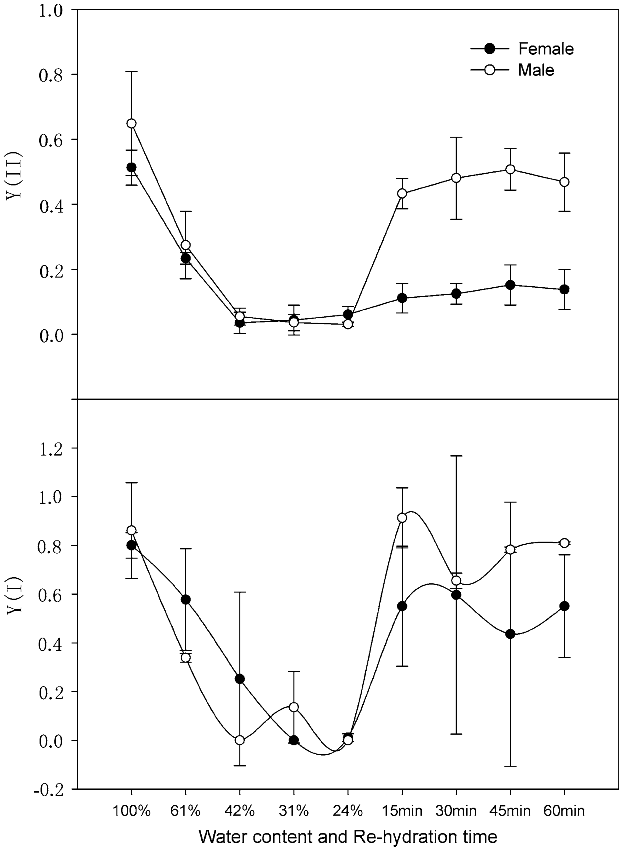

Fig. 3 Variation of the effective quantum yield of PSI, *Y*(I) and PSII, *Y*(II) of female and male parts of *P. katadai* during dehydration and re-hydration. Indicated data are the mean data of two independent experiments (±SD)

significant difference of the $F_{\mathrm{v}}/F_{\mathrm{m}}$ value between sexually different sections was found. However, after re-hydration the $F_{\mathrm{v}}/F_{\mathrm{m}}$ recovery showed obvious differences: the $F_{\mathrm{v}}/F_{\mathrm{m}}$ value of the male parts recovered much better than that of the female parts ($P < 0.05$). The $F_{\mathrm{v}}/F_{\mathrm{m}}$ of the male parts fully recovered right after being re-wetted, while the $F_{\mathrm{v}}/F_{\mathrm{m}}$ value of the female parts remained significantly lower than the initial level.

Considering the variations of photochemical quenching, the qL of the female and male parts displayed a similar pattern: qL dropped steadily in the first phase of dehydration, during which AWC dropped from 100% to AWC 42%, yet exhibited high SD during further dehydration (AWC 42–24%). With re-hydration, the qL value of both the female and male parts dropped instantly. After a certain time of re-hydration, however, the qL value of both parts showed a slight rise. During re-hydration the response of the qL between male and female parts was significantly different ($P < 0.05$): after 1 h of re-hydration, the qL of the male parts almost returned to the initial level, while the qL of the female parts remained significantly lower than the initial level (Fig. 4).

The nonphotochemical quantum yield of PSI caused by donor side limitation, *Y*(ND) and acceptor side limitation, *Y*(NA)

During dehydration, the *Y*(ND) of both sexual parts reached the highest value yet with high standard deviation values when the AWC reached 42%, whereas the *Y*(ND)s of other AWCs showed low SD values. After this point, the acceptor side limitation of sexually different parts exhibited distinct differences ($P < 0.05$).This impact leaded to a corresponding drop of *Y*(NA) and to a low level in the male parts, while, in contrast, the *Y*(NA) of the female parts raised to a high value (Fig. 5).

After re-hydration, the *Y*(NA) of the female parts dropped strongly as soon as they were re-wetted. Then the *Y*(NA) rose again, became unstable after re-hydration for 45 min, but finally stabilized. Quite differently, the *Y*(NA) of the male parts remained relatively stable and showed little rise.

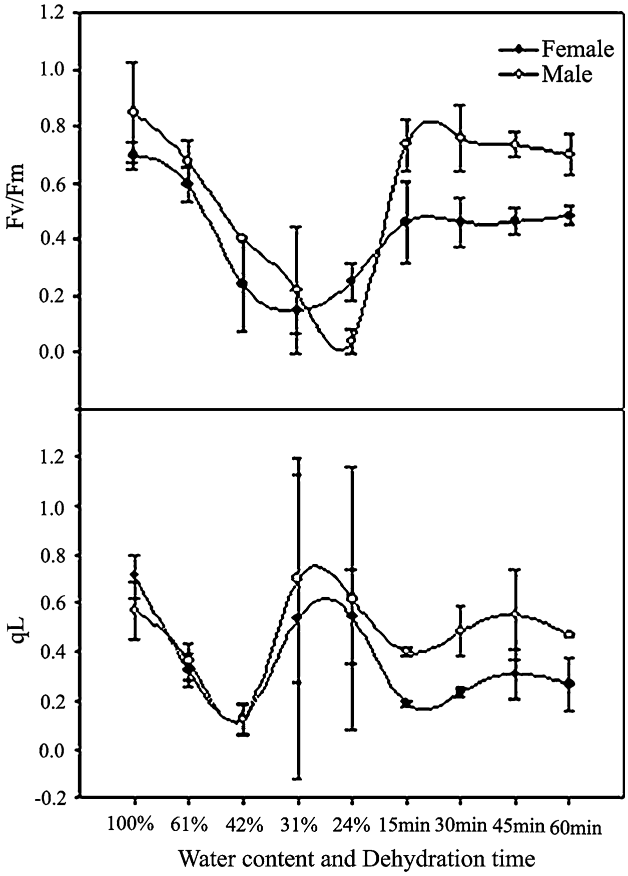

Fig. 4 Variation of the optimum quantum yield, $F_{\mathrm{v}}/F_{\mathrm{m}}$, and coefficient of photochemical quenching, qL, of female and male parts of *P. katadai* during dehydration and re-hydration. The data are the mean data of two independent experiments (±SD)

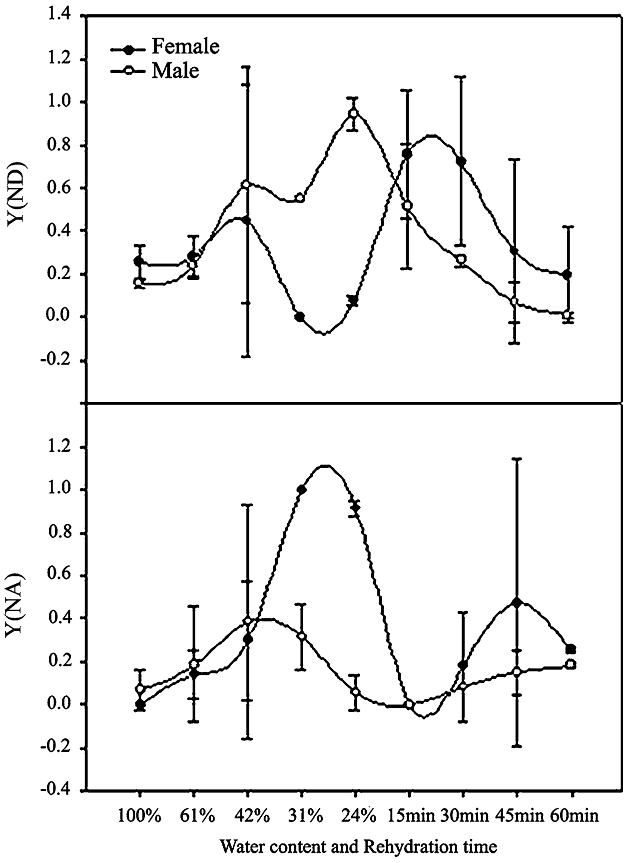

Fig. 5 Nonphotochemical quantum yield of PSI caused by donor side limitation, *Y*(ND), and acceptor side limitation, *Y*(NA), of female and male parts of *P. katadai* during dehydration and re-hydration. Data are the mean data of two independent experiments (±SD)

Rapid light curves of PSI and PSII of female and male parts of *P. katadai* during dehydration

The results of the rapid light curves of PSI and PSII (Fig. 6) showed that the light responses of both PSI and PSII were profoundly influenced by dehydration. However, after dehydration, the light response of PSI was more unstable than that of PSII. Under high degrees of dehydration (AWC 42 and 31%), the light curves of both male part and female parts manifested rapid fluctuation; but at AWC 42%, the PSI activities of the male parts were considerably stronger than those of the female parts.

Discussion

As demonstrated by the light absorption analysis, the content of phycoerythrin in female parts of *P. katadai* var. *hemiphylla* is significantly higher than that in male parts (Fig. 2) and therefore the female parts appear darker in color. In addition, the higher phycoerythrin content in the female parts might be the cause for the larger area that the female part usually occupies in the thalli. According to Yokoya et al. (2007) a higher level of phycoerythrin content could also cause higher growth rates under same illumination conditions.

Chlorophyll fluorescence has recently been recognized as an independent method for assessing algal physiology in the aquatic environment (Prasil et al. 2008). Pulse amplitude modulated (PAM) fluorometry has been favored by many researchers in investigating photosynthetic properties of algae due to its swiftness, convenience and nondestructive nature (Beer and Ilan 1998; Bischof et al. 1998; Roháček and Barták 1999; Figueroa et al. 2003; Abdala-Díaz et al. 2006; Andersson et al. 2006; Zacher et al. 2007). This technique has been proven to be useful for measuring the impact of environmental stress on the physiological state of plant photosynthesis (Prasil et al. 2008). It is assumed that the fluorescence measured originated exclusively from PSII. However, when the measuring wave length is greater than 700 nm, the fluorescence from PSI needs to be taken into consideration (Schreiber 2004). Once the PSI contribution is known, it can be subtracted from $F_{m'}$ in order to calculate the corrected $\Delta F/F_{m'}$. The PSI contribution to F_0 at a wave length greater than 700 nm in C3 plants has been estimated to be 30% (Schreiber 2004). In the present study, the contribution of PSI was assumed to be 30% of the total and was subtracted from F_0.

Lower plants do not posses any mechanism for protecting their cells from water loss. Instead, they have adapted to perform photosynthesis under a much wider range of internal water content (Bukhov and Carpentier 2004a). During emersion, *P. haitanensis*, another economically important *Porphyra* species endemic to China, can retain photosynthesis and response to the CO_2 concentration changes in the air (Zou and Gao 2002). Our results showed that the thalli of *P. katadai* can retain normal photosynthetic activity before losing 58% of their contained water. However, with water losses of the thalli, the activity of both PSII and PSII was hindered. The photosynthetic potential of PSII showed a linear relationship with dehydration. During dehydration, except for a slight variation, the optimum quantum yield (F_v/F_m) of both the female and male parts dropped steadily in the early phases (Fig. 4): the effective

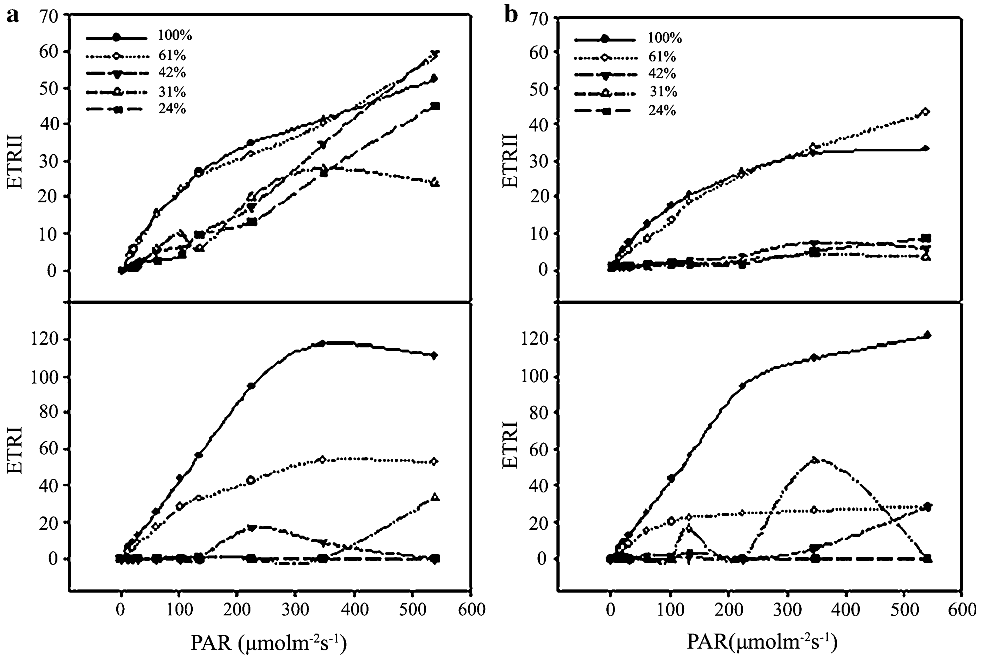

Fig. 6 *P–I* curves of PSI (ETRI vs. PAR) and PSII (ETRII vs. PAR) of female (**a**) and male parts (**b**) of *P. katadai* during dehydration, all of which were light adapted for 5 min before measurements. Five RLCs (rapid light curves) of PSI and PSII correspond to different dehydration degrees (AWC 100, 61, 42, 31 and 24%) measured in thalli exposed to increasing light intensity

quantum yield of the photosystems of *P. katadai* and the coefficient of photochemical quenching reached the bottom level at AWC 42% (Figs. 3, 4). According to Satoh et al. (1983), severe water deficiency inhibits electron flow on the water side of PSII and between the two photosystems of *Porphyra perforata*. When AWC reached 42%, the effective quantum yield of PSII (YII) became relatively stable (Fig. 3) while the nonphotochemical quantum yield of both donor and acceptor side showed strong fluctuation (Fig. 5), which indicated that their openness changed frequently and vigorously. These phenomena implied that under this condition the operation of PSIs of both parts was very unstable. All these results support the notion that the photosystems entered a special stage when the AWC of the thalli reached 42%. Thus, we deduce that during desiccation, in both female and male parts, AWC 42% is a critical stage.

Being coupled by proton translocation to the intrathylakoid lumen, electron transport pathways driven by the PSI operating alone appear to be functionally more important than electron re-cyclization around PSII (Allakhverdiev et al. 1997). Environmental stresses such as water deficiency stimulate the activity of alternative PSI-driven electron transport pathways (Bukhov et al. 2004). Therefore, the energetic and regulatory functions of PSI-driven pathways must constitute an integral part of photosynthetic organisms and provide additional flexibility to environmental stress (Bukhov and Carpentier 2004b). After re-hydration, the photosynthetic parameters of both the male and female parts showed a significant recovery within an hour. This phenomenon demonstrates their ability to restore photosynthetic functions during the transition from air to water. Under dehydration in both female and male parts, the activity of PSI showed more vigorous fluctuations than PSII (Fig. 6).In both parts of the thalli, the recovery occurs faster in PSI after re-hydration (Fig. 3). This is consistent with the results of Bukhov et al. (2004) on the photosynthetic performance of a re-hydrated lichen. The phenomena indicate that, in *P. katadai*, the activity of PSI operating alone plays an important role in the restoration of photosynthetic activities after re-hydration. During the whole process of dehydration and re-hydration the PSI of the male parts kept significantly more stable than that of the female parts (Fig. 3). Since after 1 h of re-hydration almost all the photosynthetic parameters (except YI) of the male parts, which were fully restored, were significantly better than that of the female parts (Figs. 3, 4), we conclude that the relatively steady activity of PSI of the male parts during the critical stage of dehydration constitutes a considerable advantage in regaining vigor after submersion. Furthermore, after the AWC of the thalli reached 42%, the acceptor side limitation, *Y*(NA) indicating the openness of PSI, is significantly higher in female parts compared to male parts. In the female parts, the value of *Y*(NA) raised to around 1, which means that the electron transport though PSI was nearly shut down. In the male parts, however, the acceptor side limitation only dropped correspondingly, thus showed a better transport of electrons. Therefore, we conclude that when the AWC reached 42% the PSI in the female parts was seriously affected by the malfunction of PSII, while the PSI in male parts was less affected than the female parts and thus in a better condition. It is this advantage which gives the photosystems of the male parts a better performance after re-wetting. To sum up, in *P. katadai* the susceptibility of photosynthesis to dehydration depends on the accommodative ability of PSI under severe dehydration.

A question remains, however: after severe dehydration, why is the PSI in the male part stronger compared to that in the female part? By comparing the main differences between the sexually different parts, we speculated that this may have something to do with the differences of the pigments. According to Smith et al. (1986), under severe dehydration there occurs a disruption of energy transfer between phycobiliprotein and chlorophyll A in dehydration-sensitive *prophyra* sp. *Porphyra perforata*. This disruption prevents the energy received by the phycobiliprotein from passing through the normal photosynthesis chain. Instead, the constrained energy escapes in a more or less destructive way. An increased fluorescence emission at 682 nm emanating from allophycocyanin was observed, in *P. perforata* after severe dehydration (Smith et al. 1986). This phenomenon indicates that the destructive energy may contribute to the destruction of the photosynthesis structure, including the PSI. The content of phycobiliprotein of the female parts is significantly higher than that of the male parts (Fig. 2). After severe dehydration and under illumination, the destructive energy constrained in female parts thus can be expected to be far greater than that in the male parts, with the result that the destruction of PSI in the female parts would be more severe than in the male parts. Therefore, after severe dehydration, the PSI in the male area would be stronger compared to that of the female area. However, this is only a hypothesis. To determine if this holds true, further investigations are needed.

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