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Photoinhibition of photosynthesis in the marine brown alga *Fucus serratus* as studied in field experiments

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ABSTRACT: In field experiments photoinhibition of photosynthesis in the intertidal brown alga *Fucus serratus* was investigated by means of both fluorescence and oxygen measurements. Samples were taken from thalli floating just below the water surface. During falling tides the ratio variable fluorescence/maximum fluorescence (F_v/F_m) decreased with increasing photon fluence rates. As during rising tides only samples could be measured that were previously desiccated, F_v/F_m increased. Plants living in a rock pool and, hence, not emersing during falling tides showed a considerable decrease of photosynthetic capacity due to photoinhibition. Measured algae samples were collected after experiments, kept for about 24 h in dim light for recovery and then measured again. These values were used as references in order to calculate the extent of photoinhibition. Oxygen measurements support results obtained with the fluorescence technique. In the morning photosynthetic capacity decreased with increasing photon fluence rates. Photosynthetic capacity recovered in the late afternoon and early evening when photon fluence rates decreased. However, if on a sunny day an algal sample oriented perpendicularly to the sun's rays was continuously irradiated, a strong decrease of photosynthetic capacity was observed which was not reversible under the dim light conditions of the afternoon and early evening. This indicates photodamage.

INTRODUCTION

Photoinhibition of photosynthesis has frequently been studied with various photosynthetic organisms (see reviews by Powles 1984, Kyle et al. 1987, Krause 1988). However, little work has been done on benthic marine macroalgae, although photosynthesis of these algae has been studied in detail by several authors (Mathieson & Norall 1975, King & Schramm 1976a, b, Ramus et al. 1976, Burris 1977, Dring 1981, Dring & Brown 1982, Lüning & Dring 1985, Lüning 1985). In the marine brown alga *Dictyota dichotoma* photoinhibition of photosynthesis depends on both fluence rate and duration of irradiation (Nultsch et al. 1987). An action spectrum of photoinhibition in this alga revealed that photoinhibitorily active radiation is mainly absorbed by the photosynthetic pigments, especially in the red by chlorophyll *a* and in the green by the carotenoid fucoxanthin. Blue light is less effective than its absorption by the Soret band of chlorophyll *a* would suggest, and wavelengths above 700 nm do not cause significant photoinhibition. Thus, PS II seems to be the site of photoinhibition in *D. dichotoma*. Recovery of photosynthetic capacity after strong light irradiation in *D. dichotoma* is rapid (< 1 h), suggesting that photoinhibition is a mechanism protecting the alga from photodamage.

Ramus & Rosenberg (1980) studied the diurnal photosynthetic performance of *Dictyota dichotoma*. This and other seaweeds such as *Ulva, Codium* and *Gracilaria* species were incubated in standard oxygen demand bottles exposed to daylight. On sunny days when photon fluence rates were high the authors found an early afternoon depression of oxygen production rates which seemed to be reversible in the late afternoon and early evening as long as fluence rates remained high enough to drive photosynthesis.

As terrestrial shade plants or shade-adapted leaves of plants exhibit a greater sensitivity to photoinhibition than sun-adapted ones, shade-adapted seaweeds from the subtidal region should also show a greater sensitiv-

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ity to strong light than those growing in the eulittoral (cf. Neale 1987). This has been confirmed in a recent study by Herbert & Waaland (1988) for 2 *Porphyra* species. After exposure to strong light conditions the extent of photoinhibition in the subtidal red alga *P. nereocystis* was greater than in the intertidal species *P. perforata*.

The occurrence of photoinhibition of photosynthesis under field conditions in higher plants has been shown by several authors (Björkman et al. 1988, Ögren 1988). Using chlorophyll fluorescence measurements at ambient air temperature in a willow (*Salix*) stand in Sweden, Ögren (1988) observed a decrease in the variable fluorescence/maximum fluorescence (F_v/F_m) ratio on cloudless days, but no decrease on cloudy days. Recovery of photoinhibited leaves took 7 to 16 h. Photoinhibition in marine macroalgae in their natural habitat has not been investigated so far. Therefore, in field experiments we measured the daily course of photoinhibition of photosynthesis in the brown alga *Fucus serratus* with the aid of oxygen and fluorescence techniques.

This alga was chosen as it is widespread in the lower eulittoral (Lüning 1985) and, in addition, because it is easily accessible at low tide. On sunny days *Fucus serratus* has to cope with high fluence rates at low tide so that a strong photoinhibition could be expected. However, it must be taken into account that the plants emerge at low tide so that they are also exposed for hours to desiccation, salinity and heat stresses.

MATERIAL AND METHODS

Field experiments with the intertidal brown alga *Fucus serratus* were carried out mainly in May 1989 on the rocky shore of Helgoland in the SE North Sea. The near-surface water temperature during this time ranged between 11 and 13°C. Measurements were made at places which were easily accessible as well as secure for the equipment. For both fluorescence and oxygen measurements discs of 14 mm diameter were cut out of the thalli in the region close to the apical bifurcation. Unless otherwise noted, only thalli floating just below the water surface were chosen. Thus, during falling tide, measurements could be carried out even with algae from lower on the shore. During rising tide thalli were measured which had been previously emersed. Measurements were stopped when all algae were submerged and no longer reachable.

In vivo chlorophyll fluorescence measurements were carried out at seawater temperature with a portable pulse-amplitude modulation fluorometer (PAM, Walz, Effeltrich, FRG), as devised by Schreiber et al. (1986), connected with a saturation pulse lamp. The measurement of in vivo chlorophyll fluorescence from marine macroalgae required the construction of a special seawater cuvette, surrounded by a cooling jacket. Discs of algae were darkened for 15 min in seawater before fluorescence measurements. The initial fluorescence F_o can be seen after switching on the modulated non-saturating measuring light; this represents light energy lost during migration from antenna chlorophyll *a* molecules to reaction centers. In contrast, the maximal fluorescence F_m is detectable when all primary acceptors of PS II are reduced. This was done with an additional overall saturating light pulse (700 ms) of high energy. For further explanations on chlorophyll fluorescence see Briantais et al. (1986). The ratio of F_v/F_m ($F_v = F_m - F_o$) was used as a sensitive measure for photoinhibition (Krause & Somersalo 1989). After the experiment, all discs were collected, kept for 24 h in dim light (11 µmol m^{-2} s^{-1}) in the laboratory for recovery and then measured again. In this way the full photosynthetic capacity was determined.

Simultaneously with the fluorescence measurements the oxygen production of a thallus disc in a closed plexiglas cuvette (Fig. 1) was measured with a temperature-compensated Clark electrode (EO 90, Oxi 92, WTW, FRG) under natural light and temperature conditions. The plexiglas cuvette had a glass window on the top and a volume of 35 ml. It was constructed especially for the field experiments. For protection the cuvette was surrounded by an open-topped PVC case. A battery-powered magnetic stirrer, mounted in the PVC case, ensured a sufficient flow of seawater over the front of the gold-silver electrode and provided a steady seawater exchange between the electrode and the alga chamber. The alga disc was fixed between 2 perforated plexiglas plates. To avoid depletion of

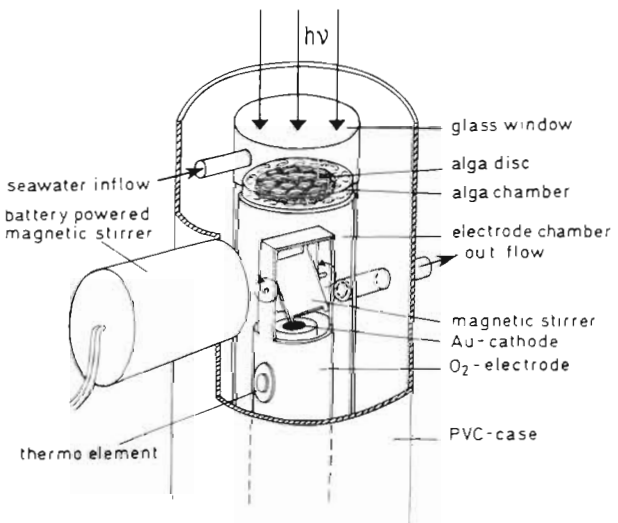

Fig. 1 Schematic diagram of the cuvette used for oxygen measurements in the field

nutrients and to prevent saturation of the seawater with oxygen, the water was periodically substituted by non-saturated fresh seawater, stored in a bottle connected to the cuvette inflow. The PVC case was fixed to the ground by an iron stake so that the alga faced the sky. With the exception of the open top it was submerged so that the alga remained at seawater temperature. The electrode was coupled to an amplifier which was connected by a long cable to the recorder kept at a safe distance from the sea. The position of the device was corrected from time to time according to the tide level. Changes in oxygen concentration per time unit (mg O_2 l^{-1} min^{-1}) were used as a measure of photosynthetic activity. After the field experiments samples were collected, kept for 24 h in dim light (11 µmol m^{-2} s^{-1}) in the laboratory for recovery, and then a fluence rate-effect curve of the photosynthetic oxygen evolution was measured for each alga disc. As light source a projector (Leitz, Wetzlar, FRG) equipped with a quartz iodine lamp was used. Different photon fluence rates were set by inserting neutral density filters. Beginning with low photon fluence rates the photosynthetic oxygen evolution was measured for 5 min at each photon fluence rate.

The spectral composition of light in different water-depths was measured with an underwater spectroradiometer (LI-1800UW, LI-COR, Lincoln, NB, USA). The fluence rate during the course of a day was recorded with a photodetector mounted on the roof of the Biologische Anstalt Helgoland, as described by Hanelt & Nultsch (1990). The photodetector was calibrated with a Radiationmeter (LI-185B, LI-COR) equipped with either a pyranometer sensor (LI-200SB) or a quantum sensor (LI-190SB).

RESULTS

On the shore of Helgoland, *Fucus serratus* plants are covered by a maximal water column of about 2 to 3 m at high tide. The spectral composition of the light measured at different depths on a relatively cloudy day (1 June 1989) is shown in Fig. 2. According to the Jerlov system of optical water types the water around Helgoland should be classified as coastal water type no. 7 with maximal transmittance at 558 nm (cf. Lüning & Dring 1979). The transmittance decreases drastically with increasing depth, so that in 3 m water depth only 22 % of 558 nm light could be measured. On this day the maximal white light photon fluence rate measured in air was 800 µmol m^{-2} s^{-1}. In a water depth of 2 to 3 m the photon fluence rate is too low to saturate photosynthesis or to cause significant photoinhibition in *F. serratus*. During falling tide the irradiance impinging on the *F. serratus* thalli increases with the decreasing sea level. Thus the algae have to adapt within 6 h to considerable and rapid changes of the fluence rate.

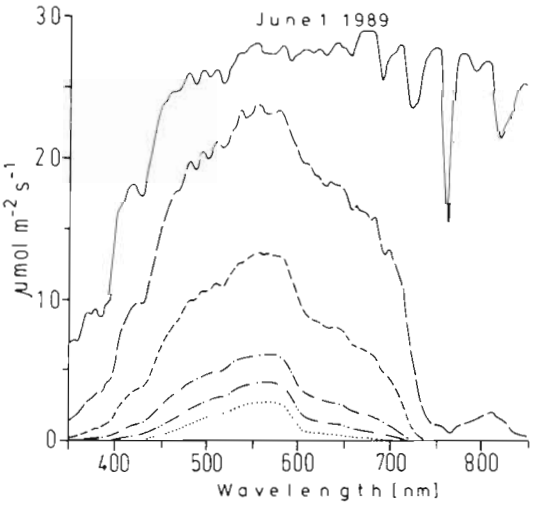

Fig. 2. Spectral composition of light in different water depths near the stand of *Fucus serratus*. From top to bottom: spectrum of 'white light' in air and spectra of impinging light measured at 1, 2, 3, 5 and 7 m water depth

Fluorescence measurements

In a first series of experiments samples of thalli floating just below the water surface were collected from different places in the eulittoral. Emersed and, hence, partly desiccated thalli were not used in order to avoid any interference by water and salt stress. Fluorescence measurements were carried out immediately after samples were cut out of the thalli. At the beginning of the experiments the samples were taken from different levels of the lower eulittoral, according to the decreasing tide level. Thus, an increasing sensitivity to light of algae taken from lower on the shore has to be considered. Moreover, as algae from lower on the shore were measured at a later time of day, they had received considerably more photons than samples taken earlier. Therefore a stronger photoinhibition should be expected. During rising tides, samples were taken from higher levels of the lower eulittoral again. These thalli were emersed before and therefore desiccated to different water contents.

As shown in Fig. 3, the F_v/F_m values of the *Fucus serratus* samples decreased during falling tide to a minimum value of 0.4 at 10:00 h, as a result of photoinhibition. These samples had not been exposed to air. On the other hand, algae measured after the turn of tide had been exposed to air for various times. Thus they were desiccated to different water contents. Samples were taken only from plants floating just below the water surface as mentioned above. Thus, the

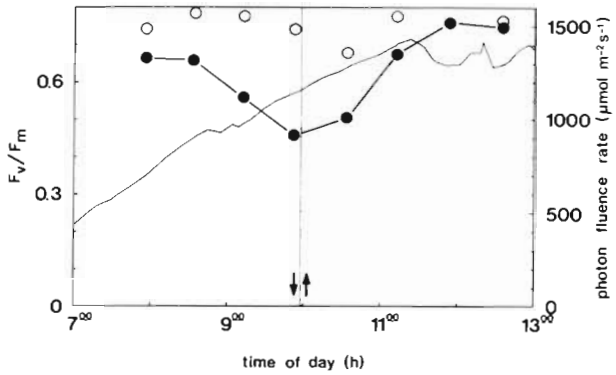

Fig. 3. *Fucus serratus*. Photosynthetic activity (●—●) of thalli floating just below the water surface during falling (↓) and rising tides (↑). Vertical line represents the turn of tide. (○) Full photosynthetic capacity of samples measured after a recovery phase of 24 h. Thin curve shows actual photon fluence rate measured on the roof of the Biologische Anstalt

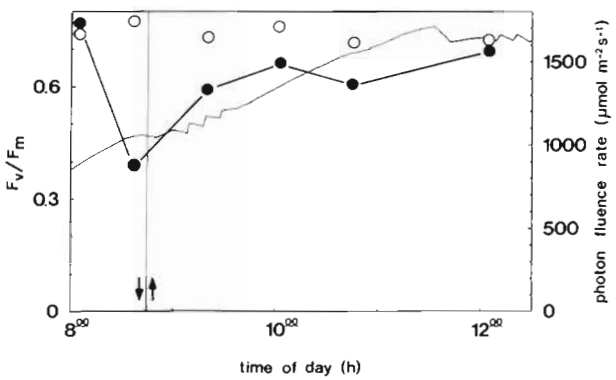

Fig. 4. *Fucus serratus*. Photosynthetic activity (●—●) thalli floating just below the water surface during falling and rising tides. (○) Controls after 24 h recovery. For further explanations see Fig. 3

first thallus measured after the turn of tide had been exposed to air for nearly 1 h, whereas the thallus measured at 12:35 h had been exposed for about 3 to 4 h. As the F_v/F_m values measured during the rising tide were higher with longer desiccation times, we assume that the current photoinhibitory state of the photosynthetic apparatus is conserved by desiccation. After recovery for 24 h in weak light in the laboratory F_v/F_m for all these samples varied only between 0.7 and 0.8, indicating a high reproducibility of the fluorescence measurements.

Fig. 4 supports the results shown in Fig. 3. If a thallus was measured before the turn of tide and therefore not exposed to air, photoinhibition was detectable. However, if thalli were measured after the turn of tide, F_v/F_m increased with the degree of desiccation.

In order to investigate whether photoinhibition can be induced even in the desiccated state, a series of experiments with samples taken from the same thallus at different times was carried out (Fig. 5). At 8:20 h,

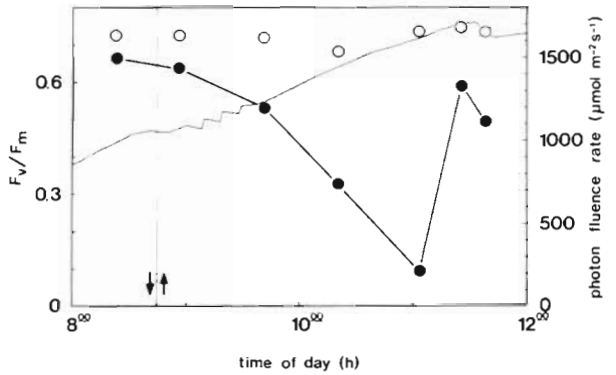

Fig. 5. *Fucus serratus*. Photosynthetic activity (●—●) of a thallus desiccated after emergence and then re-immersed. (○) Controls after 24 h recovery. For further explanation see Fig. 3

when the thallus was just emersed, no photoinhibition was detectable. Just before this thallus was submerged again by the tide at 11:05 h, F_v/F_m decreased with increasing desiccation to about 0.1. The decrease in F_v/F_m measured in the first 2 samples at 8:23 and 8:56 h was exclusively due to an increase of F_o without great changes in F_m. The further decrease of F_v/F_m caused by desiccation during the following hours was the result of a drastic decrease in F_m, whereas F_o remained unchanged. After 11:05 h the thallus was submerged again by the tide. During the following 20 min it reabsorbed the water, and the F_v/F_m value jumped up to about 0.6, due to rapid increase of F_m. F_v/F_m, however, did not reach the initial value, and decreased again, due to photoinhibition. Unfortunately, the measurements could not be continued as the habitat was no longer accessible. These 2 types of experiments were repeated during the following days. Though the absolute values (data not shown) varied depending on the individual plants, clouding and tides, the results obtained confirm those of the experiments described above.

As an *experimentum crucis*, *Fucus serratus* thalli living in a rock pool were measured. The advantage of these experiments was that the algae were always submerged in a constant water depth during ebb and flood until the whole pool was covered by the rising tide. As before, samples were taken only from thalli floating just below the water surface. At 11:00 h the pool was accessible and the experiments could be started. The F_v/F_m ratio of *Fucus serratus* was as high as the control value at this time (Fig. 6). Due to the relatively high photon fluence rates to which the algae were exposed, F_v/F_m decreased after a delay which we cannot explain during the next few hours to 0.3. A cloudy period between 13:00 and 13:45 h caused a transient increase of F_v/F_m up to almost 0.6, but at 13:45 h it was again about 0.3. In the afternoon a slow recovery of photoinhibition was observed which was

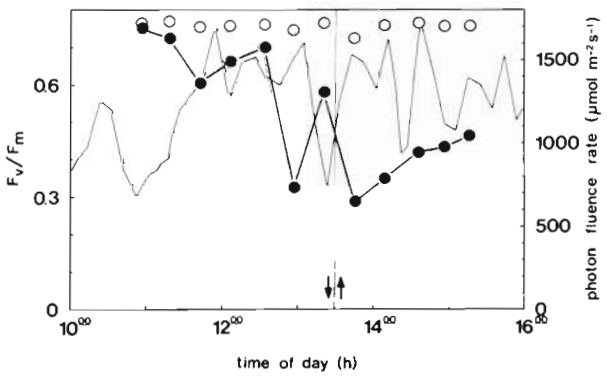

Fig. 6. *Fucus serratus*. Photosynthetic activity (●—●) of a thallus standing in a rock pool under natural irradiation and after a recovery phase of about 24 h (○). For further explanations see Fig. 3

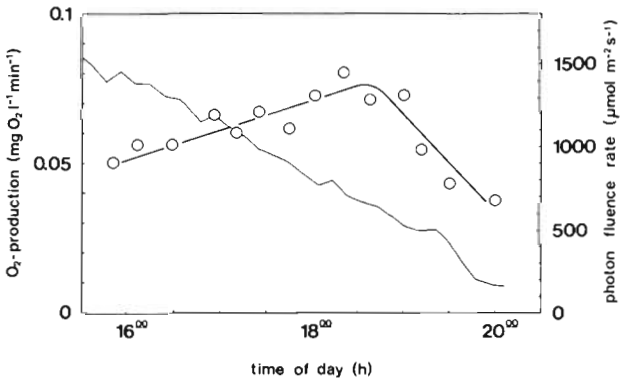

Fig. 8. *Fucus serratus*. Photosynthetic activity of a sample (○) in situ exposed to decreasing photon fluence rates (thin curve) in the afternoon and early evening

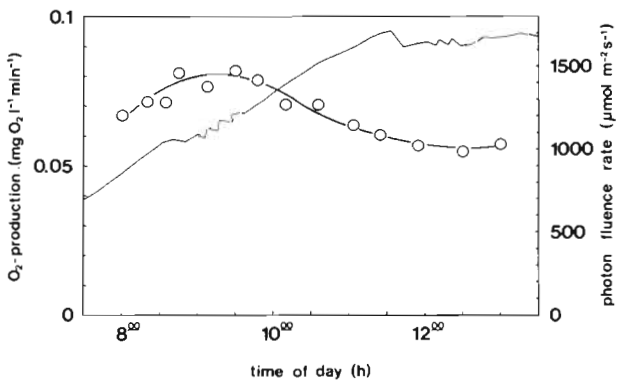

Fig. 7. *Fucus serratus*. Photosynthetic activity of a sample (○) in situ exposed to increasing photon fluence rates (thin curve) in the morning

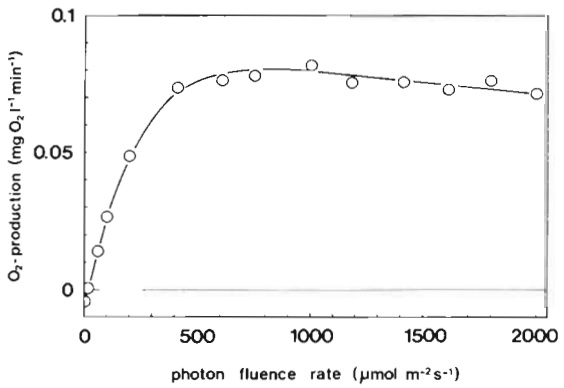

Fig. 9. *Fucus serratus*. Photon fluence rate-effect curve of photosynthetic oxygen evolution

probably due to the increasing clouding. As the algae were never desiccated during the experiments the decrease in the F_v/F_m ratio can only be the result of photoinhibition.

Oxygen measurements

In parallel to the fluorescence experiments oxygen measurements were carried out in which one disc cut out of a *Fucus serratus* thallus was exposed to daylight in situ throughout the day. In Fig. 7 photosynthetic oxygen production of a *F. serratus* sample during increasing photon fluence rates is shown. Between 8:00 and 9:15 h photosynthetic oxygen production increased until the saturation level of photosynthesis was reached at a photon fluence rate of about 1100 µmol m^{-2} s^{-1}. Then, with further increasing photon fluence rates, photosynthetic oxygen production decreased as a result of photoinhibiton.

Although oxygen measurements were carried out on the same days as the fluorescence measurements the degree of photoinhibition is not comparable because of the different total photon fluences the algae were exposed to before the measurements. Furthermore, in the case of oxygen measurements only one algal sample was measured during the day, fixed in the plexiglas cuvette covered by a constant water column. In contrast, for fluorescence measurements samples were taken from different plants growing at different depths.

On another day, the in situ recovery of photosynthetic capacity of a photoinhibited *Fucus serratus* sample during the afternoon and the early evening was measured (Fig. 8). With decreasing photon fluence rates photosynthetic oxygen evolution increased until photon fluence rates dropped below the saturation level of photosynthesis around 18:45 h. Then the photosynthetic activity decreased according to the decreasing photon fluence rate. For recovery the alga discs were kept in dim light and in subsequent laboratory experiments the photosynthetic fluence rate-effect curve of each thallus disc was measured with white light. Generally photosynthesis was saturated at photon fluence rates between 700 and 1000 µmol m^{-2} s^{-1} (one example is shown in Fig. 9). This is in good

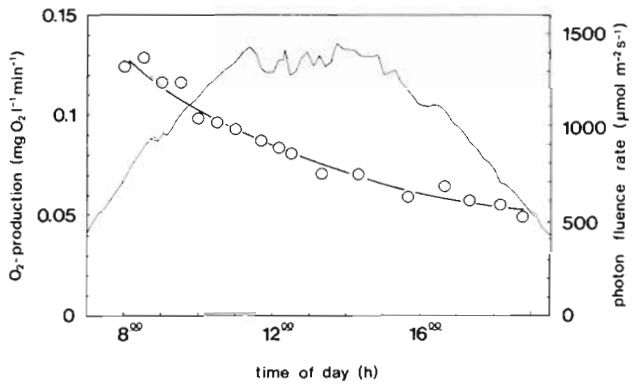

Fig. 10. *Fucus serratus*. Photosynthetic activity of a sample (○) oriented perpendicularly to incident sunlight. Thin curve: photon fluence rate

agreement with the results obtained in the field experiments (Figs. 7 and 8). A comparison shows that maximal oxygen evolution in field experiments is always reached when the photon fluence rate is as high as mentioned above. Higher photon fluence rates caused a gradual decrease of oxygen evolution as a result of photoinhibition (Fig. 9). However, the extent of photoinhibition shown in Fig. 9 is not comparable to the values shown in Fig. 7 and Fig. 8, since it is the total photon fluence impinging on the thalli during the foregoing light period that is responsible for the extent of photoinhibition, not the current photon fluence rate.

When the position of the cuvette was repeatedly adjusted so that the disc of the *Fucus serratus* thallus was always oriented perpendicularly to the sun's rays, and, hence, irradiated with high fluence rates during the whole day (Fig. 10), an almost continuous decrease in photosynthetic oxygen evolution was observed. As even with decreasing photon fluence rates no recovery could be observed, photodamage must be considered to have occurred.

DISCUSSION

Ramus & Rosenberg (1980) measured the diurnal photosynthetic O_2 production in several green, brown and red algae. They obtained varying patterns of diurnal photosynthetic performance mainly depending on the diurnal course of irradiance and the species in question. In general, they observed a maximum in the morning, followed by an afternoon depression and a late afternoon recovery. They interpreted this depression as a result of photoinhibition and its recovery. However, as they measured only the actual photosynthetic O_2 production, they could not exclude possible interferences by photorespiration, circadian periodicity in photosynthetic capacity, increase in 'dark' respiration, and chloroplast arrangement inside the cell.

For these reasons we combined oxygen and fluorescence measurements, as it is generally accepted that the F_v/F_m ratio is a sensitive and reliable measure for photoinhibition studies (Krause & Weis 1984, Baker & Horton 1987, Krause 1988, Somersalo & Krause 1988). Thus we can be sure that the observed decrease of O_2 production caused by high photon fluence rates at noon and in the afternoon is really the result of photoinhibition, i.e. a decline in photosynthetic capacity, and that any interference by photorespiration and 'dark' respiration can be ruled out. For the same reason it could be confirmed that the increase of photosynthetic activity in the late afternoon is due to recovery from photoinhibition. A circadian periodicity of photosynthetic activity does also not contribute to the daily change of photosynthetic capacity for 2 reasons: (1) A decrease in photosynthetic capacity depends exclusively on the actual fluence rate and is independent of the time of the day. Thus a significant photoinhibition can occur even in the later afternoon when after a very cloudy day the sun comes out relatively late. (2) If circadian rhythms contributed to the daily changes of photosynthetic capacity, they should be visible also in the controls measured after recovery in dim light. Finally, it is highly improbable that circadian rhythms in the chloroplast arrangement are responsible for the daily changes in photosynthetic capacity. The chromatophore displacements observed in *Fucus vesiculosus* are strictly fluence rate dependent and do not show any periodicity (Rüffer et al. 1978, Nultsch et al. 1979). Moreover, Nultsch et al. (1981) have shown that the photosynthetic activity in the brown alga *Dictyota dichotoma* is independent of the chromatophore arrangement. Recently, Hanelt & Nultsch (1990) observed in field experiments that in *D. dichotoma* the chromatophores are mostly in the high intensity position during the day, provided that the photon fluence rate is not too low, as for example in a water depth of several meters.

It is well known that uncovered algae from the intertidal zone show a decrease in photosynthetic activity as a result of a decrease in water content (Wiltens et al. 1978, Dring & Brown 1982, Öquist & Fork 1982). Thus the strong decline in the F_v/F_m ratio (Fig. 4) is the result of desiccation rather than of photoinhibition. After the thalli were submerged again, recovery was rapid, but not complete. This may be due to photoinhibition, because at this time of day high photon fluence rates were measured. According to Dring & Brown (1982), however, the recovery from severe desiccation in 3 *Fucus* species and 2 other brown algae took about 2 h. Thus, a complete recovery could not be expected within about 25 min. After the resoaked thallus was kept in dim light for 24 h, complete recovery was observed. However, the only partial recovery can also

be explained in the following way: the more the thalli are desiccated, the less sensitive they are to light and, hence, the less is the inhibitory effect. In largely desiccated thalli light does not cause photoinhibition at all. Moreover, it seems that the photoinhibitory state is conserved by moderate desiccation so that the thalli show the same photoinhibition state after re-absorbing water as before their emergence. This would explain why the thalli measured at about 11:50 and 12:36 h (Fig. 3), which emerged between about 7:00 and 8:00 h, did not show any inhibition, whereas the other two that emerged later were significantly photoinhibited. If this interpretation were correct, we might conclude that the mechanisms of F_v/F_m decrease caused by either photoinhibition or desiccation are different.

As marine tidal algae during the day are exposed to varying photon fluence rates due to both clouding and tides, photoinhibition seems to play an important role in the regulation of photosynthesis of non-desiccated thalli. In general it is fully reversible during the dim light period in the later afternoon and early evening, which is relatively long in temperate latitudes. Thus we may conclude that photoinhibition is a protective mechanism which prevents the photosynthetic apparatus from photodamage under strong light conditions. Though we have shown that long-term exposure to direct sunlight can cause irreversible decrease of photosynthetic capacity, i.e. photodamage, this may rarely occur under natural conditions for the following reasons. Contrary to the situation in the O_2-measuring cuvette where the thallus is fixed with respect to the direction of the sunbeam the thalli floating in the water continuously change their orientation to the sun. Moreover, light is reflected in part at the moving water surface and the transmitted light is scattered by plankton and suspended particles. If the thallus becomes immobile during low tide, photosynthetic activity is decreased by desiccation as mentioned above, thus preventing an overload of the photosynthetic apparatus.

In the literature the term photoinhibition is used with different meanings. On the one hand the term is often equated with 'light dependent damage to the photosynthetic apparatus' (Osmond & Chow 1988) or with 'the first stage of photodamage' (Critchley 1988). On the other hand, it is increasingly regarded as a mechanism protecting photosynthetic organisms from photodamage (Nultsch et al. 1987, Sibbald & Vidaver 1987, Krause 1988, Somersalo & Krause 1988, Krause & Somersalo 1989, Havaux 1989). We consider that the results of our field experiments with *Fucus serratus* strongly support the latter opinion. Moreover, in algae occupying different positions on the shore the different abilities to perform photoinhibition and its recovery (Herbert & Waaland 1988) suggest that photoinhibitoin could be a mechanism by which light exerts an effect on the distribution of algae in the intertidal belt.

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