Ecological studies of aquatic moss pillars in Antarctic lakes
3. Light response and chilling and heat sensitivity of photosynthesis

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Abstract: The light-photosynthesis relation was measured using a PAM chlorophyll fluorometric method in a moss, *Leptobryum* sp., which is the primary component of aquatic moss pillars, in cultured *Leptobryum* sp. on an agar plate, and in both aquatic and terrestrial forms of *Bryum pseudotriquetrum*. The morphology of the plate-cultured *Leptobryum* sp. was clearly different from the sample growing on an aquatic moss pillar; the leaves and shoots were considerably thickened and enlarged in the former.   In spite of the great difference of morphology, photosynthetic light responses such as light-PS II yield, -non-photochemical quenching and the relative rate of electron transport of both samples were nearly the same.   On the other hand, the responses of *B. pseudotriquetrum* collected from a moss pillar and terrestrial habitat differed greatly.   Light-PS II yield and light-ETR relationships of the *Leptobryum* sp. showed rather shade-plant type response, low effective PS II yield at any light intensity and low maximum ETR with low light saturation point, while *B. pseudotriquetrum* from a terrestrial habitat showed rather 'sun-plant' type responses. Aquatic *B. pseudotriquetrum* showed the lowest values of effective PS II yield and ETR at almost all light intensities among the present samples.   Chilling/heating stress was experimentally added to the aquatic *Leptobryum* sp., and it was found that both maximum and effective yield of PS II showed quite narrow and cryophilic relationships with treatment temperatures.   These photosynthetic features observed in the *Leptobryum* sp., shade-plant type light response and very naïve sensitivity to the changes of temperature, suggest that the species can perform photosynthetic growth within the aquatic habitat; however, it cannot survive or prevail in the terrestrial habitat in severe East Antarctica.

key words: moss pillar, photosynthesis, light curves, temperature sensitivity, Antarctic lakes

Introduction

Discovery of a luxuriant moss community, 'moss pillars', in shallow oligotrophic East Antarctic lakes (Imura *et al.*, 1999, 2003) is opening a new window on the ecology of Antarctic mosses.   Mosses, in general, are known as amphibious plants (Ignatov and Kurbatova, 1990), and hence, distributions in both terrestrial and aquatic environments

have been reported even in Antarctica (Savicz-Lyubitskaja and Smirnova, 1959; Light and Heywood, 1973, 1975; Priddle and Dartmall, 1978; Priddle, 1979; Kasper *et al.*, 1982; Kanda and Iwatsuki, 1989; Kanda and Ohtani, 1991). These papers mainly focused on finding species in lakes, taxonomical treatments, and morphological descriptions of mosses in aquatic environments, and such aquatic mosses are sometimes reported as one of the 'submerged forms', slender shoots with small leaves and somewhat etiolated morphology, of terrestrial mosses distributed around the lakes (*e.g.,* Seppelt, 1983; Kanda and Ohtani, 1991). This suggests that the aquatic environment is not suitable for the growth of some mosses but they can live somehow live in it. However, the massive existence of the aquatic mosses, which create moss pillars in some lakes (Imura *et al.*, 2003; Kudoh *et al.*, 2003a), may indicates that they have some adaptive features to grow and to form a huge biomass in an aquatic environment.

In the present paper, the light response of photosynthesis of the primary structural component of the moss pillar, *Leptobryum* sp., was studied. Then the result was compared with that of the sub-component moss, *Bryum pseudotriquetrum*, which grows among the moss pillars and in a terrestrial habitat in East Antarctica. Further, the effects of chilling and heat stress on these mosses were experimentally tested. These studies were conducted to determine the properties of photosynthesis of *Leptobryum* sp., so as to explain why they succeed in some Antarctic lakes but not in the surrounding terrestrial habitats, from the point of view of photosynthetic reactions.

Materials and methods

Samplings and samples used

Samples of moss pillars were collected on 9 February 1999 from a lake Kuwai Ike (69°29′S, 39°35′E), by using a handy throw-in dredge from the shore of the lake. The collected samples were transferred into plastic bottles (2-L), and kept in dark and cool (never frozen) conditions for a few days. The samples were then incubated in tap water under 5℃ and 20 μmol m^{-2}s^{-1} with 14 L/10 D light cycle condition in a laboratory for later analyses. Many shoots of the moss appeared and stood up from the moss pillar during incubation for several months. We used these shoots for the present photosynthetic measurements as 'aquatic samples'. The *Leptobryum* sp. and *Bryum pseudotriquetrum* shoots were distinguished with visual morphological features (*e.g.,* Kudoh *et al.*, 2003a). Some shoots of *Leptobryum* sp. were picked up from the moss pillar and cultured on an agar plate (1% w/w) with diluted Knop's solution (Bopp, 1952) for *ca.* 4 months, and its morphological difference of shoots between moss pillar samples and cultured plants was checked. And the light response of the plate-culture (plate-cultured sample, hereafter) was also checked to compare it to the moss pillar samples as described below.

B. pseudotriquetrum actively growing in terrestrial and aquatic habitats (found among moss pillars) were collected for comparative study of the photosynthetic light response. Terrestrial samples were collected at a coastal area of Amundsen Bay (66°55′S, 52°30′E) on 23 February 2000. Aquatic samples were collected from moss pillars sampled by SCUBA diving (Kudoh *et al.*, 2003a) in lake B-4 Ike (69°29′S, 69°31′E) on 19 January 2000. Several shoots of the species were taken from both samples and were

kept in plastic sealed bottles with a little water for a few days under cool (5–10℃) and *ca.* 20μ mol m^{-2}s^{-1} light conditions until the photosynthetic measurements described below.

Light response measurement

Light intensity dependence (light response curves) of PS II quantum yield, non-photochemical quenching (NPQ) and relative electron transport rate (ETR) were measured by means of a PAM chlorophyll fluorometer (Teaching-PAM, Walz). A bud (1–3 mm) from each shoot was dissected in de-ionized water with a micro-blade. The sample was then placed in a special suspension cuvette TEACH-SC, positioned in the detector system and allowed to stand in the dark for 30 min to make the sample become dark adapted at *ca.* 5℃.

Measurements of rapid light-response curves were made using DA-TEACH data acquisition software with a built-in programmed protocol using a personal computer. First, the minimum/maximum yields (F_o and F_m) of fluorescence under a measuring light and a pulsed saturation light were measured in the dark-adapted sample, and then actinic illumination, which was supplied from the built-in LED, with 10 steps of intensity from 10 to 850μ mol m^{-2}s^{-1} were exposed. Each actinic light was illuminated for 2 min and a saturation pulse was exposed at the end of each step to measure the fluorescence yield under a different illuminated condition.

The effective quantum yield of PS II and the NPQ parameter were determined using the fluorescence yields of F_m, F_t and F_m'. F_t and F_m' are fluorescence just before saturation pulse exposure (F_t) and that induced by the pulse (F_m'), respectively, under variable actinic light conditions, as,

$$\text{PS II yield} = (F_m' - F_t)/F_m' = \Delta F/F_m', \tag{1}$$
$$\text{NPQ} = (F_m - F_m')/F_m'. \tag{2}$$

And the relative electron transport rate (ETR) can be derived from the product of PS II effective quantum yield and quantum flux density, as,

$$\text{ETR} = \text{PS II yield} \times \text{PAR} \times \text{C} \tag{3}$$

PAR denotes the flux density of incident photosynthetically active radiation (μ mol m^{-2} s^{-1}). In the present study, the coefficient C is assumed to be 0.42, which has been proposed as a mean value of green leaves among higher plants (Schreiber *et al.*, 1994). For the present experiments, duplicate buds of all samples were analyzed.

Chilling/heat sensitivity analysis

The photosynthetic process consists of light-driven primary reactions and the consecutive enzymatic reactions. If photosynthesis is proceeding under steady-state conditions, approximately the same number of electrons released from PS II should be observed. Chilling/heat stress, which might damage the enzymatic reactions, will change the rate of the electron flow, and so we can readily analyze the stress intensity by measuring the relative rate of electron flow by means of the same PAM chlorophyll fluorometer.

Buds from the aquatic *Leptobryum* sp. were cut and suspended in a small amount

of de-ionized water ($ca.\,200\,\mu l$) in cryovials.   Each bud was kept under a given temperature from –20 to 50℃ for 10 min in darkness.   Then, the samples were trans-ferred to a 5℃ incubator, in which the species was grown, and incubated for 1 hr in the dark.   Triplicate samples at each temperature treatment were analyzed.

Damages within PS II caused by the present chilling/heat treatment were deter-mined by measuring the maximal PS II quantum yield using a PAM fluorometer, at first, then actinic illumination of 120 μ mol m^{-2}s^{-1} was turned on for 5 mim followed by a saturation pulse to measure the effective PS II quantum yield in order to access the overall damages in the photosystem (for more detail, see a manual written by Schreiber, 1997, which is available from the web site: http: //www.walz.com).

Results

Morphological difference of *Leptobryum* sp. induced by the culture condition

Shoots of *Leptobryum* sp., which extended from the moss pillar during incubation within a watered culture bottle for several months, showed rather slender stems with small leaves compared with the cultured plants on the agar plate (Fig. 1).   The morphological properties of the former sample were very similar to those collected from the lake (*cf.* Kudoh *et al.*, 2003a).   The plate-cultured plant had nearly twice-thickened stems and 2–4 times wider leaves at similar temperature and light intensity, and the same incubation period.

Fig. 1.   Morphological features of *Leptobryum* sp. incubated on a moss pillar (left) in water and cultured on an agar plate (right).
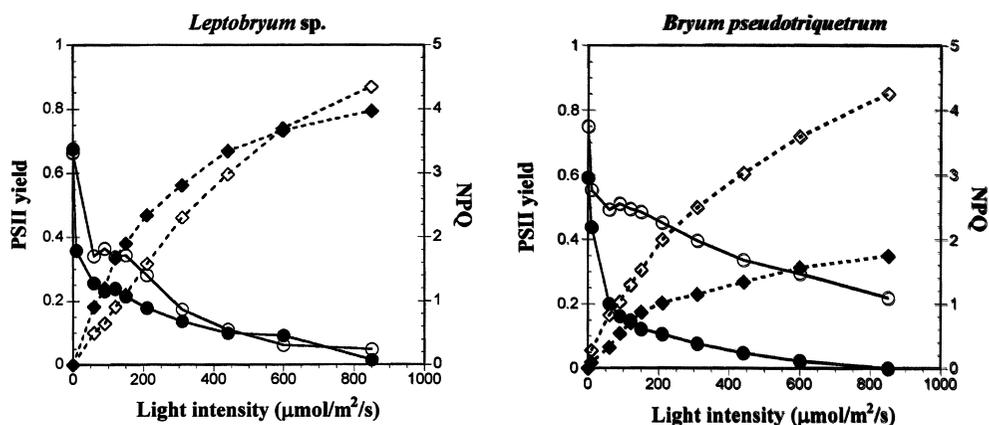
Fig. 2. Light-PS II yield and light-NPQ curves of *Leptobryum* sp. (left) and *B. pseudotriquetrum* (right). Closed and open circles in the panels indicate PS II yields of aquatic and plate-cultured *Leptobryum* sp., respectively (left), or aquatic and terrestrial *B. pseudotriquetrum,* respectively (right). Closed and open diamonds in the panels indicate NPQ of aquatic and plate-cultured *Leptobryum* sp., respectively (left), or aquatic and terrestrial *B. pseudotriquetrum,* respectively (right).

Light responses of *Leptobryum* sp. collected from a moss pillar sample, and in other samples.

Quantum yield of PS II of all samples measured under dark-adapted condition (maximal quantum yield of PS II) showed rather high values between 0.5 and 0.8 (Fig. 2). The yield of the aquatic samples, *Leptobryum* sp., sharply decreased to *ca.* 0.35 when actinic illumination was turned on, and the values gradually decreased with increased actinic light intensity. At the highest actinic light in the present setting, 850 μ mol m^{-2}s^{-1}, almost no quantum yield was measured. Plate-cultured *Leptobryum* sp. samples showed slightly higher values than those measured in aquatic samples, but the difference was not so large. On the other hand, terrestrial *B. pseudotriquetrum* showed consistently high values under all actinic light intensities. Even at the highest setting of the present actinic light intensity, the effective yield was >0.2, which indicated the occurrence of active electron flow and thus photosynthetic activity at that light intensity. In contrast, aquatic *B. pseudotriquetrum* samples showed the lowest yield under almost all actinic light intensities of the four, and showed no yield at the highest light intensity.

Non-photochemical quenching (NPQ) was calculated using eq. (2) and drawn in Fig. 2. NPQ values of both aquatic and plate-cultured *Leptobryum* sp. samples showed similar patterns of increase with the increment of actinic light intensity (Fig. 2 left), while those between terrestrial and aquatic *B. pseudotriquetrum* were greatly different (Fig. 2 right). Steep increases with increase of actinic light intensity were observed in both *Leptobryum* sp. samples and terrestrial *B. pseudotriquetrum*; however, the increase was small in aquatic *B. pseudotriquetrum*.

The relative electron transport rate, which was calculated from the data in Fig. 2 using eq. (3), showed a large difference among samples; terrestrial *B. pseudotriquetrum* showed the highest, but the rate from a moss pillar was the lowest rate at any light
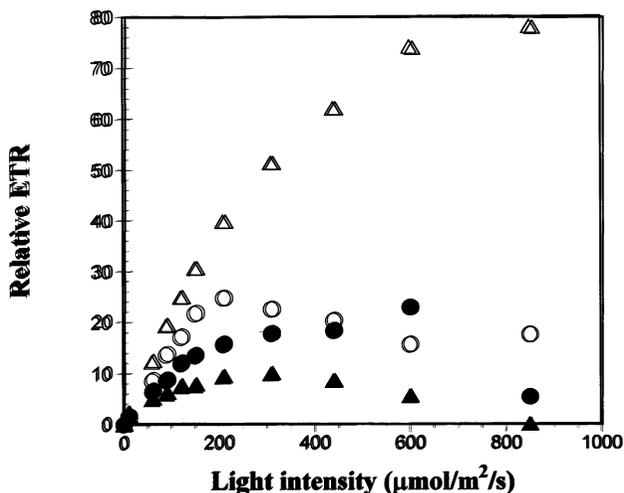
Fig. 3.   Light-ETR curves of mosses calculated using the PS II yield data in Fig. 2.   Closed and open circles indicate the relative ETR of aquatic and plate-cultured *Leptobryum* sp. samples, and closed and open triangles are the rates of aquatic and terrestrial *B. pseudotriquetrum* samples, respectively.

intensity (Fig. 3).   The rates of aquatic and plate-cultured samples of *Leptobryum* sp. ranged between the rates of terrestrial and aquatic *B. pseudotriquetrum,* and the former showed slightly lower rates than the latter.

      The light saturation point of terrestrial *B. pseudotriquetrum* $< 850 \mu$ mol m^{-2}s^{-1}, was higher than those of the test samples.   The points shown in aquatic *Leptobryum* sp. as well as the plate-cultured sample, were *ca.* $200–400 \mu$ mol m^{-2}s^{-1}, and the point of aquatic *B. pseudotriquetrum* also showed a similar value.   The light response curve, higher ETR and higher saturation point in terrestrial *B. pseudotriquetrum,* suggested that this species has adapted to a much lighter environment, while those obtained from the other samples, slower ETR and lower saturation point, seemed to be shade-plant type responses.

Chilling/heat sensitivity of *Leptobryum sp.*

      The chilling/heat sensitivity of photosystems of the aquatic *Leptobryum* sp. was experimentally checked.   Maximal PS II yield, which was measured using a dark-adapted sample and light-driven primary reactions within PS II, showed rather constantly high values of *ca.* 0.7 after temperature stress of 0–30℃ (Fig. 4).   But the maximal yield suddenly decreased when the sample was chilled or heated over below/above this temperature range.   The degree of the decreases of the yield was nearly 80% after –20℃ chilling stress for 10 min, and the maximal yields at 40 and 50℃ of heat treatments were nearly 50% and 100% reduced, respectively.

      The effective yield of PS II, which was measured under actinic light exposure and indicates overall photosynthetic yield, was clearly suppressed out of the 0–5℃ temperature range.   The different suppression patterns between the maximal and effective
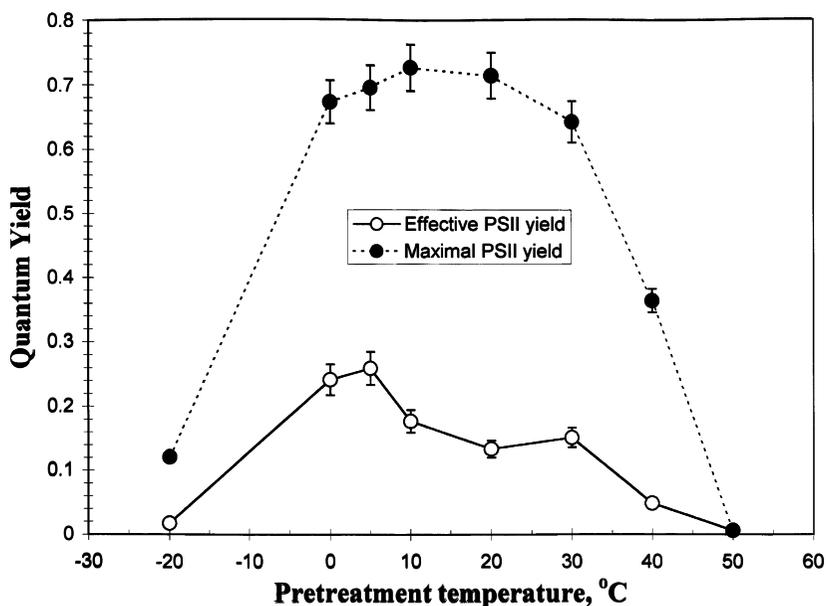
Fig. 4.   Chilling and heating sensitivity of photosystems of a moss pillar *Leptobryum* sp.   The vertical bar on each circle indicates the standard deviation among analyses.

yields, rather wide chilling/heat resistance observed in the former, indicates that PS II reaction centers are considerably more chilling/heat resistant than the overall process. This means that the overall process of *Leptobryum* sp. seemed highly chilling/heat sensitive to the point that almost no photosynthetic activity was observed after the sample was frozen at −20℃ for 10 min; or the activity was suppressed by *ca.* 30% when it experienced a high temperature of 10℃ for 10 min.

Discussion

At the lake bottom, where moss pillars are prevailing, the light intensity is not so strong as on the surrounding terrestrial habitat because of attenuation by water, ice and snow (Kudoh *et al.*, 2003b).   Even during the ice-free season (January–February), the light intensity reaching the moss habitat was *ca.* 50% of ground level and it further decreased to < 10% during the rest of the ice-covered season while the light intensity at the terrestrial habitat in summer was sometimes > 2000 μmol m^{-2}s^{-1}.   Lake bottom temperature in such a lake was rather stable with slight seasonal changes (0–12℃) compared to the terrestrial moss habitat (Kudoh *et al.*, 2003b).   The present study aimed to give answers to the hypothesis that mosses growing at lake bottoms have the ability to perform photosynthetic growth under dim light and stable low temperature.

It is well known that mosses change their morphological features when they are submerged (Lodge, 1959; Priddle, 1979; Kanda and Ohtani, 1991).   Such morpholog-ical changes, pointed out in previous papers (Lodge, 1959; Priddle, 1979; Kanda and

Ohtani, 1991), might affect the photosynthetic activity of mosses because size, thickness and color of the leaves often differ significantly (Kanda and Ohtani, 1991). Kanda and Ohtani (1991) reported that *B. pseudotriquetrum* collected from a lake in the same vicinity showed morphologically different features from the terrestrial ones; rather slender and elongated stems, small leaves and sometimes etiolated shoots were observed in the submerged samples, which are similar to the changes in the present *Leptobryum* sp. between aquatic and agar plate-cultures.

The light-PS II yield and light-ETR curves of both aquatic *Leptobryum* sp. and *B. pseudotriquetrum* samples showed shade-plant type light responses relative to the terrestrial *B. pseudotriquetrum* (Figs. 2 and 3). Under all light conditions terrestrial *B. pseudotriquetrum* showed higher PS II yield and ETR; however, the same species that grew in moss pillar (aquatic samples) showed the lowest values. Photosynthetic responses of *B. pseudotriquetrum* might be depressed concomitantly with such morphological changes, that is, $>50\%$ of slower ETR at every light intensity and great difference of light saturation point.

On the other hand, in *Leptobryum* sp., which was a primary component of a moss pillar (Imura *et al.*, 1999; Kudoh *et al.*, 2003a), light responses showed only slight differences between the aquatic samples and plate-cultured samples (Figs. 2 and 3), in spite of the great difference of morphological features (Fig. 1). These indicate the possibility that the photosynthetic light response of *Leptobryum* sp. is not depressed or enhanced greatly by the morphological changes due to transfer from terrestrial to aquatic habitats, or from aquatic to terrestrial conditions as shown in *B. pseudotriquetrum*. Another possible reason for the great differences in light response between terrestrial *B. pseudotriquetrum* and other samples is cultivating conditions; mosses grown in a moss pillar or cultured on a plate experienced only limited light and cool conditions for several months due to the experimental procedure, while *B. pseudotriquetrum* harvested in a terrestrial habitat experienced the higher natural irradiance of the Antarctic summer before our sampling from the habitat. This might explain why the light response measured in the terrestrial samples showed sun-adapted features, although we tried to allow all samples to stand under the same conditions for a few days before measurements. Further confirmation for the present estimations should be taken based on systematically designed culture experiments, or comparative measurements using natural *Leptobryum* sp. in a terrestrial habitat; however, this species has not been found in Antarctica (Imura *et al.*, 1999, 2003).

Very little change of the light-NPQ response was recorded for *Leptobryum* sp. samples under different culture conditions as shown in the light-PS II yield, while light-NPQ and light-PS II yields responses between terrestrial and aquatic samples of *B. pseudotriquetrum* were greatly different (Fig. 2). These differences of light response induced by the culture (or habitat) condition between species suggest that the latter species has more flexible photosynthetic plasticity than the former; or, in other words, the former species has only a limited plasticity of photosynthesis, that might have merit at the light-shade environment.

According to recent physiological studies on plant photosynthesis, which have investigated photo-damages to and light protection of photosystems, plants have several strategies to regulate the flow of light energy into their photosystems so as to protect

them from unrecoverable damage, which is easily induced, especially under low temperature (reviewed by Aro *et al.*, 1993; Sonoike, 1998; Ort, 2001).   There is no doubt that light-NPQ properties observed in the present mosses are one of the strategies to protect their photosystems under their habitat light and temperature conditions.   Steep increase of NPQ with increase of actinic intensity in *Leptobryum* sp. possibly suggests that the species can dissipate excess strong light energy so as to protect their light-shade adapted photosystems.   In spite of the similarity of the light-NPQ response between terrestrial *B. pseudotriquetrum* and *Leptobryum* sp., light-PS II yield at all light intensities was quite large.   This suggests that the terrestrial *B. pseudotriquetrum* shows efficient light-photosynthesis usage even if it has similar dissipation ability to *Leptobryum* sp.   This seems to be the most efficient photosynthesis under all light intensities while protecting their photosystems, but the highly efficient light-PS II yield and the light-NPQ properties were lost in the aquatic samples (Fig. 2 right).   Such efficient photosystems under limited light condition may be difficult to maintain due to high maintenance cost.   Then the aquatic *B. pseudotriquetrum* may lose the strong light protection ability through NPQ; however, further precise studies are required for confirmation of the present hypothesis.

Sensitivity to the chilling/heating stresses of the present *Leptobryum* sp. suggests that photosystems of the species are cryophilic; stress is easily induced when the temperature increases above 10℃ for only 10 min, and the primary response at PS II was clearly decreased when the sample experienced temperature above 30℃ for 10 min (Fig. 4).   Chilling treatment at −20℃ in the present experiment also induced considerable decrease in the quantum yield of PS II.   This indicates that the species is not simply a cryophilic organism but possesses a sensitive photosystem that protect it against freezing.   The lake bottom habitat, where moss pillars are prevalent is rather stable concerning temperature with slight seasonal changes and never shows sub-zero temperature; hence, the species does not necessarily possess the photosynthetic ability to withstand the wide temperature range or freezing that might occur in a terrestrial habitat.

In the present study, we summarized our preliminary experimental results on the photosynthetic light response and its temperature sensitivity to describe the features of mosses constituting moss pillars in lakes in the vicinity of the Sôya Coast, East Antarctica.   The rather shade-adapted type light response of the photosynthesis and its narrow optimum range of temperature have been discussed, leading to a hypothesis that the ecological success of *Leptobryum* sp. as a primary component of moss pillars, is due to its slightly higher photosynthetic performance under submersible condition compared to *B. pseudotriquetrum,* which was one of the most prevailing species in the terrestrial habitat in the vicinity.   However, further studies are needed for confirmation.

References

Aro, E-M., Virgin, I. and Andersson, B. (1993): Photoinhibition of photosystem II. Inactivation, protein damage and turnover. Biochim. Biophys. Acta, **1143**, 113–134.

Bopp, M. (1952): Entwicklungsphysiologische Untersuchungen am Laubmoose Protonemen. Zeitschr. f. Bot., **40**, 119–152.

Ignatov, M.S. and Kurbatova, B. (1990): A review of deep-water bryophytes with new records from USSR. Hikobia, **10**, 393–401.

Imura, S., Bando, T., Saito, S., Seto, K. and Kanda, H. (1999): Benthic moss pillars in Antarctic lakes. Polar Biol., **22**, 137–140.

Imura, S., Bando, T., Seto, K., Ohtani, S., Kudoh, S. and Kanda, H. (2003): Distribution of aquatic mosses in Sôya Coast region, East Antarctica. Polar Biosci. **16**, 1–10.

Kasper, M., Simmons, G.M., Parker, B.C., Seaburg, K.G. and Wharton, R.A. (1982): *Bryum* Hedw. collected from lake Vanda, Antarctica. Bryologist, **85**, 424–430.

Kanda, H. and Iwatsuki, Z. (1989): Two aquatic mosses in the lakes near Syowa Station, Continental Antarctica. Hikobia, **10**, 293–297.

Kanda, H. and Ohtani, S. (1991): Morphology of the aquatic mosses collected in lake Yukidori, Langhovde, Antarctica. Proc. NIPR Symp. Polar Biol., **4**, 114–122.

Kudoh, S., Tsuchiya, Y., Ayukawa, E., Imura, S. and Kanda, H. (2003a): Ecological studies of aquatic moss pillars in Antarctic lakes. 1. Macro structure and carbon, nitrogen and chlorophyll *a* contents. Polar Biosci., **16**, 11–22.

Kudoh, S., Watanabe, K. and Imura, S. (2003b): Ecological studies of aquatic moss pillars in Antarctic lakes. 2. Temperature and light environment at the moss habitat. Polar Biosci., **16**, 23–32.

Light, J.J. and Heywood, R.B. (1973): Deep-water moss in Antarctic lakes. Nature, **242**, 535–536.

Light, J.J. and Heywood, R.B. (1975): Is the vegetation of continental Antarctica predominantly aquatic? Nature, **256**, 199–200.

Lodge, E. (1959): Effects of certain cultivation treatments on the morphology of some British species of *Drepanocladus*. J. Linn. Soc. London, **56**, 218–224.

Ort, D.R. (2001): When there is too much light. Plant Physiol., **125**, 29–32.

Priddle, J. (1979): Morphology and adaptation of aquatic mosses in an Antarctic lake. J. Bryol., **10**, 517–529.

Priddle, J. and Dartmall, H.J.G. (1978): The biology of an Antarctic aquatic moss community. Freshwater Biol., **8**, 469–480.

Savicz-Lyubitskaya, L.I. and Smirnova, Z.N. (1959): New species of *Bryum* Hedw. from Bunger Hills. Inf. Bull. Sov. Antarkt. Eksped., **7**, 34–39 (in Russian).

Seppert, R.D. (1983): The status of the Antarctic moss *Bryum korotkevicziae*. Lindergia, **9**, 21–26.

Schreiber, U. (1997): Chlorophyll fluorescence and photosynthetic energy convertion: Simple introductory experiments with the TEACHING-PAM Chlorophyll Fluorometer. Effeltrich, Heinz Walz GmbH, 73 p.

Schreiber, U., Bilger, W. and Neubauer, C. (1994): Chlorophyll fluorescence as a nonintrusive indicator for rapid assessment of in vivo photosynthesis. Ecol. Stud., **100**, 49–70.

Sonoike, K. (1998): Various aspects of inhibition of photosynthesis under light/chilling stress: photoinhibition at chilling temperatures versus chilling damage in the light. J. Plant Res., **111**, 121–129.