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Regulation of photosynthesis by radiation quality in the lichen *Evernia prunastri*

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Abstract

In *Evernia prunastri*, photosynthetic gas exchange was saturated with yellow radiation (SOX) at 400 μmol m^{-2} s^{-1}, and then red (R), far-red (FR), or blue (B) radiations at irradiance of 15 μmol m^{-2} s^{-1} were added. Because of photosynthesis saturation, any stimulation or decay in CO_2 assimilation by any radiation quality could be attributed to the involvement of a non-photosynthetic photoreceptor. Thus CO_2 assimilation, effective quantum yield, and photochemical quenching were enhanced when R was included, and decreased with FR. Blue radiation completely abolished CO_2 fixation. Hence different spectral radiation qualities may activate non-photosynthetic photoreceptors such as phytochrome and blue photoreceptors, which are involved in regulating the photosynthetic activity in *E. prunastri*.

Additional key words: chlorophyll fluorescence; photochemical quenching; photoreceptors; quantum yield; spectrum quality.

Introduction

Lichens are nutritionally specialised fungi that derive carbon and in some cases nitrogen from the algal or cyanobacterial phycobionts. Mycobiont and photobiont live together in an integrated thallus. Carbon is acquired by the photobiont through photosynthesis, which is only active when the lichen is wet and exposed to light. It is not known yet whether or how in these symbiotic organisms saccharide resources and photosynthesis are regulated to maintain an optimal balance between energy input and expenditure. Nevertheless, radiant energy is the main factor in the regulation of the symbiotic state (Palmqvist 2000). Plants have developed several mechanisms to sense photon numbers and quality to overcome changes in their environment in order to optimise their survival. They can detect almost all facets of radiation such as direction, duration, spectral quality, quantity, and solar angle, through specialised photoreceptor molecules that allow them to sense irradiation (Sharma 2001). This is of vital importance in terrestrial systems because canopies produce a drastic modification in the spectrum due to differential photon absorbance and dispersion. In addition, plant density and morphology decrease the overall irradiance that reaches the leaf surface (Ballaré *et al.* 1991, Smith 1994). Variations in spectrum quality underneath the canopy reduce the red : far-red (R : FR) and blue : red (B : R) ratios, which act as environmental signals detected by specific photoreceptors to generate the appropriate response. Modification in the R : FR ratio induces morphological and physiological transformations because of changes in the photosynthetic pattern (Smith 1982).

Many of the photoresponses elicited by R and FR show a unique feature: the reversibility of action. The responsible for this characteristic reversibility is the photoreceptor phytochrome (Pratt 1985). Phytochrome exists in two interconvertible forms: the inactive form (P_r), which absorbs R, and the physiological active form (P_{fr}), which absorbs FR. These forms are inter-convertible. Higher plants may avoid shade as a competitive strategy (the so-called shade avoidance syndrome) when R : FR is reduced and shade avoidance reactions are phytochrome-mediated (Ballaré *et al.* 1997, Schmitt 1997, Smith and Whitelam 1997). However, nothing is known about this response in lichens yet. Ahmad and Cashmore (1993) isolated a gene corresponding to the HY4 locus of *Arabidopsis thaliana*, this gene encodes a protein with significant

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Abbreviations: Chl – chlorophyll; DM – dry mass; FR – far red radiation; I_C – compensation irradiance; LPSL – low pressure sodium lamps; P_N – net photosynthetic rate; PAR – photosynthetically active radiation; PPFD – photosynthetic photon flux density; R – red radiation; R_D – dark respiration rate; SOX – yellow photosynthetic radiation; WL – "white light"; Γ – CO_2 compensation concentration.
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homology to microbial DNA photolyases, which have a structure consistent with a flavin-type-blue photoreceptor.

In studies on the effect of radiation quality in photosynthetic organisms, photosynthesis and photomorphogenesis must be distinguished. Is the process aim of study controlled by radiation quantity through a greater or smaller photosynthetic response? Alternatively, is it regulated by specific non-photosynthetic photoreceptors? To solve this problem, we saturated photosynthesis in the lichen *E. prunastri* with yellow radiation (SOX) provided by low pressure sodium lamps (LPSL), supplemented with B, R, and FR at low irradiance (15 μmol m^{-2} s^{-1}).

We studied the response of photosynthetic CO_2 exchange and chlorophyll *a* (Chl *a*) fluorescence in the lichen *E. prunastri* incubated under different photomorphogenic conditions induced by radiation quality. The maximum emission radiation of LPSL is situated at 590 nm and bandwidth is 15 nm, providing photosynthetically active radiation (PAR). There are no photoreceptors other than photosystems, known to be activated/deactivated by SOX (Rich *et al.* 1987). Any response observed can be attributed to the different spectral qualities added.

Materials and methods

Biological material: Thalli of the epiphytic lichen *Evernia prunastri* L. (Ach.) were collected from the stems of *Quercus pyrenaica* Willd. in Valsain (Segovia, Spain) at 1 200 m of altitude. In this species of lichen, the fungi are lichenised to the green phycobiont *Trebouxia* sp. Samples were kept in the dried state for no more than 4 d. Prior to experimentation, thalli were hydrated and pre-conditioned in a growth chamber during 3 d at 17 °C, 12 : 12 "white-light" (WL) : dark photoperiod at a photosynthetic photon flux density (PPFD) of 100 μmol m^{-2} s^{-1}. Lichens were moistened twice a day at the beginning of the light and dark cycles by spraying them with de-ionised and bi-distilled water. Dry mass (DM) was estimated after incubation at 80 °C for 72 h.

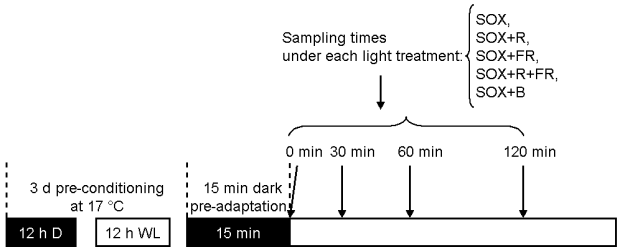

Fig. 1. Spectral treatments. After pre-conditioning during 12 h in darkness (12 h D) followed by 12 h in "white light" (12 h WL), thalli were pre-adapted during 15 min in darkness (15 min D) irradiated with yellow photosynthetic radiation (SOX) at a PPFD of 400 μmol m^{-2} s^{-1}, either supplemented or not with 15 μmol m^{-2} s^{-1} of red (R), far-red (FR), R+FR, and blue (B) radiations for 2 h, sampling at 0, 30, 60, and 120 min.

Spectral treatments: One g of dry lichen thalli was taken from the growth chamber at the end of the light period after pre-conditioning and transferred to Petri dishes. Thalli in a growth chamber at 17 °C were irradiated with SOX at a PPFD of 400 μmol m^{-2} s^{-1}, either supplemented or not for 2 h with 15 μmol m^{-2} s^{-1} of R, FR, R+FR, or B radiations. Sampling was done every 30 min (Fig. 1). Although area is a common parameter used for photosynthesis studies, we chose mass due to the fruticose nature of the lichen.

WL was provided by white fluorescent lamps (F20 W/CW Osram, Germany), SOX by low pressure sodium lamps (*Philips SOX 135 W*), and B by blue fluorescent tubes (*General Electric 20 W/Blue*) with two plexiglas filters *Rohm PG-627+PG-602*. R was provided by red fluorescent tubes (*General Electric 20 W/Red*) with two plexiglas frames *PG-501*, and FR by *Linestra* lamps (*Osram NU4/20W*) equipped with two filters *PG-501+ PG-627* (Fig. 2). Spectral PPFDs were measured by a *Licor-1800* spectroradiometer (*Licor*, Lincoln, Nebraska, USA) provided with a cosine corrected planar sensor (2π).

CO_2 exchange rates were recorded by an *LCA-4* Infra Red Gas Analyser (*Analytical Development Company*, Hoddesdon, UK). Net photosynthetic rate (P_N) was determined at different water contents of the thalli and different SOX irradiances according to Sancho and Kappen

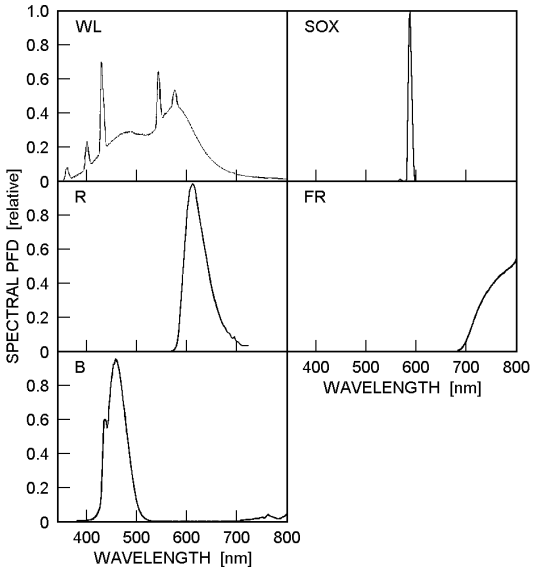

Fig. 2. Relative emission spectra of the lamps used for the treatments. "White light" (WL), yellow (SOX), red (R), far-red (FR), and blue (B).

(1989), Lange *et al.* (1995a,b), Lange and Green (1996). In order to study a possible implication of photoreceptors other than photosynthesis in regulating P_N, P_N was measured under SOX either supplemented or not with B, R, FR, and R+FR. All experiments were run at the water content at which P_N and effective quantum yield were optimal (17 °C, 350 cm^3 m^{-3} external CO_2 for 2 h at constant PPFD and humidity). For this purpose, thalli were sprayed every 15 min with bi-distilled and deionised water throughout irradiation in order to avoid desiccation and keep the optimal water content constant (Fig. 3). Water content of the thalli was controlled by weighing before and after each measurement. P_N and fluorescence parameters were measured at the indicated times (Fig. 1).

***In vivo* Chl *a* fluorescence** of photosystem 2 was measured with a portable PAM fluorometer (*PAM 2000*, *Walz*, Efeltrich, Germany) as described by Schreiber and Bilger (1993). The *PAM 2000* allows the running of pre-programmed experimental sequences to evaluate the dependence of the fluorescence parameters on the actinic irradiance produced by an R-emitting diode (λ = 650 nm). F_0 and F_m were determined in 15-min dark pre-adapted thalli. Samples were then exposed for 10 min to an intermediate R irradiance of 125 μmol m^{-2} s^{-1} to activate Calvin cycle enzymes and radiation acclimation. Irradiance was then increased from 3 to 300 μmol m^{-2} s^{-1} in 11 intervals lasting 6 min each. At the end of each irradiation step, a saturating WL pulse was given to measure F_t and F_m, which allows the calculation of the effective quantum yield ($\Delta F/F_m'$) and photochemical quenching (q_P) according to the following equations:

$$\Delta F/F_m' = (F_m' - F_t)/F_m'$$
$$q_P = (F_m' - F_t)/F_m' - F_0'$$

Statistics: Means of 2 to 6 independent measurements from each of three separate thalli are presented. Values for the different radiation treatments were compared by one way ANOVA analyses followed by Fisher's LSD test (Sokal and Rohlf 1987).

Results

Thalli were exposed to different hydration grades to study whether the water content of the thallus affected photosynthesis. In general terms, under SOX as the water content augmented, P_{max} (maximal photosynthetic rate) decreased while the compensation irradiance, I_C increased (Fig. 3*A*). In WL the behaviour was similar. In both cases the photosynthetic efficiency did not show significant differences except for thalli with a water content of 600 cm^3 kg^{-1}(DM). Photosynthetic parameters of photosynthesis-irradiance curves in both SOX and WL for *E. prunastri* derived from Edwards and Walker equation are shown in Fig. 3*A,B* and Table 1. The optimum water content of the thalli (600 cm^3 kg^{-1}) was chosen to carry out the rest of the experiments. The highest P_N was recorded at the lowest water content of the thalli. Similar behaviour was observed under WL (Table 1, Fig. 3*B*), whilst at higher water contents, P_{max} was lower under WL than under SOX. This is a common behaviour in lichens due to inability of CO_2 diffusion in water-saturated thalli (Lange *et al.* 1995a).

Saturation of P_N is required to study the effect of non-photosynthetic photoreceptors in CO_2 fixation (Fig. 4). Thalli were exposed to saturating SOX (due to the fact that there is no photomorphogenic receptor known up to date, activated by yellow radiation), supplemented with a small percentage of different spectral qualities. Dark respiration rate (R_D) was constant throughout the entire time course. When thalli were incubated under SOX without addition of other spectral quality (control), there was a rapid shift from respiration to CO_2 fixation during the first 5 min of incubation, reaching P_{max} after 15–20 min (2.4 μmol m^{-2} s^{-1}). Then, P_N dropped dramatically below the CO_2 compensation concentration (Γ) after 60 min. Water contents of lichens optimal for photosynthesis comprise narrow ranges, difficult to maintain over extended periods of time under high irradiation. However, it is unlikely that the decline in P_N was due to desiccation, because humidity was constant at the optimal water content while under irradiation, and so the hydration level of thalli did not change, as we tested by weighing the thalli before and after each measurement.

Only 15 μmol m^{-2} $s^{-1}$of R added to SOX produced a very different effect in the photosynthetic pattern. As it

Table 1. Photosynthetic parameters at a photosynthetic photon flux density (PPFD) of 400 μmol m^{-2} s^{-1} under yellow radiation (SOX) and "white light" (WL), estimated according to Edwards-Walker fitting (1987). WC, water content of the thalli [cm^{-3} kg^{-1}(DM)]; P_{max}, maximal photosynthetic rate [μmol(CO_2) m^{-2} s^{-1}]; I_C, compensation irradiance [μmol(CO_2) m^{-2} s^{-1}]; $I_{0.5}$, semi-saturation irradiance [μmol(CO_2) m^{-2} s^{-1}]; α, photosynthetic efficiency [mol(CO_2) mol^{-1}(photon)]; r, Pearson correlation coefficient; n = 10. a, b, c represent significant differences between the different water contents of thalli, p<0.05.

	WC	P_{max}	I_c	$I_{0.5}$	α	r
SOX	500 [a]	4.25	83.01	104.54	0.049	0.98
	600 [a]	4.68	98.43	116.81	0.047	0.99
	1100 [b]	2.42	101.55	70.00	0.048	0.98
	1300 [c]	2.07	132.02	82.63	0.040	0.96
WL	500 [a]	4.25	72.60	109.80	0.034	0.97
	600 [a]	5.20	80.20	139.50	0.035	0.99
	1100 [b]	2.10	100.40	42.00	0.058	0.99
	1300 [c]	0.53	116.00	15.10	0.040	0.99

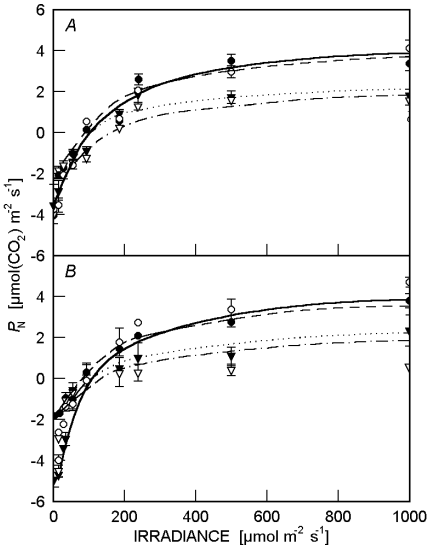

Fig. 3. Irradiance response curves of net photosynthetic rate (P_N) at different water contents of the thalli. 50 (●), 60 (○), 110 (▼), and 130 (∇) cm^{-3} kg^{-1}(DM). Experiments were done in triplicate. Separate thalli and standard deviations are shown as *double-sided bars*. Curves were fitted according to Edwards and Walker (1987).

happened for SOX, after switching the lights on, photosynthesis was activated and the thalli reached P_{max} after 20–30 min (2.5 μmol m^{-2} s^{-1}). However, P_N never fell below Γ. Thus probably a small quantity of R had the effect of enhancing and maintaining P_N at high irradiances.

When SOX was supplemented with FR, P_N was 5-fold lower than the rates obtained for SOX and S+R (P_{max} = 0.5 μmol m^{-2} s^{-1}). It returned to R_D values after 45 min. FR prevented the first activation of photosynthesis above Γ and had an inhibitory effect on P_N, when compared to SOX or SOX+R. When SOX was supplemented with R+FR, P_N was lower than with R or FR, below Γ. This fact indicated that FR had a negative effect. The same effect was observed under SOX+B. Photosynthesis was completely stopped, and P_N never went above Γ. At the end of the time course, P_N equalled R_D. As a summary, SOX and SOX+R promoted photosynthesis, while SOX+FR, SOX+(R+FR), and SOX+B inhibited it.

The effective quantum yield ($\Delta F/F_m'$) and photochemical quenching (q_P) were measured to relate the photochemical events of the process to CO_2 fixation. $\Delta F/F_m'$ is the photochemical efficiency of irradiated PS2. The addition of a small quantity of R to SOX not only maintained CO_2 fixation, but also reached the highest efficiency in electron transport through the thylakoid transport chain (Fig. 5). After 60 and 120 min under the rest of the radiation treatments, the efficiency increased, although this did not parallel CO_2 fixation. There was an important drop in P_N under SOX just after 30 min. This seemed to indicate again that R was required to maintain photosynthesis.

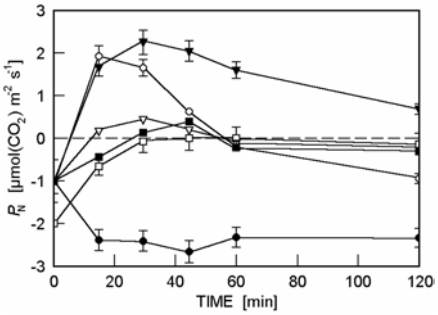

Fig. 4. Net photosynthetic rate (P_N) *versus* time curves. Thalli were irradiated with yellow radiation (SOX) at constant PPFD of 400 μmol m^{-2} s^{-1}, either supplemented or not with 15 μmol m^{-2} s^{-1} of red (R), far-red (FR), R+FR, and blue (B) radiation for 2 h. Darkness (●), SOX (○), SOX+R (▼), SOX+FR (∇), SOX+(R+FR) (■), and SOX+ blue (□). Experiments were done in triplicate in separate thalli and standard deviations are shown as *double-sided bars*.

q_P indicates the proportion of photons captured by PS2 promoting photochemical work. The highest q_P values were obtained under SOX+R (Fig. 5), which is coincident with the highest $\Delta F/F_m'$ and P_N. After 30 min, q_P increased and was constant in SOX+B. This could explain why P_N equals R_D from 60 min onwards. q_P was different between SOX and SOX+B after 120 min exposure to SOX.

Discussion

The values obtained for CO_2 fixation are in agreement with the $\Delta F/F_m'$ and q_P for SOX and S+R. R promoted CO_2 assimilation as well as the $\Delta F/F_m'$ and the photochemical work (q_P), whilst FR and B had a negative or inhibitory effect. We suggest that the different spectral qualities affect the regulation of photosynthesis in *E. prunastri*. This implies the involvement of non-photosynthetic photoreceptors. Algae photoreceptors are mainly related to chloroplast development and both B and R up- or down-regulate the photosynthetic apparatus (Hegemann *et al.* 2001). Similar results were observed in the red macroalga *Porphyra umbilicalis*: B decreased the growth rate when compared to R (Figueroa *et al.* 1995). In other red macroalga, *Porphyra leucosticta*, radiation quality affected the growth rate morphogenetically, by inhibiting (B) or promoting (R) growth (Aguilera *et al.* 1997).

The different non-photosynthetic photoreceptors might be acting upon enzymes of the photobiont metabolism. Such effect may be exerted at the CO_2 fixation level

(Fig. 3). This effect can be observed comparing the P_N under SOX (Fig. 3*A*) with P_N under WL (Fig. 3*B*). Despite the fact that WL comprises all visible spectrum and that the photosynthetic parameters are somewhat higher (Table 1), the behaviour in terms of photosynthetic efficiency is rather similar under SOX and WL. In optimum hydrated poikilohydric systems, coupled cyclic electron transport may occur concurrently with linear electron transport under saturating irradiation, particularly in lichens, because more electrons are available for reducing photosystem 1 (PS1) (Heber *et al.* 2000). Therefore, enzymes such as for example ribulose-1,5-bisphosphate carboxylase/oxygenase, nitrate reductase (Gordillo *et al.* 2001a,b), and carbonic anhydrase (Palmqvist and Badger 1996) would demand electrons from the electron transport chain, which explains why the $\Delta F/F_m'$ and q_P are maintained at high efficiencies. *E. prunastri*'s photobiont is a green alga from the genus *Trebouxia* (Galun 1988). The relationship between CO_2 exchange and relative electron transport rate (rETR) through PS2 was determined in other trebuxioid lichens (Palmqvist *et al.* 1997), showing that this relationship is non-linear. Moreover, in some cases the lowest ETR was coincident with the highest CO_2 exchange rates. This could be due to quenching mechanisms, which are inversely proportional to CO_2 fixation. In any case, the relationship between ETR and CO_2 exchange is very complex in poikilohydric organisms, and the mechanisms for the regulation of photosynthesis are different from those found in vascular plants (Green *et al.* 1998).

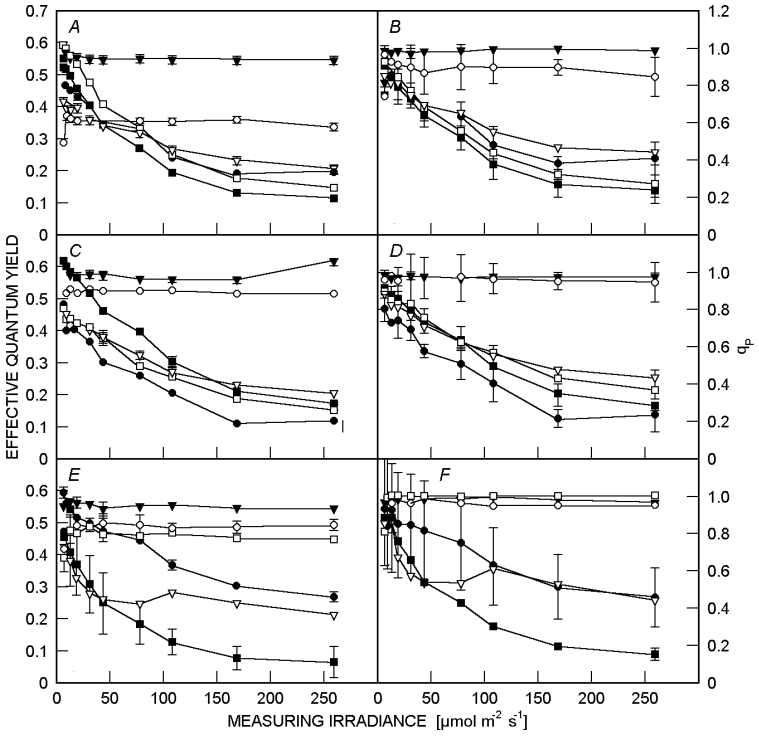

Fig. 5. Effective quantum yield $[(F_m' - F_t)/F_m]$ (*A, C, D*) and photochemical quenching (q_P) (*B, D, F*) at 30 min (*A, B*), 60 min (*C, D*), and 120 min (*E, F*) of exposure to different radiation types. Darkness (●), SOX (○), SOX+R (▼), SOX+FR (▽), SOX+(R+FR) (■), and SOX+ blue (□). Experiments were done in triplicates and standard deviations are shown as *bars*.

According to the response obtained, particularly under SOX+R, SOX+FR, and SOX+(R+FR), phytochrome could be involved in the regulation of photosynthesis at some stage. We show that FR had a negative effect upon CO_2 fixation even when R was added. Under irradiance saturating photosynthesis, addition of FR can cause an imbalance in excitation energy between PS1 and PS2 since FR is preferentially absorbed by PS1. In order to discriminate against FR effects induced *via* absorption by photosynthetic pigments, we run a classical phytochrome experiment consisting of a 5 min R pulse of low PPFD followed by a 10 min FR pulse followed by darkness. We tested for CO_2 fixation under these conditions (Fig. 6). CO_2 assimilation was always lower than Γ due to the low irradiance used. However, R_D increased when FR was applied after 5 min of R, showing a possible implication of phytochrome.

In contrast to the data presented in this study, B stimulated photosynthesis of brown algae in saturating R irradiance, probably by stimulating carbon concentration mechanisms such as the activation and release of CO_2 (Dring 1989, Schmid and Dring 1996).

The importance of the relationship between photomorphogenic photoreceptors and photosynthesis has been

widely demonstrated: phytochromes A and B are involved in *A. thaliana* flowering *via* photosynthesis (Bagnall and King 2001). R and B regulate respiration activity in *Euglena gracilis* (Wolff and Kunne 2000). In the aquatic angiosperm *Vallisneria gigantea*, the regulation of the orientation movement of chloroplasts in epidermal cells is the result of co-operation between phytochrome and photosynthetic pigments under low PPFD (Dong *et al.* 1995). We suggest that phytochrome is involved in the regulation of CO_2 assimilation in *E. prunastri*.

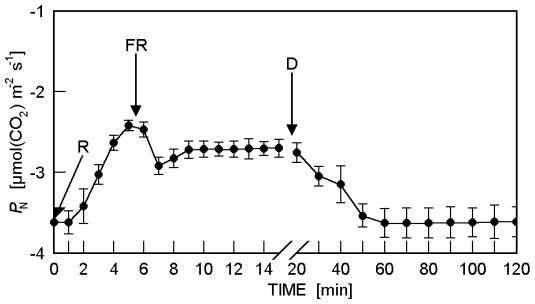

Fig. 6. Net photosynthetic rate (P_N) *vs*. time curves. Thalli were irradiated for 5 min with 15 μmol m^{-2} s^{-1} of red (R) followed by 10 min of 15 μmol m^{-2} s^{-1} far-red (FR), followed by darkness (D) up to 2 h. Experiments were done in triplicate in separate thalli. Standard deviations are shown as *double-sided bars*.

R radiation is absorbed by PS2 and PS1. Both photosystems act as sensors to regulate photosynthetic acclimation in the long term (Chow *et al.* 1990). These authors used short "end-of-day" FR pulses to increase FR : R, finding that the shift in the spectral proportion was detected by phytochrome. Vascular plants, green algae, and cyanobacteria respond to temperature or irradiance changes through changes in the redox state of the thylakoid electron transport chain (Huner *et al.* 1996). This mechanism of sensing the redox state is an important way of monitoring abiotic changes. PS1 and PS2 act as sensors of radiation quantity, modulating their relationship with phytochrome in such a manner that the spectral ratio R : FR not only acts as a signal, but also modifies the quantity of photons received by both photosystems (Anderson 1986).

The inhibitory response obtained for SOX+B could point to a blue photoreceptor (Cashmore 1997). The B family of photoreceptors is responsible for responses such as inhibition of chloroplast development in the brown algae *Macrocystis pyrifera* (Apt *et al.* 1995) and inhibition of growth in the red macroalga *P. leucosticta* (Aguilera *et al.* 1997). In most microalgae, B enhances the transcription of several genes encoding for Chl and heme biosynthesis; regulates the ratio of the light-harvesting complex LHC2 to its reaction centre RC2 by stimulating transcription of genes encoding Chl-binding proteins; controls the expression of the Calvin's cycle enzymes (Hegemann *et al.* 2001), and also regulates the circadian clock in *Chlamydomonas* (Mittag 2001). The data strongly indicate an induction of R_D by B, which might compensate gross photosynthesis, probably due to fungal respiration, which is a major factor in the carbon balance of lichens. Even more, respiratory activity could be enhanced by B either in the algal or the fungal partner, or in both. For instance, Bader *et al.* (1992) demonstrated that B enhanced the respiratory activity under photosynthetic conditions in *Chlorella*. Therefore, B could control the development of the algae and ultimately this would contribute to the regulation and maintenance of symbiotic equilibrium.

As concluding remarks, we suggest that the different spectral radiation qualities used in this study activate different non-photosynthetic photoreceptors (probably phytochrome and a B-photoreceptor), that ultimately regulate photochemistry and CO_2 assimilation in *E. prunastri*. The eco-physiological meaning of photon perception in some lichens can be understood not only if we consider that in the field, at the end of the day, R : FR decreases, but also that this ratio is very small under the canopy, even during the day. This is because leaves of plants and trees forming the canopy prefer R (Huner *et al.* 1996) and so, the proportion of FR underneath the canopy is increased with respect to other spectral qualities. This has an obvious effect in PS1, but also regulates the ratio P_{fr} : P_r, which enables the perception of shade and detection of neighbouring plants, acting as a light-regulatory switch throughout the plant life cycle (Kendrick and Kronenberg 1994). Unfortunately, there are not any data about the shade avoidance syndrome in lichens and we can not conclude anything with regard to this from our experiments. However, lichens have little control over their hydration status and rapid physiological and optical responses allow them to thrive through repeated dehydration cycles. According to Mackenzie and Campbell (2001), interaction of the photobiont with the mycobiont cortex might develop wavelength-depending mechanisms for screening radiation during hydration/dehydration cycles in order to generate photoprotection specific to the absorbance spectra of each particular photobiont's light-harvesting antennae. Lichens, as many other organisms, do not merely respond to their environment, they also have the capacity to adjust their physiology and behaviour in anticipation of changing environment. Lower eukaryotes, especially, are able to acclimate only to environmental changes that happen periodically. The major rhythmic changes are the day/night cycle and the hydration/dehydration state (this being of particular importance in the location were lichens were collected, as day would correspond to dehydration and night to hydration). The machinery that prepares an organism for these changes is a biological or circadian clock. The mechanism of such clocks can be part of a molecular pathway in which different photoreceptors are involved in order to help coping with the environment.

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