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Photosynthetic Fluorescence Induction and Oxygen Production in Corallinacean Algae Measured on Site

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Abstract: Photoinhibition of photosynthesis was measured in two Mediterranean Corallinaceae, *Jania rubens* and *Corallina mediterranea*, using pulse-amplitude modulation (PAM) fluorescence and oxygen production on site. Both algae were found to be adapted to low irradiances of solar radiation and easily inhibited by exposure to excessive radiation. Both algae were impaired even in their natural habitat under overhanging rocks which protected them from direct solar radiation, except for a few hours in the early morning. Recovery from photoinhibition of both the photosynthetic quantum yield, defined as F_v'/F_m', and oxygen production took several hours and was not complete. Judging from both parameters indicated above, *Jania* seems to be even more sensitive than *Corallina*, even though the former alga was found in more exposed habitats.

Key words: Corallinaceae, *Corallina*, *Jania*, oxygen measurements, PAM fluorescence, photoinhibition, Rhodophyta, solar radiation.

Abbreviations and Symbols

F_o:	initial fluorescence in the dark-adapted state, all reaction centers are open (oxidized)
F_m:	maximal fluorescence in the dark-adapted state, all reaction centers are closed (reduced)
F_v:	variable fluorescence, calculated as $F_m - F_o$
F_o', F_m' and F_v':	the same for the light-adapted state
F_t:	current steady-state fluorescence
PAM:	pulse amplitude modulated fluorometer
PAR:	photosynthetically active radiation
qP:	photochemical quenching of chlorophyll fluorescence determined by $q_P = (F_m' - F_t)/(F_m' - F_o')$
qN:	non-photochemical quenching of chlorophyll fluorescence calculated by $q_N = 1 - (F_m' - F_o')/(F_m - F_o)$

Introduction

During the past few years rapid technological progress has made it possible to assess photosynthesis in plants on site, eliminating the necessity of transferring the specimens into the laboratory which often creates a stress situation for the organisms and produces a number of artifacts. One of these developments is the miniaturization and computer-control of equipment for pulse amplitude modulation (PAM) fluorescence (Schreiber et al., 1986).

Light-induced chlorophyll fluorescence changes can be successfully used to obtain valuable information on the numerous factors which control the photosynthetic apparatus (Briantais et al., 1986; Renger and Schreiber, 1986; Krause and Weis, 1991) based on fluorescence quenching analysis (Quick and Horton, 1984; Schreiber et al., 1986). Intensive investigations have led to a better understanding and interpretation of the complex processes, but the discussion is still far from being settled (Walker, 1992; Schreiber and Bilger, 1993; Schreiber et al., 1994). The basic assumption of fluorescence quenching analysis is that two different processes with different time kinetics can reduce the maximal fluorescence yield, F_m. The faster of the two processes is photochemical quenching which is quickly suppressed by the application of a short saturating pulse which closes all reaction centers of PS II. The second process is non-photochemical quenching which occurs on a much slower time-scale and is thought to be mainly based on the energization of the thylakoid membrane involving a number of different quenching mechanisms (Schreiber et al., 1995; Krause and Weis, 1991).

In order to obtain quantitative information on the status of the photosynthetic apparatus Genty et al. (1989) and Weis and Berry (1987) developed empirical expressions for quantum yield based on fluorescence parameters measured during quenching analysis. This approach has the advantage that the analysis does not require previous knowledge of the dark fluorescence parameters. The validity of these expressions has been supported by concomitant gas exchange measurements.

PAM fluorescence techniques were first used for higher plants to evaluate their ecophysiological status in the field. With the development of more sensitive equipment, the techniques were later successfully applied for measurements in macroalgae and unicellular algae, even in dilute suspensions. However, available commercial equipment first hampered successful measurements because of limited sensitivity which was not suitable for dilute suspensions of algae. Another problem was that several algal groups showed qualitatively different behavior from higher plants and thus has been interpreted as functional and structural differences (Büchel and Wilhelm, 1993; Ting and Owens, 1992). Specifically, the

Bot. Acta 109 (1996) 285 – 291

regulatory mechanisms seem to be vastly different in various algal taxonomic groups. Recent investigations indicate that it may be advantageous to utilize shorter saturating pulses than for higher plants for several groups of algae and cyanobacteria (Schreiber et al., 1995).

Another tool for the assessment of ecophysiological properties of algal photosynthesis is the measurement of oxygen exchange *in situ*. For this purpose a portable and submergible device has been developed which allows computer-controlled measurements in the water column under solar irradiation in real time (Häder and Schäfer, 1994a, b).

The aim of the present paper is to determine the photosynthetic parameters of two Mediterranean Corallinaceae under solar irradiation on site. Specifically, the question is discussed whether current irradiation values impair photosynthesis in the two algae in their natural habitat.

Materials and Methods

Plant material

The common Mediterranean red algae *Corallina mediterranea* and *Jania rubens* (Corallinaceae) were used for the experiments. The algae were collected from an east-facing rocky shore of Saronikos Gulf, near Korinth, Greece (37° 58′ N, 23° 0′ E). All samples were retrieved from under overhanging rocks close to the surface where they were exposed to direct sunlight only during a few hours in the early morning. The experiments were carried out during the summers of 1994 and 1995.

Measurements of PAM fluorescence

A portable pulse amplitude modulated fluorometer (PAM 2000, Walz, Effeltrich, Germany) was used to determine *in vivo* chlorophyll fluorescence on site (Schreiber et al., 1986). Thalli were freshly harvested and mounted in open UV-B translucent Plexiglas frames (GS 2458, Röhm and Haas, Darmstadt, Germany) submersed in shallow water in the shade for half an hour. After this dark adaptation PAM fluorescence was measured and the optimal photosynthetic quantum yield determined. The specimens were then exposed to solar radiation to induce photoinhibition, indicated by a decrease in the effective photosynthetic quantum yield, and PAM fluorescence was evaluated again. Subsequently, the samples were shaded again, and the recovery of quantum yield was determined at predefined time intervals for up to 6 h. In another type of experiment thalli were collected every hour from sunrise to sunset, and the fluorescence parameters were determined immediately after harvest. The PAM fluorometer allows preprogrammed experimental sequences to be run; i.e., it is possible to determine the dependence of the fluorescence parameters on the irradiance of actinic light provided by a red light-emitting diode (LED).

Oxygen exchange measurements

Oxygen exchange was measured under solar radiation at the surface or in the water column with a submersible device (Häder and Schäfer, 1994a, b). The oxygen concentration is determined with a Clark-type electrode; simultaneously PAR irradiance, temperature and depth are measured. After amplification the signals are routed to an analog/digital card located in a laptop computer. The computer program samples the data at frequent intervals, determines mean values, displays the data and stores them on the hard disk drive. Linear regression of the oxygen concentration is calculated in order to determine oxygen produced or consumed per unit time.

The kinetics of photoinhibition was determined in thalli exposed to solar radiation immediately after harvest. After an initial measurement of dark respiration, net oxygen production was assayed until photoinhibition was manifest. In another type of experiment the thalli were exposed at various depths in the water column. Recovery was investigated by storing the samples at 5 m depth for a predefined period of time in a translucent container. At the end of all experimental runs the exposed area of the thalli was measured and their dry weight determined.

Statistics

At least eight independent PAM fluorescence measurements were taken from different parts of the thallus or different specimens from which mean values and standard deviation were calculated. Photosynthetic oxygen exchange was measured at least three times for each treatment. All experimental runs were repeated several times and Student's *t*-tests were performed, where appropriate.

Measurement of solar radiation

Solar irradiance was measured during the experiments in three wavelengths bands (UV-B, 280–315 nm, UV-A, 315–400 nm, PAR, 400–700 nm) using a newly-developed filter instrument (ELDONET, Real Time Computer, Möhrendorf, Germany). The instrument takes readings at 1 s intervals in each channel and integrates them over 1 min intervals. The data are graphically displayed and stored in a computer after analog/digital conversion, and doses are calculated on an hourly and daily basis for each channel. Typical irradiances under clear skies were 390 W m^{-2} for PAR, 38 W m^{-2} for UV-A and 0.95 W m^{-2} for UV-B at local noon under cloudless skies.

Results

In order to determine the dependence of the fluorescence parameters on actinic light a preprogrammed automatic experiment was performed using freshly harvested samples (Fig. **1**). Before the run the samples were dark-adapted for 30 min and F_o and F_m measured. Then the thalli were allowed to adapt to light using the built-in red light emitting diode at an irradiance of 23.3 W m^{-2}. After these initial measurements the actinic light irradiance was increased in 11 steps from 1 to 79 W m^{-2}. In *J. rubens* (Fig. **1a**) the steady state fluorescence, F_t, dropped slightly from an initial value of 0.44. F_o' followed a similar pattern at slightly lower values. In contrast, F_m' showed a much steeper decline from a higher initial value with increasing irradiances. The photosynthetic yield had an optimal value at about 2.5 W m^{-2} and declined with increasing irradiances. The photochemical quenching dropped only slightly from its initial value close to 1. In contrast, non-photochemical quenching rose from values near 0.2 to about 0.8. Thalli of *C. mediterranea* were harvested from the same site and subjected to the same experimental run (Fig. **1b**). In

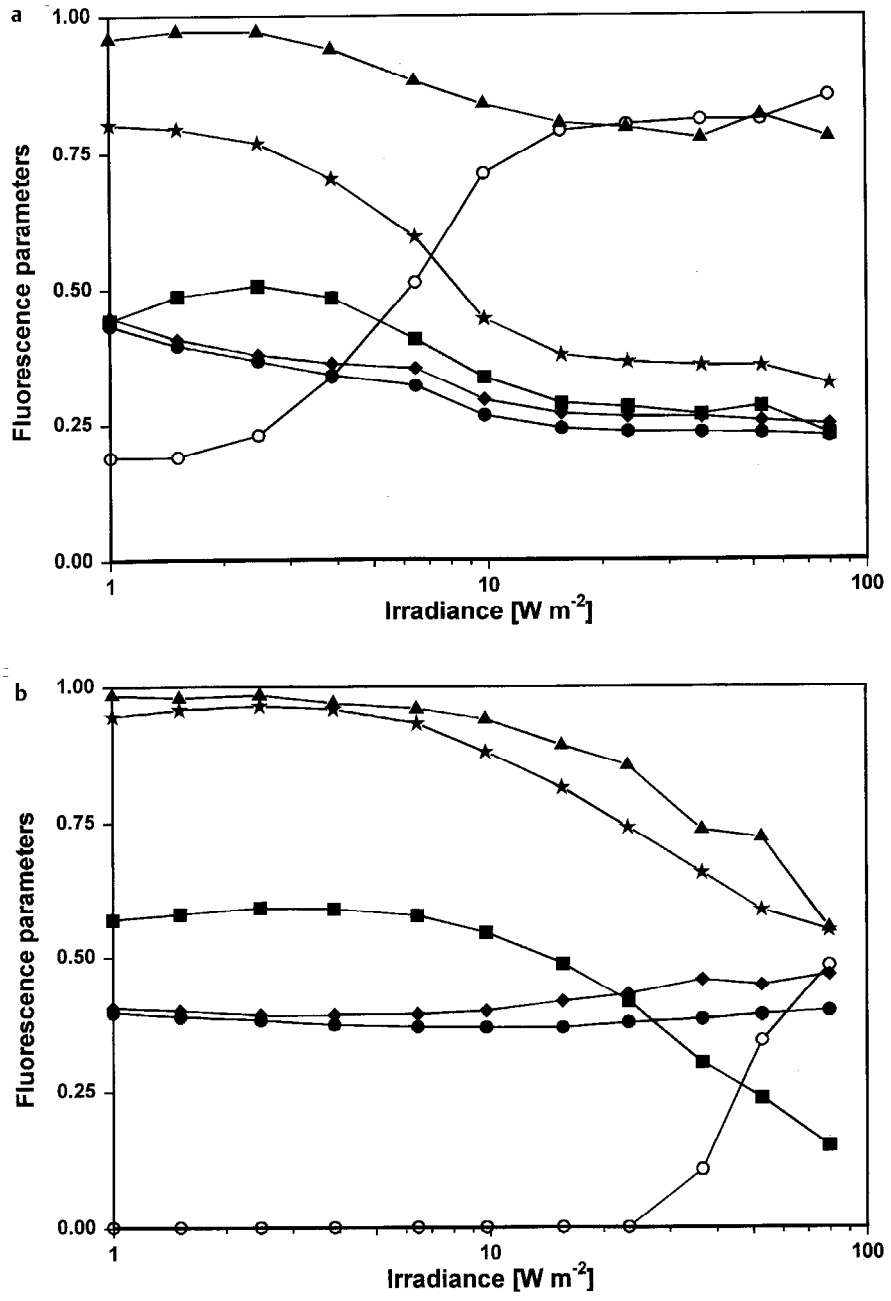

Fig. 1 Fluorescence parameters measured in *Jania rubens* (**a**) and *Corallina mediterranea* (**b**) in dependence of fluence rate of actinic red light. Before the experiments the thallus was adapted to an intermediate fluence rate of 23 W m^{-2} for 10 min and then exposed to increasing irradiances for periods of 6.5 min each. At the end of each period the fluorescence parameters were determined. The results shown here are representative data of three independent measurements. Diamonds: F_t, squares: photosynthetic quantum yield, triangles: photochemical quenching, open circles: nonphotochemical quenching, asterisks: F_m' and closed circles: F_o'.

contrast to *Jania*, in *Corallina* F_t rose slightly, and F_o' remained almost constant with increasing irradiances. F_m started at higher values and dropped only to values of about 0.6. The yield remained almost constant for low irradiances but fell to about 0.2 at high irradiances. The photochemical quenching decreased more than in *Jania* but the non-photochemical quenching was zero at most irradiances and only started to rise at high irradiances.

Thalli of *Corallina* were harvested and kept in a shallow rock pool suitable for on-site measurements with the PAM instrument. The optimal quantum yield was determined after 30 min of dark adaptation (Fig. **2**). Then the thalli were exposed to solar radiation for 30 min during which time the yield decreased substantially. After exposure the thallus was shaded again and recovery measured at predetermined intervals. In this experiment the thalli were exposed in a UV-transmitting Plexiglas container which kept the algae in place so that exposure and measurement area could be controlled, but sea water circulated through the container. At the end of the 6 h recovery period the yield was also determined in algae subjected to the same treatment, except for exposure to solar radiation, in order to determine whether there were any other stress factors, besides high solar irradiance, affecting the yield. The high yield value indicates that experimental handling had not affected the photosynthetic capacity of the algae. The same experiment was repeated with *Jania* thalli harvested from the same site. As compared to *Corallina*, the yield decreased even further after solar exposure and the recovery was slower and only partial. Also, the control values after the treatment were lower than before the experiment.

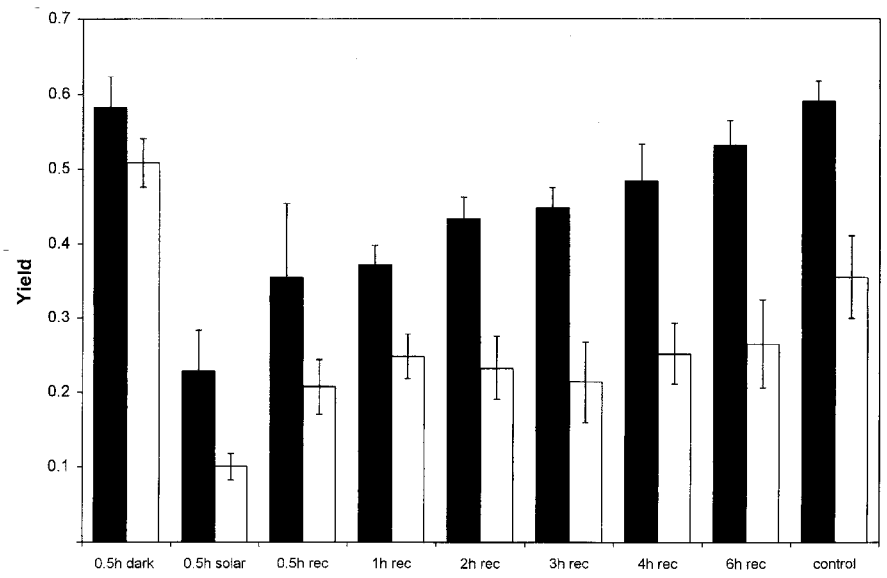

Fig. 2 Photosynthetic quantum yield of *J. rubens* (open bars) and *C. mediterranea* (closed bars) measured after adaptation in the shade; after exposure to solar radiation in a rock pool, and during recovery (in the shade). For each data point at least eight measurements were averaged and the standard deviation calculated.

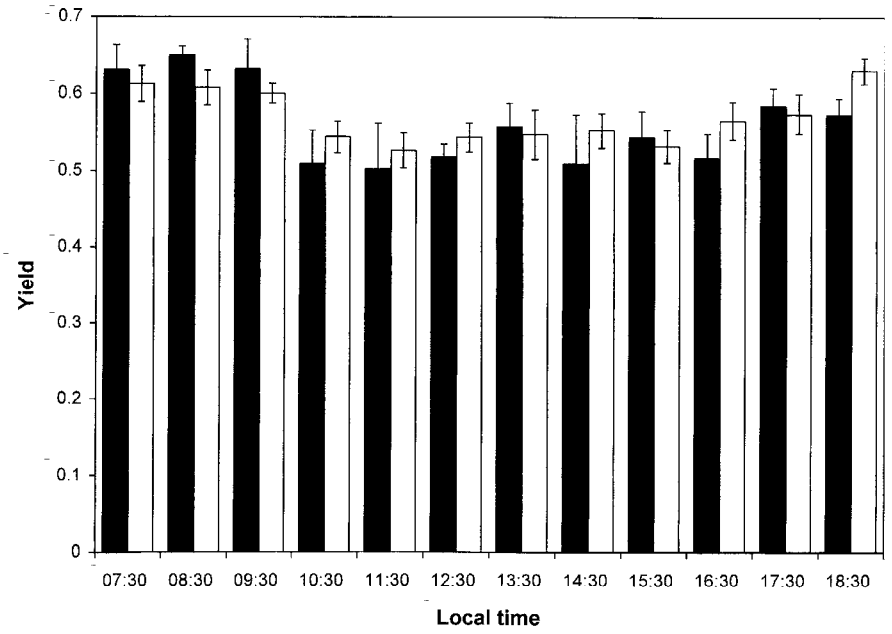

Fig. 3 Photosynthetic quantum yield of *J. rubens* (open bars) and *C. mediterranea* (closed bars) measured from dawn to dusk. Thalli were retrieved from their growing site and measured immediately after harvest. For each data point at least eight measurements were averaged and the standard deviation calculated.

In the experiments described above the thalli were exposed to direct solar radiation in a shallow rock pool where they received considerably higher solar radiation than at their growth site. In order to determine whether photoinhibition also occurs at their natural site, algae were harvested from dawn to dusk at 1 h intervals and the yield was determined immediately after harvest. The algae received direct solar radiation from sunrise to about 11.00 h. The samples of both algae showed maximal yield values of about 0.6 for the first few hours (Fig. **3**). After 9.30 h the yield decreased significantly and recovered only very slowly over the day, even though for most of the day the algae did not receive direct sunshine.

Thalli of *Jania* were harvested and immediately transferred into the instrument to measure oxygen exchange. The thalli showed significant dark respiration. When exposed to solar radiation close to the surface, oxygen production started to decline after a few minutes of exposure, and negative values were recorded after about 16 min (Fig. **4a**). Similar behavior was found in *Corallina*, but in this alga oxygen production remained almost constant for a longer exposure time than in *Jania* (Fig. **4b**). Finally, photoinhibition also commenced in this alga. After complete cessation of oxygen production, samples were stored at 5 m depth in a translucent container. In both algae partial recovery of photosynthetic oxygen production could be determined after 2 h, but in no case was full recovery to the initial values observed (data not shown).

In another type of experiment a sample of *Jania* was harvested and, after measuring dark respiration, it was exposed at different depths between 5 m and 0 m, starting at the lowest level (Fig. **5a**). It is interesting to note that the highest net photosynthetic oxygen production was found at 0 m at full sunlight, even though the sample was harvested from a shaded area. Differences between the various depths were not very striking even though the irradiances differed by more

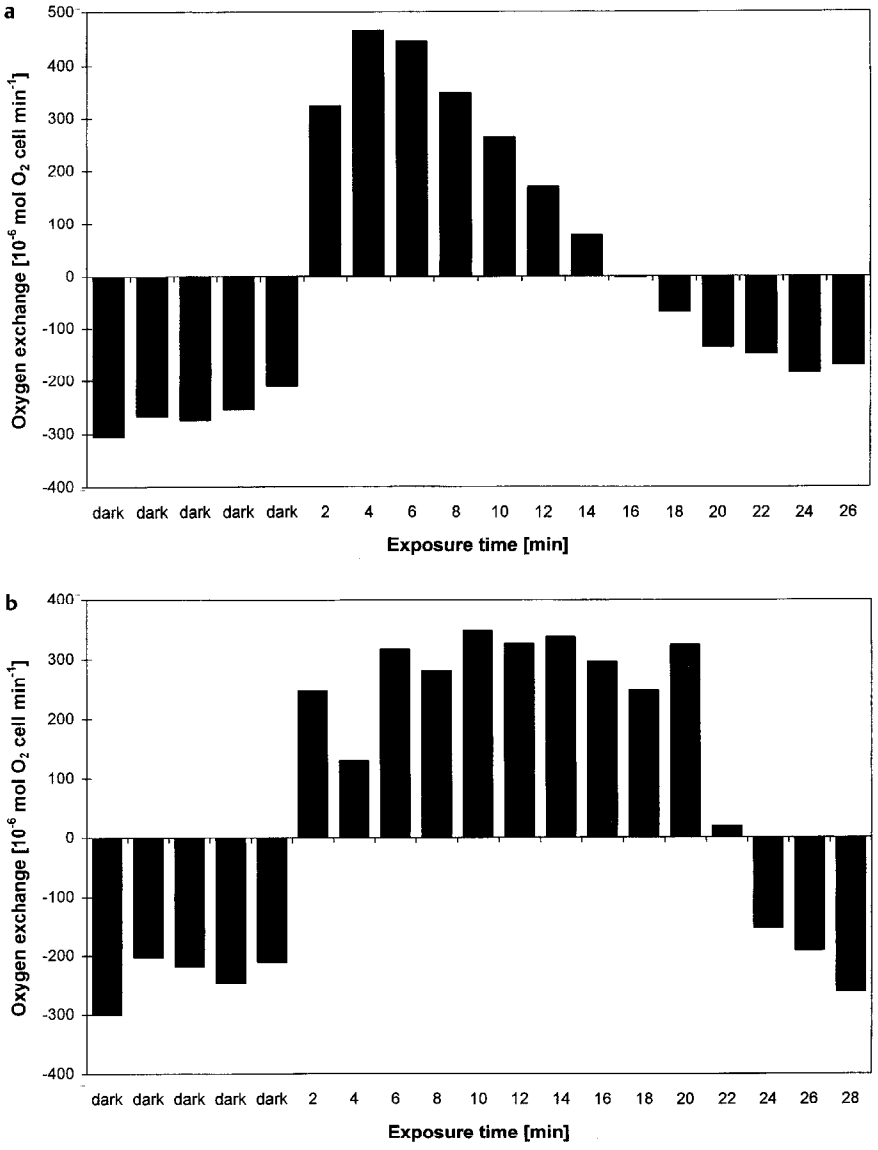

Fig. 4 Photosynthetic oxygen exchange of *J. rubens* (**a**) and *C. mediterranea* (**b**) measured under solar radiation at the surface. Before exposure, dark respiration was determined and then oxygen exchange measured and integrated over 2 min periods each. The data shown here are representative data of one of three independent measurements.

than a factor of two between surface and 5 m. Exposure time at the surface was too short (4 min) to induce photoinhibition. Somewhat different behavior was recorded for *Corallina* (Fig. **5b**). In this alga the highest oxygen production values were found at 5 m, but also in this case the differences were not very significant.

Discussion

Solar irradiation of high fluence rates induces photoinhibition in higher plants (Björkman and Demmig, 1987; Schreiber et al., 1994), macroalgae (Hanelt et al., 1992, 1993; Franklin et al., 1992; Larkum and Wood, 1993) and phytoplankton (Helbling et al., 1992; Leverenz et al., 1990; Herrmann et al., 1995). Excessive solar radiation induces photo-oxidative stress caused by light-dependent generation of active oxygen species (Foyer et al., 1994). The mechanism of photoinhibition is still controversial (Crofts and Yerkes, 1994), but it can be regarded as an active physiological regulatory process to protect the photosynthetic apparatus from excessive radiation. A key reaction of this process is the turnover of PS II D1 protein (Sundby et al., 1993). During photoinhibition the photosynthetic quantum yield and photochemical quenching decrease and often the non-photochemical quenching increases.

Both Corallinaceae used for this study are adapted to low solar irradiances and thrived best in the shade of overhanging rocks. In contrast to *Corallina*, *Jania* was also found in other, more exposed habitats but there it was often shaded by other algae, or the outer layers of the thallus were dead and served as shading for the innermost photosynthetically active branches. In contrast to other algae adapted to direct solar radiation, recovery from exposure to direct sunlight was slower and not complete (Häder et al., 1996a, b). One important result is that the photosynthetic quantum yield is not optimal even in the natural habitat of the algae. It is even more surprising that recovery takes several hours after direct solar radiation stopped. When compared, *Jania* seems to be the more sensitive species and also recovery takes longer and is less complete than in *Corallina*.

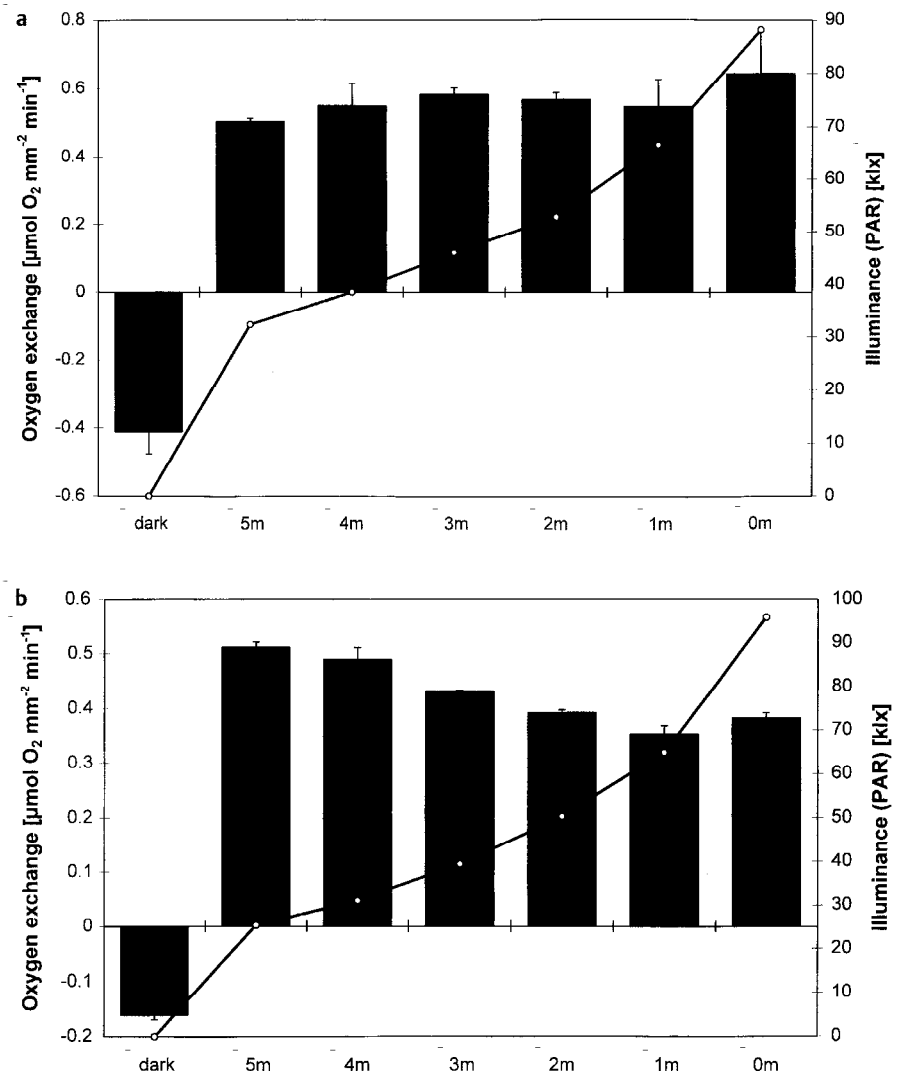

Fig. 5 Oxygen exchange of *J. rubens* (**a**) and *C. mediterranea* (**b**) in darkness and subsequently at increasing depths from 5 m to 0 m in comparison to PAR irradiance. Temperature was 23 °C. For each data point three measurements were averaged and the standard deviation calculated.

It is interesting to note that inhibition of oxygen production and photosynthetic yield followed different kinetics. A similar result was found in the brown alga *Dictyota dichotoma* (Hanelt et al., 1994). In this organism increasing white light fluence rates caused a decrease of oxygen production and a concomitant decrease in the photosynthetic quantum yield. Simultaneously, an increase in zeaxanthin was found, which is supposed to play an important role in photoprotection mechanisms in the chloroplast under light stress (Uhrmacher et al., 1995). Dithiothreitol, an inhibitor of the de-epoxidase of the xanthophyll cycle suppressed the conversion from violaxanthin to zeaxanthin and, simultaneously, the decrease of the initial fluorescence, F_o, as well as the photosynthetic yield, F_v/F_m.

Considering the natural irradiation conditions, the putative protection mechanism of the xanthophyll cycle against photoinhibition by visible light could be modulated by ultraviolet radiation in the range of 280–315 nm (UV-B). Pfündel et al. (1992) could show that the xanthophyll cycle itself is a target of UV-B radiation. Their results indicate an inhibition of the de-epoxidase, whereas the decrease of the violaxanthin availability is caused by a decrease of PS II activity. In the latter case the results of several investigations implicate the quinone Q_A as a primary site of UV-B damage, and damage to plastoquinone molecules may then induce degradation or damage of the D1 protein of PS II (Greenberg et al., 1989; Melis et al., 1992). Consequently, the exposure of organisms adapted to low solar irradiance to full sunlight may result in an increase of photoinhibition or photodamage caused not only by high visible light and UV-B but also by a potentiated effect of both.

Algae seem to differ in several respects from higher plants in their regulatory mechanisms and capacity (Büchel and Wilhelm, 1993). Further investigations, including inhibition and recovery kinetics, are necessary to elucidate the mechanisms of photoinhibition and photodamage.

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