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Photoinhibition as a regulative mechanism of photosynthesis in marine algae of Antarctica

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ABSTRACT

Photosynthetic activity, photoinhibition and recovery of photosynthesis in the brown alga Adenocystis ultricularis *and in the red alga* Palmaria decipiens *were studied in field experiments on King George Island (Antarctica) in February 1993. Experiments were carried out with a portable fluorometer and an oxygen-measuring device constructed especially for field studies. Both algal species show photoinhibition of photosynthesis observed in fluorescence and oxygen measurements during the course of a day. The kinetics of photoinhibition and recovery of photosynthesis were very fast at low water temperature albeit enzymatic reactions are involved in these processes. The brown alga* A. utricularis *reacts faster than brown macroalgae of the tropic and moderate latitudes. Thus, it may be questioned whether the turnover-cycle of the* D_1 *-protein of photosystem II is involved in the molecular process of photoinhibition, unless the enzymatic processes involve in photoinhibition or recovery are adapted to low temperatures in the Antarctic species. A comparison of the reactivity to changing light conditions of the intertidal* A. utricularis *and* P. decipiens *with maximal growth rate in the subtidal zone shows that the brown intertidal alga responds to a strong light stress much faster and with a higher photoinhibitory degree as the red alga. In addition, recovery of the brown intertidal alga is much faster than the recovery of* P. decipiens. *This indicates that a relation between photoinhibition and zonation of these algae exists. Both algal species can cope with excessive light conditions as a results of photoinhibition. Thus, photoinhibition of photosynthesis is rather a regulatory mechanism than a photodamage in marine algae so that photosynthesis can acclimate to strong light conditions especially occuring when low tide concides with high irradiance around noon.*

Key words: Antarctica, fluorometry, low temperature adaptations, marine algae, photoinhibition, photosynthesis.

Fotoinhibición como mecanismo de regulación de la fotosíntesis en algas marinas de la Antártica

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RESUMEN

La actividad fotosintética, la fotoinhibición y la recuperación de fotosíntesis en el alga café Adenocystis utricularis *y en el alga roja* Palmaria decipiens *se estudiaron en experimentos de terreno en isla Rey Jorge, Antártica, en febrero de 1993. Los experimentos se llevaron a cabo con un fluorómetro portátil y un aparato para medición de oxígeno construido específicamente para trabajos en terreno.*

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Ambas especies de algas mostraron fotoinhibición de fotosíntesis observadas en fluorescencia y mediciones de oxígeno durante el transcurso del día. La dinámica de la fotoinhibición y recuperación de la fotosíntesis fueron muy rápidas en agua a bajas temperaturas, aunque hay reacciones enzimáticas involucradas en estos procesos. El alga café A. utricularis *reacciona más rápido que las macroalgas café del trópico y latitudes templadas. Así, se puede preguntar cuándo el ciclo de renovación de la proteína* D_1 *del fotosistema II está involucrado en los procesos moleculares de fotoinhibición, a menos que el proceso enzimático involucrado en fotoinhibición o recuperación esté adaptado a bajas temperaturas en las especies antárticas. Una comparación de la reactividad a los cambios de las condiciones de luz de* A. utricularis y P. decipiens *intermareal con máximo rango de crecimiento en zonas submareal, muestran que las algas café intermareal responden mucho más rápido al stress de luminosidad fuerte y con un alto grado fotoinhibitorio como en el alga roja. Además, la recuperación del alga café intermareal es mucho más rápida que aquella en* P decipiens. *Esto indica que existe una relación entre la fotoinhibición y la zonación de estas algas.*

Ambas especies de algas pueden competir con excesivas condiciones de luz como resultado de la fotoinhibición. Así, la fotoinhibición de fotosíntesis es más bien un mecanismo regulador que uno fotodañino en las algas marinas, de tal manera que, la fotosíntesis puede aclimatarse a condiciones de luz fuerte que ocurre especialmente cuando la baja marea coincide con la alta irradiancia alrededor del mediodía.

Palabras claves: Antártica, fluorometría, adaptaciones a baja temperatura, algas marinas, fotoinhibición, fotosíntesis.

INTRODUCTION

Photosynthetic activity of marine algae is depressed by strong sunlight in the field (Coutinho and Zingmark, 1987; du Preez *et al.*, 1990; Ramus and Rosenber, 1980). In field investigations it has been shown that the depression, caused by photoinhibition, follows a diurnal pattern (Huppertz *et al.*, 1990; Henley *et al.*, 1991, 1992; Hanlet, 1992; Hanlet *et al.*, 1993). In the morning photosynthetic activity is high, but increasing fluence rates of sunlight photoinhibition commences. The highest degree of photoinhibition and, hence, the lowest photosynthetic activity occurs between noon and the early afternoon. In the late afternoon photosynthesis recovers, and in the evening almost full recovery of photosynthetic capacity is reached. Photosynthesis depends on the tide level, because the water column covering the algae protects photosynthesis against high fluence rates. Therefore, the highest degree of photoinhibition is observed in those algae floating near the water surface (Hanlet *et al.*, 1994).

Photoinhibition of photosynthesis, occuring in excessive light intensities, is a photoprotective mechanism which impairs photosystem II so that excesive absorbed energy is rendered harmless by thermal dissipation (c.f. Krause and Weis 1991). Otherwise, the harmulf excessive abosorbed energy increases the rate of photodamage of the D^1 -protein which would exceed the rate of its repair process. This leads to a breakdown (degradation) of the D^1 -protein (Andersson *et al.*, 1992) and, hence, the plant suffers from a loss of photosynthetic activity. The increase of the thermal energy dissipation could be due to an increase of the zeaxanthin content of the PS II antenna (Adams III and Demmig-Adams, 1992) and/or by increasing the amount of inactive PS II centers (e.g. PS II_β centers), which may be able to protect photosynthetic active centers (Öquist and Chow, 1992).

In the mechanisms of photoinhibition and recovery of photosynthesis enzymatic steps are involved. Therefore, photoinhibition and recovery are temperature dependent. Richter *et al.* (1990) reported that the breakdown of D^1 -protein as well as the concomitant loss of variable fluorescence were largely prevented when spinach thylakoids were photoinhibited at 0°C. Isolated thylakoids of irradiated *Curcurbita* leaves, however, showed a faster photoinhibition of PS II at low temperature (Aro *et al.*, 1990). Greer *et al.* (1986) observed that in *Phaseolus* the rate of recovery was slow below 15°C and optimal at 30°C. These contradictory results indicate the different adptation strategies of the plants to the environmental temperature conditions. E.g. winter cereals are resistant to short-term photoinhibition and have even an increased capacity for photosynthesis at low temperatures, whereas overwintering evergreens become dormant during the cold hardening period and generally remain susceptible to photoinhibition (Huner *et al.*, 1993).

Antarctic algae are exposed to low temperatures and a short vegetation period. However, light saturated photosynthesis, dark respiration and carbon fixation of antarctic macroalgae at 0°C are very similar to those of the temperate algae at higher temperature (Thomas and Wiencke, 1991). Moreover, Wiencke *et al.* (1993)

have shown that photosynthesis of these algae is adapted to the low light intensities and cold environment. Thus, the question arises, how these dim light adapted antarctic algae react in response to the strong light conditions which are due to both the daily course of sunlight and low tide. Photosynthesis of temperate as well as of tropic algae shows a fast decrease due to photoinhibition if the fluence rate of sunlight becomes excessive (Hanelt, 1992; Hanelt *et al.*, 1993, 1994). As the vegetation period in the tropic and temperate latitudes is longer and the fluence rate of daylight much higher than in Antarctica it might happen that the net production becomes too small after photosynthesis is impaired by photoinhibition. Moreover, the low temperature of the antarctic water body is expected to have an effect on the turnover rate of the enzymatic processed involved in photosynthesis. Therefore, it was of great interest to investigate photosynthesis of antarctic macrophytes in field experiments which has been done in February 1993 on the coast of the Sea-Elephant Bay of King George Island.

MATERIAL AND METHODS

In January 1993 an excursion to the Chilean antarctic station Presidente Eduardo Frei Montalva on King George Island (South Shetland Islands) commenced. The Sea-Elephant Bay near the station was suitable for our field experiments because macroalgae were growing in the intertidal zone and, hence, could be investigated *in situ*. The brown alga *Adenocystis utricularis* (Bory) Skottsberg grew in the middle and lower eulittoral and the red alga *Palmaria decipiens* (Reinsch) Ricker in the lower eulittoral and subtidal zone. However, thalli of the red one collected in the sublittoral were much larger than those growing in the eulittoral.

In vivo chlorophyll fluorescence was measured with a small portable pulse-amplitude-modulation fluorometer (PAM 2000, Walz, Effeltrich, Germany) connected to a portable computer (Poquet PC, Santa Clara, USA). It is a further developed system based on the principle devised by Schreiber *et al.* (1986). As a measure of photoinhibition the ratio of variable to maximal fluorescence Fv/Fm of the dark adapted plant was used (cf. Krause and Weis, 1991). Fv = Fm - Fo, in which Fo is the initial fluorescence, i.e. when all reaction centers of PS II are active or «open», and Fm is the maximal fluorescence, i.e. when all PS II centers are «closed». As shown earlier (Hanelt, 1992; Hanelt *et al.*, 1992, 1993), the results of oxygen measurements are consistent with those of fluorescence measurements. In addition to the oxygen measurements, Δ F/Fm' was determined, the fluorescence ratio which is reported to represent the actual quantum yield of photosynthesis (Genty *et al.*, 1989; Havaux *et al.*, 1991, Schroeter *et al.*, 1992). Δ F is the difference of the respective maximal fluorescence (Fm') of a light adapted plant and the fluorescence level caused by daylight (F_t), $\Delta F = Fm' - F_t$.

Pieces of the phylloids were cut out under water and mounted on the end of the fiber optics of the fluorometer exposed in air nearby. Then the quantum efficiency Δ F/Fm' in sunlight was recorded. The exposition of the algae to direct sunlight in air caused a drastic decrease of the fluorescence ratio, mainly due to a very strong energy-dependent quenching q_E. In order to obtain resolvable Δ F/Fm' values the algal sample was exposed in a position averted from the sun in this way reducing the irradiance impinging on the alga to 10 - 20% of direct sunlight. Subsequently, the alga was transferred into a self constructed seawater cuvette. After application of a 30 s far red pulse ($\approx$ 30 µmol m^{-2} s^{-1}), used to oxidize the electron transport chain, the alga was darkened for 10 min. Fo was measured with a pulsed, red measuring light ($\approx$ 0.3 µmol $m^{-2}s^{-1}$, 650 nm) and Fm was determined with a 600 ms completely saturating white light pulse ($\approx$ 4500 µmol $m^{-2}s^{-1}$). In addition, the quantum efficiency Δ F/Fm' of a red, non-saturating fluence rate (10 µmol $m^{-2}s^{-1}$, 655 nm) was measured following the Fv/Fm measurement to determine the effect of photoinhibition on the efficiency of photosynthesis.

Oxygen production rate of a thallus disc, cut out of the phylloid, was measured with a temperature-compensated Clark electrode (Oxi 92, WTW, Germany) under natural light and temperature conditions. The measuring device is described in detail by Huppertz *et al.* (1990) and Hanel (1992). However, it was modified by replacing the glass window of the cuvette by a quartz glass transmitting also UV. In contrast to the fluorescence measurements only one piece of a thallus disc was transferred into the oxygen cuvette and exposed to daylight in the surf zone the whole time. Photosynthetic capacity was determined with the completely saturating fluence rate of daylight. The measure photosynthetic efficiency in the non-saturating region of photosinthetic the algae were irradiated with 60 µmol m^{-2} s^{-1} light of 650 nm produced by a light emitting diode (LED). This LED mounted in a cap was put on the top of the cuvette only temporarily for a

few minutes every hour. Oxygen production rate is expressed in percent of the production rate measured in the non-photoinhibited control. All experiments were done in filtered, natural seawater.

Irradiance was recorded in air continuously with a LI-COR data-logger (LI-1000, LI-COR, Lincoln, NB, USA) equipped with a flat head sensor (LI-190 SA). Underwater light measurements were made with an underwater spherical quantum sensor (LI 193 SA) and compared to the light intensity above the surface measured with a flat head sensor. A continuous underwater recording was not possible because at rising tide the surf was too strong and, in addition, the sensor could not securely fastened on the ground.

The graphics show only a selection of typical time courses of photosynthesis, because it is not possible to standardize field experiments due to the diversity of the daily course of sunlight and different points of time of low high tide.

UV-A and UV-B radiation was measured with an International Light radiometer (IL 1440A) equipped with an UV-A detector (SL021, spectral range 325 to 338 nm) and an UV-B detector (SEL240, spectral range 245 to 320 nm).

RESULTS

The water body near the coast of King George Island was very clear in comparison to standard coastal water. In the Fildes bay at a depth of 10 m a light transmittance of about 25% (spectral range of 400 - 700 nm, Fig. 1) and even of about 35% on another day was measured. This water can be classified as a Jerlov (1951) oceanic type II, though the measurements were carried out near the coast. On the contrary, light transmittance at the end of the surf zone in the Sea-Elephant Bay (about 3 m from the coast) was very low, because pieces of disintegrated algae and other drift material decreased the water transmittance.

Fig. 2 shows a daily course of photosynthesis of the brown alga *Adenocystis utricularis*. The weather conditions were very good so that high photon fluence rates (PFR) of sunlight occurred. Clouding decreased the fluence rate only ocasionally for a short time. In the morning the fluorescence ratios Fv/Fm and Δ F/Fm' were high showing full photosynthetic activity of non-inhibited thalli. A reduction of the Fv/Fm ratio indicates the occurrence of photoinhibition. The Δ F/Fm' value is a measure for the quantum yield or phothosynthetic efficiency in this case determined with a fluence rate of 10 μmol m^{-2} s^{-1} of a red 655 nm actinic light after the Fv/Fm measurement. Decreasing Δ F/Fm' values indicate a decreasing quantum yield of photosynthesis. With increasing PFR both fluorescences ratios decreased. The decline between 11:15 and 13:30 became slower as the dirt at the end of the surf zone decreased the irradiance under water transiently. Minimal ratios were observed between 13:20 and 14:50 that photosynthesis of the uncovered thalli was strongly photoinhibited. With rising tide photosynthesis of the submerged thalli recovered very fast in less than 2 h, so that it had fully recovered in the early evening and/or in thalli living at a depth of more than 0.5 m. The Δ F/Fm' curve was only slightly different from Fv/Fm curve which shows that the decrease in the quantum efficiency (Δ F/Fm') if a non-saturating fluence rate was mainly caused by photoinhibition of photosynthesis (indicated by Fv/Fm).

Simultaneously the oxigen production of an *A. utricularis* thallus was measured. A piece of the thallus was monted on the electrode and then exposed perpendicularly to the sun beam at 10:00. Photosynthetic capacity measured with the saturating sunlight decreased during the first hour of the measurement (Fig.3). Subsequently, photosynthesis recovered and the capacity increased and reached its maximum already in the early afternoon. However, after the thallus was collected under water at 10:00 it was exposed to full sunlight near the water surface. This caused strong photoinhibition which can be shown much better by the low photosynthetic efficiency measured with the red non-saturating light. After the alga was transferred into the cuvette the efficiency increased continuously because photosynthesis recovered. In the evening this red light saturates also the fully recovered photosynthesis and caused the same oxygen production rate as it was caused by sunlight. Thus, even the oxygen measurements showed that in the algal sample photoinhibited in the morning photosynthesis recovered due to decreasing PFR's, specially in the afternoon.

Fig. 4 shows the results of fluorescence measurements with the red alga *Palmaria decipiens*. Again, photosynthesis of thalli under water was not photoinhibited around 10:00. A litte later, however, a strong decrease in the photosynthetic activity was observed. Thus, photoinhibition occurred already 2 hours before the water column covering the alga decreased to 1 cm as a result of falling tide (marked by the first arrow).

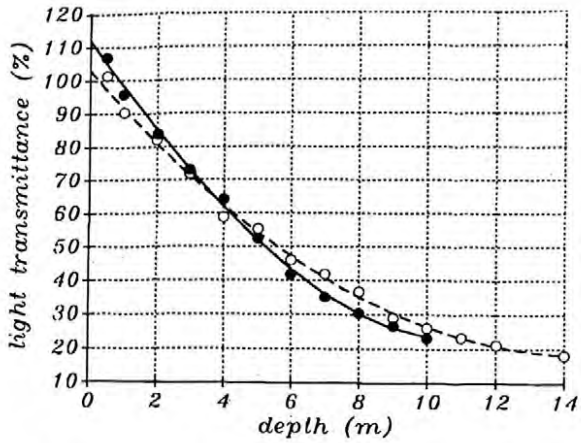

Fig. 1. Light transmittance of the water body in the Fildes bay at 14:00, 17 February 1993. Measurements near Presidente Eduardo Frei station (•) and near the Uruguayan station (o).

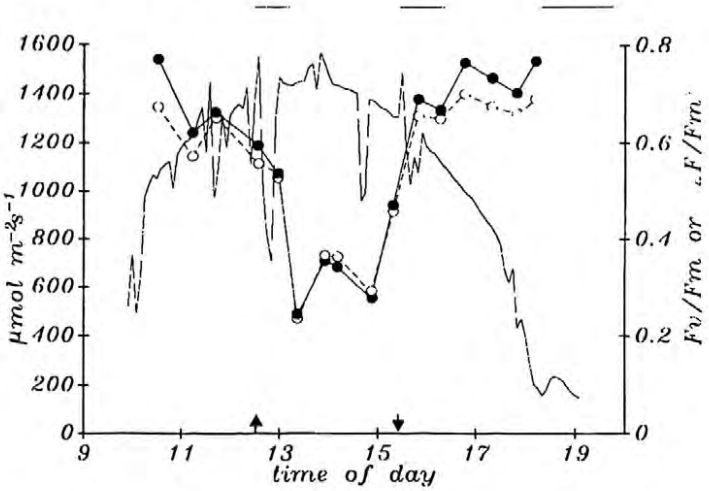

Fig. 2. *Adenocystis utricularis*. Daily course of Fv/Fm (• - •) of thalli adapted to strong sunlight. Δ F/Fm' (o — o), the quantum efficiency of a sunlight adapted plant measured with a red control light (10 µmol m^{-2} s^{-1}, 655 nm). The thin line shows the photon fluence rate µmol m^{-2} s^{-1}) measured in air. The first arrow (↑) shows the moment when the algae were uncovered by falling tide and the second arrow (↓) when they are covered again by rising tide.

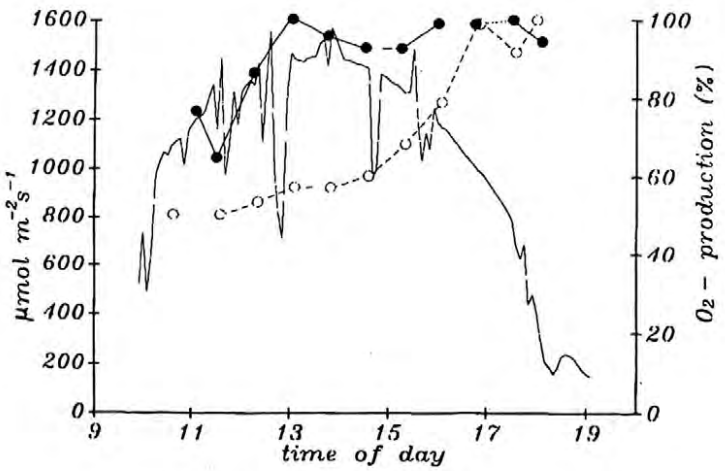

Fig.3. *Adenocystis utricularis*. Daily course of oxygen production of a thallus disc *in situ* exposed to daylight near the water surface on a sunny day. Photosynthetic capacity (• – •) measured with saturating sunlight, photynthetic efficiency of the same thallus (o - o) measured with 60 µmol m^{-2} s^{-1} of 650 nm control light for a few minutes. The thin line shows the photon fluence rate (µmol m^{-2} s^{-1}) measured in air.

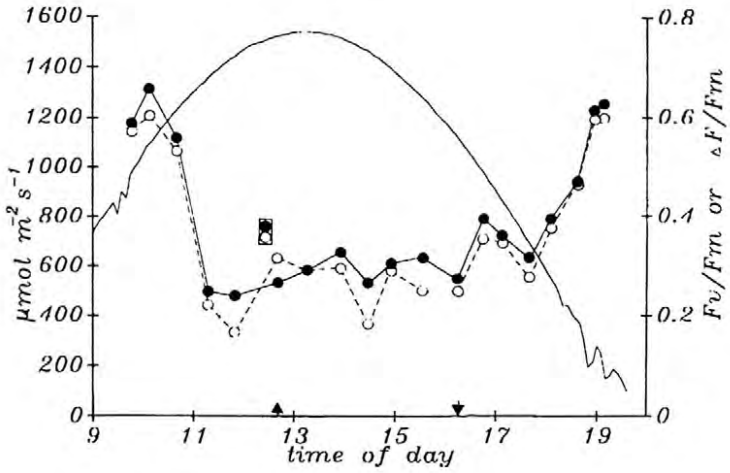

Fig.4. *Palmaria decipiens*. Experimental details as in Fig. 2. The circles surrounded by a square show the fluorescence values of a thallus which was shadowed by a group of larger thalli.

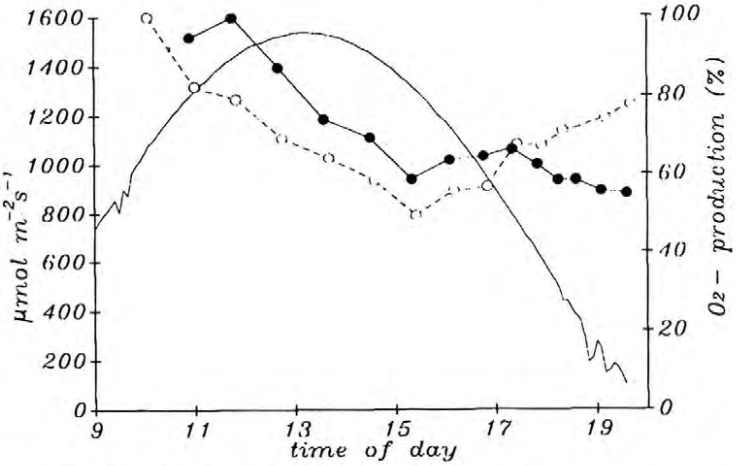

Fig. 5. *Palmaria decipiens*. Experimental details as in Fig. 3. After 17:50 the curve of the photosynthetic capacity (• - •) decreased again because sunlight was not longer sufficient to saturate photosynthesis.

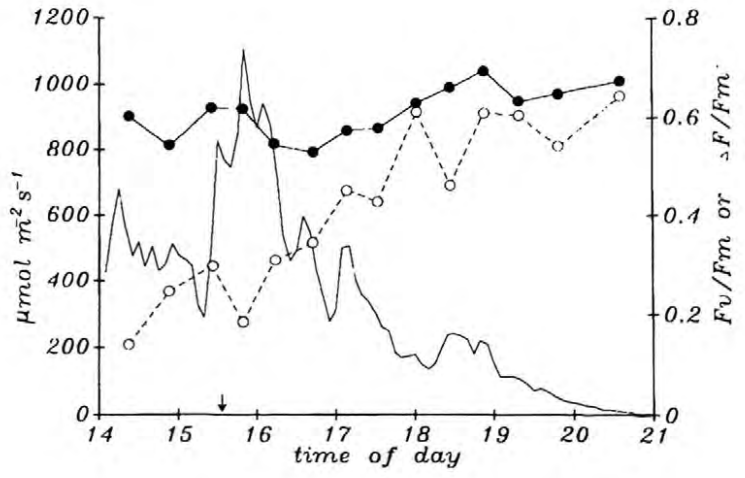

Fig. 6. *Palmaria decipiens*. Daily course of Fv/Fm (• - •) and Δ F/Fm' (o – o) of thalli irradiated with daylight on a cloudy day. The thin line shows the photon fluence rate (µmol m^{-2} s^{-1}) measured in air. The arrow on the abacissa marks the moment of low tide.

Then photosynthesis remained on a low level for about 6h 30 min, though the algae were always covered by a water column of about 1 cm. During this long period of inhibition the fluorescence ratios showed a slight increase.

However, significant recovery commenced very late in the evening and after an increasing water column covered the algae again (second arrow). The values measured at 12:28 (the circles surrounded by a square, Fig. 4) show the fluorescence ratios of a thallus which was shadowed by larger algal thalli. Both ratios are higher than those of thalli exposed to direct sunlight, because the shadowed algae are less photoinhibited than the irradiated ones.

Oxigen production of *P. decipiens* is shown in Fig. 5. Photosynthetic capacity measured with saturating sunlight decreased at high fluence rates until 15:20 the minimum was reached. Then the capacity increased because photosynthesis recovered during decreasing PFR. At 17:50 the capacity decreased again, because the PFR of the sunlight impinging at an acute angle on the alga in the evening was not sufficient to saturate photosynthesis. Nevertheless, the continuous of the photosynthetic efficiency after 15:20 measured with the non-saturating PFR (60 µmol m^{-2} s^{-1}. 650 nm) shows that photosynthesis recovered steadily.

On a cloudy day the PFR was low and, hence, photosynthesis of *P. decipiens* was only slightly photoinhibited (Fig. 6), especially after the transient increase of PFR in the early afternoon during low tide (low tide marked by an arrow). In this experiment Δ F/Fm' was measured with indirect sunlight. In the beginning Δ F/Fm' was low in the early afternoon, but increased later. At 20:36 the quantum yield had also fully recovered. Δ F/Fm' was much lower than Fv/Fm the early afternoon because the photosynthetic efficiency was lowered due to the energy-dependent quenching mechanism (q_E) which is caused by a high Δ pH over the thylakoid membranes. This mechanism is defined as an intrinsic regulatory mechanism of photosynthesis.

A comparison between covered and uncovered thalli of *P. decipiens* is shown in Fig. 7. The submerged thalli which were collected directly under the water surface showed a decrease of Fv/Fm at the high PFR during the course of the day. The fast decline of the PFR in the afternoon caused a fast recovery of photosynthesis in this case. Thalli uncovered during falling tide became desiccated with time. This may be the reason for the delayed decrease of Fv/Fm and slightly lower Fv/Fm values. Moreover, also recovery was delayed. In *A. utricularis,* no difference between uncovered and covered thalli were observed (data not shown). This may be due to the special morphology of its thallus which is like a little water filled bag.

In addition, the differences in the photoinhibitory pattern between the brown *A. utricularis* and the red *P. decipiens* were compared also under controlled laboratory conditions (Fig. 8a, b). A higher photoinhibitory fluence rate caused a higher degree of photoinhibition on both algae. However, the brown alga was much faster and to a higher degree inhibited than the red alga *P. decipiens*. In dim light photosynthesis of both algae recovered. Again the recovery of the brown alga was much faster than that of the red alga. Thus, the brown alga *A. utricularis* acclimate to changes in the light environment much faster and to a higher extent than the red *P. decipiens.*

DISCUSSION

Photoinhibition depends on temperature (Ludlow, 1987; Öquist *et al.*, 1987). The repair cycle of PS II is inhibited by low temperatures (5°C), whereas the first step of photoinhibition, determined by the reduction state of the primary electron acceptor Q_A, is temperature independent (Ottander *et al.*, 1993). However, acclimations in response to short-term stress conditions are different from adaptations to long-term environmental conditions. Thus, a short stress of high temperature and high fluence rate acted together in *Ulva rotundata* in decreasing photosynthetic efficiency and capacity (Henley *et al.*, 1992). However, in the surf zone of the Sea-Elephant Bay the water temperature in February changed only between 1.8°C during bad weather and maximally 8.4°C on a sunny, calm day. Air temperature was generaly below the water temperature so that emerged algae were cooled by the wind and the thalli did not heat up significantly. Thus, temperature stress in the day time did not occur. Nevertheless, the daily courses of photoinhibition show clearly how fast *Adenocystis utricularis* reacts in response to the changing light conditions, and low temperature do not decrease its rate. On the contrary, the kinetics of photoinhibition and recovery were much faster than those observed in the tropic algae (Hanlet, 1992; Hanlet *et al.*, 1994). Apparently, this antarctic alga is well adapted to the low temperature environment.

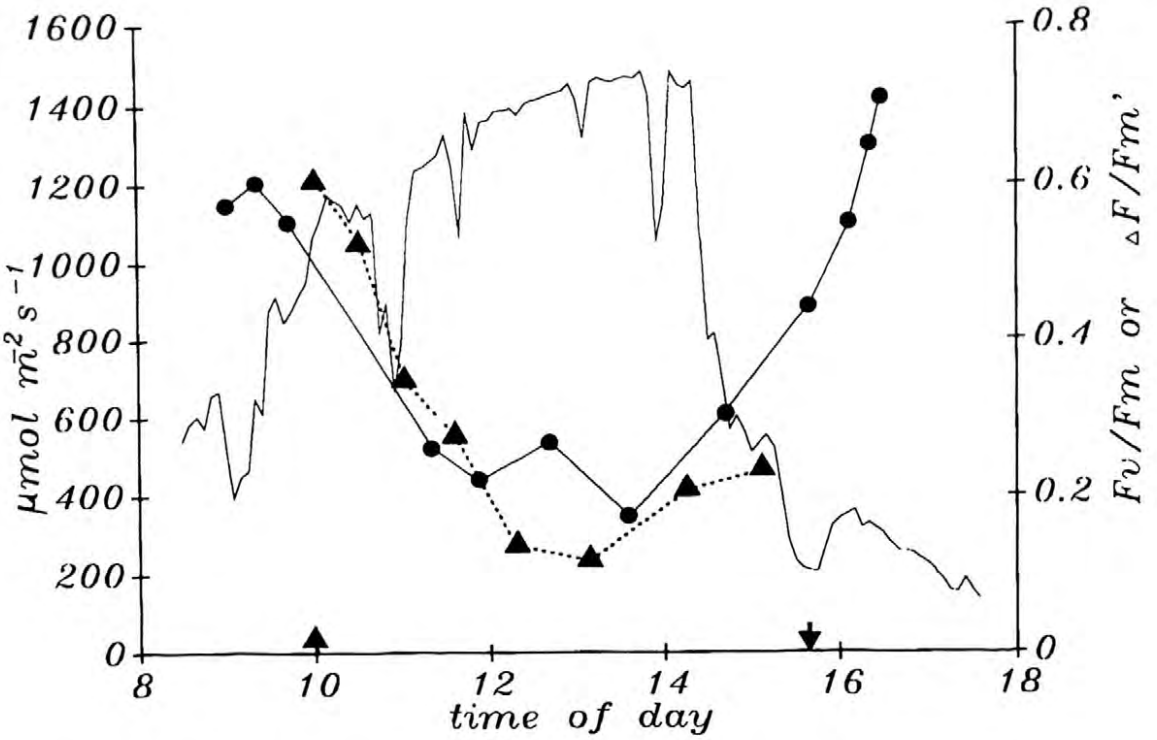

Fig.7. *Palmaria decipiens*. Fv/Fm of thalli below the water surface (• - •) and of those which were uncovered and, hence, were exposed to an additional desiccation stress (.. Δ ..). The thin line shows the photon fluence rate (µmol m^{-2} s^{-1}) measured in air, in the afternoon became cloudy. The first arrow (↓) shows the moment when the algae are uncovered by falling tide and the second arrow (↑) when they are covered again by rising tide.

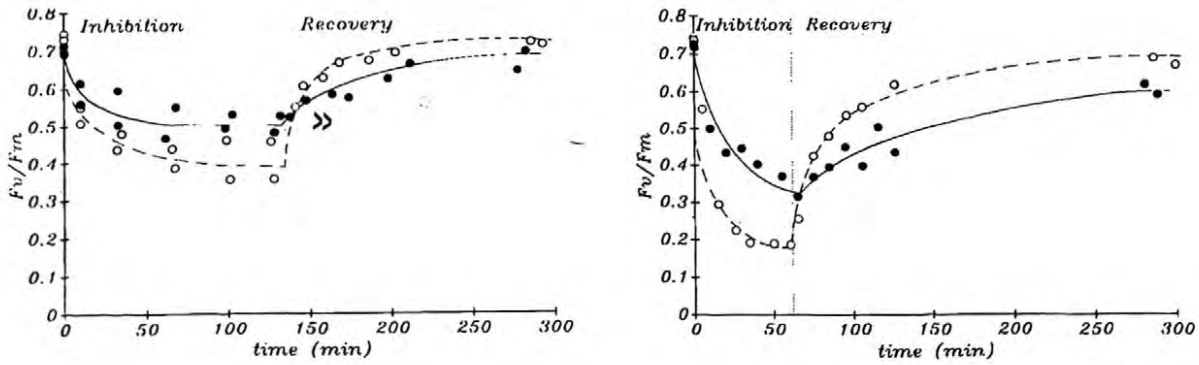

Fig.8. Fv/Fm of each two different thalli of *Palmaria decipiens* (• - •) and *Adenocystis utricularis* (o - o). A) Photosynthesis was inhibited for 2 h with 300 µmol $m^{-2}s^{-1}$ white light so that photosynthesis could recover. B) Photoinhibition cuased by 1000 µmol $m^{-2}s^{-1}$ for 1 h and recovery in 2 µmol $m^{-2}s^{-1}$ white light for 4 h. The dotted vertical line marks the change from the inhibitory to the recovery period.

There are two possibilities to explain this finding: either the enzymes of the PS II repair cycle are adapted to the low temperature, or the turnover of the D_1-protein does not play a significant role in both photoinhibition and recovery of photosynthesis in antarctic algae. Schnettger *et al.* (1992) and Huner *et al.* (1993) have discussed that the fast mechanism of recovery may be independent of the «slow repair» via D_1 turnover. *A. utricularis* supports this hypothesis because it reacts initially with a fast inhibition or recovery phase when it was exposed to strong and dim light conditions, respectively. After strong photoinhibition the kinetics of recovery were in the first hour very fast, but later they slowed down until photosynthesis was fully recovered.

The photoinhibition kinetics of the subtidal red alga *P. decipiens* were slower and the degree of photoinhibition and recovery were lower than in the intertidal brown alga *A. utricularis*. Moreover, three sunny days in connection with low tide around noon time were sufficient to bleach the *P. decipiens* thalli in the middle and lower intertidal zone whereas no changes in *A. utricularis* thalli were observed. If the capacity for photoinhibition in marine algae is a mechanism to acclimate the photosynthetic apparatus to changing light conditions, these results give further evidence that a relation between photoinhibitory sensitivity and the algal zonation in the littoral exists, as demonstrated earlier (Hanelt, 1992; Hanelt *et al.*, 1993; Hanelt *et al.*, 1994) In this connection, it should be mentioned that a circannual rhythm in the photosynthetic performance of *P decipiens* may exist (Weykan and Wiencke, 1992) so that this alga did not show its maximal photosynthetic capacity in February.

Huppertz *et al.* (1990) demonstrated that the photoinhibitory degree of phototosynthesis in *Fucus serratus* was conserved by desiccation. Moreover, Dring and Brown (1982) reported that desiccation decreases photosynthesis. In our experiment, desiccated *P. decipiens* thalli show only slight changes in the photoinhibitory degree. *A. utricularis* does not desiccate because it is moistened by the water inside the cavity of its tubular thallus.

Low light adapted higher plants respond to light stress with significant photoinhibition, whereas strong light adapted plants are not as sensitive to light stress (Demming-Adams and Adams III, 1992). Wiencke *et al.* (1993) demonstrated that antarctic algae are also dim light adapted plants. Acordingly, they react with significant photoinhibition to light stress, as shown in these studies. Nevertheless, the investigated algae are able to cope with light stress and to optimize photosynthesis under strong light conditions. Thus, in an ecological context they can acclimate to strong light in a short time.

In February on a sunny day a maximal UV-A fluence rate of 22.5 W m^{-2} and a maximal UV-B fluence rate of 2.57 W m^{-2} was measured in air around noon. Harmful doses of UV-B may reach a depth of 10 m in clear ocean waters, and algae living in strong-light habitats develop protective mechanisms (secreening compounds) against UV-B inhibition (Larkum and Wood, 1993). In addition, these authors showed that only a 1/10 of the UV-B fluence rate which was measured on King George Island decreases photosynthesis and Fv in several algae. Thus, an influence of the natural UV-radiation on the algae investigated in these studies cannot be excluded. However, the fluence rates of the antarctic UV-radiation are not unusually high because in the temperate zone of Helgoland, an island in the SE North Sea, the same rates are reached in Spring.

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