

Photosynthetic performance of the Chlorophyte *Ulva rigida* measured in Patagonia on site

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ABSTRACT

The photosynthetic performance was analyzed in the common Chlorophyte, *Ulva rigida* in Patagonia, Argentina. A portable PAM instrument was used to measure the photosynthetic quantum yield both on site and under seminatural conditions. Solar radiation was recorded in parallel with a filter dosimeter in three wavelength ranges, UV-A, UV-B and PAR. The algae responded with photoinhibition to exposure of 15 min of solar radiation when the thalli were kept in a fixed position but recovered in the subsequent shade conditions within several hours. 30-min exposure of free floating thalli caused a less profound photoinhibition. The photosynthetic quantum yield was also determined over whole days under clear skies, partly cloudy and rainy conditions in free floating thalli in a large reservoir of water and in thalli on site growing in rock pools. While most of the effect was due to visible radiation, the UV wavelength range, and especially UV-B, considerably enhanced the decrease in photosynthetic quantum yield. Fluence rate response

curves showed that the species is a typical shade plant which developed profound non-photochemical quenching at intermediate and higher irradiances. Fast induction and relaxation kinetics indicated a fast adaptation of the photosynthetic capacity to the changing light conditions as well as a fast decrease of PS II fluorescence upon exposure to solar radiation. There was negligible bleaching of chlorophylls and carotenoids due to exposure to solar radiation.

INTRODUCTION

Aquatic ecosystems account for about half of the primary biomass production on our planet, matching the combined productivity of all terrestrial ecosystems [1]. While most of the aquatic productivity is due to phytoplankton [2] macroalgae have a significant share especially in coastal areas. Almost all macroalgae are sessile organisms and cannot adapt to the changing irradiation conditions by vertical migration in their habitat [3,4].

The vertical distribution of the species on the coast is controlled mainly by light availability [5,6], and the photoprotective capabilities of a species probably define its upper growth limit. Macroalgae are exposed to excessive solar PAR (photosynthetic active radiation, 400 –

700 nm) as well as UV radiation, (UV-B 280 – 315 nm and UV-A 315 – 400 nm) especially in the upper eulittoral and the supralittoral [7,8]. Photosynthetic organisms, algae and terrestrial plants, show various degrees of photoinhibition when exposed to high solar radiation [9-11] or even irreversible photodamage. Photodegradation of the D1 protein in photosystem II (PS II) causes chronic photoinhibition resulting in a decrease in the photosynthetic electron transport [12]. This adaptive mechanism protects the photosynthetic apparatus from excessive radiation energy. Dynamic photoinhibition is another regulatory mechanism based on the xanthophyll cycle found in higher plants and many macroalgae, but not in Rhodophytes [4,13]. Excess solar radiation energy, which is thermally dissipated, reduces the quantum yield of PS II; this process is reversible within minutes to hours. These adaptive processes of the photosynthetic apparatus in algae are summarized in recent reviews [3,4].

The photosynthetic quantum yield can be calculated from the measured fluorescence parameters [14]. The calculation does not require the knowledge of the dark fluorescence parameters F_0 and F_m . The validity of this approach has been verified by parallel gas exchange measurements [15].

Quenching analysis can be performed based on the measured PAM signals fluorescence. The analysis assumes that two parallel processes, photochemical and non-photochemical quenching (qP and qN), decrease the maximal fluorescence yield F_m . Photochemical quenching is caused by the utilization of the radiation energy in the photosynthetic apparatus. Non-photochemical quenching is due to the built-up of a pH gradient across the thylakoid membrane [9,16].

Many photosynthetic organisms show a pronounced decrease in the photosynthetic yield between noon and the early afternoon believed to be due to dynamic photoinhibition [8,17]. In

marine algae this pattern is overlaid by the tidal rhythm. The coincidence of low tides and high solar angles [8,18] results in the highest radiation stress. Macroalgae are subjected to a complicated pattern of irradiances controlled by the daily cycle, the tidal rhythm and the changing cloud cover. Photoinhibition was found in macroalgae from the tropics and the temperate zone [7,19] but also in Arctic and Antarctic macroalgae [20,21].

Due to the high proportion of PAR in solar radiation this wavelength band is responsible for most of the photoinhibition. However, in the top few meters of the water column a significant percentage of photoinhibition is caused by UV-B (and less so by UV-A) radiation [8,22-30], although UV-B contributes only 1 % of the radiation energy reaching the Earth's surface. The unproportionally high photoinhibition by solar UV has been found in a number of marine algal [4,10] and phytoplankton species [31]. The UV-related photoinhibition is highest in algae located at or above the water surface during low tide.

The aim of the present paper is to characterize the photosynthetic performance of a widespread green macroalga, *Ulva rigida*, under natural conditions at their growth site on the Patagonian coast, Argentina.

MATERIALS AND METHODS

Measurement of solar radiation

Solar radiation was continuously measured from dawn to dusk with a three-channel filter instrument [32] (ELDONET, Real Time Computer, Möhrendorf, Germany) located on the roof of the Estación de Fotobiología, Playa Unión (EFPU) during the whole measurement period in three wavelength bands (UV-B, 280 - 315 nm; UV-A, 315 - 400 nm; PAR, 400 - 700 nm). The irradiance is averaged over 1-min intervals and recorded on the host computer. All data are transferred to the central server of the ELDONET network where they are available

on the Internet (<http://www.ib.pi.cnr.it/eldonet/index.html>).

Plant material

Specimens of the common Chlorophyte *Ulva rigida* were harvested every morning from tidal pools on an east-facing rocky shore south of Playa Union (65° 3' W, 43° 19' S, Rawson, Patagonia, Argentina) during low tide. The water temperature was around 17° C and the salinity 34 ‰ during the experimental period. Specimens were collected immediately before the experiment and mounted in custom-made UV transparent Plexiglas holders (GS 2458, Röhm and Haas, Darmstadt, Germany) with open sides which allowed sea water to flow through the holders. Some of the holders were sandwiched with UV cut-off filter foils to exclude short wavelength radiation below 320 nm (Montagefolie, Nr. 10155099, Folex, Dreieich, Germany) or below 395 nm (Ultraplan UV Opak, Digefra, Munich, Germany). The transmission spectra of these filter foils have been published by Figueroa et al. [33]. The sample holders with the specimens, four replicates for each treatment, were kept in shallow water on site, in the shade of a black plastic foil for 30 min. After the dark period the specimens were exposed to solar radiation during local noon for 15 or 30 min in shallow water and subsequently transferred back into the shade for recovery of the photosynthetic yield. The fluorescence parameters (see below) were determined after the dark period, after the exposure time and at predetermined times during the recovery period.

For another set of experiments, plants were collected and kept in a large volume of seawater in a dark container during transport to the laboratory. For exposure to solar radiation, thalli were either mounted in the Plexiglas holders described above or allowed to freely float in flat open plastic containers floating on top of a large open surface with running water to keep

the temperature constant. A third set of experiments was carried out in Bahía Bustamante (250 km south of Rawson) where the effective photosynthetic quantum yield was measured in algae in a natural rock pool during low tide without removing the thalli from their growth site.

Measurements of PAM fluorescence

Photoinhibition can be determined by oxygen measurements [34] or using the pulse amplitude modulation (PAM) fluorometer [35]. The *in vivo* chlorophyll fluorescence parameters were determined non-invasively with a portable pulse amplitude modulated fluorometer (PAM 2000, Walz, Effeltrich, Germany). This method determines chlorophyll *a* fluorescence signals from photosystem II (PS II): First the background chlorophyll fluorescence signal F_0 is induced in dark-adapted organisms by a red light source, which is weak enough not to cause the PS II reaction centers to close. On this background a saturating white light pulse is flashed which induces maximal fluorescence, F_m , during which the PS II reaction centers are closed. The maximal fluorescence (F_m') is usually lower in light-adapted plants while F_0' is usually higher. The overall photosynthetic quantum yield Y was calculated using the equation [14]

$$Y = (F_m' - F_t) / F_m' = F_v' / F_m'$$

where F_m' is the maximal fluorescence in a light-adapted plant and F_t the current steady state fluorescence. Dark-adapted plants were used to determine the optimal quantum yield.

The photochemical quenching (qP) of chlorophyll fluorescence can be determined from the fluorescence parameters as

$$qP = (F_m' - F_t) / (F_m' - F_0')$$

and the non-photochemical quenching as

$$qN = 1 - (F_m' - F_0') / (F_m - F_0)$$

The PAM fluorometer also allows to run pre-programmed experiments. One of these runs is designed to measure induction curves with on-

line quenching analysis. First the measuring light is switched on and a saturation pulse is applied to determine F_o and F_m followed by the recording of the fluorescence yield at 10 ms sampling rate. The fluorescence yield decreases after the F_m measurement and approaches F_o . Then the actinic irradiation is switched on and the series of saturating pulses every 20 s started. The quantum yield, q_N and q_P are calculated after every saturating pulse.

The relaxation kinetics of q_N can be determined immediately following the induction curve. Before that, the alga should have reached a steady state fluorescence and developed non-photochemical fluorescence quenching. The thalli are exposed to the actinic light, and F_o and F_m are determined. The sampling rate is 30 ms. Two saturating light pulses are elicited to measure the quenching parameters in the light-adapted state and then the actinic light is turned off. Subsequently, saturating light pulses are applied with increasing time intervals between pulses following the function $t = 10 \times 1.2^{n-1}$. The halogen lamp can be used instead of the built-in red light emitting diode (LED) in order to induce strong q_N .

In addition to the induction curves described above rapid induction kinetics can be determined at 1000 μ s sampling rate. F_o is determined after the measurement light is switched on and before the actinic light modulated at 20 kHz is switched on for 2 s providing information on the donor and acceptor side properties of PS II. In order to monitor the relaxation kinetics, the recording continues for another 2 s after the end of the actinic light pulse. The re-oxidation of the various acceptor pools in PS II can be enhanced by switching on a far red background light simultaneously. These kinetic curves were also determined before and during exposure to solar radiation. Algae were exposed to solar radiation during cloudless conditions in a large volume of water to control the temperature.

The irradiance dependence of important fluorescence parameters as well as photochemical and non-photochemical quenching are determined by applying increasing actinic light levels. F_o and F_m are determined in dark-adapted thalli before the experimental sequence followed by a 10 min irradiation period at an intermediate irradiance to adapt the sample to light and to activate the Calvin cycle enzymes. Then the actinic light from a red LED is increased every 6.5 min from its lowest level to the maximum. Before each measurement a far red pulse is applied to oxidize the electron transport chain.

Chlorophyll determination

Thalli were exposed to a full day of solar radiation and the chlorophyll concentration was determined in comparison to control thalli kept in dim light. Same amounts of fresh weight were extracted in 10 ml of absolute methanol for 2 h. The fluorescence of the methanolic extract was measured in a Turner Designs fluorometer (TD 700) before and after acidification and concentration of chlorophyll calculated from these readings. The fluorometer was calibrated using pure chlorophyll *a* from *Anacystis nidulans* (Sigma C 6144). The absorption spectra of the algae were also determined from the methanolic extract (before acidification) from 250 to 750 nm [36] using a UV-visible spectrophotometer (Hewlett-Packard 8453E). After extraction the thalli were dried at 40° C for 24 h and the dry weight determined.

Statistics

Mean values and standard deviation were calculated from a minimum of eight independent measurements on independent thalli. All experiments were repeated several times on different days. Student's *t* tests were determined to verify whether the different irradiance treatments caused statistically significant differences.

RESULTS

The irradiance-response curve for *Ulva* shows a slow and steady decline of the F_m' value from over 1.6 to 0.6 (Fig. 1). The photochemical quenching decreases only little from an initial value of close to 1 to 0.6 at 79 W m^{-2} . The yield is stable near 0.68 for lower irradiances and decreases to 0.2 at the maximal irradiance. F_o' and F_t do not vary significantly while the non-photochemical quenching increases from 0.12 to 0.84 indicating a high degree of photoinhibition.

After the first saturating pulse the induction curve with quenching analysis measured at 10 ms sampling rate, showed a fast drop of F_t and a parallel pattern for F_m' followed by a transient rise to an intermediate maximum. After that, both parameters decline to a value of about 0.65 (Fig. 2A). The non-photochemical quenching q_N runs antiparallel to F_t and F_m' . The PAM halogen lamp was used in this experiment in order to induce a significant non-photochemical quenching of 0.65. Both the yield and photochemical quenching remain at a

low level over the recording period. The relaxation kinetics of q_N was determined immediately after the induction at 30 ms per data point (Fig. 2B). The non-photochemical quenching gradually declines over the recording period while F_m' steadily increases. Both the yield and photochemical quenching step up after the first two saturating pulses and thereafter continue to increase at a lower rate, while F_t follows an antagonistic pattern.

When exposed to 15 min of unfiltered solar radiation in the Plexiglas holders floating in a larger volume of seawater the effective photosynthetic quantum yield for the PAR treatment declined from above 0.7 to about 0.35 (Fig. 3). However, within 30 min of exposure, the yield had recovered to 0.62 when the algae were kept in the shade, and continued to increase during the rest of the recovery period. The specimens that were exposed to full solar radiation (UVR+PAR) had a significantly larger inhibition after the exposure time as indicated by the Student *t* test, but the inhibition in the treatment that received UV-A+PAR did not differ significantly from the exposure to the PAR-

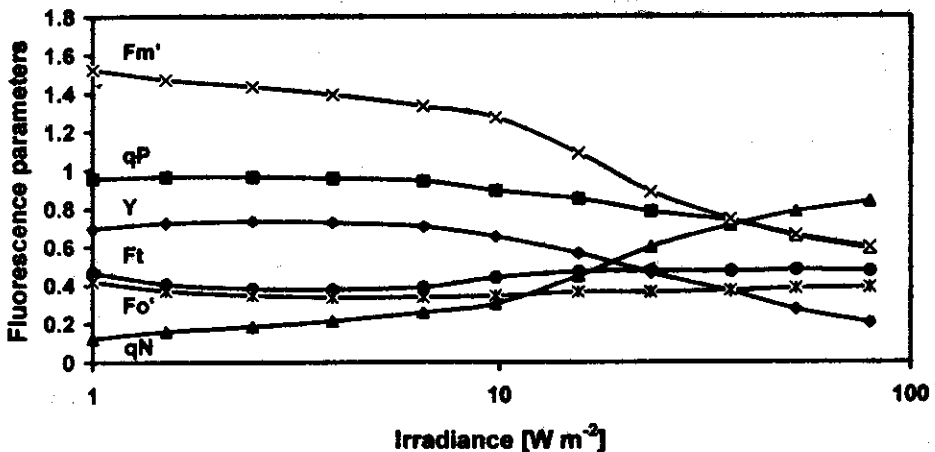


Figure 1: Fluorescence parameters measured in *U. rigida* in dependence of the fluence rate of the actinic red light.

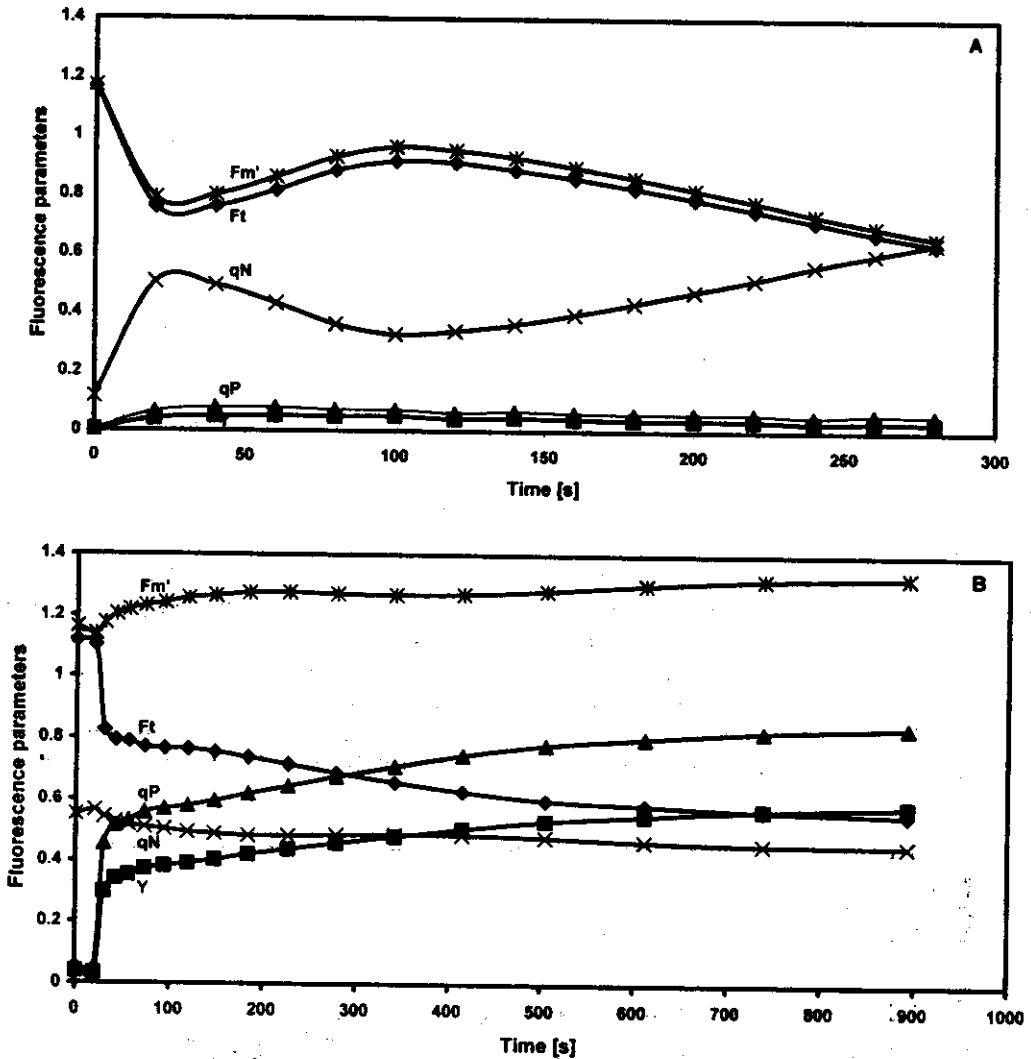


Figure 2: A Induction curve with quenching analysis and B relaxation kinetics of *U. rigida* at 10 ms sampling rate.

only treatment. During recovery the values from the three treatments did not differ significantly from each other. Control specimens treated the same way as the exposed samples except for the exposure period showed a simi-

lar yield as the dark-adapted plants before exposure. This control indicates that the experimental conditions did not affect the yield; therefore it is safe to conclude that the effect is only due to exposure to solar radiation.

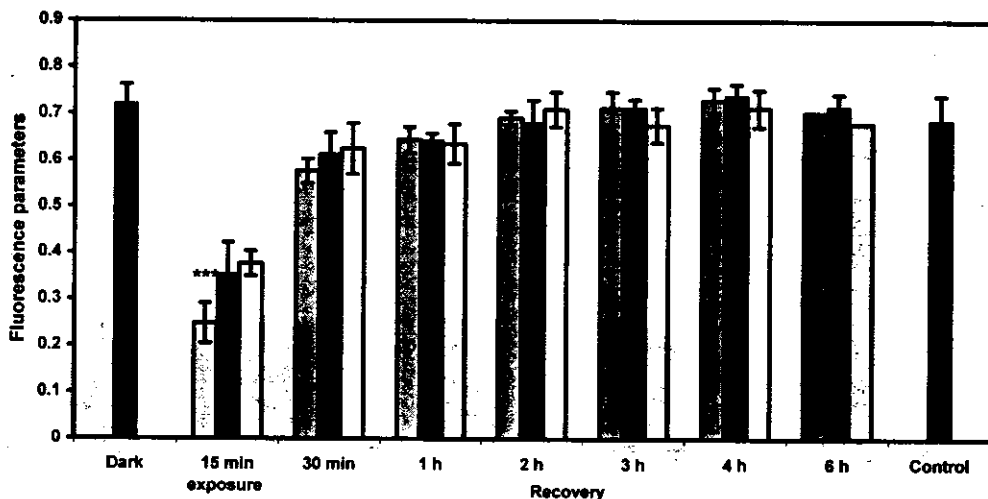


Figure 3: Photosynthetic quantum yield of *U. rigida* measured after 15 min of exposure to solar radiation, in Plexiglas holders, and after increasing recovery times (details in the text). The specimens were exposed either to unfiltered solar radiation (gray bars), radiation filtered through a 320 nm cut-off filter foil (black bars) or filtered through a 395 nm cut-off filter foil (White bars).

In the experiment described above the thalli were confined in one position in the Plexiglas containers so that exposure and yield measurements were done always on the same surface. To closer mimic the natural situation thalli were allowed to freely float in a larger volume of sea water and exposed continuously over the day (data not shown). A significant photoinhibition was observed during noon and the early afternoon hours on a day with only scattered clouds. Additional photoinhibition due to UVR was not so obvious as the algae were already stressed by high PAR. Photoinhibition due to PAR was less pronounced on a cloudy-rainy day. However, differences between samples exposed to unfiltered solar radiation and those exposed to PAR were significant. In another experiment photoinhibition was also studied in a completely natural environment at Bahia Bustamante. The rock pool was accessible only during low tide and cov-

ered by 1 to 2 m of water during high tide. The first measurement was at 11 h local time shortly after the retreat of the water under clear sky and showed a high yield around 0.63 (Fig. 4). Measurements were repeated on an hourly basis and indicated a steep drop to around 0.2. Similar patterns of the yield were seen on subsequent days.

The fast induction kinetics at 1000 μ s sampling rate indicates the involvement of several components of PS II (Fig. 5). There are at least two distinct rise components which lead to a transient fluorescent maximum. Subsequently, the fluorescence declines to a steady state at a lower level. After the actinic light was switched off, the decay shows at least two components. The kinetics was measured before and at regular time intervals during exposure to solar radiation under clear skies. Even after 15 min the fluorescence level had dropped dramatically. The first component decreased less

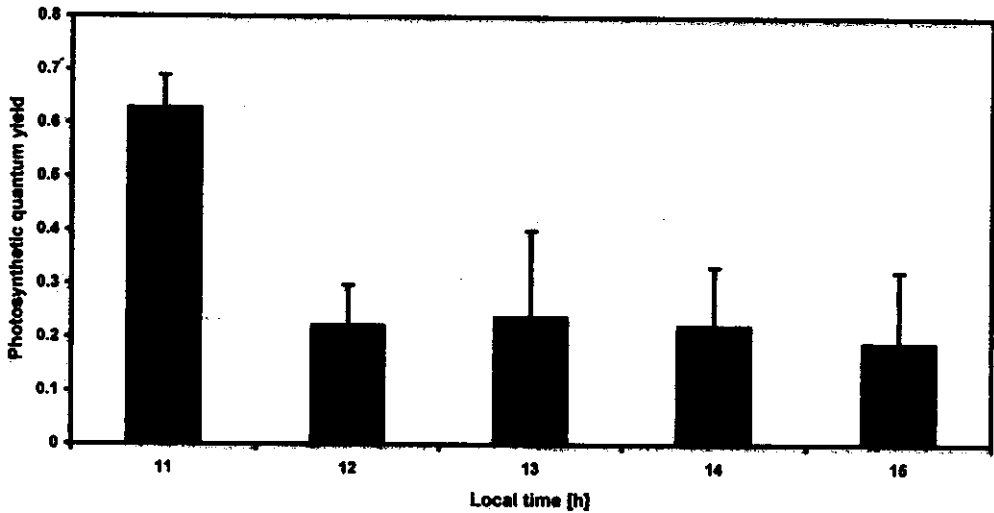


Figure 4: Photosynthetic quantum yield of *U. rigida* in its natural environment in a rock pool in Bahía Bustamante measured at hourly intervals during low tide.

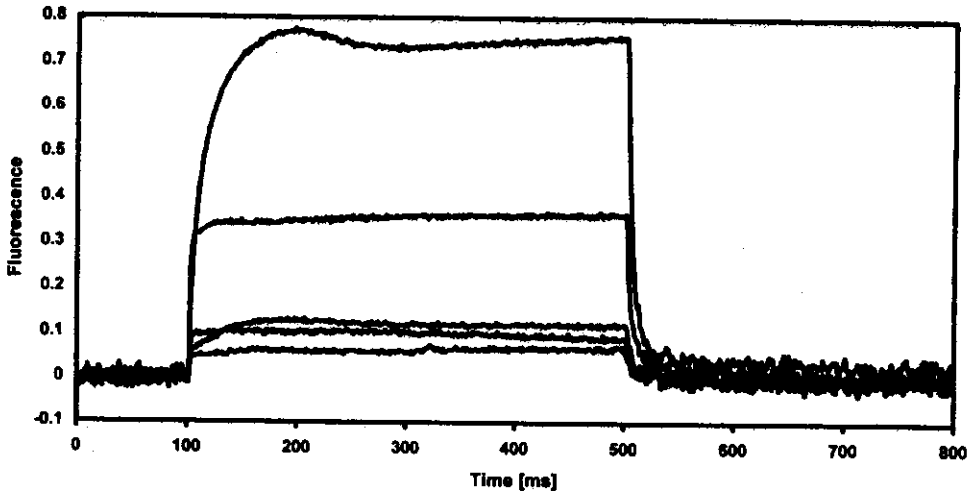


Figure 5. Rapid induction and relaxation kinetics at $1000\mu\text{s}/\text{data point}$ in *U. rigida*.

strongly and thus became more obvious. After 60 min the maximal fluorescence yield had dropped to 4 % of its initial value. Thalli were exposed free floating in a large

volume of sea water for 8 h centered around local noon on a clear day. Methanolic extracts were prepared from exposed samples and control samples kept in dim light. The absorption

spectra do not differ markedly, indicating minimal bleaching due to solar radiation.

4. DISCUSSION

Even toward the end of the summer solar radiation in the Argentinean Patagonia is characterized by intensive PAR (400 – 700 nm) and UV (280 – 400 nm). During the experimental period the UV-B range (280 – 315 nm) was measured above 1.7 W m^{-2} . Since the studied macroalgae populate shallow rock pools in the highest intertidal zone they are exposed to almost unfiltered solar radiation during low tides but are well protected during high tide which is between 2 and 3 m higher than low tide.

Judging from the drastically changing exposure conditions in the habitat the algae need to accomplish positive net photosynthesis at low and intermediate irradiances. In contrast, during excessive irradiation they need effective preventive mechanisms to protect themselves from photooxidative damage. In higher plants and macroalgae the regulatory mechanisms designed to ameliorate light stress include adjustment of the antenna size, thermal dissipation of excess excitation energy, antioxidant systems and the fast repair of photooxidative damage [37]. Non-photochemical quenching is believed to be due to the build-up of a proton gradient across the thylakoid membrane and the protonation of carboxyl groups on the light harvesting complex (LHC) of PS II. Another part of non-photochemical quenching, membrane energization, qE, is linked with the violaxanthin cycle [12]: at low and intermediate irradiances zeaxanthin is converted to antheraxanthin and finally to violaxanthin, while the sequence is reversed during exposure to excessive irradiation. Zeaxanthin is believed to be in close contact with the excited chlorophyll to pick up the excess excitation energy and dissipate it thermally before the chlorophyll can undergo intersystem crossing to the long-lived triplet state which may transfer its energy to

(triplet) oxygen upon which the highly photooxidative singlet oxygen is produced. Recently, also the xanthophyll lutein has been discussed to play a role in non-photochemical quenching [37].

One of the PS II LHC-associated smaller proteins, PsbS, with up to then unknown function, has recently been found to be involved in the mechanism of non-photochemical quenching. It is a 22 kDa, four helix protein which binds chlorophylls and xanthophylls. A mutant which lacks the psbS gene showed a drastically impaired non-photochemical quenching in *Arabidopsis thaliana* [37].

The fluence rate-response curve indicates that *U. rigida* possesses an effective adaptation mechanism to adjust to the prevailing light conditions. Judging from the irradiances at which non-photochemical quenching commences and photochemical quenching declines, this alga is a typical shade plant adapted to effectively harvest and utilize light energy at low fluence rates. This implies that the algae need effective protective mechanisms for high light conditions. The induction and relaxation kinetics of qN indicate that the algae can adapt to changing light conditions within minutes. During exposure to unfiltered solar radiation the fluorescence signal decreases within 15 min to less than 20 % of its initial value. The relaxation kinetics of qN provide information on the different parts of non-photochemical quenching induced by high irradiance. This process decreases the availability of radiation energy for photosynthesis and thus the quantum yield as it relaxes it by thermal dissipation.

The investigated species shows a high photosynthetic quantum yield after dark adaptation or in its natural habitat at the end of the night. Exposure as short as 15 min to unfiltered solar radiation causes significant photoinhibition when the thalli are confined to the same position, not freely floating as in their natural habitat; but almost complete recovery was found

within a few hours. However, when exposed for 30 min or longer, recovery takes much longer and may be incomplete during the 6 h recovery period. This observation corresponds with results found in a number of eulittoral Mediterranean and Atlantic species [4]. Surface-adapted algae recover much faster from exposure to unfiltered solar radiation than algae adapted to deeper water [22-30]. Ecologically more important is the finding that the algae suffered photoinhibition when exposed freely floating or at their natural grow site during low tide. Therefore, it may be necessary to reconsider our conception about the timing of maximal photosynthesis in supralittoral and subtidal macroalgae. Obviously the algae show optimal photosynthetic quantum yield either early in the morning and evening hours during low tide or when high tides coincide with high solar angles. These independent factors thus result in a complicated pattern of the photosynthetic yield. It will be interesting in the future to determine if this behavior is endogenously regulated. A remarkable observation is the fact that solar UV has a significant share in photoinhibition under natural conditions even though the incident energy represents only a small fraction in solar radiation.

The results from the exposure studies are based on short-term experiments and do not allow conclusions on possible long-term adaptation. However, the results from the measurements at the growth site of the thalli show that the algae are photoinhibited when the sun is at high angles under cloudless or partly cloudy conditions, indicating that these algae have adapted to the light conditions protecting themselves against excessive radiation using very effective adaptation mechanisms which operate on a minute scale.

ACKNOWLEDGMENTS

This work was financially supported by the European Community (ENV4-CT97-0580 and

EV5V-CT94-0425; DG XII, Environmental Programme) to D.-P. H. and the Fundación Antorchas, Argentina (A-13669/1-3) to E. W. H. This is contribution N° 25 of Estación de Fotobiología Playa Unión.

Abbreviations: Fo, initial chlorophyll fluorescence in a dark-adapted plant; Fm, maximal fluorescence in a dark-adapted plant; Fv, variable fluorescence = Fm - Fo; Fo', Fm' and Fv', the same for the light-adapted state; Ft, current fluorescence of a light-adapted plant; LHC, light harvesting complex; PAM, pulse amplitude modulation; PAR, photosynthetic active radiation; PS II, photosystem II; qE, energy quenching; qN, non-photochemical quenching; qP, photochemical quenching.

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