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# Photosynthesis of the mediterranean green alga *Caulerpa prolifera* measured in the field under solar irradiation

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Abstract

Photoinhibition of photosynthesis was investigated in the Mediterranean green alga *Caulerpa prolifera* by using pulse amplitude modulation (PAM) chlorophyll fluorescence and oxygen evolution. After exposure to solar radiation at the water surface, oxygen production decreased drastically within 20 min; this inhibition of photosynthesis was only partially restored during the subsequent hours in the shade. Oxygen measurements at different depths showed optimal photosynthesis at a depth of 5 m. Exposure to solar radiation at the surface also caused a drastic decline in the effective photosynthetic quantum yield. Also these effects only partially recovered indicating that they are mainly caused by reversible photoinhibition and to a smaller extent to nonreversible photodamage. Photoinhibition occurs in this alga even in its natural habitat when the sun is at large angles. Despite the fact that UV-B accounts for a very small fraction of solar radiation, it has a considerable effect on photosynthesis while UV-A seems to contribute only a small amount to photoinhibition in *C. prolifera*.

*Keywords:* *Caulerpa prolifera*; Chlorophyta; Oxygen measurements; Pulse amplitude modulation fluorescence; Photoinhibition; Solar radiation; Ultraviolet radiation

## 1. Introduction

In the past, ecophysiological investigations of photosynthesis have been limited to gas exchange measurements including oxygen evolution and carbon dioxide uptake [1]. In recent years the technique of pulse amplitude modulation (PAM) fluorescence was introduced as an alternative and supplementary tool [2–5]. In contrast with steady state fluorescence, PAM fluorescence gives an insight into the regulatory processes of photosynthetic energy allocation and the physiological status of the photosynthetic apparatus in vivo.

While the initial measurements were restricted to the laboratory, recent miniaturization and the development of computer-controlled measurements of the PAM fluorometer allows the equipment be to operated in the field [6]. In addition, submersible devices have been developed for assessing oxygen exchange in the field under natural conditions of solar radiation and temperature [7,8]. Especially for macroalgae, it is preferable to perform the measurements in the field, since the transport of the specimen into the laboratory induces a number of difficulties caused by thermal stress and changes in irradiance and salinity for the plants.

Most ecophysiological work on photosynthetic processes has concentrated on higher plants [5,9]. However, about 50% of the primary biomass production on our planet is based on aquatic ecosystems thus matching the productivity of all terrestrial ecosystems taken together [10,11]. Although most of the productivity is due to phytoplankton, macroalgae have a fair share in it. With a few exceptions macroalgae are sessile and consequently they have to cope with the changing irradiance regime of solar radiation. Light is probably the most important among several factors controlling the vertical distribution of macroalgae in the littoral [12].

Being adapted to lower irradiances than those of unfiltered solar radiation, macroalgae face a serious light stress when exposed to higher irradiances [13,14]. Excess irradiation causes reversible photoinhibition [15–19] or even irreversible photodamage. The phenomenon of photoinhibition has been interpreted as a reversible interruption in the photosyn-

Abbreviations: $F_o$, 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); $F_o'$ and $F_m'$, the same for the light-adapted state, $F_v$, variable fluorescence, calculated as $F_m - F_o$; $F_t$, current steady state fluorescence; PAM, pulse amplitude modulated fluorometer; PAR, photosynthetic active radiation; *qP*, photochemical quenching of chlorophyll fluorescence; *qN*, non-photochemical quenching of chlorophyll fluorescence; UV-B, ultraviolet-B radiation (280–315 nm); UV-A, ultraviolet-A radiation (315–400 nm)

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thetic electron transport chain [20] and serves as a protective mechanism by which excessive irradiation is thermally dissipated [5]. Photoinhibition can be detected both with oxygen and with PAM (pulse amplitude modulated fluorescence) measurements [6,21].

For reasons yet unknown chlorophyll fluorescence is almost exclusively produced from photosystem II. Transient changes in the irradiation result in changes in the allocation of excitation energy to photochemistry, fluorescence and non-radiative energy dissipation, respectively, which is reflected in changes of the fluorescence patterns. Therefore measurement of the fluorescence parameters allows the determination of photochemical and non-photochemical quenching (which compete with fluorescence emission) of the photosynthetic apparatus [22,23].

In addition to visible radiation (photosynthetic active radiation, PAR 400–700 nm) also UV-A (315–400 nm) and UV-B (280–315 nm) are important stress factors in terrestrial and aquatic plants [14,24] even though their relative energy contribution is much less than that of PAR in the solar spectrum [25–27]. Inhibitory effects of UV-B on photosynthesis and chlorophyll fluorescence of several species of marine benthic algae and phytoplankton have been documented [21,28,29].

Recent research has indicated several targets of short wavelength radiation in the photosynthetic apparatus: UV-B impairs the D1 protein associated with photosystem II [30,31]. Damage of the water splitting site of photosystem II and of the reaction centre of photosystem II have been documented [32,33].

The aim of this article is to describe the effects of exposure to solar radiation in the field of photosynthetic oxygen production and fluorescence induction in the green Mediterranean macroalga, *C. prolifera*.

## 2. Material and methods

### 2.1. Plant material

Thalli of the common mediterranean alga *Caulerpa prolifera* were collected from a depth range of 5–25 m by diving on the coast of Saronikos Gulf, near Korinth, Greece (37° 58′ N, 23° 0′ E). The algae grew on a sandy substrate in front of a rocky shore facing east. The thalli were transported in a light-tight container and immediately subjected to the measurements. The experiments were carried out in the summers of 1994 and 1995.

### 2.2. Measurements of oxygen exchange

The samples were transferred from the dark containers into a chamber developed to measure oxygen exchange in the water column under solar radiation [7,8]. During the handling, care was taken not to damage the sensitive algae and to keep them under shaded conditions. In a typical experiment, dark respiration was determined first, followed by measurements of net oxygen production at various depths in the water column. Subsequently, the sample was exposed at the water surface (but still submerged) until photoinhibition was reached (negative oxygen production). The algae were stored at a depth of 5 m in a translucent container for regeneration of their photosynthetic capacity and finally the oxygen production was again measured. In another experiment, the kinetics of photoinhibition was determined in thalli immediately after harvest. After exposure, the area of the thallus was measured as well as the dry weight.

### 2.3. Measurements of fluorescence induction

In vivo induced chlorophyll fluorescence was measured on site with a portable pulse amplitude modulated fluorometer (PAM 2000, Waltz, Effeltrich, Germany) as described by Schreiber and Bilger [34]. PAM fluorescence measurements are based on the determination of the ground fluorescence $F_o$ induced by low irradiation of a dark adapted sample (all reaction centers in the open state). Upon a single saturating flash, maximum fluorescence, $F_m$, is observed indicating that all reaction centers are closed. The difference between $F_o$ and $F_m$ is called variable fluorescence, $F_v$. From the ratio $F_v/F_m$ the optimal quantum yield can be calculated [35]. Irradiation with high fluence rates of the previously dark-adapted sample usually leads to a decrease of $F_m$, now called $F_m'$, and an increase or a decrease in $F_o$, leading to $F_o'$. From these measured values and the currently encountered fluorescence, $F_t$, the photochemical quenching $qP$ can be calculated [36], i.e., the amount of excitation energy funnelled into the photochemical processes.

$$qP = (F_m' - F_t)/(F_m' - F_o')$$

The nonphotochemical quenching $qN$ is calculated from

$$qN = 1 - (F_m' - F_o')/(F_m - F_o)$$

The nonphotochemical quenching includes all nonradiative processes dissipating excitation energy; however the underlying molecular mechanism is still controversial [36]. The overall effective quantum yield of photochemical energy conversion can be determined from $(F_m' - F_t)/F_m'$ [37].

In a typical experiment, freshly harvested thalli were mounted in UV-B translucent Plexiglas frames (GS 2458, Röhm and Haas, Darmstadt, Germany) and kept in a shallow rock pool under a shading cover for at least 30 min. After dark adaptation the fluorescence parameters were measured and the optimal quantum yield was determined. The algae were then exposed to solar radiation and the fluorescence parameters measured again. Subsequently, the samples were covered and the recovery of the effective photosynthetic yield was determined periodically during the following hours. In another experiment, four parallel samples were exposed under different cut-off filters which removed short wavelengths (WG 295, WG 335, WG 360 and GG 400, all from

Schott and Gen., Mainz, Germany). The experimental procedure was similar to the one described above.

To determine the daily variation in the effective quantum yield at the growth site, thalli were collected every hour from sunrise to sunset, and the fluorescence parameters were measured immediately after harvest. The PAM fluorometer provides preprogrammed experimental runs which can also be modified by the user. One run allowed us to determine an actinic irradiance series. Before the run $F_m$ and $F_o$ were determined in the dark adapted sample. In the first step the sample is exposed to an intermediate irradiance (23 W $m^{-2}$) of red light produced from an array of light emitting diodes for 10 min for light adaptation and the activation of the Calvin enzymes; subsequently a series of 11 levels of irradiation, starting from the lowest, are applied, each lasting 6.5 min. At the end of each irradiation period a saturating white light pulse is used to determine the fluorescence parameters, $F_t$, $F_m'$ and the effective quantum yield. For the correct determination of $qP$ and $qN$, a far red light pulse is given before the saturating light pulse to determine $F_o'$.

### 2.4. Statistics

For the PAM measurements (except the actinic irradiance series) at least 8 individual measurements were taken from which the mean values and standard deviation were calculated. Photosynthetic oxygen exchange was measured at least three times for each irradiation. All experimental runs were repeated several times.

### 2.5. Measurement of solar radiation

Solar radiation was measured in three wavelengths bands (UV-B, 280–315 nm, UV-A, 315–400 nm, PAR, 400–700 nm) using a permanently installed instrument (ELDONET, Real Time Computer, Erlangen, Germany) developed recently by the German group. The instrument employs commercially available, waterproof filter sensors (Gröbel, Ettlingen, Germany) and takes readings at 1 s intervals which are integrated over 1 min. After amplification and analog/digital conversion the data in the three channels are graphically displayed and stored in a computer. Hourly and daily doses are calculated for each wavelength band. 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.

## 3. Results

### 3.1. Oxygen exchange measurements

A thallus of *C. prolifera* harvested from a depth of 4 m showed a pronounced respiration when transferred into darkness (Fig. 1). When exposed to unfiltered solar radiation just below the water surface, oxygen production (integrated over 5 min intervals) increased to over 0.2 $\mu$mol $mm^{-2}$ $min^{-1}$. Shortly afterwards, the oxygen production decreased sharply due to photoinhibition, and the 20 min value was already negative. Oxygen uptake increased further up to 25 min of exposure. In another experiment, a sample was harvested from a depth of 5 m and after dark respiration was exposed at decreasing depths between 5–0 m (Fig. 2). Maximal oxygen production was encountered at the surface; however, the values did not differ much between the different depths.

Freshly harvested algae (from 20 m) were exposed just under the water surface and oxygen production was recorded until negative values were encountered (photoinhibition). The sample was then stored at 5 m in a translucent container for 2 h and 10 min. Subsequently, the oxygen exchange was determined in darkness and at decreasing depths from 4–0 m;

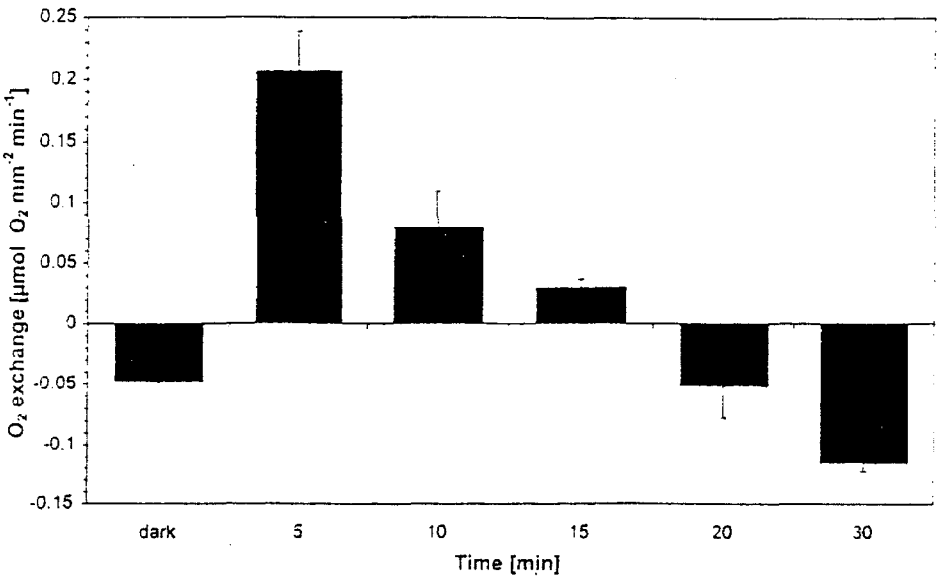


Fig. 1. Photosynthetic oxygen exchange (±S.D.) of *C. prolifera* harvested from 5 m and measured under solar radiation at the surface. Before exposure, dark respiration was determined and then oxygen exchange measured integrated over 5 min periods each.

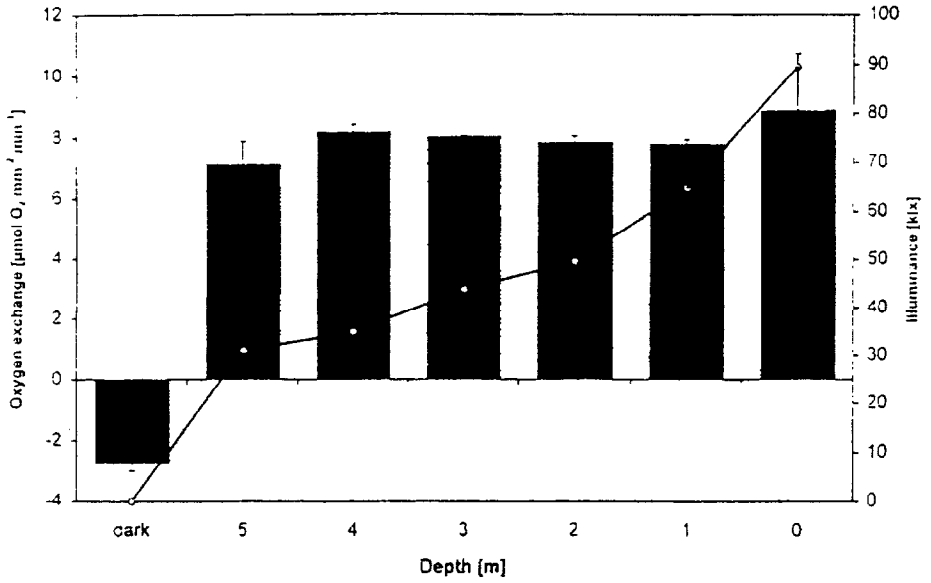


Fig. 2. Photosynthetic oxygen exchange ( ± S.D.) of *C. prolifera* harvested from 5 m and measured under solar radiation at different depths from 5–0 m. Before exposure, dark respiration was determined and then oxygen exchange measured integrated over 4 min periods each. Light intensity is indicated as illuminance since the light sensor in the instrument has a sensitivity curve which closely resembles that of the human eye.

the sample had not fully recovered from photoinhibition but regained a net positive oxygen production. Similar results were obtained with *C. prolifera* harvested from different depths; however, specimen retrieved from deeper water showed a faster photoinhibition than those from lower depths (4–25 m, data not shown).

### 3.2. PAM fluorescence measurements

In order to determine the fluorescence parameters thalli were harvested from 5 m and kept in a shallow rock pool suitable for on site measurements with the PAM instrument. The optimal quantum yield was determined immediately after dark exposure for 30 min (Fig. 3). The thalli were then exposed to unfiltered solar radiation for 45 min and finally shaded for recovery. Measurements of the effective quantum yield (in at least 8 samples each) were performed during the following 5 h. Immediately after solar exposure the yield had dropped to less than 25% of its initial value and recovered up to 80% of its original value. In order to determine whether the samples were stressed by the handling and slightly higher surface temperatures, unexposed control samples were kept under the same conditions except for solar radiation. These dark-adapted samples showed the same yield as the initial measurements immediately after harvest indicating that there were no significant stress factors except solar radiation.

A similar experiment was performed with thalli harvested from 18 m and exposed under cut-off filters which removed

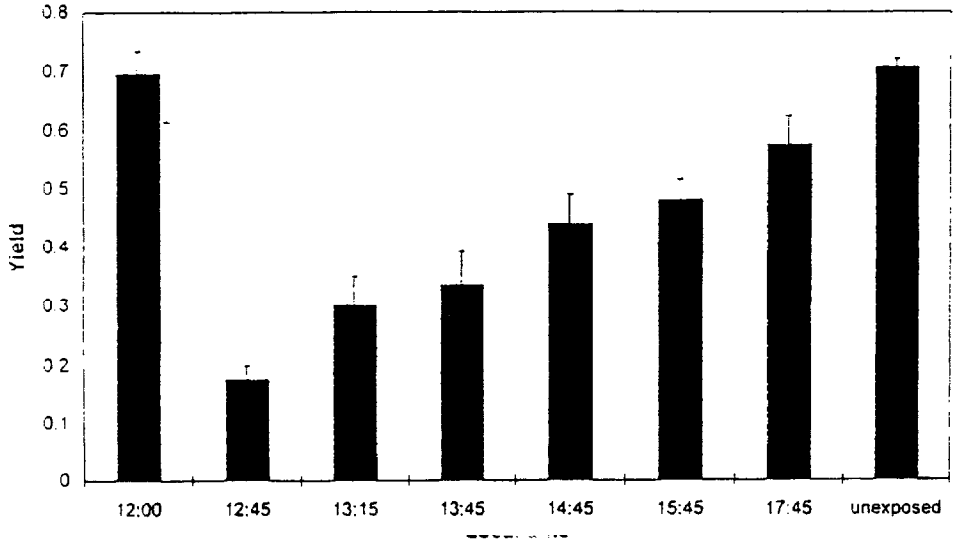


Fig. 3. Photosynthetic quantum yield of *C. prolifera* harvested from 5 m was measured after 30 min of adaptation in the shade, after 45 min of exposure to solar radiation in a rockpool and during recovery (in the shade). The rightmost bar indicates the yield for thalli subjected to the same experimental procedure ... for solar radiation. For each data point at least eight measurements were averaged and the standard deviation calculated.

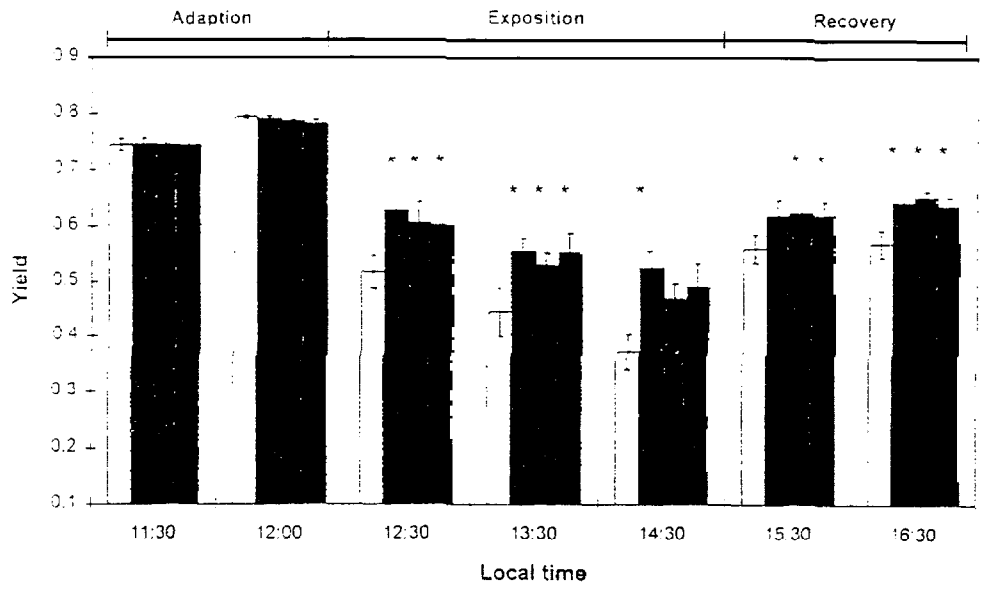


Fig. 4. Photosynthetic quantum yield of *C. prolifera* harvested from 18 m was measured before and after 30 min of dark adaptation, during 2.5 h of exposure to solar radiation (12:00–14:30 local time) in a rock pool and during recovery (in the shade). The thalli were exposed under the following cut-off filters (100x100 mm): WG 295 (open bars), WG 335 (hatched bars), WG 360 (dotted bars) and GG 400 (solid bars). For each data point at least eight measurements were averaged and the standard deviation calculated. Asterisks indicate those values which significantly ($p$ 0.05) deviate from the values measured for the WG 295 filter in each time group.

increasing portions of the short wavelength radiation (Fig. 4). Since solar radiation reaching the earth hardly contains any radiation below 295 nm the sample filtered under the WG 295 filter can be regarded as control. The effective quantum yield values of the samples exposed under the WG 295 filter are significantly lower than those of the samples exposed under the other cut-off filters during both exposition and recovery. Statistical significance is indicated by the Student's t-test. The inhibition was lower than in the experiment described above (Fig. 3) due to the fact that the algae were not kept flat but were allowed to float upright which greatly reduced the solar irradiation.

In the previous two sets of experiments, the thalli were exposed to solar radiation in a shallow rock pool, but the algae were collected from a deeper habitat (between 5–25 m). In order to determine whether photoinhibition occurs at their natural site, algae were harvested from 5 m from dawn to dusk at 1 h intervals and the yield was determined immediately after harvest. The samples showed a maximal quantum yield of 0.8 for the first sample which was harvested before sunrise (Fig. 5). In the subsequent samples the value decreased continuously as solar irradiance increased at the habitat. The lowest value was >25% below the maximal value. From 15:20 onward the algae were shaded by the rocky

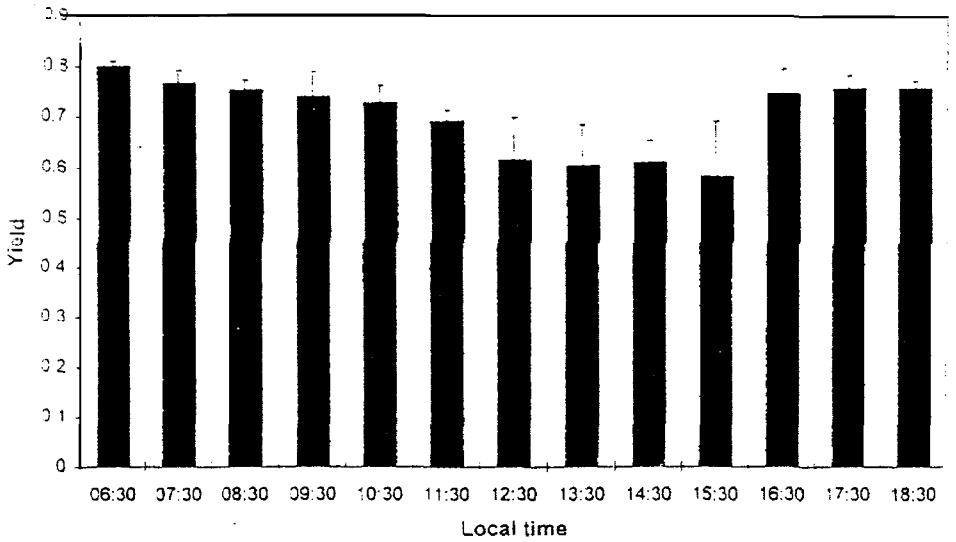


Fig. 5. Photosynthetic quantum yield from dawn to dusk of *C. prolifera* harvested from 5 m. Thalli were retrieved from their growing site and measured immediately after harvest. For each data point at least eight measurements were averaged and the standard deviation calculated.

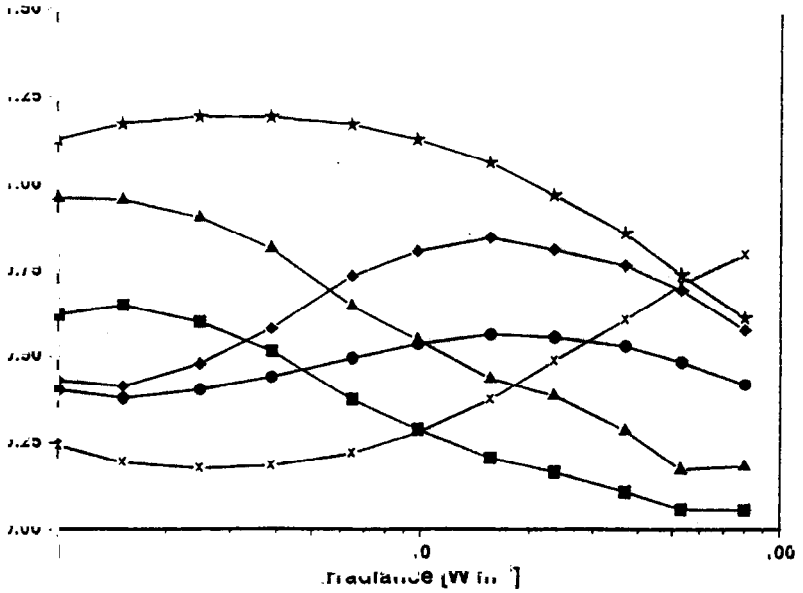

Fig. 5. Fluorescence parameters measured in *C. prolifera* harvested from 5 m depth in dependence of the fluence rate of the actinic red light. Before the experiments the thallus was adapted to an intermediate fluence rate of 23 W m$^{-2}$ for 10 min and then exposed to increasing irradiances for periods of 6.5 min each. At the end of each period the fluorescence parameters were determined. Diamonds: $F_t$, squares: photosynthetic quantum yield, triangles: photochemical quenching, crosses: nonphotochemical quenching, asterisks: $F_m'$ and circles: $F_o'$.

shore. Starting with the next measurements (16:30) the yield sharply increased to almost the initial morning value.

In order to determine the dependence of the fluorescence parameters on the actinic light, an automatic run was performed on samples freshly harvested (Fig. 6). First the sample was dark adapted with $F_o$ and $F_m$ being measured (data not shown). The thallus was then allowed to adapt to light using the built-in red light emitting diode with an irradiance of 23 W m$^{-2}$. The steady state fluorescence, $F_t$, increased from a low value to an optimum at an irradiance of 16 W m$^{-2}$ and subsequently fell again. $F_o'$ followed a similar pattern. In contrast, $F_m'$ had an optimum at a lower irradiance of 3.9 W m$^{-2}$ and declined gradually from there. The photosynthetic quantum yield had an optimal value of about 0.65 at low irradiances and declined at higher irradiances. The photochemical quenching started with values close to 1 (indicating optimal energy exploitation for photosynthesis) and decreased to values below 0.1. In contrast, non-photochemical quenching rose from low values near 0.2 to about quadruple of that.

## 4. Discussion

The phenomenon of photoinhibition after exposure to solar irradiation of high fluence rates has been observed both in macroalgae [18,38,39] and phytoplankton [40–42]. In contrast with photodamage, photoinhibition can be regarded as an active physiological regulatory process characterized by a reduction in the photosynthetic quantum yield and in the capacity of photosynthetic $O_2$ evolution to protect the photosynthetic apparatus from excessive radiation. In the present article, photoinhibition in the green alga *C. prolifera* was determined using measurements of both PAM fluorescence and oxygen production.

Unfiltered solar radiation as well as radiation depleted of UV-B or UV-B and UV-A impaired the photosynthetic capacity in *C. prolifera*. Unfiltered solar radiation causes a strong photoinhibition even after short exposure, as indicated by a fast decrease in the photosynthetic quantum yield and of oxygen production. The algae seem to be adapted to greater depths where fluence rates of solar radiation are lower due to attenuation in the water column. At a depth of 5 m at the test site the PAR irradiance was measured to be less than 50% of the surface irradiance. Therefore it is not surprising that the oxygen production of algae exposed to surface irradiation ceases within 20 min of exposure, and that optimal oxygen production is encountered at a depth of 5 m while various degrees of photoinhibition occur at lower depths. However, even at their habitat the algae are partially photoinhibited by solar radiation especially when the sun is high. This inhibition is readily reversed later in the day. In contrast, photoinhibition resulting from exposure at the surface up to a point where no net photosynthetic oxygen production is encountered could not be fully repaired within more than 2 h indicating some photodamage by this treatment.

In addition, PAM fluorescence measurements indicated a fast decline in the photosynthetic yield during a 45 min exposure to unfiltered solar radiation and only partial recovery during the subsequent 5 h. Solar radiation deprived of the UV-B component resulted in a significantly reduced degree of photoinhibition, while further removal of longer wavelength components in the UV-A range caused only small amendments which could not be distinguished at all during recovery. These results indicate that solar PAR has a major impact on the photosynthetic yield and photoinhibition; how-

ever, solar UV-B radiation also has a strong effect which is confirmed by results reported by Helbling et al. [40] and Larkum and Wood [31]. UV-A does not seem to be very effective in *C. prolifera* which is in contrast with findings in phytoplankton, where inhibition elicited by UV-A had about the same or even higher efficiency than that induced by UV-B [43].

In the fluence rate response curves induced by red light, an increase in non-photochemical quenching and a decrease in the photochemical quenching were observed. These data are in agreement with investigations on red algae [18], the unicellular green alga *Chlamydomonas* [41] as well as on willow leaves [44].

Björkman [45] and Demmig and Björkman [46] showed that the decrease in effective quantum yield due to photoinhibition is linearly related to the decrease in the optimal quantum yield of photosynthesis. Increases in $F_o$ can indicate a damage of PS II not readily reversible [9,46]. An increase in $F_o$ and a decrease in $F_m$ after exposure to high fluence rates of solar light was also shown by Henley et al. [47] and Franklin et al. [39] in shade-grown *Ulva rotundata*. These authors assumed that the decrease in effective quantum yield and the increase in $F_o$ indicate damage of PS II as the effect was only partially reversible after several hours. A decrease in $F_o$ might indicate a reversible regulatory mechanism such as photoprotection via thermal dissipation [46].

The primary targets of UV (UV-B and/or UV-A) in the photosynthetic apparatus are still obscure especially in algae which seem to differ in several respects from higher plants in their regulatory mechanisms and capacity [23]. Further investigations, including recovery kinetics and action spectra are necessary to study the mechanisms of photoinhibition and photodamage and reveal the primary targets of photoinhibition.

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