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Photosynthetic Responses of Mastigophora diclados (Brid. ex Web.) Nees Ecotypes to Excess Light in Consequence of their Microhabitats in Reunion Island: a Fluorescence Induction Study

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Abstract. Three hours of high light treatment caused a 50% or 20% decrease in F_v/F_p in the shade and sun types of *Mastigophora diclados*, respectively. In the case of the shade type moss, the decrease in F_v/F_p was due to a decrease in F_v and an increase in the F_0 parameter indicating a pronounced inactivation of functional PS II reaction centres. This was associated with an increase in the F_i parameter. However, in the sun-type moss the F_0 parameter decreased and the F_i remained constant, suggesting that the non-radiative dissipation of excitation energy in the antenna pigment beds may play a more important role in the sun-type moss. This was associated with a higher R_{fd} parameter. At low light intensity the F_v/F_p of the sun type moss recovered completely after 1 h, while the recovery of the shade-type moss was partial (70%) even after 3 h.

Keywords: chlorophyll fluorescence, photosynthesis, photoinhibition, insular environment, light acclimation, Mastigophora diclados

Abbreviations used

Chl: chlorophyll; F_v/F_p: optimal quantum yield of photosystem II; F_v: variable fluorescence; F_0: initial level of fluorescence; F_i: intermediate level of fluorescence; F_p: plateau level of fluorescence; F_s: steady-state level

of fluorescence; LHC II: light-harvesting chorophyll a/b protein complex; PS II: photosystem II; RCs: reaction centres; R_F: maximal rise in induced fluorescence; R_{fd}: fluorescence decrease ratio.

Introduction

Islands in the Pacific and Indian Ocean situated above "hot spots" have become special sites of plant evolution due to their distance from the continents. Some 80–90% of the flora on these islands consists of indigenous plants to be found nowhere else on Earth, whose conservation is of international importance for maintaining the diversity of the biosphere. In these high-rainfall areas soil erosion is very intensive. Under these circumstances, the moss flora of "moss forests" has a very significant ecological role. By storing and passing on great quantities of suddenly falling precipitation they protect the soil underneath from its erosive influence, thereby ensuring the maintenance of the conditions necessary for the settling of rare plant species. As a result of tropical windstorms or, not infrequently, human intervention, the closed tree stratum of these rain forests open up, changing the light conditions of the area. In such cases, the high light stress reactions of species in the various moss associations takes on ecological significance.

The ability of plants to adapt to the light conditions of their environment enables them to colonise different habitats, ranging from the arid, strongly lit deserts to the shady ground level of the tropical rain forests. It is well documented that the chloroplasts of shade plants living on the ground level of forests have a modified structure compared with that of sun plants. The grana of the larger shade-type chloroplasts have more thylakoid membranes, than the smaller sun-type chloroplasts (Lichtenthaler, 1981; Melis and Harvey, 1981). In addition, the quantity of light-harvesting chlorophyll a/b protein complex (LHC II) is also greater in the shade-type chloroplasts, compared to the PS II core, which is in accordance with the ratio of stacked/unstacked regions and with the greater chlorophyll a/b ratio (Simpson, 1981; Anderson et al. 1973). There is also a significant difference in the quantity of electron transport chain components. In the chloroplasts of shade plants there is less cytochrome b-559, cytochrome b-563, cytochrome f and plastoquinone relative to the quantity of chlorophyll (Boardman et al. 1972). These structural differences are also revealed in the functional differences of the thylakoid membrane: in shade plants, the PS II and PS I activity measured at saturation light intensity is lower, as is the photophosphorylation, which becomes saturated at very low light intensity. The CO_2 fixation me-

asured at saturation light intensity also changes parallel with the functions of the electron transport chain (Boardman et al. 1972).

Under natural circumstances the light intensity is often significantly greater than is required for plant growth and the light energy absorbed by the leaves is more than the photosynthetic electron transport chain can utilise. Under these circumstances the long-lived triplet chlorophyll may generate reactive singlet oxygen, which may, among other things, cause irreversible damage to the D_1 protein (Aro et al. 1993). This may be reflected in a reduction in the quantum yield of CO_2 fixation and O_2 evolution (Powles, 1984). To avoid photooxidative damage these plants have developed several protective mechanisms, including the process known as the repair cycle of PS II (Aro et al. 1993). The protective role of zeaxanthin is also well documented (Demmig–Adams, 1990; Demmig–Adams and Adams, 1992), as is that of State I–State II transitions (Horton, 1989). At the level of water-soluble enzymes, various anti-oxidant enzyme systems may be of importance (Asada and Takahashi, 1987). In several cases, when the measure of light damage overtakes the efficiency of protective processes, photoinhibition causes a decrease in plant growth (Ögren, 1988; Ögren and Evans, 1992). The sensitivity of plants to photoinhibition at a given light intensity level greatly depends on genetic adaptation, the actual physiological conditions, and sun-shade acclimation. In addition, photoinhibition, as a physiological symptom, is also greatly dependent on other environmental factors. Photoinhibition is stronger when high light intensity is combined with other stress factors such as low or high temperature, lack of CO_2, or UV-b stress.

This paper investigates the reactions to intensive light stress of the shade and sun type species of *Mastigophora diclados*, a moss species which occurs in habitats with significantly different light conditions in Reunion Island part of the Mascarine Archipelago.

Materials and Methods

Plant Materials

The photosynthetic responses to excess light of the sun and shade types of *Mastigophora diclados* (Brid. ex Web) Nees were studied in a mountainous tropical rain forest. The sun and shade types of *M. diclados* to be investigated were selected from an *Acacia heterophylla*-dominated rain forest on the Belouve plateau (1400 m above sea level) on the island of Reunion. The sun and shade types of this moss species were collected from habitats subjected to high (800–1500 $\mu mol\,m^{-2}\,s^{-1}$ PPFD) and low (100–200 $\mu mol\,m^{-2}\,s^{-1}$ PPFD) light conditions 24 hours before the measurements. The light treat-

ments and measurements were carried out on the upper photosynthetically active parts of the samples.

Light Treatment

The photoinhibition of photosynthesis in the moss types was induced by a 1200 μmol m^{-2} s^{-1} photosynthetic photon flux density (PPFD) of white light (Schott KL-1500, Germany) for three hours. During recovery the samples were transferred to low light conditions (40 μmol m^{-2} s^{-1}). The chlorophyll a fluorescence induction parameters were determined every hourly at 20 °C after a short (5 min) dark adaptation in the 90–100% water state.

Determination of Chlorophyll Fluorescence Parameters

The in vivo chlorophyll fluorescence measurements on intact moss segments were carried out with a computerised portable chlorophyll fluorometer after a 30-min (control samples) or 5-min (light treated samples) dark adaptation. The fluorescence was excited by a light-emitting diode (Stanley KR5004X) of 200 μmol m^{-2} s^{-1} PPFD and detected by a BPX-60 (Siemens) photodiode. The fast and slow fluorescence induction was excited for 1200 ms and for 5 min respectively.

Results

Fluorescence induction parameters of the control shade- and sun-type mosses

Kautsky and Hirsch (1931) observed changes in the time dependence of the fluorescence of chlorophyll a (*Chl* a) when the dark-adapted photosynthesising sample was exposed to light. Since then, the investigation of *Chl* a fluorescence transients (Kautsky effect or fluorescence induction) has been used as a sensitive, non-destructive tool for studying the different processes of photosynthesis (Papageorgiou, 1975). Fluorescence induction may be divided into two parts: (i) a fast initial stage from F_0 to F_p, characterised by an increase in the intensity of fluorescence, followed by (ii) a slow decrease in the intensity of fluorescence to the steady-state fluorescence level (F_s). This increase in fluorescence in the fast stage can be attributed to changes in the first stable electron acceptor (Q_A) of PS II in the redox state, thus the parameters of the fast stage provide a good insight into the electron transport processes of PS II. On the basis of the data in Table 1 it can generally be said that under stress-free conditions there is only a very slight (though significant) difference between the parameters of the shade-type and sun-type *M. diclados* plants. This indicates that acclimation to different light conditions is also revealed in the functional modification of PS II.

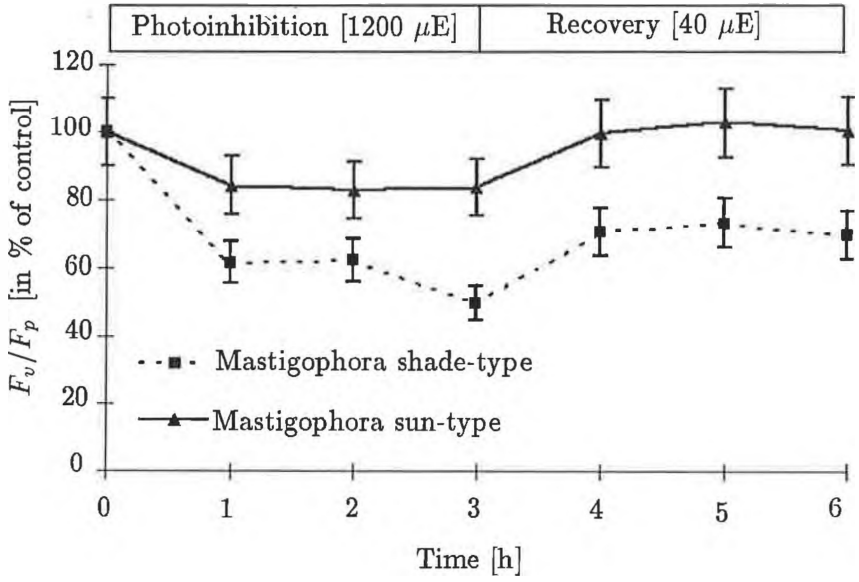

Fig. 1 Optimal quantum yield (F_v/F_p) of PS II during photoinhibition (at 1200 μmol^{-2} s^{-1}) and recovery (at 40 μmol^{-2} s^{-1}). Fluorescence was excited with 200 μE m^{-2} s^{-1} light intensity and the samples were dark-adapted (5 min) before the measurement.

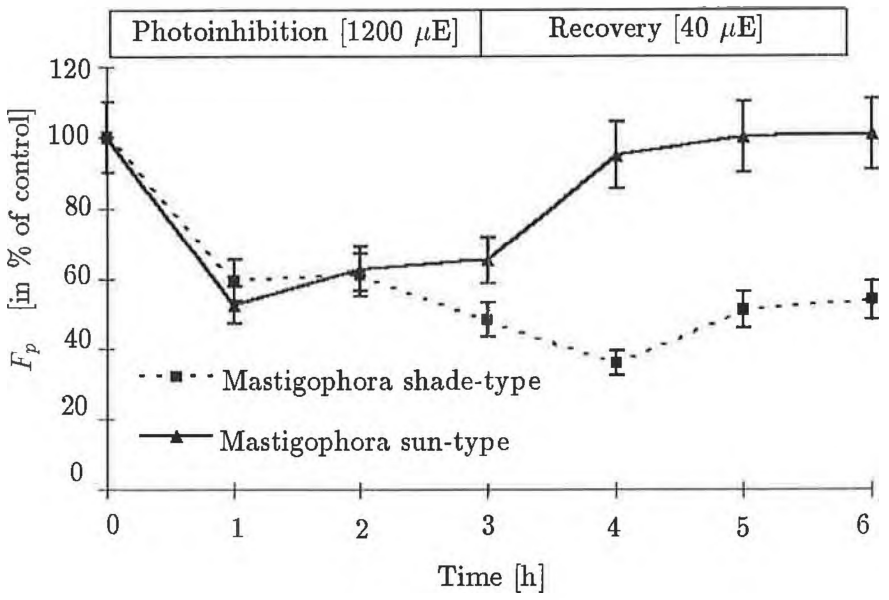

Fig. 2 Changes in maximal fluorescence level (F_p) at a measuring light intensity of 200 $\mu mol^{-2}\,s^{-1}$, during photoinhibition (at 1200 $\mu mol^{-2}\,s^{-1}$) and recovery (at 40 $\mu E\,m^{-2}\,s^{-1}$). Fluorescence was excited with 200 $\mu mol^{-2}\,s^{-1}$ light intensity and the samples were dark-adapted (5 min) before measurement.

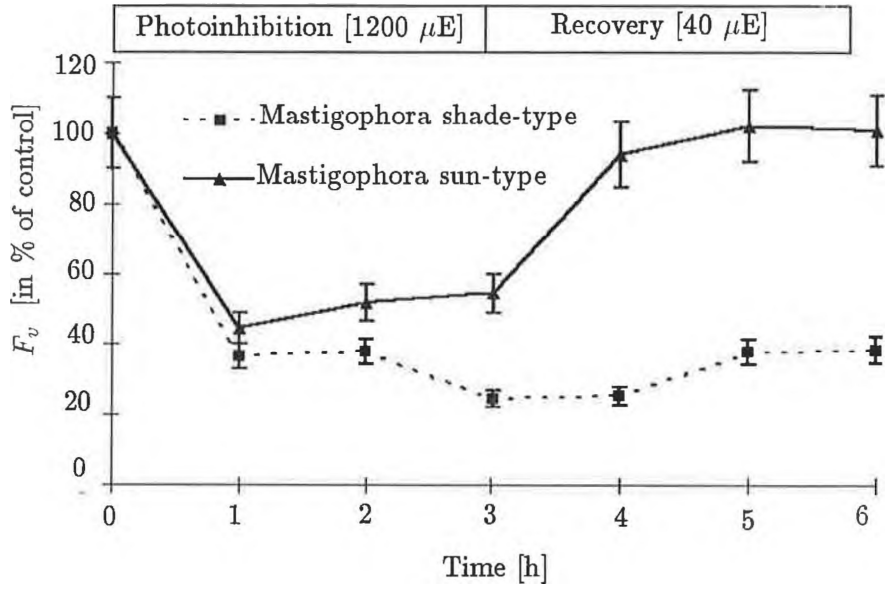

Fig. 3 Changes in variable fluorescence (F_v) during photoinhibition (at 1200 μmol^{-2} s^{-1}) and recovery (at 40 μE m^{-2} s^{-1}). Fluorescence was excited with 200 μE m^{-2} s^{-1} light intensity and the samples were dark-adapted (5 min) before measurement.

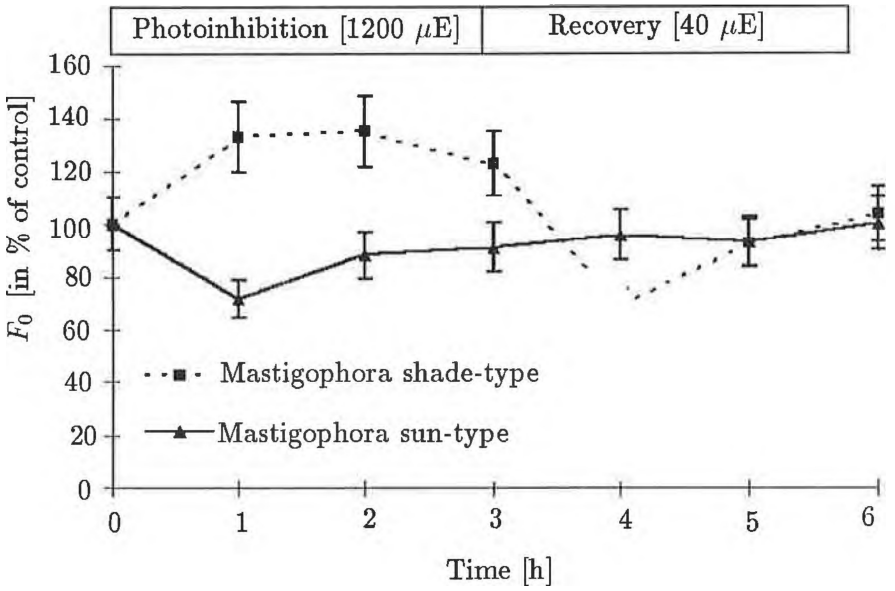

Fig. 4 Changes in initial fluorescence level (Fo) during photoinhibition (at 1200 $\mu E\,m^{-2}\,s^{-1}$) and recovery (at 40 $\mu mol^{-2}\,s^{-1}$). Fluorescence was excited with 200 $\mu mol^{-2}\,s^{-1}$ light intensity and the samples were dark-adapted (5 min) before measurement.

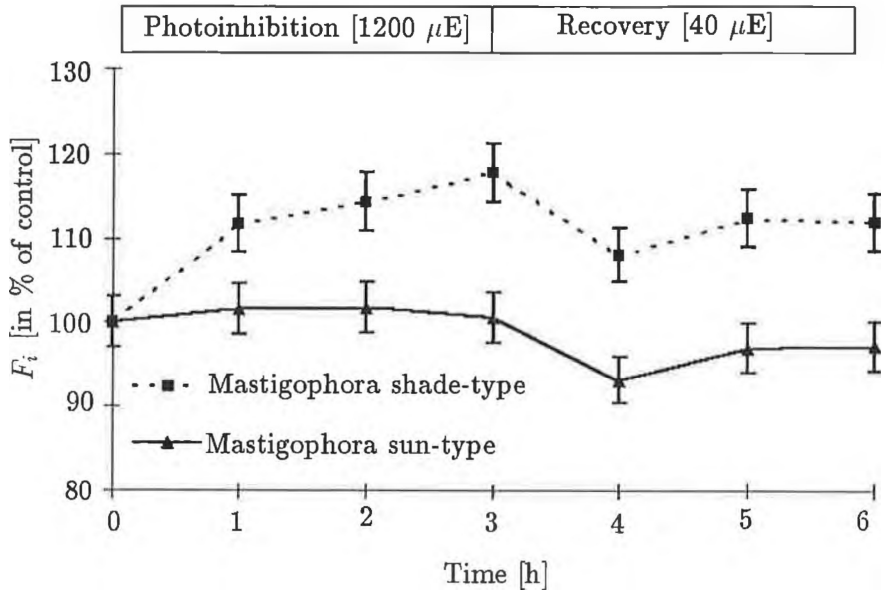

Fig. 5 Changes in intermediate fluorescence level (F_i) during photoinhibition (at 1200 μmol^{-2} s^{-1}) and recovery (at 40 μE m^{-2} s^{-1}). Fluorescence was excited with 200 μE m^{-2} s^{-1} light intensity and the samples were dark-adapted (5 min) before measurement.

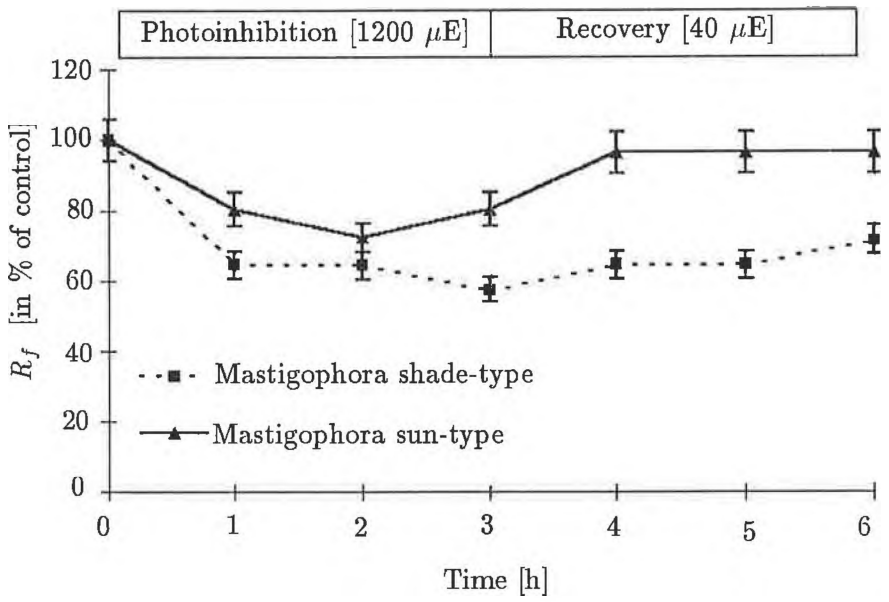

Fig. 6 Changes in the maximum rate of fluorescence rise $[(dF_v/dt)_{max} = R_f]$ during photoinhibition (at 1200 μmol^{-2} s^{-1}) and recovery (at 40 μE m^{-2} s^{-1}). Fluorescence was excited with 200 μE m^{-2} s^{-1} light intensity and the samples were dark-adapted (5 min) before measurement.

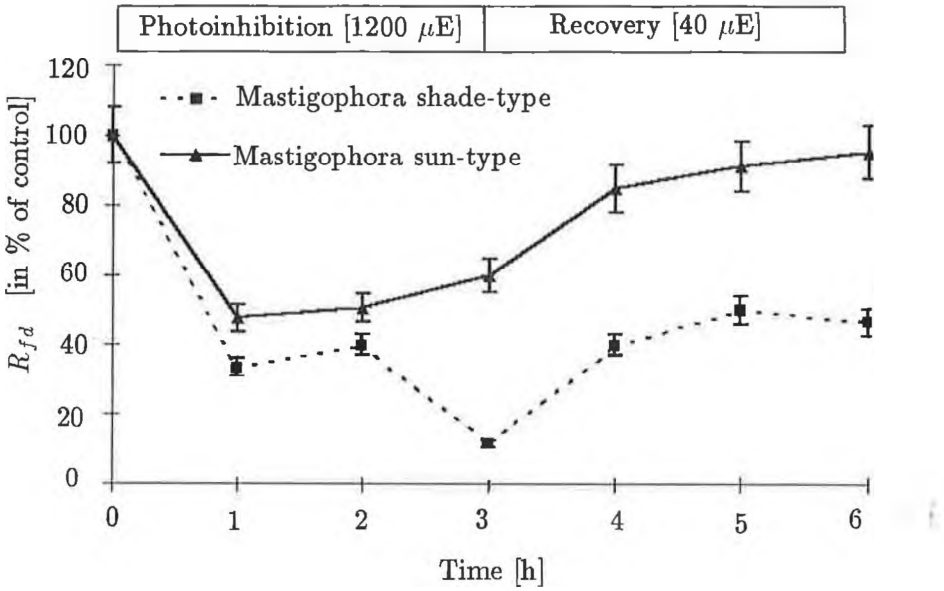

Fig. 7 Changes in the fluorescence decrease ratio (R_{fd}) during photoinhibition (at 1200 μmol^{-2} s^{-1}) and recovery (at 40 μmol^{-2} s^{-1}). Fluorescence was excited with 200 μmol^{-2} s^{-1} light intensity and the samples were dark-adapted (5 min) before measuring.

The F_v/F_p parameter, indicative of the optimal quantum efficiency of PS II, is significantly higher in the shade-type Mastigophora. This difference is even more striking for the $F_v(F_p - F_0)$ parameter and to a lesser degree for the F_0 parameter. Between the initial fluorescence level (F_0) and the maximum or plateau level (F_p) there is an intermediate level (F_i). This parameter is linked to the heterogeneity of PS II and the activity of the electron transport between Q_A and Q_B. In the present case the F_i expressed as a percentage of F_p is high in both plants, being higher in the sun-type than in the shade-type moss. Nevertheless, this difference in F_i is not significant. The maximal steepness of the increase in fluorescence intensity from F_i to F_p is indicated by the parameter R_f [$R_f = (dF_v/dt)_{\max}$]. This steepness is related to the capacity of PS II to reduce the PQ pool. At the low light intensity (200 μmol^{-2} s^{-1}) used for exciting fluorescence and photosynthesis, this parameter is also about 12% higher in the shade-type mosses.

For plant samples photosynthesising in a steady-state situation, the ratio of fluorescence decrease [$R_{fd} = (F_p - F_s)/F_s$] at a given light intensity signals the ratio of the quenched and non-quenched portions of fluorescence and correlates well with the potential photosynthetic capacity of the plant (Strasser et al. 1987). As can be seen in Table 1, under the present circumstances there was no significant difference between the shade- and sun-type mosses.

Ffluorescence induction parameters of shade- and sun-type mosses during photoinhibition and recovery

When plants are exposed to light intensity much higher than their growth conditions, the inhibition of photosynthesis can be observed. *Chl* a fluorescence has proved to be a suitable tool for detecting damage to the photosynthetic apparatus, including PS II (for review, see: Powles, 1984; Krause, 1988). As can be seen in Fig.1, the 1200 μmol^{-2} s^{-1} light intensity caused an approx. 40% decrease in the optimal quantum efficiency of PS II (F_v/F_p) after one hour in the shade-type *M. diclados*, decreasing further to 50% in the third hour of photoinhibition. In the sun-type *M. diclados* this decrease amounted to about 20% and this value did not change after a further 2 hours of light treatment. It can be seen in Fig. 2 that the maximal fluorescence level (F_p) induced by the given light intensity (200 μmol^{-2} s^{-1}), exhibited a decrease of about 40% after one hour in both types, compared to the non-photoinhibited control. In the shade-type mosses a further 10% decrease could be observed, while the sun-type mosses showed a slow, non-significant increase. A significant difference could not be observed between the two groups until the end of the third hour. After the 3-hour light treatment the decrease in variable fluorescence (F_v) revealed kinetics similar to the changes in the F_p level. Nevertheless, the decrease in F_v after 1-hour was

more pronounced, (about 60%) in both types, later reaching 70–80% in the shade-type, while in the sun-type a slow increase occurred. As a result, by the end of the third hour the parameter linked with the electron transport processes of PS II showed an inhibition of about 80% in the shade-type mosses and only 50% inhibition in the sun-type. The initial fluorescence level (F_0) stems from the light-harvesting antenna pigments and is not connected to the electron transport processes of PS II. Its value is proportionate to the quantity of antenna pigments and at a given concentration its increase may signal the loss of functional connection between the PS II core and the LHCs. During photoinhibition, the F_0 level shifts in opposite directions in the shade-type and sun-type plants (Fig.3). The F_0 level of the shade-type *M. diclados* increased by 30% in the first hour and this value hardly changed during continued photoinhibition. The F_0 level of the sun-type *M. diclados*, however, decreased by 30%, which also revealed only a slight further decrease in the following two hours. During the recovery period the F_v/F_p parameter of sun-type mosses shifted back to the level of the control by the end of the first hour, which was also true of the F_p and F_v parameters. The situation was quite different for the shade type. The optimal quantum efficiency of PS II, which had suffered 50% inhibition, reached only 70% of the control after an hour, and qas still at this level after 3 hours. Figures 2, 3 and 4 show that this slight increase could be attributed to a decrease in the high F_0 level, since the F_v exhibited practically no recovery, being 30% of the control even in the third hour of recovery. It can thus be said that the 3-hour (1200 μmol^{-2} s^{-1}) light treatment caused slowly reversible damage to the primary processes of PS II, which did not relax even after 3 hours, in the shade-type mosses, and a quickly reversible inhibition, which relaxed in 1 hour, in the sun-type mosses. As Figure 5 shows, there was a significant difference in the F_i parameters, proportionate to the number of inactive PS II reaction centres in the different types of *M. diclados*, during photoinhibition and recovery. During the first two hours of inhibition, an increase in F_i was observable in the shade type. However, in the third hour a 20% increase occurred compared to the control. At low light intensity, this value was 10–15% higher than the control even after three hours. In the case of mosses grown at higher light intensity, the F_i did not change significantly during photoinhibition and only a slow decrease was observable during recovery.

As was mentioned above, the R_f parameter is proportionate to the maximum reduction of the plastoquinone pool by PS II. Figure 6 shows that the electron transport processes taking place within the active PS II prior to the reduction in the PQ pool lose some of their efficiency during photoinhibition in both groups. In the shade-type *Mastigophora* this decrease was

about 40% by the end of photoinhibition and later, even after 3 hours at low light intensity, it was only 70% of the control. On the other hand, the R_f parameter of the sun-type *M. diclados*, which exhibited a less pronounced decrease, started to increase after the second hour of photoinhibition and reached the control level after the first hour of recovery.

The R_{fd} parameter signalling the potential photosynthetic capacity (Figure 7) decreased greatly during the first hour of photoinhibition in both groups and reached 90% in the shade type in the third hour. In the sun type the maximal decrease was about 50% and after the first hour a slow increase was observable, which became more intense when the high (1200 μmol^{-2} s^{-1}) light intensity ceased. By the end of the recovery period, the R_{fd} parameter of the sun-type *M. diclados* was the same as that of the control, while in the shade type it was only 40% of the control.

Discussion

The results of this investigation show that there are differences between the photosynthetic parameters of *M. diclados* growing in habitats with various light conditions, even in the default state. The functional parameters observed indicate that at the low light intensity level (200 μmol^{-2} s^{-1}) used in the measurements, photosynthesis in general and PS II in particular operated more efficiently in *M. diclados* grown at low light intensity. This is confirmed by the higher F_v/F_p value, which is associated with the functioning of the PS II reaction centres, the primary processes of photosynthesis. Previous studies (Chu and Anderson, 1984) indicate that a higher F_0 level may also indicate the presence of more extensive LHC linked to the reaction centres. At low light intensity, which may provide a more efficient excitation energy supply for the reaction centres. In these plants the PS II reaction centres can reduce the PQ pool within a short time as indicated by the greater R_f parameter (Table 1), which may also be due to the fact that in the shade-type plants the size of the PQ pool is generally smaller than in the sun type (Boardman et al. 1972). Both groups, however, are characterised by a high level of F_i. The increase in fluorescence from F_0 to the first inflectional point or intermediate peak (F_i) can be attributed entirely to the variable fluorescence yield from the PS II$_\beta$ centres (Cao and Govindjee, 1990). The PS II$_\beta$ centres are incapable of reducing the PQ pool and thus of oxidising water, nor do they take part in the operation of the linear electron transport chain. The question is, how these plants are able to reach a relatively high level of R_{fd} with such a large proportion of inactive PS II reaction centres. As is well known, at a given light intensity $R_{fd} = (F_p - F_s)/F_s$ (Strasser et

al. 1987), that is, R_{fd} equals the ratio of quenched to non-quenched fluorescence. The responsibility for the decrease in fluorescence during the slow stage of fluorescence induction lies with the photochemical and the various types of non-photochemical quenching processes (Krause and Weis, 1991). The high R_{fd} value indicates that the quenching processes are intense, and at the low light intensity applied, can be expected to consist principally of photochemical quenching. The prerequisite of the greater part of photochemical and, at this low light intensity, non-photochemical quenching is the operation of the linear electron transport chain, which can only be generated by active PS II RCs. It is possible that the functionally inactive but physically intact PS II RCs take part in the elimination of excitation energy in the form of heat (Öquist et al. 1992).

As a result of adaptation to different light conditions, the functional parameters of the photosynthetic apparatus based on fluorescence induction were significantly different during photoinhibition and following recovery. The 3-hour, 1200 μmol^{-2} s^{-1} light intensity treatment reduced the efficiency of the primary processes, especially of charge separation, in PS II in both groups. This was manifest in the changes in F_v/F_p and, to an even greater extent, in the F_v parameter. However, the decrease in the optimal quantum efficiency of PS II was more vigorous in *M. diclados* grown at low light intensity. On the basis of the R_f parameter it can be said that there was a retardation not only in charge separation in the RCs but also in the reduction of the PQ pool by PS II. While the decrease in these processes in *M. diclados* grown at high light intensity seemed to be reversible during recovery following photoinhibition, the values equalling those of the control after 1 hour, in mosses grown at low light intensity these changes were irreversible or very slowly reversible. So what protective mechanisms have evolved against photoinhibition in *M. diclados* grown at high and low light intensity? The fact that as a result of high light intensity both the F_0 level and the number of inactive Q_B non-reducing RCs indicated by F_i increased suggests that the heterogeneity of PS II may have an important role in the process of photoinhibition and/or in the protective mechanism against photoinhibition in shade-type mosses. The literature mentions two main aspects of PS II heterogeneity: PS II antenna heterogeneity, also known as α, β, heterogeneity, and PS II reducing side heterogeneity. On the basis of PS II antenna heterogeneity there are two different PS II populations with different antenna sizes. The dominant form is PS II$_\alpha$, localised in the grana regions and responsible for water oxidation and plastoquinone reduction. PS II$_\beta$ is often localised in the intergrana or stroma thylakoids and only contains PS II Core and *Chl* a-b LHC II-inner components, with no LHC II-peripheral antenna (Melis, 1985; Greene et al. 1988; Guenther et

al. 1988). Beside this, the PS II centres are incapable of electron transfer from Q_A to Q_B. These are the PS II Q_B-non-reducing centres (Greene et al. 1988; Guenther et al. 1988). These two labels often indicate the same inactive PS II RC. According to Guenther et al. (1990), the Q_B non-reducing centres are intermediate stages in the damage and repair processes of PS II. For theoretical reasons, however, although these centres are incapable of charge stabilisation, through charge separation and recombination. The ability to trap excitation energy and thus to non-photochemically dissipate the absorbed light energy is preserved (Cleland et al. 1986; Styring et al. 1990). Considering all this, it seems possible that by maintaining a large number of photoinhibited, functionally inactive but structurally intact reaction centres, mosses grown at low light intensity achieve the controlled dissipation of light energy.

Unlike the mosses grown at low light intensity, *Mastigophora* plants grown at high light intensity shoved no increase in F_i during photoinhibition suggesting that the inactive Q_B-non-reducing centres play a lesser role in protecting against photooxidative damage. At the same time, a decrease was recorded in both F_p and, to a smaller degree, in F_0. These symptoms are also known to be charateristic of the energy-dependent fluorescence quenching connected to the pH gradient through the thylakoid membrane, and to low lumen pH and the accumulation of zeaxanthin (Dau, 1994). It is also well documented that sun-type plants are characterised by a high xanthophyll/β carotene ratio (Aro et al. 1986). At the same time, the PS II repair cycle associated with the D_1 protein turnover also plays an important role in repairing photooxidative damage (Öquist et al. 1992). In addition, both processes are relaxed in the dark or at low light intensity within 0.5–1 hour, as observed during the dark relaxation of *M. diclados* grown at high light intensity.

All this seems to suggest that the protective strategies against high light stress in shade-type and sun-type *Mastigophora* are different, and that this could be related to the amount of light energy available in their given habitat. The sun-plant strategy appears at high light intensity. The high light intensity provides ample energy for the growth of the plant as well as for the energy-intensive *de novo* D_1 protein synthesis linked to the PS II repair cycle and for producing a greater pool of xanthophyll pigments. On the other hand, when the shade-type *M. diclados* is exposed to very high light intensity it apparently lacks the capacity to counterbalance oxidative damage with the help of a fast turnover repair cycle. Instead, photoinhibited, inactive PS II reaction centres are accumulated, because the turnover of the repair cycle is slow compared to the velocity of the photooxidative damage. Thus, with the help of heat dissipation by inactive RCs photoinhibition induces

the stable regulation of PS II in the shade-type *M. diclados.* However, if the light intensity is too high compared to the capacity of these processes, the photosynthetic apparatus may suffer photooxidative damage, which is only slowly reversible, or irreversible, because of the slowness of the repair cycle.

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