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2.1 Photoinhibition in Antarctic Mosses

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Summary: Photoinhibition of *Grimmia antarctici* during the summer at Casey, East Antarctica, was indicated by a reduction in photosynthetic capacity (light saturated photosynthetic rate), photosynthetic efficiency (photon yield of O_2 evolution), photochemical quantum yield (ratio of variable to maximum fluorescence) and rate of fluorescence quenching when plants were exposed to moderate light at low temperature. We suggest that photoinhibition is a major factor limiting bryophyte productivity in Antarctic ecosystems.

Zusammenfassung: Bei *Grimmia antarctici* wurde im Sommer bei der Station Casey, East Antarctica, eine Lichthemmung festgestellt. Sie trat in Erscheinung als Verminderung der photosynthetischen Kapazität (Photosyntheseraten bei Lichtsättigung), der photosynthetitischen Effizien (Photonenausbeute der O_2-Freisetzung), der photochemtschen Quantenausbeute (Verhältnis von variabler zu maximaler Fluoreszenz) und der Rate der Fluoreszenzlöschung, wenn die Pflanzen bei niedrigen Temperaturen Schwachlicht ausgesetzt wruden. die Autoren betrachten die Lichthemmung als einen wesentlichen Faktor, der die Produktivität der Moose in antarktischen Ökosystemen einschränkt.

1. INTRODUCTION

The low productivity of plant communities at high latitudes is generally attributed to low summer growth temperatures and short growing season. Water stress and nutrient availability are frequently cited as additional influences. Light, on the other hand, is not usually regarded as a determining factor during summer (CALDWELL et al. 1978). Although maximum irradiance in polar regions is lower than elsewhere, this is thought to be compensated by longer photoperiods during the growing season. The fact that maximum photosynthetic rates are achieved at comparatively low light intensities in bryophytes (VALANNE 1984) is also consistent with the view that constraints on productivity due to limiting solar radiation are relatively unimportant in Antarctic and Arctic bryophyte communities. The possibility that growth at high latitudes may be limited by excessive light is far more likely.

Inhibition of photosynthesis by strong light, referred to in the older literature as photoinactivation, photolability or solarisation and more recently as photoinhibition, has been known for a long time (POWLES 1984) and numerous examples of photoinhibition under normal environmental conditions are reported (eg. HARRIS & PICCININ 1977, BELAY 1981, WHITELAM & CODD 1983, BJÖRKMAN & HOLMGREN 1963, JURICK et al. 1979). Although we are not aware of any systematic investigation of the effect of high light on the photosynthetic capacity of polar bryophytes under field conditions the observations of OECHEL & SVEINBJÖRNSSON (1978) are consistent with photoinhibition of *Pogonatum alpinum* at mid-day during midsummer. Maximum photosynthetic rates and light saturation were aboserved simultaneously at 0800 h. As solar radiation and temperature increased during the morning, the rate of CO_2 exchange decreased rapidly. As these authors noted "since temperatures remained below the optimum, the observed decreases in photosynthesis may have been the result of photoinhibitory processes". RASTORFER & HIGINBOTHAM (1968) also noted an interaction between low temperature and high light intensity leading to a marked depression in photosynthesis in *Bryum sandbergii*. They distinguished this effect from "solarisation" since, under the conditions of their experiment both high light and cold were needed to produce the reponse.

Photoinhibition is a reflection of damage to the photosynthetic apparatus by light. It involves a reduction in photosynthetic capacity, independent of gross changes in pigment concentration. The threshold of light intensity required to cause damage depends on the light harvesting and photosynthetic capacity of the plant. Any light in excess of that which can be utilised in photosynthesis is potentially damaging. Circumstances which reduce the rate of the dark (carbon reduction) reactions of photosynthesis reduce the level of light required to drive these reactions and hence, increase sensitivity to photoinhibition. Low temperature, limited availability of water and nutrients are obvious examples. All are encountered in polar regions. This suggests that productivity at high

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latitudes may be severely limited by photoinhibition. On the other hand, it is well known that higher plants from thermally contrasting habitats have adapted to extreme environments through genetic variation in the photosynthetic apparatus (BERRY & BJÖRKMAN 1980). If bryophytes have done the same, photoinhibition may not be a major constraint on plant productivity in Arctic and Antarctic ecosystems.

The aim of this study was to discover whether *Grimmia antarctici* Card., one of the dominant bryophyte species in East Antarctica, experiences photoinhibition under summer growth conditions.

The effect of stress on photosynthetic capacity was investigated by comparing under standard conditions, rates of 0_2 evolution and fluoresence characteristics of plants previously exposed to different environments. Light saturated photosynthetic rates and photon yields of oxygen evolution were estimated from photosynthesis/light intensity curves. The former provide a measure of photosynthetic capacity; the latter an indication of photosynthetic efficiency (BJÖRKMAN & DEMMIG 1987). The results were correlated with measurements of chlorophyll fluoresence at room temperature. These reflect underlying photosynthetic reactions (LAVOREL & ETIENNE 1971, PAPAGEORGIOU 1975) and, as CRITCHLEY & SMILLIE (1981) have shown, provide a simple means of following the development of photoinhibition under stressful conditions.

2. MATERIALS AND METHODS

Casey (66° 17'S, 100° 32'E) is located on the north-west corner of Bailey Peninsula, an island in the Windmill Group joined to the mainland by a thick permanent ice sheet extending from the polar plateau (HOLLIN & CAMERON 1961). The terrestrial vegetation consists entirely of algae, lichens and bryophytes extending over several hectares of ice-free, windswept terrain. Although the plant cover is relatively sparse and total productivity low, there are numerous sites where the moss turf is abundant. Such sites are often composed of a single bryophyte species and free of any obvious algal and lichen contaminants. *Grimmia antarctici* Card. was collected from a site about 0.5 km south of the base immediately prior to each experiment and the cushions kept moist in shallow trays inside or outside the laboratory under the conditions specified.

2.1 *Photosynthesis measurements*

Rates of 0_2 exchange were determined on green shoots ca. 3 mm in length shaved from the top of the moss cushions. The cut shoots were equlibrated in water for 15—20 min before the turgid fresh weight of the sample (between 10—30 mg) was determined under carefully standardised conditions, i. e. drained for 60 s on blotting paper and weighed immediately on a pre-tared digital balance (Sartorius Model 1702).

Photosynthesis/light intensity (photon flux density, PFD) curves were obtained for each sample using a Rank oxygen electrode essentially as described by ALLEN & HOLMES (1986). Known weights of tissue were placed in the chamber with 4 ml 20 mM Hepes buffer (pH 7.6) containing 20 mM potassium bicarbonate. The temperature was maintained at 20° C by circulating water from a controlled temperature bath through the water jacket of the chamber. Oxygen consumption in darkness (dark respiration) was determined at the start of each run. The light proof covering over the chamber was then removed and rates of oxygen exchange determined over a range of PFDs. Light was provided by a slide projector. PFD within the chamber was controlled by neutral filters in front of the lamp housing and by varying the distance between the lamp and the chamber. PFDs were measured on the far side of the chamber with a LI-COR data logger (Li 1000) and quantum sensor (Li 190 sa). The values given are for photosynthetically active radiation (400—700 nm) and underestimate the levels inside the chamber by a small but consistent amount. Photosynthetic rates determined on replicate samples (n = 3—6) from the same moss cushion were generally highly reproducible (SE mean < 10%).

2.2 *Fluoresence measurements*

Chlorophyll fluoresence induction kinetics were measured at 20° C on the surface of moss cushions after an appropriate dark adaption period (10—20 min). The instrument used was a portable fluorometer (Model SF 10, Richard Brancher Research LTD, Ottawa) connected to a chart recorder (Rikadenki R-02). The measuring probe of the SF10 was placed at different positions on the surface of the clump and irradiated for 4 or 10 secs. Between 5 and 10 transients from different positions on each clump were obtained. Photochemical quantum yield was estimated from the ratio of variable to maximum fluorescence (F_v/F_m) and quench rate was determined (in

arbitrary units) from the slope of the decline from the fluoresence peak (LAWLOR 1987). The fluoresence characteristics were remarkably uniform over each moss cushion. The SE of the mean of photochemical quantum yield was < 5%; that of the mean quench rate was < 1%.

3. RESULTS

3.1 *Light-saturated photosynthetic rates*

The effect of high light and cold on the photosynthetic capacity of *Grimmia* is illustrated in Fig. 1. In this experiment a cushion of *Grimmia* approx. 100 cm^2 was transferred from an exposed site to the laboratory (15—20° C). After 8—10 h in dim natural light (50 $\mu E\ m^{-2}s^{-1}$), followed by 90 min darkness, the clump was sampled and 0_2 exchange measured at 20° C over a range of PFDs. Immediately after sampling, the moss cushion was divided into two portions. One was transferred to medium (500 $\mu E\ m^{-2}\ s^{-1}$) and the other to high (1000—1800 $\mu E\ m^{-2}\ s^{-1}$) light on a snow bank for 100 and 150 min respectively. The temperature on the top of the bank was 0° C. After exposure to light and cold the moss clumps were returned to the laboratory and allowed to equlibrate to room temperature in darkness for about 90 minutes before samples were taken for 0_2 exchange measurements. The initial response (curve 1) provided a measure of the light saturated photosynthetic rate and light saturation point of *Grimmia* at the time of transfer to bright light and cold. Exposure to moderate light and cold (curve 2) produced a 40% reduction in the light saturated photosynthetic rate and a 30% reduction in in the PFD required to produce saturation (from c. 700 to 500 $\mu E\ m^{-2}\ s^{-1}$). The effect of direct sunshine and intermittent cloud (1000—1800 $\mu E\ m^{-2}\ s^{-1}$) at low temperature (curve 3) was even more dramatic. Photosynthesis was almost completely inhibited and there was no net gain in 0_2 at any light intensity.

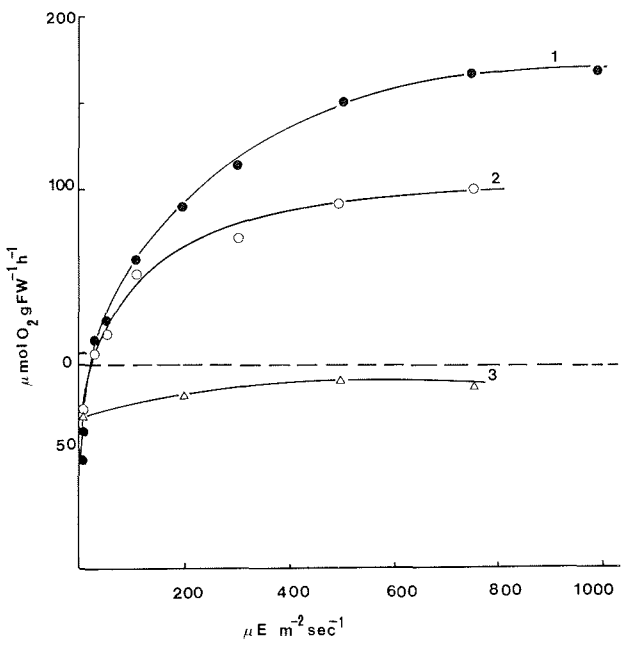

Fig. 1: Net photosynthetic rates of *Grimmia* at 20° C as a function of PFD ($\mu E\ m^{-2}s^{-1}$) following (1) pretreatment in dim light —•— (2) exposure to moderate light (500 $\mu E\ m^{-2}s^{-1}$) at 0° C for 100 minutes — o — (3) exposure to bright light (1000—1800 $\mu E\ m^{-2}s^{-1}$) at 0° C for 150 minutes —Δ—

Fig. 2 shows the effect of time of exposure to moderate light and cold on dark respiration and light saturated photosynthetic rates at 20° C. Respiration was realtively unaffected: light saturated photosynthetic rates were severely depressed. The inhibitory effect of light and cold was rapid. Covering the moss cushion with a block box led to a rapid recovery. These findings imply (1) damage to the photosynthetic apparatus was due to a combination of light and cold and not to low temperature, per se; (2) measurements of photosynthetic capacity at temperatures substantially above the treatment temperature underestimate the extent of photoinhibitory damage

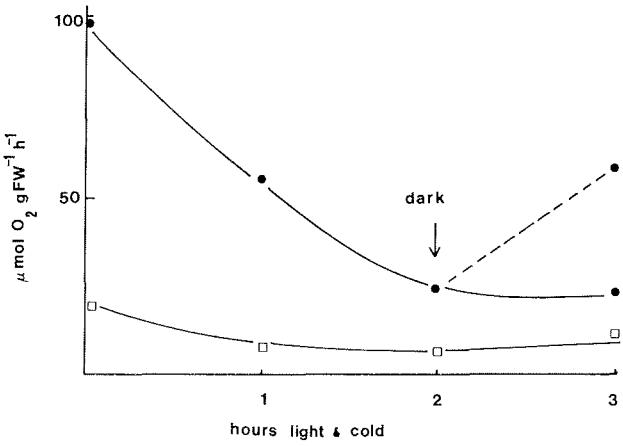

Fig. 2: Effect of time of exposure of Grimmia to moderate light (500 μE m^{-2} s^{-1}) at low temperature (0° C) on light saturated photosynthesis (—•—) and dark respiration (—❑—) rates at 20° C.

in the field, by an amount equal to the recovery that occurs during equilibration to the measurement temperature.

3.2 *Fluorescence characteristics*

Cushions of *Grimmia* were selected from moist, snow free areas and from beneath 30 cm of snow on a sunny day with scattered cloud. The air temperature was just above zero (1—2° C) and the light levels varied between 600 and 1000 μE m^{-2} s^{-1}. The moss clumps were put into plastic bags containing wet paper towels and taken immediately to the laboratory. Between 5 and 10 fluoresence transients were recorded for each cushion after a minimum of 20 min dark adaptation at room temperature and mean photochemical quantum yields and quench rates determined. The moss cushions, designated 1—5 in Fig, 3 were treated as follows.

(1) Exposed site: 20 min dark
(2) Exposed site: 160 min dark
(3) Frozen site: 20 min dark
(4) Frozen site: thawed in darkness (160 min dark)
(5) Frozen site: thawed in light (140 min 600—1000 μE m^{-2} s^{-1} at 2° C) followed by 20 min dark.

Photochemical quantum yield, indicated by the ratio of variable to maximum (F_v/F_m) fluoresence in Fig. 3a provided a measure of photochemical processes associated with PS II. Photochemical quantum yield (F_v/F_m) was higher in frozen plants (3) and plants thawed in darkness (4) than in plants from exposed situations (1) or in frozen plants subjected to bright light and cold (5). The 30% lower photochemicl quantum yield of plants from exposed (snow-free) situations and the 40% reduction in photochemical yield when snow cover was removed prematurely are both indicative of photoinhibition under field conditions. From the similarity of the photochemical quantum yields in treatments 1 and 5, we suggest that it makes little difference whether the snow is removed gradually by wind and melt or rapidly by digging, the end result is the same: inhibition of PS II photochemistry by excess light.

Quenching of fluoresence is thought to reflect phosphorylation by thylakoids and is correlated with the assimilation of CO_2. Our results (Fig. 3b) indicate that photosynthesis was occurring in *Grimmia* from exposed sites (1) but not under 30 cm of snow (3). Maximum rates of quenching were observed in moss from snow covered sites which were allowed to thaw in darkness (4). However, exposure to light during thawing inhibited whatever recovery processes were involved (5).

The apparent constancy of the photochemical quantum yield in *Grimmia* thawing in darkness (3 and 4 in Fig. 3a) is confirmed by the time course of fluoresence attributes shown in Fig. 4. Under our experimental conditions there was a lag of about 40 minutes in the development of quenching capacity in frozen material and the maximum rate was achieved in just over two hours.

The main findings of this experiment are summarised in Fig. 5. With the exception of *Grimmia* cushions which

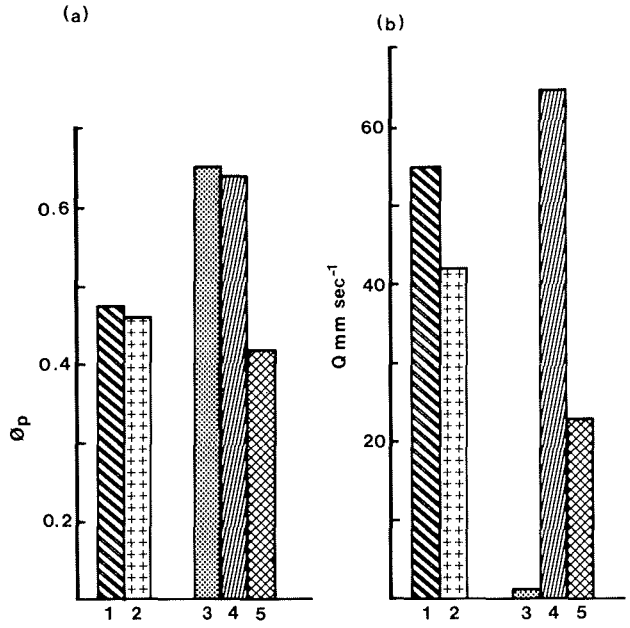

Fig. 3: (a) Photochemical quantum yield Øp (F_v/F_m) and (b) rate of quenching (mm s^{-1}, arbitrary scale) of *Grimmia* from exposed, and snow, covered (frozen) sites as follows: (1) exposed site: 20 min dark; (2) exposed site: 160 min dark; (3) frozen site: 20 min dark; (4) frozen site: 160 min dark; (5) frozen site: 140 min light (600—1000 µE $m^{-2}s^{-1}$) at 2° C followed by 20 min dark.

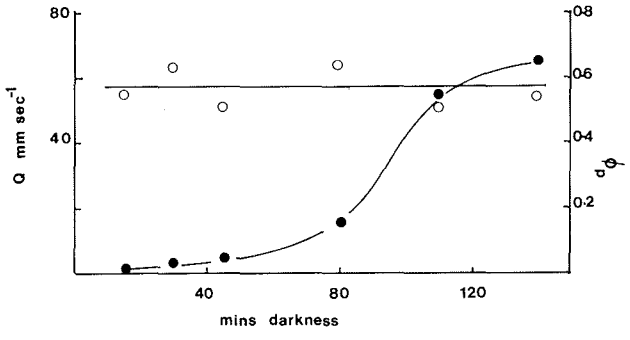

Fig. 4: Photochemical quantum yield Øp (F_v/F_m) — o — and quench rate (Q mm s^{-1}) — • — of frozen *Grimmia* allowed to thaw in darkness at room temperature (20° C).

had not been exposed to bright light since the previous summer and which were still frozen, there was a direct relation between photochemical quantum yield and the rate of fluoresence quenching. Both were greatest in plants which were allowed to thaw in darkness (4) and least in those which were exposed to light while still frozen (5). Plants from snow free sites which had presumably made the transition from (winter) darkness to full sunlight more gradually (1, 2) were intermediate in both photochemical quantum yield and quenching ability. These results are consistent with damage to the photosynthetic apparatus by light.

3.3 *Photon yield of oxygen evolution*

Estimates of the photon yield of O_2 evolution in unstressed and stressed plants were made from detailed measurements of photosynthetic rates over 0—10 µE $m^{-2}s^{-1}$ (treatments 1 and 2 in Fig. 1). The rates of O_2 evolution were converted from a fresh weight to area basis using a conversion factor of 0.0184 g per cm^2 calculated from the fresh weight of shoot tips in 1 cm^2 of moss cushion. The results are shown in Table 1. Photochemical quantum yields (F_v/F_m) from the same moss cushions are also shown.

Exposure of unstressed *Grimmia*, to moderate light (500 µE $m^{-2}s^{-1}$) at low temperature (0° C) led to a reduction

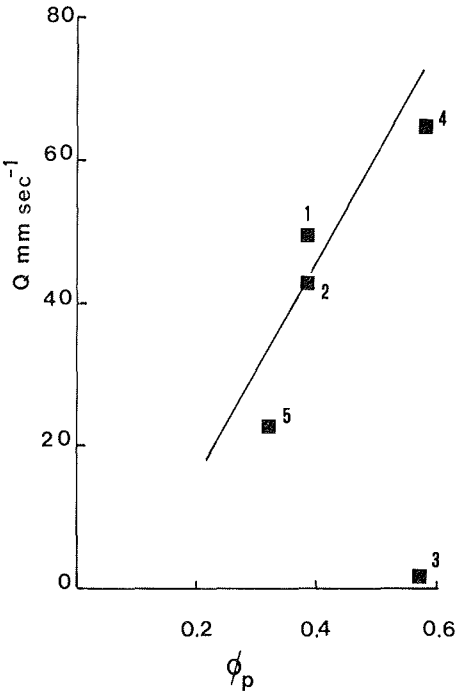

Fig. 5: Quench rate (Q mm s^{-1} arbitrary units) as a function of photochemical quantum yield in *Grimmia*. Numbers assigned to each point identify particular treatments as in Fig. 3.

	Photon yield mol O_2 mol photon^{-1}	F_v/F_m
Initial: unstressed	0.08	0.62
Stressed: 500 uEm^{2}s^{-1} at 0°C for 100 mins.	0.028	0.39

Tab. 1: Photon yield of O_2 evolution and photochemical yield (F_v/F_m) of Grimmia after 8–10 hr in dim light 50 µE m^{-2}s^{-1}) at room temperature (initial . . . . unstressed) and after exposure to moderate light at low temperature (stressed).

in both photon yield and F_v/F_m ratio. The former reflects a reduction in the efficiency with which light was converted to stable chemical products; the latter an adverse effect on PS II photochemistry. Both are evidence of photoinhibition.

4. DISCUSSION

The first symptom of photoinhibition is impaired electron transport. The end result is a reduction in both light limited and light saturated photosynthesis. This paper provides evidence of all three in *Grimmia antarctici* under normal summer growth conditions. We therefore conclude that productivity of this endemic Antarctic species is limited by damage to the photosynthetic apparatus by light.

When light saturated photosynthetic rates of unstressed *Grimmia* are converted from a fresh weight to dry weight or area basis (1 g fresh weight = 0.2 g dry weight; 54 cm^2) it becomes apparent that they are 5—7 times higher than most published rates for bryopthytes (KALLIO & KÄRENLAMP 1975, ILKS & PROCTER 1975, KALLIO & SAARNIO 1986) and are comparable with rates reported for angiosperms (SALSBURY & ROSS 1985). We attribute this to our experimental procedures rather than to an innately greater capacity of *Grimmia* for photosyntheis. High rates of photosynthesis were also observed in Antarctic and temperate ecotypes of *Ceratodon*

and *Bryum* under similar conditions unpublished). In contrast to most other workers we measured photosynthetic capacity in plants under non-limiting conditions of water and CO_2 rather than actual rates of photosynthesis in the field. Furthermore, in our experiments, *Grimmia* cushions were allowed to adjust to low light levels at temperatures in the optimum range for several hours before photosynthesis was measured using a liquid phase O_2 electrode system. Usually photosynthesis is measured under actual or simulated field conditions using an infra-red gas analyser (IRGA).

The simplest interpretation of the high photosynthetic rates of *Grimmia* reported in this paper is that they reflect the photosynthetic capacity of unstressed plants. High rates were always observed after *Grimmia* had been in the laboratory for a few hours, suggesting that light-damaged thylakoids recovered during this time. This interpretation is consistent with direct evidence of recovery of photosynthetic capacity at low temperature in darkness (Fig. 2). It is also consistent with the high photochemical quantum yield and rate of fluoresence quenching of plants from snow covered sites which were allowed to thaw in darkness (Fig. 3, treatment 4).

Room temperature fluoresence is widely used to detect effects of environmental stress on photosynthesis. It is generally accepted that reductions in F_v/F_m ratios and rates of fluoresence quenching reflects reduced photosynthetic activity. Interpretation of room temperature fluoresence transients is based on theoretical considerations (KITAJIMA & BUTLER 1976) and comparison with 77K fluoresence. The currently accepted view (LAWLOR 1987) is that the rapid rise in fluoresence when chlorophyll is excited reflects electron transport characteristics: quenching of fluoresence after the peak is thought to reflect phosphorylation. The ratio of variable to maximum fluoresence (F_v/F_m) is determined by photochemical processes in the thylakoids and reflects the efficiency of PSII photochemistry. Quenching is associated with the induction of CO_2 assimilation and the utilisation of excitation energy. Impaired electron transport, reflected in a reduction of F_v/F_m, results in a reduction in ATP synthesis and quenching. However, assimilation of CO_2 can also be limited by other factors such as levels of key Calvin cycle enzymes. When this is the case, photochemical quantum yield (F_v/F_m) may be high but the rate of quenching low. We conclude from these theoretical considerations and the results in Fig. 3 that:

(1) freezing overwinter does not impair photochemical efficiency. The highest photochemical quantum yield (F_v/F_m) was observed in *Grimmia* which was still protected by 30 cm of snow (treatment 3).

(2) the high photochemical qunatum yield in frozen *Grimmia* (treatment 3) in the absence of quenching implies that photosynthesis is limited by low activity of enzymes essential for carbon reduction.

(3) thawing frozen Grimmia in darkness (treatment 4) does not impair its photochemical efficiency (i. e. no reduction in F_v/F_m) and enables the C reduction reactions of photosynthesis to proceed (i. e. there is a dramatic increase in quenching).

(4) thawing in light (treatment 5) on the other hand, leads to a reduction in the efficiency of photochemical reactions associated with PS II (i. e. reduction in F_v/F_m) and a reduction in quenching.

(5) since the photochemical quantum yield of plants in exposed situations (treatment 1) is similar to that of plants thawed in light and substantially less than that of plants thawed in darkness, plants in the field are damaged by excess light.

Overall, the fluoresence data reported here are entirely consistent with evidence of photoinhibition provided by direct measurements of photosynthetic rates. They are also consistent with photon yields for O_2 evolution determined before and after exposure of *Grimmia* to moderate light and cold.

In contrast to photochemical quantum yield (F_v/F_m) which reflects the efficiency of PSII photochemistry, the photon yield of O_2 evolution (mol O_2 mol photons^{-1}) provides a measure of the efficiency of the entire photosynthetic process. BJÖRKMAN & DEMMIG (1987) have recently used photon yields of O_2 evolution and 77K fluoresence to characterise the photosynthetic attributes of vascular plants of diverse origins. They argue that "on the assumption that plants use the same photosynthetic pathways and are equally efficient in converting photons into chemically-bound energy, one would expect them to have identical photon yields as long as the functional integrity of the system remains intact". Their results indicated that photon yields of O_2 evolution were

excellent indicators of stress and that there was a strong correlation between photon yield and F_v/F_m.

BJÖRKMANN & DEMMIG (1987) obtained a mean value of 0.106 SE 0.001 for the photon yield of O_2 in 37 C_3 vascular plants. The mean value for 5 C_4 species was 0.069 SE 0.004. We obtained a maximum value for *Grimmia* of 0.08. This was correlated with a F_v/F_m ratio of 0.62. When *Grimmia* was exposed to moderate light at low temperature these values decreased to 0.028 and 0.39 respectively.

BJÖRKMAN & DEMMIG (1987) observed a similar reduction in photon yield and F_v/F_m in a shade plant exposed to bright light. In relatively unstressed *Hedera canariensis* with a mean photon yield of 0.08, the F_v/F_m ratio was 0.67: in light stressed plants with mean photon yield of 0.028, F_v/F_m was 0.3.

Although our results are preliminary and further replication is needed, the match between BJÖRKMAN and DEMMIG's data and our own is unlikely to be fortuitous and leads to two important conclusions:

(1) Assuming *Grimmia* is typical, photosynthetic efficiency of bryophytes is similar to that of the higher plants.

(2) Excess light in high latitudes is a major environmental influence and bryophytes in exposed situations are subject to severe photoinhibition on bright days. The level of stress is comparable to that of a shade adapted plant exposed to sunlight for several hours. However in the case of shade adapted vascular plants, prolonged exposure to high light is not the norm, although it may be endured from time to time. In the case of bryophytes on the windswept, snow free morraine at Casey low temperature and high light are constant features during summer and photoinhibition is chronic.

Overall, our results are consistent with the finding of KALLIO & SAARNIO (1986) from transplant experiments that mosses experience stress in polar habitats. Since the maximum light saturated photosynthetic rates and photon yields of unstressed *Grimmia antarctici* were similar to those of cool temperate plants, low rates of photosynthesis in this endemic Antarctis species during summer cannot be attributed to low photosynthetic capacity. The combined effects of bright light and low temperature are extremely stressful and photoinhibition is a major factor limiting bryophyte productivity.

5. ACKNOWLEDGEMENTS

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References

Allen, J. F. & N. G. Holmes (1986): Electron transport and redox titration. — In: M. F. Hipkins & N. R. Baker (eds). Photosynthesis energy trans duction — a practical approach., 103—141, IRL Press, Oxford.

Belay, A. (1981): An experimental investigation of inhibition of phytoplankton photosynthesis at lake surfaces. — New Phytol. 89: 61—74.

Berry, J. & O. Björkman (1980): Photosynthetic response and adaptation to temperature in higher planta. — Ann. Rev. Plant Physiol. 31: 491—543.

Björkman, O. & B. Demming (1987): Photon yield of 0_2 evolution and chlorophyll fluoresence characteristics at 77K among vascular plants of diverse origins. — Planta 170: 489—504.

Björkman, O. & P. Holmgren (1963): Adaptability of the photosynthetic apparatus to light intensity in ecotypes from exposed and shaded habitats. — Physiol. Plant. 16: 889—914.

Caldwell, M. M., D. A. Johnson & M. Fareed (1978): Constraints on tundra productivity: Photosynthetic capacity in relation to solar radiation utilisation and water stress in Arctic and alpine tundras. — in, Vegetation and production ecology of an Alaskan Arctic tundra, L. L. Tieszen (ed), 323—342 Springer-Verlag, New York, Heidelberg, Berlin.

Critchley, C. & R. Smillie (1981): Leaf chlorophyll fluoresence as an indicator of high light stress (photoinhibition) in *Cucumis sativus* L. Aust. — J. Plant Physiol. 8: 133—141.

Dilks, J. & M. Proctor (1975): Comparative experiments on temperature responses of bryophytes: assimilation, respiration and freezing damage. — J. Bryol. 8: 317—336.

Harris, G. & B. Piccinin (1977): Photosynthesis by natural phytoplankton populations. — Arch. Hydrobiol. 80: 405—457.

Hollin, J. & R. Cameron (1961): IGY glaciological work at Wilkes Station, Antarctica. — J. Glaciol. 3, (29) 833—842.

Jurik, T., J. Chabot & B. Chabot (1979): Ontogeny of photosynthetic performance in *Fragaria virginiana* under changing light regimes. — Plant Physiol. 63, 542—547.

Kallio, P. & L. Kärenlampi (1975): Photosynthesis in mosses and lichens. — In, Photosynthesis and productivity in different environments. — In: J. P. Cooper (ed) IBP Prog. 3, 393—428, Cambridge Univ. Press, Cambridge, London, New York, Melbourne

Kallio, P. & E. Saarnio (1986): The effect on mosses of transplantation to different latitudes. — J. Bryol. 14, 159—178.

Kitajima, M. & W. Butler (1975): Quenching of chlorophyll fluoresence & primary photochemistry in chloroplasts by dibromothymoquinone. — Biochim. Biophys. Acta 376: 105—115.

Lavorel, J. & A.-L. Etienne (1971): In vivo chlorophyll fluoresence. — In: J. B. Barber (ed), Primary processes of photosynthesis, 203—268, Elsevier/North Holland Biomedical Press Amsterdam.

Lawlor, D. W. (1987): Photosynthesis: metabolism, control and physiology. Longman Scientific & Technical, Longman, London.

Oechel, W. & B. Sveinbjörnsson (1978): Primary production processes in Arctic bryophytes at Barrow, Alaska. — In: L. Tieszen (ed), Vegetation and production ecology of an Alaskan Arctic tundra, 269—298, Springer/Verlag, Berlin, Heidelberg, New York.

Papageorgiou, G. (1975): Chlorophyll fluoresence: an intrinsic probe of photosynthesis. In, Govindjee (ed) Bioenergetics of photosynthesis, 319—371, Academic Press, New York.

Powles, S. (1984): Photoinhibition of photosynthesis by visible light. — Ann. Rev. Plant Physiol. 35: 15—44.

Rastorfer, J. & N. Higinbotham (1968): Rates of photosynthesis and respiration of a moss *Bryum sandbergii* as influenced by light intensity and temperature. — Amer. J. Bot: 55 (10): 1225—1229.

Salsbury, F. & G. Ross (1985): Plant Physiology. — Wadsworth Pub. Co., Belmont California.

Valanne, N. (1984): Photosynthesis and photosynthetic products in mosses. — In: A. F. Dyer & J. G. Duckett (eds), The experimental biology of bryophytes., 257—273, Academic Press, London.

Whitelam, G. & G. Codd (1983): Photoinhibition of photosynthesis in the cyanobacterium *Microcystis aeruginosa*. — Planta 157: 561—566.