Oecologia (1997) 110:25–31

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Effects of continuous and repeated dehydration on carbon fixation by bryophytes from the maritime Antarctic

Received: 15 April 1996 / Accepted: 28 September 1996

Abstract The effects of dehydration and rehydration on carbon exchange in 14 bryophytes from the maritime Antarctic were investigated using an infra-red gas analysis system. Continuous long-term (1–12 months) and repeated (1–6 one-month cycles) desiccation responses were investigated under controlled conditions. Loss of photosynthetic rate increased with length of dehydration period in all species, although some desiccation tolerance was observed even in those bryophytes from the most hydric habitats. Percentage retention of photosynthetic rate increased from hydric to xeric species, but this pattern was not repeated in terms of absolute rates of carbon fixation due to the high initial rates in the hydric species. Repeated cycles caused a greater loss of photosynthetic rate than continuous dehydration in hydric species, but the opposite situation occurred in mesic and xeric mosses. The latter groups were possibly better able to utilise the short periods of rehydration during cycles. In most bryophytes an increase in the percentage loss of photosynthetic rate following dehydration-rehydration occurred from spring to summer to autumn samples. This pattern was clearest in the hydric species and reduced in the xeric species. These variations were largely due to changes in the initial rates of photosynthesis during the growing season. It is suggested that this increased photosynthetic capacity is stress-sensitive, and is lost during either desiccation or winter freezing; the base photosynthetic capacity, being stress-tolerant, survives either of these events. The results obtained support the hypothesis that water availability is of importance in determining the distribution of bryophytes in the Antarctic. However, only the broad scale of variation in plant communities could be explained by these observations; other factors must be important in determining the finer scale of species distribution and community composition. The results are applicable to attempts to model the productivity of Antarctic bryophytes from known or predicted environmental data.

Key words Antarctica · Bryophytes · Carbon fixation · Dehydration cycles · Desiccation tolerance

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Introduction

Antarctic terrestrial ecosystems are dominated by bryophytes and lichens and are of relatively low biodiversity (Smith 1984, 1993). As a result of this simple structure they provide useful test systems for the study of plant communities in which fundamental questions concerning the distribution and interactions of plant species may be addressed in the absence of otherwise common complicating factors such as competition, grazing or anthropogenic influence. Bryophytes are particularly suitable as experimental organisms as they are easily sampled and usually provide relatively large physiological responses (Proctor 1982; Longton 1988).

Studies on the distribution of bryophytes in Antarctica have demonstrated clear gradations in community structure. These can be readily differentiated by the hydric status of the habitat, varying from stream-edge communities that are almost continuously wet to epilithic communities that are often dehydrated and reliant upon precipitation for wetting (Smith 1972, 1984, 1993; Longton 1988). It has been postulated that water availability is the major environmental factor determining the survival, productivity and distribution of species, and, hence, community structure of these ecosystems (Wilson 1990; Kennedy 1993a). If this hypothesis is correct, Antarctic bryophyte ecosystems would provide the opportunity to study the control of plant community structure in the simplest possible case, i.e. where the greatest part of the observed variation in communities can be attributed to a single environmental factor.

Antarctic bryophytes are exposed to varying periods of desiccation during the short summer (December to March), the frequency and length of these events, and hence the water content of the bryophytes, being habitat-dependent (Collins 1977; Goddard 1979; Pickup 1991; Kennedy 1993b). In addition, freezing during winter (April to November) may lead to longer periods of water deficiency due to the indirect effects of water removal from the cells by the freezing of external water (Burke et al. 1976).

The desiccation tolerance of mosses, particularly those from habitats that are subject to some degree of drying, is well established (reviewed in Longton 1980; Richardson 1981; Proctor 1982, 1990). Some correlation between the hydric status of habitat and water relations of bryophytes has been demonstrated in temperate mosses (Clausen 1952, 1964; Proctor 1984), but less information is available for polar mosses. Gimingham and Smith (1971) described a relationship between the ability of Antarctic mosses to take up and retain water and their habitat. Kappen et al. (1989) found lower rates of photosynthesis and some adaptation to desiccation-stress in xeric compared to mesic ecodemes of *Schistidium antarctici*, although Wilson (1990), working on the same species (identified as *Grimmia antarctici*) found no difference in the photosynthetic capacity of the two forms. Fowbert (1996) reported lower water content optima for growth in a mesic than a hydric species and higher growth rates in hydric species. However, none of these investigated the ability of the mosses to survive dehydration events. A direct correlation between desiccation tolerance and habitat has yet to be demonstrated and assessment of the role that this may play in the distribution of Antarctic bryophytes remains incomplete.

There are no reports of the relative effects of continuous and repeated dehydration-rehydration cycles in polar bryophytes, although studies of lichens have suggested that repeated cycles are less detrimental than continuous desiccation, or even beneficial in some cases (Kershaw 1985).

This paper investigates the effects of medium- and long-term desiccation and repeated dehydration-rehydration cycles on gas exchange by Antarctic bryophytes from a range of habitats. The role that desiccation-stress might play in determining the distribution of these plants and the extent to which it may explain the communities observed is considered.

Materials and methods

Experiments were carried out on 13 mosses and one liverwort collected from sites on Signy Island, South Orkney Islands. These are listed in Table 1 along with the collection site, growth form and general habitat. The species selected covered the range of forms and habitats that occur on Signy Island (Smith 1972).

Samples of 50 mm diameter and thickness dependent on the general habit of the bryophyte (Table 1) were returned to the laboratory. Water was added, if necessary, to ensure that the samples were fully hydrated. These were then left for three days to acclimatize to the experimental conditions (10 °C and 150 μmol m^{-2} s^{-1}), sufficient time to achieve full recovery from any field dehydration (M.C. Davey, unpublished work).

General experimental methods

Experiments were carried out in a constant temperature room at 10 °C (room ± 1.5, thallus ± 0.3 °C), an irradiance of 150 μmol m^{-2} s^{-1} provided by fluorescent lamps and a relative humidity of 25%. The irradiance used was saturating for these mosses at the

Table 1 Bryophyte species used, collection sites, habitat characteristics, growth form and sample thickness. Species are listed in order from the most hydric to the most xeric

Species	Collection site	General habitat	Growth form	Sample thickness (mm)
Marchantia berteroana Lehm. et Lindenb.	South Factory Cove	Hydric	Thallus	5
Calliergon sarmentosum (Wahlenb.) Kindb.	East Factory Cove	Hydric	Carpet	20
Brachythecium austro-salebrosum (C.Muell.) Kindb.	East Factory Cove	Hydric	Cushion	20
Drepanocladus uncinatus (Hedw.) Warnst.[a]	East Factory Cove	Hydric	Carpet	20
Drepanocladus uncinatus (Hedw.) Warnst.[b]	East Factory Cove	Hydric	Carpet	20
Racomitrium austro-georgicum Par.	Moraine Valley	Mesic	Cushion	20
Chorisodontium aciphyllum (Hook. f. et Wils.) Broth.	East Factory Cove	Mesic	Turf	20
Polytrichum alpestre Hoppe.	East Factory Cove	Mesic	Turf	20
P. alpinum Hedw.	Berntsen Point	Mesic	Turf	20
Tortula saxicola Card.	Marble Knolls	Xeric	Cushion	20
Andreaea depressinervis Card.	East Factory Cove	Xeric	Cushion	20
Ceratodon cf. *purpureus* (Hedw.) Brid.	Paternoster Valley	Xeric	Turf	10
Schistidium antarctici (Card.) Savicz. et Smirn.	Paternoster Valley	Xeric	Cushion	10
Andreaea gainii Card.	East Factory Cove	Xeric	Cushion	10

[a] *Drepanocladus uncinatus* from wetter site
[b] *D. uncinatus* from drier site

experimental temperature (Davey and Rothery, in press). Prior to gas exchange measurements, any excess water was removed by tamping with tissue paper and samples left in the dark for 1 h.

Gas exchange measurements were made using a Binos II infrared gas analysis (IRGA) system in open differential mode. Both analysis and reference chambers were of 40 cm^3 capacity and incorporated small fans to ensure thorough mixing of the airstream. Air flowrate was 500 ml min^{-1} controlled using Platon GT rotameters. Samples were placed in the analytical chamber for two minutes, sufficient time to reach equilibrium, and the carbon dioxide differential noted. Respiration was measured, the samples left to acclimatize in the light for 1 h and net photosynthesis then measured.

Results were converted from ppm CO_2 differential to carbon gain or loss using the equation appropriate to rotameters given by Janác et al. (1971) (Eq. 3.21, p. 163). Gross photosynthesis was calculated as the difference between carbon exchange in the light and the dark.

At the end of experiments samples were dried at 105 °C for 24 h, weighed, ashed at 550 °C for 24 h, reweighed and ash-free dry weight (AFDW) calculated.

Long-term dehydration experiments

Fifty samples of each bryophyte were collected on three occasions: spring (November 1993), summer (January-February 1994) and autumn (April 1993). Respiration and photosynthesis were measured and the samples left to dry. After 1 month ten replicates of each species were chosen at random, rehydrated for 3 days, respiration and photosynthesis remeasured and AFDW determined. This procedure was repeated after 2, 3, 6 and 12 months.

Repeat dehydration-rehydration cycles

Ten samples of each bryophyte were collected on two occasions: early summer (December 1994) and late summer (March 1994). Respiration and photosynthesis were measured and the samples left to dry. After 1 month the samples were rehydrated for 3 days, respiration and photosynthesis remeasured and the samples again allowed to dehydrate. This procedure was repeated monthly to 6 months (six dehydration-rehydration cycles). AFDW was then determined.

Results

In no experiment was there any pattern to the changes in the respiration rates of the bryophytes. These fluctuated widely, both in direction and magnitude, and no predictable effects of continuous or repeated dehydration were observed. As a result of variations in respiration, the rates of net photosynthesis also varied unpredictably. Therefore, all following discussion will refer to the effects of dehydration on the rates of gross photosynthesis which showed consistent patterns of change.

Long-term dehydration experiments

In general, a decrease in gross photosynthetic rate was observed in all species over the course of all three experiments. Typical curves are shown in Fig. 1 for *Polytrichum alpinum*. Results are presented both as a percentage of the photosynthetic rate determined before dehydration and as an absolute photosynthetic rate. Curves obtained from samples collected at different seasons followed similar patterns: a fall in photosynthetic rate being followed by a levelling of the curve as a residual rate was maintained even after long periods of dehydration. In some species, particularly those from xeric habitats, the period of major decrease was preceded by a period of steady photosynthesis, lasting for between one and three months before a decline was observed. An example is given for *Andreaea gainii* in Fig. 2. Also seen in Fig. 2 is an increase in the rate of photosynthesis in some samples above that measured at the start of the experiment. Again this was a feature of some samples from the more xeric habitats.

The percentage retention curves can be characterized by the slope of the curve from the start of the experiment (at 100%) to the end of the steepest fall in the curve. These data are presented in Table 2, where the more negative the figure given the greater the loss in photosynthetic rate. Two patterns emerge: loss of photosynthetic rate increased from the xeric to hydric species, and from spring to autumn samples for most species. The second of the two trends is also seen in Fig. 1a where samples of *P. alpinum* collected in the spring retained a greater percentage of their photosynthetic rate than those collected in the summer, which in turn were

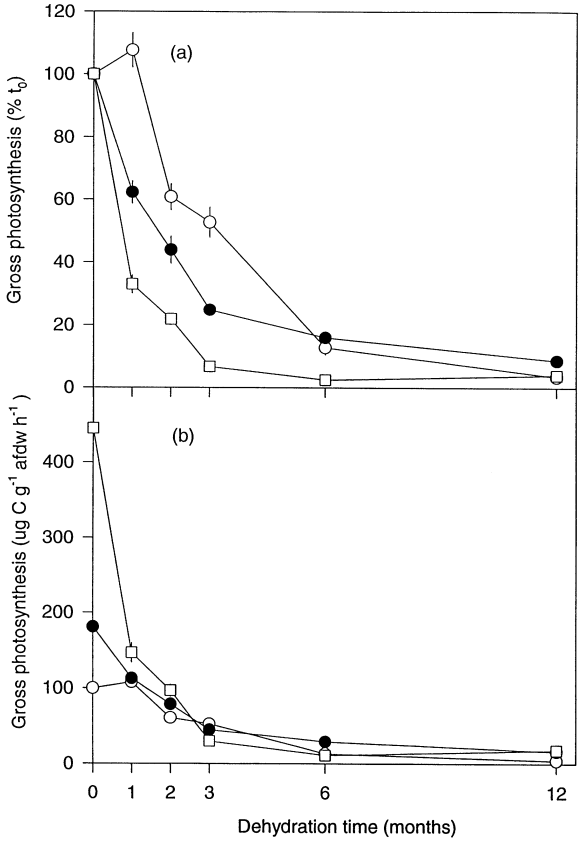

Fig. 1a,b Effects of continuous dehydration on gross photosynthesis by samples of *Polytrichum alpinum* collected in ○ spring, ● summer and □ autumn. Results are presented as means of either **a** percentage of pre-dehydration rate or **b** absolute rate as means. *Error bars* indicate SEs ($n = 10$); where not shown these were smaller than the symbols used

greater than those collected in the autumn. Figure 1b demonstrates that this difference is attributable to differences in the initial rates of photosynthesis between the samples. The initial absolute rate of photosynthesis increased from spring to summer to autumn, and it is this increase that was lost during the first months of dehydration, after which photosynthetic loss was the same in all three sets of samples. Similar effects were observed in the other species.

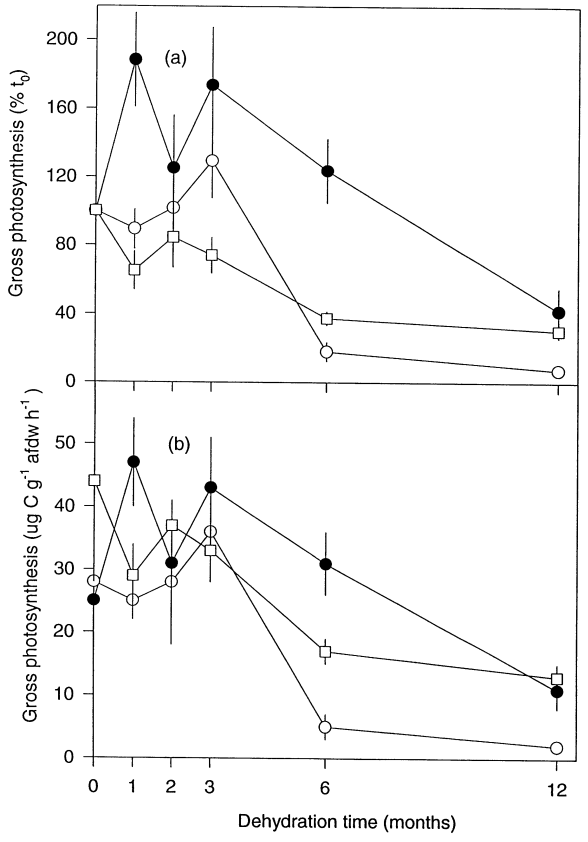

Fig. 2a,b Effects of continuous dehydration on gross photosynthesis by samples of *Andreaea gainii*. Results are presented as means of either **a** percentage of pre-dehydration rate or **b** absolute rate as means. Symbols and error bars as Fig. 1

As the absolute rates of photosynthesis from each season were similar, after the first month of dehydration, the results from the subsequent months can be amalgamated. The mean rates of photosynthesis are given in Table 3. Although there were some notable results, particularly the high retention of photosynthetic rate in *Tortula saxicola* and *Ceratodon* cf. *purpureus*, there was no clear pattern to the rate of gross photosynthesis maintained by the samples. The correlation between percentage loss of photosynthetic rate and the hydric status of the habitat seen in Table 2 appears to be largely attributable to differences in the initial rates of photosynthesis in mosses from different habitats.

Repeat dehydration-rehydration experiments

There were few differences in results between the samples collected in early summer and those collected in late summer. The two sets of results were amalgamated and are given in Fig. 3. As in the long-term experiments, loss of photosynthetic rate increased from xeric through mesic to hydric species, although the differences between the xeric and mesic species were less clear than those between the mesic and hydric species.

Trends in the absolute rate of photosynthesis were again less obvious than those for the percentage photosynthesis (Table 4). Apart from bryophytes where no

Table 2 Retention of gross photosynthetic rate over long periods of dehydration

Species	Retention of photosynthesic rate (% · month^{-1})		
	Spring	Summer	Autumn
M. berteroana	9	17	9
C. sarmentosum	77	65	9
B. austro-salebrosum	23	56	17
D. uncinatus[a]	90	81	67
D. uncinatus[b]	90	84	64
R. austro-georgicum	100	91	89
C. aciphyllum	105	93	56
P. alpestre	93	85	85
P. alpinum	85	74	47
T. saxicola	96	92	84
A. depressinervis	101	89	89
C. cf. *purpureus*	211	102	85
S. antarctici	92	89	86
A. gainii	106	124	89

[a] *D. uncinatus* from wetter site
[b] *D. uncinatus* from drier site

Table 3 Absolute rates of gross photosynthesis (μC·g^{-1} AFDW · h^{-1}) as mean of three long-term dehydration experiments

Species	Gross photosynthesis after number of months			
	2	3	6	12
M. berteroana	31	28	42	1
C. sarmentosum	42	33	22	11
B. austro-salebrosum	54	25	6	9
D. uncinatus[a]	65	46	24	1
D. uncinatus[b]	60	40	16	4
R. austro-georgicum	39	35	18	10
C. aciphyllum	42	37	24	16
P. alpestre	66	56	24	13
P. alpinum	79	43	18	13
T. saxicola	105	98	79	56
A. depressinervis	50	43	20	17
C. cf. *purpureus*	53	43	26	35
S. antarctici	70	61	36	4
A. gainii	32	37	18	9

[a] *D. uncinatus* from wetter site
[b] *D. uncinatus* from drier site

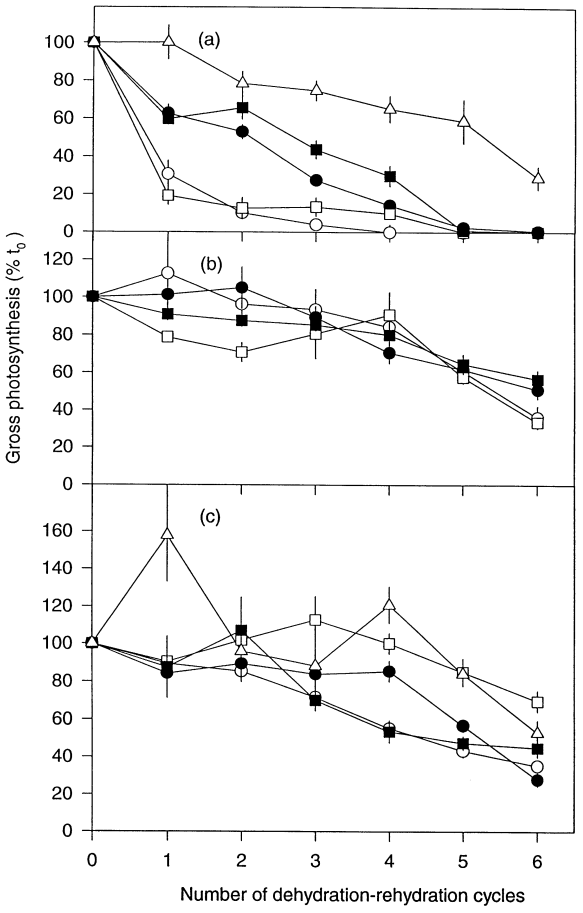

Fig. 3a–c Effects of dehydration-rehydration cycles on gross photosynthesis expressed as a mean percentage of pre-dehydration rate. **a** Hydric species: ○ *Marchantia berteroana*, ● *Calliergon sarmentosum*, □ *Brachythecium austro-salebrosum*, ■ *Drepanocladus uncinatus* from wetter site, Δ *D. uncinatus* from drier site. **b** Mesic species: ○ *Racomitrium austro-georgicum*, ● *Chorisodontium aciphyllum*, □ *Polytrichum alpestre*, ■ *P. alpinum*. **c** Xeric species: ○ *Tortula saxicola*, ● *Andreaea depressinervis*, □ *Ceratodon* cf. *purpureus*, △ *Andreaea gainii*. *Error bars* as Fig. 1

retention was observed, the interspecific differences were small, particularly after the second cycle, and no pattern of results attributable to the habitat of the plants was detected.

These data may also be compared to those from the long-term experiments. The ratio of the percentage retention of the bryophytes (from early summer samples) after 1-, 2-, 3- and 6-monthly cycles to that from long-term experiments (from spring, summer or a mean of the two as appropriate dependent upon the dates of sample collection) after the same number of months is given in Table 5. The data for 1 cycle/month should be 1.0 as the two treatments were identical to this point, and this is generally observed. At later times, numbers below 1.0 indicate that the repeatedly dried samples retained photosynthetic capacity less well than the continuously dried samples, and the reverse for numbers above 1.0. The clearest results were after six cycles/months where the hydric species from repeat experiments suffered far more than the continuously dried samples, whereas the mesic and hydric species have survived slightly better in the repeat experiments.

Discussion

As would be expected from previous work on bryophytes from both Antarctic and other ecosystems (Proctor 1982; Longton 1988), dehydration events led to a reduction in the rate of photosynthesis, this loss increased with the length of the dehydration period. However, all species retained some photosynthetic capacity for 6–12 months. Although such survival is typical of mesic and xeric bryophytes (Proctor 1982; Longton 1988), some previous studies have reported that hydric mosses, often the same species as used here, are highly drought-sensitive and die after a few hours, desiccation (Oechel and Sveinbjörnsson 1978; Longton 1988; Sveinbjörnsson and Oechel 1992). Such apparent contradictions suggest that drought-tolerance is possible in these species, but is not always manifested and may

Table 4 Absolute (μg C· g^{-1} AFDW· h^{-1}) rates of gross photosynthesis after monthly dehydration-rehydration cycles

Species	Months						
	0	1	2	3	4	5	6
M. berteroana	227	132	46	18	0	0	0
C. sarmentosum	210	107	100	58	30	5	1
B. austro-salebrosum	286	74	47	38	28	0	0
D. uncinatus[a]	143	91	104	39	43	1	0
D. uncinatus[b]	87	106	76	84	56	51	25
R. austro-georgicum	38	34	36	30	32	23	14
C. aciphyllum	48	51	68	44	34	30	24
P. alpestre	78	63	71	80	71	45	26
P. alpinum	99	94	101	98	79	64	56
T. saxicola	128	95	110	85	71	55	45
A. depressinervis	85	70	86	84	73	48	24
C. cf. *purpureus*	55	53	58	73	55	47	38
S. antarctici	97	92	86	66	52	46	43
A. gainii	40	78	39	33	48	34	21

[a] *D. uncinatus* from wetter site
[b] *D. uncinatus* from drier site

Table 5 Ratios of percentage photosynthetic retention in repeat dehydration-rehydration experiments to those in long-term dehydration experiments after a given number of monthly cycles/number of months

Species	Ratio of retention of photosynthesis after number of cycles/months			
	1	2	3	6
M. berteroana	1.0	1.5	0.6	0.0
C. sarmentosum	1.0	1.4	1.0	0.2
B. austro-salebrosum	0.8	0.9	1.9	0.0
D. uncinatus[a]	1.1	1.6	0.6	0.0
D. uncinatus[b]	1.1	1.0	1.5	0.7
R. austro-georgicum	1.0	1.0	0.9	1.2
C. aciphyllum	1.0	1.4	1.0	1.6
P. alpestre	1.0	1.4	1.9	1.2
P. alpinum	0.9	1.7	1.9	16.2
T. saxicola	0.9	1.3	1.1	1.0
A. depressinervis	0.9	1.3	1.3	1.2
C. cf. *purpureus*	1.4	1.3	1.5	1.2
S. antarctici	1.1	1.0	1.3	1.4
A. gainii	1.0	0.9	1.1	1.7

[a] *D. uncinatus* from wetter site
[b] *D. uncinatus* from drier site

be linked to pre-dehydration acclimation conditions, as observed in the seasonal variations in tolerance discussed later, and previously recorded for temperate mesic bryophytes (Clausen 1952). The desiccation periods survived by the bryophytes were in excess of any likely to be encountered in the maritime Antarctic where plants are wetted at least once a year by snowmelt and regularly during the summer by precipitation (Goddard 1979; Walton 1984; Longton 1988).

A clear trend of increasing percentage retention of photosynthetic rate was observed from hydric to mesic to xeric species after both single and repeat dehydration-rehydration cycles. Loss of photosynthetic rate in the hydric species following dehydration represented a large proportion of the initial capacity. However, no species was as drought-sensitive as those bryophytes from wet, temperate habitats which can be killed by even slight drying (Clausen 1952; Proctor 1982). These results were not repeated in the values for absolute rates of photosynthesis, which show no trend with habitat in single drying events and separated only the hydric species in the repeated cycles. The present study considered only the recovery of photosynthetic capacity following dehydration and rehydration. Neither the fate of the carbon fixed, whether to growth in those species not damaged by drying or to the repair of damaged membranes in other species, nor the loss of carbon through solute leakage via such damaged membranes following rehydration (Brown and Buck 1979) were determined. It is likely that less damaged species will be able to return more rapidly to the utilization of fixed carbon for growth.

Comparison of continuous and repeated drying regimes demonstrated that the hydric species suffered greater loss of photosynthesis during repeated cycles. This suggests that the dehydration-rehydration event was more damaging to hydric bryophytes than the time spent desiccated, a conclusion supported by the large loss of photosynthetic rate that occurred in these species after a single cycle. In contrast, in mesic and xeric species greater recovery was observed from repeated cycles. Studies on temperate mosses have shown greater survival after repeated wet/dry cycles, attributed to "drought-hardening" (Dilks and Proctor 1976a). It is also likely that the rehydration period during each cycle (3 days) was sufficient for some growth to occur in those species in which return to positive net photosynthesis was rapid.

In most species a decrease in percentage retention of photosynthesis was observed as the growing season progressed. Measurements of absolute rates of photosynthesis demonstrated that these differences were almost entirely due to variations in the initial rate of photosynthesis determined at t_0. As all samples were given adequate time to rehydrate/acclimatize to the test conditions it is unlikely that these differences were due to variations in the hydric state of the samples collected. Instead, the photosynthetic capacity of the bryophytes increased as the growing season progressed, and was reduced during winter. It is suggested that during desiccation, the stress-sensitive component of the photosynthetic capacity was lost whilst the stress-tolerant component remained. This hypothesis is supported by the observation that the seasonal changes were greatest in hydric and mesic species that were not subject to summer desiccation, and small or undetectable in xeric species that were subject to regular drying events to return the photosynthetic capacity to its base level.

Similar seasonal tolerance patterns of spring maxima and autumn minima have been described for mosses from temperate regions (Proctor 1982). Dilks and Proctor (1976b) reported a higher rate of photosynthesis by the hydric liverwort *Plagiochila spinulosa* at t_0 during summer than the rest of the year, with this increase being lost on dehydration and, although results for mesic and xeric species were less clear, demonstrated a decrease in t_0 photosynthesis-relative desiccation-tolerance through the growing season. Such considerations may also be important in some reports of desiccation-hardening of mosses following dehydration pre-treatments (Dilks and Proctor 1976a). However, other studies have described increases in desiccation-tolerance in terms of factors other than photosynthesis at various times of year (reviewed in Proctor 1982). It is clear that there are interspecific differences in the patterns of desiccation-tolerance in bryophytes, and that a single mechanism is probably not applicable in all scenarios.

The above hypothesis and pattern of reduced desiccation-tolerance during summer may seem contrary to the idea of "drought-hardening" and increased desiccation-tolerance during dry periods in Antarctic and temperate bryophytes (Proctor 1982; Longton 1988). However, this is only the case if summer is regarded as the major period of bryophyte desiccation. If instead, the less severe, but continuous, long-term dehydration brought about by the indirect effects of freezing (Burke

et al. 1976), which affect bryophytes in the same manner to direct dehydration (Dilks and Proctor 1975), is the major source of desiccation stress, then the results are consistent.

The distribution of bryophytes and the composition of plant communities in Antarctica are often explained by the differences in the availability of water between habitats (Smith 1984; Kennedy 1993a). The results presented here partially support this view. The species from hydric habitats are drought-sensitive, particularly to repeated drying events, and this may explain their inability to colonise areas of limited water availability. However, the separation of mesic and xeric species is less convincing, and the results cannot be used to explain the fine-scale distribution of species within habitats of similar water availability. It is clear that, even in these simple ecosystems, the distribution of plant species cannot be satisfactorily explained by a single environmental factor.

Although the minimum experimental dehydration period of one month was greater than that likely to be encountered in northern maritime Antarctica (Goddard 1979; Walton 1984; Longton 1988), they could be encountered in southern maritime or continental Antarctica, where some of these species also occur (Longton 1988). In addition, the results are still applicable to short-term dehydration events. The results were very similar to those obtained in short-term dehydration-rehydration experiments on samples collected at the same time of year (M.C. Davey, unpublished work). Therefore, the results can be used with some confidence in relation to any dehydration event that is observed in environmental monitoring programmes, and can be readily applied to models of bryophyte growth in response to known or predicted environmental conditions in the manner already attempted for lichens (Bölter et al. 1989; Schroeter et al. 1995).

Acknowledgements Thanks are due to the British Antarctic Survey for providing facilities for this work. Dr. R.I. Lewis Smith provided advice throughout. Dr. P. Convey commented on an earlier draft of the manuscript.

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