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Effects of solar radiation and solar radiation deprived of UV-B and total UV on photosynthetic oxygen production and pulse amplitude modulated fluorescence in the brown alga *Padina pavonia*

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Abstract

The effects of solar radiation on photosynthetic oxygen production and pulse amplitude modulated (PAM) fluorescence were measured in the marine brown macroalga *Padina pavonia* harvested from different depths from the Greek coast near Korinth. In fluence rate-response curves the light compensation point for photosynthetic oxygen production increased and the saturation level decreased with increasing exposure time to solar radiation. Cutting off the UV-B wavelength range (280–315 nm) from solar radiation reduced the inhibition of photosynthesis, and the organisms were less affected when all of the UV radiation was filtered out. Algae collected from 7 m depth were much more prone to photoinhibition than those harvested from rock pools exposed to unfiltered solar radiation. During continuous exposure to solar radiation, rock pool algae showed photoinhibition after longer periods of time than specimens from 7 m or from dark adapted habitats. When subjected to unfiltered solar radiation the ratio of the variable fluorescence to the maximal fluorescence F_v/F_m ($F_v = F_m - F_o$) rapidly declined with increasing exposure time. However, again algae from 7 m depth were more prone to photoinhibition than rock pool algae. The differences between the two ecological strains were less obvious when UV-B or total UV was removed from solar radiation. Only in the latter case a complete recovery was observed after 2 h while, when exposed to unfiltered sunlight, only the rock pool algae recovered completely within that time.

Keywords: Clark electrode; Oxygen measurements; *Padina pavonia*; Pulse amplitude modulated fluorescence; Phaeophyta; Photoinhibition; Solar radiation; Ultraviolet radiation

1. Introduction

In contrast to phytoplankton, macroalgae show a distinct and fixed pattern of vertical distribution in their habitat [1]. While some organisms inhabit the area above the tidal zone (supralittoral) exposed only to the spray from the surf, others populate the zone which is characterized by the regular temporal change in the tides (eulittoral or midlittoral). Still others are restricted to the range below the tidal zone (sublittoral).

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In addition to the degree of exposure to air, another important factor controlling the abundance and species distribution of algae is sunlight exposure. While some algae are adapted to the bright solar radiation at the surface by, for example, being exposed in rock pools, the other extreme is represented by algae which thrive only in crevices or under overhanging rocks where light exposure is limited to a small fraction of diffuse radiation. The difference between the various exposures can be substantial, ranging from over 1000 W m^{-2} on clear days at the surface to a few percent of this radiation which reaches, for exdample, the understorey of a kelp forest. The record lowest occurrence of algae was found in some rhodophyta at a depth of 268 m in the Bahamas (0.001% of the surface light), but reportedly growth in these organisms is extremely slow being in the order of a few cells per year [1].

In recent years there has been increasing interest in the ecology of macroalgae being adapted to such extremes in irradiance [2]. Another area of interest is how an organism can adapt to the rapidly changing light conditions in its environment. Experiments by Hanelt and co-workers [3–5] have shown that in many macroalgae net photosynthesis is limited to a specific range of irradiances. Under suboptimal irradiances photosynthetic activity decreases and may fall below the light compensation point where respiration dominates the oxygen exchange. At the other extreme, excessive radiation may damage the photosynthetic apparatus of the cells [6–8].

Under excessive radiation in both higher plants and macroalgae photoinhibition can be observed which can be measured as a decrease in photosynthetic activity [4–6,9–12]. The D1 protein is one of the key targets of excessive radiation [13,14]; it is thought to be altered in its secondary structure which is recognized by a protease. One of the recovery mechanisms of the photoinhibitory damage is the replacement of the degraded D1 protein by newly synthesized protein. Photoinhibition has been confirmed by PAM (pulse amplitude modulated) fluorescence measurements [15]; this method uses transient changes of chlorophyll fluorescence [16,17]. The photosynthetic apparatus can be protected from excessive irradiation by relaxation of excited chlorophyll states via carotenoids [18] and by inactivation of photosystem II reaction centers [19,20].

In addition to visible radiation, solar ultraviolet radiation is a strong environmental stress factor which modifies the photosynthetic activity of both terrestrial and aquatic plants [21–24]. In several species of marine benthic algae and phytoplankton, inhibitory effects of UV-B (280–315 nm) on photosynthesis and chlorophyll fluorescence have been documented [25–27]. UV-B seems to affect several targets in photosynthesis: it impairs the D1 protein associated with photosystem II, which results in a decrease of the noncyclic photosynthetic electron transport [28,29]. The water splitting site of photosystem II and the reaction center of photosystem II are damaged by ultraviolet radiation [30,31] and, finally, the integrity of the membranes is affected, caused by a decrease in the lipid content and that of membrane transport systems [32].

The aim of this paper is to describe the effects of Mediterranean solar radiation on photosynthetic oxygen production, photoinhibitory events and their recovery under dim-light conditions in the brown alga, *Padina pavonia*.

2. Materials and methods

2.1. Plant material

Padina pavonia was collected from east-exposed rocky shores on the coast of Saronikos Gulf, near Korinth, Greece (37° 58' N, 23° 0' E). Two ecologically different populations were identified: one grew in rock pools exposed to full solar radiation only a few centimeters below the water surface. The other population was harvested by diving to a depth of about 7 m where it was exposed to lower irradiances (Secchi disk depth was about 11 m; ca. 34% of surface visible light). The thalli were harvested on the evening before the measurements and kept in a large quantity of seawater overnight outside the laboratory. Until the algae were subjected to the measurements they were kept in the shade.

2.2. Exposure to light

Whole *Padina* thalli were exposed in open glass Petri dishes (diam. 5 cm) which were kept in a water bath at a constant temperature of about 26°C. The

algae were covered with one of three long pass filters: WG 295 cut-off filter, which hardly removes any wavelengths from solar radiation (% transmission: UV-B: 74%, UV-A: 89%, PAR: 91%); this was done to warrant similar conditions as in the case of the other filters (see below). WG 335 absorbs wavelengths shorter than 335 nm (UV-B: 0%, UV-A: 70%, PAR: 91%) and GG 400 absorbs wavelengths shorter than 400 nm (UV-B: 0%, UV-A: 1%, PAR: 86%); all filters were 3 mm thick (Schott and Gen., Mainz, Germany).

The plant material was exposed to solar radiation between 11.30 a.m. and 3.30 p.m. (local noon was at about 1.35 p.m.) in June and August/September 1994. The fluence rates for the components of solar radiation (UV-A, UV-B and visible) were determined with a bandpass radiometer (RM-10, Dr. M. Gröbel, Karlsruhe, Germany) previously calibrated against a spectroradiometer (Optronic 752; Orlando, Florida). During noon time the measurements yielded about 418 W m^{-2} PAR (= 105 klx) in the visible range, 54 W m^{-2} in the UV-A band and about 2.14 W m^{-2} in the UV-B band (representative data, measured on 8 August, 1994). On cloudless days the daily variation of irradiation was less than 10% at noon.

2.3. Measurements of oxygen exchange

Photosynthetic oxygen exchange was measured before and after regular intervals of solar radiation using a Clark type electrode [33]. Samples of the algae were selected and transferred into a closed chamber filled with filtered sea water (2 ml volume) which was agitated with a magnetic stirrer. The samples were irradiated with actinic white light produced from a 250 W slide projector (Prado, Leitz, Wetzlar, Germany) equipped with a quartz halogen lamp (Xenophot, Osram, Berlin, Germany). The irradiance was adjusted by inserting neutral density filters (Schott and Gen., Mainz, Germany). After a pre-irradiation of 2 min with the respective irradiances the photosynthetic activity of the algal samples was recorded over a time-period of about 4 min and calculated in terms of mol O_2 per cell and min. Respiration was nearly not affected under all irradiation conditions. The absolute oxygen concentrations were within the range of 70 to 90% oxygen saturation. The area of the thallus piece irradiated in the chamber was measured and the number of cells per unit area was determined with a light microscope and an image analysis system connected to it [34,35].

2.4. Measurements of fluorescence induction

In vivo chlorophyll fluorescence was measured at room temperature with a pulse amplitude modulated fluorometer (PAM 100, Waltz, Effeltrich, Germany) as described by [15]. Before and after predetermined periods of exposure to solar radiation the initial fluorescence F_o and the maximal fluorescence F_m were measured and the ratio F_v/F_m were determined, where F_v is $F_m - F_o$. Before the measurements the thalli were dark-adapted for 10 min to guarantee an oxidized electron transport chain. Prolonged dark adaptation to 30 min showed no change in F_o (data not shown). The ground fluorescence F_o was induced by 1 μs, low irradiance red light pulses (11 mW m^{-2}; emission peak at 650 nm, applied at a frequency of 1.6 kHz) emitted from a LED (type USBR, Stanley). Maximal fluorescence F_m was induced by a saturating pulse of white light (800 ms; 770 W m^{-2}) transmitted by a fiber optic connected to a halogen cold light lamp (KL 1500 electronic, Schott).

2.5. Photosynthesis measurements in the water column

Photosynthetic activity of the algae on site, above and in the water column, was assayed using an instrument described recently [36,37]. The device is water tight, so that it can be lowered into the water column. It is made from PVC with a screwed-on solid Plexiglas top which allows the penetration of solar UV-B irradiation (GS 2458, Röhm and Haas, Darmstadt, Germany). The sample cuvette is integrated into the top and has a volume of 20 ml. The alga thallus is contained in the top half of the cuvette separated from the bottom half by a grid to allow water exchange. The medium in the bottom half is agitated by a magnetic stirrer, and the oxygen electrode is inserted into the cuvette from below avoiding enclosed bubbles. The preamplifier and polarization source for the electrode [38] are cast into polyester resin, and all connectors are water tight to

prevent shorting by salt water bridges which may be caused by unintentional seawater spills. Integrated into the top of the device there is a silicon photodiode (type BPW 21, Siemens, Germany) which measures in the PAR wavelength band (400–700 nm) as well as an NTC resistor for temperature measurements.

The analog signals from the electronics are routed via a control unit, which includes an amplifier, to an A/D converter card (Kolter electronic ADC12LC) housed in the extension box of a laptop computer (Vobis Highscreen 486 DX33). A computer program allows the experimental data to be displayed on the computer screen in graphical and numerical form and to be stored in disk files. Furthermore, the program calculates the slopes of the oxygen concentration curve versus time, thus determining the oxygen production. Oxygen concentrations in the chamber were in the same range as for the laboratory measurements. The samples were freshly collected and transferred to the measurement chamber. First dark respiration was measured and then the samples were exposed to solar radiation between 11.30 and 3.30 p.m.

3. Results

Fluence rate-response curves of photosynthetic oxygen exchange in *P. pavonia* were measured for algae harvested from 7 m depth after increasing times of exposure to solar radiation (WG 295, Fig. 1). The control curve (before exposure) showed a steep increase in oxygen production with increasing irradiance, and the compensation point was found at 5 W m^{-2}. Saturation was reached at an irradiance which corresponds to about 25% of solar radiation. When a fluence rate-response curve was measured after 10 min of exposure to solar radiation the compensation point was shifted to higher irradiances and the saturation level was lower than in the control curve. This trend continued with increasing exposure time and, after 40 min of solar radiation, no net photosynthetic oxygen production could be induced by any irradiance. When the cells were left in dim light for 2 h, oxygen production had partially recovered. The experiment was repeated with thalli exposed under a WG 335 filter (which essentially removes all UV-B radiation). In this case the 10 min curve saturated slightly above the control curve and the 20 min curve was even higher (Fig. 1). Also in contrast to the thalli exposed under the WG 295 filter, 40 min of exposure did not completely block photosynthetic oxygen production. A similar result was obtained when exposing the thalli under a GG 400 filter which removes most of the UV (UV-A and UV-B) radiation (Fig. 1).

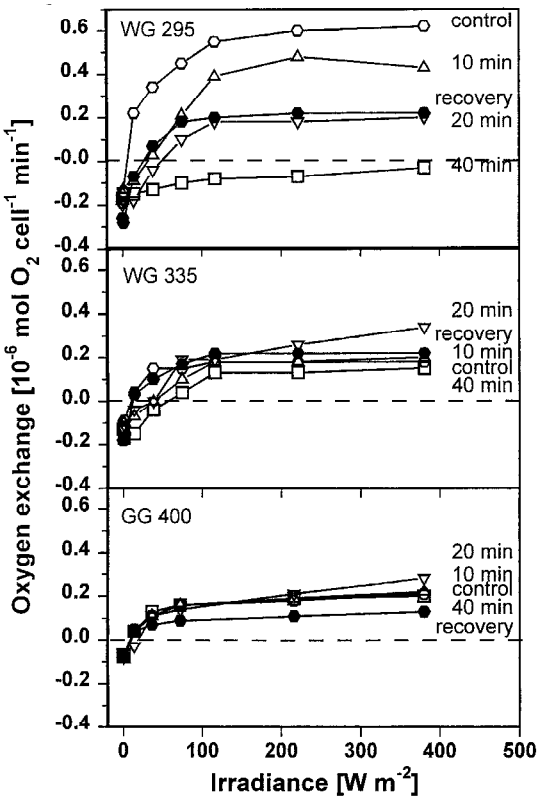

Fig. 1. Fluence rate-response curves of photosynthetic O_2 production in *Padina pavonia* harvested from 7 m depth in white light before (control, ○) and after exposure to solar radiation for different time intervals (10 min, △; 20 min, ▽; 40, min □) as well as recovery (●) of photosynthetic O_2 production from a 40 min exposure measured after 2 h in dim light. Solar radiation was filtered through a WG 295, WG 335 or GG 400 filter, respectively.

This series of experiments was repeated with algae collected from a rock pool just below the water surface (Fig. 2). In contrast to algae harvested from 7 m depth, in rock pool algae solar radiation passed

through the WG 295 filter induced a higher saturation level than in the control after 10 min of exposure (Fig. 2). In addition, the compensation point of the control was found at 13 W m^{-2}. Also the 40 min curve saturated above the compensation level. Values were closer together in the samples irradiated under the WG 335 filter (Fig. 2) and the GG 400 filter (Fig. 2). Small differences in the absolute saturation levels are due to biological scattering between individual thalli.

Photosynthesis in *Padina* was measured in a submersible device using solar radiation as actinic light. A thallus harvested from a rock pool was

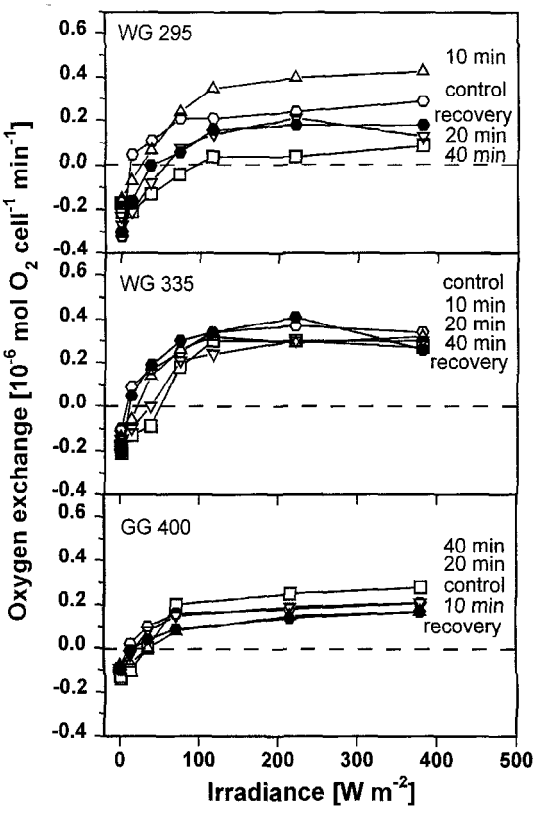

Fig. 2. Fluence rate-response curves of photosynthetic O_2 production in *Padina pavonia* harvested from a rock pool in white light before (control, ○) and after exposure to solar radiation for different time intervals (10 min, △; 20 min, ▽; 40 min, □) as well as recovery (●) of photosynthetic O_2 production from a 40 min exposure measured after 2 h in dim light. Solar radiation was filtered through a WG 295, WG 335 or GG 400 filter, respectively.

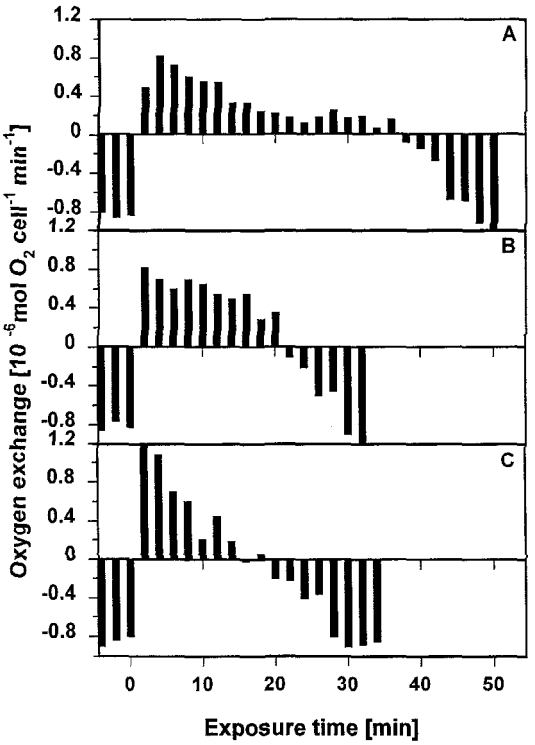

Fig. 3. Oxygen exchange of *Padina pavonia* harvested from a rock pool (**A**), 7 m depth (**B**) and from under an overhanging rock (**C**) measured at the water surface under unfiltered solar radiation in dependence of the exposure time. In the first 5 min of the experiment the algae were kept in darkness and respiration rate was determined. The temperature was 27°C.

transferred to the instrument and oxygen exchange was determined immediately afterwards. For the first 5 min the alga was kept in darkness and the respiration rate was measured (Fig. 3A). Subsequently, the sample was exposed to solar radiation at the water surface. Photosynthetic oxygen production commenced shortly after exposure. After an initial peak oxygen production decreased and net respiration is evident after about 36 min. In an alga harvested from 7 m photosynthesis stopped after about 22 min and the thallus showed respiration (Fig. 3B). This behavior was even more pronounced in a *Padina* thallus harvested from under an overhanging rock where solar irradiance was less than 10% of direct sunlight. In this sample net oxygen production ceased after only 14 min of solar exposure (Fig. 3C).

When exposed to solar radiation both F_o and F_m

Table 1
Effects of solar radiation (WG 295 filter) on F_o and F_m in an alga harvested from 7 m

Exposure time (min)	F_o	F_m
0	0.181	0.498
10	0.139	0.164
20	0.137	0.156
40	0.117	0.129
Recovery (2 h)	0.154	0.295

decreased with exposure time (Table 1). The photosynthetic quantum efficiency, as determined by F_v/F_m in PAM measurements [12], of *Padina* thalli before and after different exposure times to solar radiation are shown in Fig. 4. Exposure of 10 min under a WG 295 filter caused a significant decrease in F_v/F_m, which remained about constant with exposure up to 40 min. Rock pool algae showed a consistently higher value than algae harvested from 7 m. After 2 h in dim light, rock pool algae showed a complete recovery while 7 m algae had only partially recovered. After 5 min of exposure the inhibition was about 50% of the control (data were from a different experiment and therefore not shown). When exposed under the WG 335 filter, the inhibition was less dramatic than in the algae exposed under the WG 295 filter and the differences between rock pool and 7 m algae were not significant. When exposed under the GG 400 filter, inhibition was even less pronounced, especially after short exposure times and recovery was complete for both ecological strains from different depths.

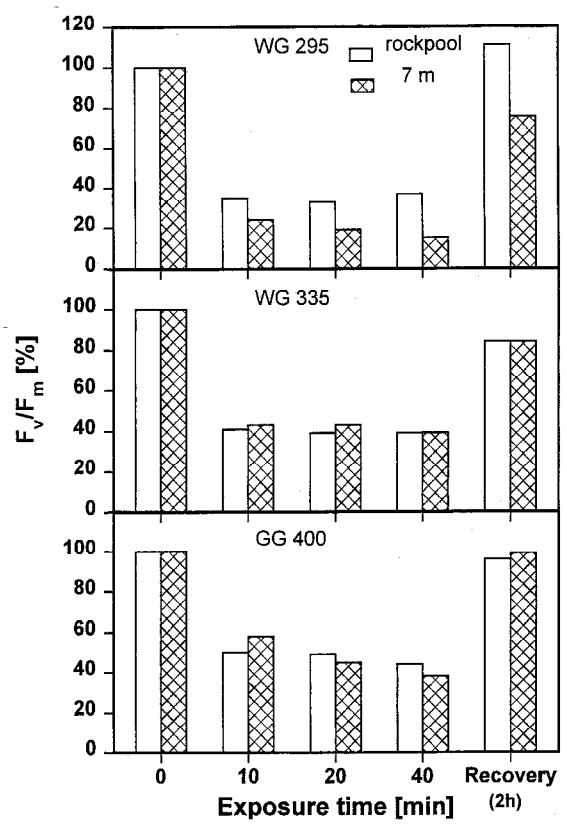

Fig. 4. Ratio of chlorophyll fluorescence F_v/F_m in *Padina pavonia* harvested from a rock pool (open bars) and 7 m depth (hatched bars), respectively, before and after increasing times of exposure to solar radiation passed through a WG 295, WG 335 or GG 400 filter, respectively. The absolute value of F_v/F_m of the control of *Padina pavonia* from the rockpool was 0.66 and from 7 m depth 0.72.

4. Discussion

Previous investigations have demonstrated that exposure of macroalgae to solar radiation of high fluence rates causes photoinhibition which is characterized by a reduction in the quantum yield and in the capacity of photosynthetic O_2 evolution [3,4,7,39]. Similar results were obtained in phytoplankton [8,40]. In the present work photoinhibition of photosynthesis in *Padina pavonia* induced by high levels of solar radiation was investigated measuring chlorophyll fluorescence parameters and the measurement of oxygen evolution, both of which yielded comparable results. The extent of photoinhibition depends on the fluence rate and the duration of exposure as well as on the spectral distribution of solar radiation. Algae adapted to different levels of solar exposure in their habitat showed different degrees of photoinhibition.

Judging from the exposure under different filters all wavelength bands of solar radiation (UV-B, UV-A and visible) impaired the photosynthetic capacity in *Padina pavonia*. Exposure to unfiltered solar radiation resulted in a fast decrease in oxygen production in algae adapted to greater depth in the water column or shaded habitats while algae harvested from the surface were less affected. Though belonging to the

same species, the samples collected from different habitats differed considerably in their morphology. Thalli from the rock pool are smaller than thalli from 7 m depth and show more calcification.

The physiological differences between the two strains were further stressed by the fact that the compensation points as well as the saturation values were differently affected by previous exposure to solar radiation. Also the degree of inhibition of the photosynthetic capacity was markedly different in the two strains. Also in other algae, such as *Halimeda tuna*, different ecological strains have been described which are adapted to different depths [41]. Comparative studies on the red alga *Porphyra perforata* which grows in the high-intertidal zone and the shade-adapted, subtidal *Porphyra nereocystis* showed that the rate of photodamage was much higher in *P. nereocystis* than in *P. perforata*. Photoinhibition resistance in *P. perforata* appears to be due to a reduced rate of photoinhibition damage rather than to a higher rate of photoinhibition repair [42].

Visible radiation represents the major part of sunlight and causes a significant effect on photosynthetic oxygen production. In addition, UV-B, which only amounts to 0.3% in solar radiation, had a pronounced effect. Grobe and Murphy [43] showed that the growth rate of the intertidal alga *Ulva expansa* was inhibited significantly under solar radiation with enhanced UV-B. A quantitatively comparable inhibition by UV-B has been obtained by Helbling et al. [8] and Larkum and Wood [27]. However, the effect of short wavelength UV radiation is more obvious in oxygen measurements than in PAM fluorescence measurements.

The fast decrease in the ratio F_v/F_m after the onset of solar irradiation indicates a sharp drop in photosynthetic quantum yield. The effects of exposure to solar radiation were observed even after shorter exposure times than in the oxygen measurements. In the PAM experiments the differences between the two different strains were not as pronounced as in photosynthetic oxygen production measurements. These data are in agreement with investigations carried out with red algae [4], green algae [40], as well as with willow leaves [44]. Björkman [45] and Demmig and Björkman [46] reported that the decrease in F_v/F_m is linearly related to the decrease in the optimal quantum yield of photosynthesis. In the present experiments the quenching of F_v and the decrease in F_v/F_m was basically caused by a decrease of F_m while F_o slightly decreased. In contrast, in the shade-grown green alga, *Ulva rotundata*, F_o increased after exposure to high fluence rates of solar light [47,7]. They assumed that the decrease in F_v/F_m and the increase in F_o indicates damage of PS II, which might be plausible because the duration of exposure lasted for several hours and the effect was only partially reversible. This result was confirmed in higher plants by Demmig and Björkman [46] and Demmig-Adams [48]. However, after longer exposure F_o resumed the level of the control which might indicate a reversible regulatory mechanism such as photoprotection via thermal dissipation [46].

Several mechanisms have been reported for the inhibition of photosynthesis. In addition to damage of the water splitting site of photosystem II recently a significant role of the D1/D2 complex in photoinhibition was discussed [49]. Some experiments indicate that excessive radiation causes a small conformational change in the proteins which are subsequently degraded by a protease of unknown origin [50]. Whether or not UV radiation and visible radiation affect the same sites in the D1 protein has not yet been revealed. The ecological relevance of this mechanism under natural conditions is debated by Baker [49]. In any case, a decline of the D1 protein band was demonstrated after prolonged irradiation [14] by using specific antibodies produced against the protein [51].

Depending on the length of solar exposure a complete or partial recovery can be observed both in the PAM and the oxygen measurements. This indicates that at least part of the observed effects is due to reversible photoinhibition. However, longer exposure, especially to shorter wavelengths, causes nonreversible effects which can be interpreted as photodamage. Similar effects have been described in other aquatic systems; in some cases the degree of damage increases even after the actual exposure time [52–54]. Future experiments including time kinetics and selective short wavelength irradiation are necessary to determine the individual components of the complex response of the algae upon exposure to solar radiation.

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