

## Ecology of *Rhacomitrium lanuginosum* (Hedw.) Brid.

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### Abstract

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*Ecology of Rhacomitrium lanuginosum* (Hedw.) Brid. REP KEVO SUBARCTIC RES STAT  
10. 43—54. Illus. 1973. — Net photosynthesis and its dependence on temperature, light  
and moisture have been studied in *Rhacomitrium lanuginosum* (Hedw.) Brid. strains  
from Spitsbergen, Finnish Lapland, S Finland, W Norway, the British Isles, Austrian  
Alps and from S Georgia. The effect of freezing was also studied. The optimum  
temperature in high light intensities of 12000—15000 lux was ca.  $+5^{\circ}\text{C}$ , and the mini-  
mum  $-8^{\circ}$  to  $-10^{\circ}\text{C}$  in all the different strains. The maxima show larger variation  
between ca.  $+25^{\circ}$  to  $+30^{\circ}$  in short-time experiments. The activation after low tempera-  
ture of  $-30^{\circ}\text{C}$  is very rapid — ca. 60 % during the first three hours in all strains.  
It seems that there are hardly any forms clearly adapted to e.g. arctic and temperate  
regions in this very cosmopolitan moss, as regards the temperature. The moss is "preadapt-  
ed" to a very wide ecological temperature variation. Moisture conditions must be very  
important to the distribution of this plant. The rhythm of light may have some signi-  
ficance as an ecological factor, and the high demand of light restricts the habitats to  
open rocks and bogs. Comparisons are made to *Pleurozium schreberi*.

### 1. Introduction

*Rhacomitrium lanuginosum* (Hedw.) Brid.  
is a widely distributed moss species in the  
maritime Arctic (STEERE 1954) where it may  
be one of the most common and abundant  
mosses (HERZOG 1926) forming stands particu-  
larly on non-calcareous slopes (cf., however,  
TALLIS 1958) at rather high elevations, but also  
close to the sea level. It is common e.g. in  
Ellesmere Land (BRASSARD 1971), in the whole  
of Greenland (HOLMEN 1960), in Spitsbergen  
(STÖRMER 1940; observations also by the au-  
thors) and in the Siberian Arctic (LAZARENKO  
1957). It is widely distributed in the temperate  
zones, too, particularly in oceanic climate re-

gions and on mountains all over the globe  
(HERZOG 1926; TALLIS 1958). Although the  
species is to be regarded mainly as oceanic in  
its ecological demands, it must be ecologically  
quite adaptable, considering its occurrence in  
less oceanic distributional regions, e.g. in Lap-  
land and in many continental areas in the Ar-  
ctic.

In fact this moss is a real cosmopolitan.  
Many attempts have been made to divide the  
species into intraspecific taxa (PODPERA 1954),  
but apparently the great variability caused by  
external conditions has confused the taxonomy  
(cf. TALLIS 1959). Is the moss really so flexible  
that the same genetical constitution can respond  
"advantageously" to the wide environmental

temperature, moisture and light variations and stand the competition of different plant species with different adaptational types? Or are there ecologically distinct races, genetically adapted to different environments (i.e. different "provenances" as in all vascular plants with wide distributional areas)? These questions (cf. RASTORFER 1972) were among the stimuli leading to this investigation. In the frames of IBP it is also important to investigate whether the various growth rates in different parts of the globe reflect differences of the environment, or various response types of a plant called *Rhacomitrium lanuginosum*.

## 2. Material and methods

The *Rhacomitrium* material used was from the following areas:

1. The Subarctic Research Station Kevo in Utsjoki, Finnish Lapland (lat. 69°45'N). The moss grows there on the boulder field of Jesnälvaara mountain at the height of about 250 m. The species is not very rare in the area but does not form continuous stands. These northernmost mountains in Lapland have some oceanic features, which seem to determine the distribution of *Rhacomitrium lanuginosum* in Finland (JALAS 1955). The habitat is, however, not well protected against the low temperature in the winter time because the snow cover may be rather low or temporarily absent. Thus temperatures of e.g. -20° to -30° must belong to the environmental features for the species in this season, as shown in the description of the area (KALLIO 1964; KALLIO et al. 1969).

2. South Finland, Yläne, Nousiainen and Turku (lat. 60°27'N). The species grows on open weathered acid granite rocks as rounded isolated tufts, often partly covered by *Cladonia* lichens. This area is the most oceanic corner of Finnish mainland, but when compared with W Norway very continental.

3. Spitsbergen (Svalbard), Ny Ålesund (lat. 78° 55'N), a real arctic area, on the heaths near the sea level. Material collected by the Kevo expedition in August 1972.

4. West Norway, Bergen (lat. 60°23'N), one of the most oceanic areas in Fennoscandia, specimens representing an epilithic *Rhacomitrium lanuginosum* society, typical of areas with high precipitation (LYE 1966), this material sent by conservator D. Moe.

5. Ireland, Glengary (lat. 54°12'N), material sent by Dr. G. G. Doyle.

6. Scotland (lat. 57°10'N) to SW of Banchory, north side of valley of River Avon, Aberdeenshire, dry, granite block scree. This material was sent by Dr. R. L. Lewis Smith.

7. Wales, Llandegfan Common, Anglesey (lat. 53° 14'N) from siliceous rocks, collected by Prof. Richards. — The localities 4—7 represent oceanic areas.

8. The Austrian Alps at the height of 600 m, P. burger See near Innsbruck (lat. 47°17'N), material sent by Dr. W. Moser.

9. South Georgia, Royal Bay (lat. 53°30'S), moderately exposed rock ledge, ca. 150 m N side of Moltke Harbour. This material was collected at the end of January 1972 and held out of doors until April, then transported in a ship's vegetable store, the voyage taking five weeks. Thereafter the material was "cultivated" out of doors in Birmingham for four months, and was sent to our laboratory by Prof. S. W. Greene.

*Pleurozium schreberi* was taken as a representative of a more chionophilous habitat and of a forest ecosystem having also depauperate forms towards the north (STEELE 1954: 427). This moss is, however, a panboreal species reaching up to the Arctic (HERZOG 1926: 232), and is common particularly in subarctic and temperate zones in Europe and in Siberia (KATENIN & BOCK 1970) as well as in N America.

Specimens from Kevo and Turku area were compared. Some measurements were also made with *Hylocomium proliferum* and some other species from Turku. The mosses were sent to our laboratory mostly by air and the experiments were started as soon as possible. Often, however, this took some days, and meanwhile the mosses were kept in a culture cabin at the temperature near 0°C and the light intensity ca. 4000 lux. In culture cabins the mosses retain their activity unchanged for many weeks. The net photosynthesis was studied by URAS, Infra-Red gas analyzer, the technique being the same as in earlier experiments by the authors (cf. KALLIO & HEINONEN 1971). The moss was moistened with distilled water so that the water % was between 200 % and 400 % dwt. Thereafter the specimens were transferred to assimilation chambers, in sizes 0.5 or 0.9 dm<sup>3</sup>. These chambers are thermostated and equipped with a moistening bottle. In the experiments in which responses to different temperatures were measured, the temperature was changed in steps of 5°, and one hour was the shortest interval between the measurements. The flow of air was 10 liters/hour.

The light intensity in these experiments was 12000—14000 lux. This is the saturated light intensity for *Rhacomitrium*; for *Pleurozium* this is apparently too high an intensity. An illumination of 6000 lux in the rhythm of 12 + 12 hours was used in longer experiments. It was possible in these conditions to keep the specimens continuously in the assimilation chambers for many days with the activity being constant. The moisture did not change significantly during five days, owing largely to the reduction of the air flow to two liters/h for the night time.

The moss was mounted in a Petri dish, diameter 9 cm. The density of the tuft was kept as normal as possible. The moss carpet was cut so that it was 2 cm (*Rhacomitrium*) or 3 cm thick (*Pleurozium*, *Hylocomium*).

Responses to the low temperature were examined in all strains. The activity was measured first at 0°, after which the temperature was lowered at a rate of 6°/hour down to -30°C, where it was kept over night (i.e. for 12—16 hours). Thereafter the temperature was raised at the same rate. The activity after the cold treatment and the "recovery" were observed. This method was used by the authors in their lichen experiments (KALLIO & HEINONEN 1971; cf. also KAPPEN & LANGE 1972).

Experiments inquiring into the possible stress of nitrogen deficiency for the net photosynthesis in mosses were carried out as follows: fresh moss material was submerged into a solution of KNO<sub>3</sub> (0.1 or 0.01 g/liter dist. water). A control moss was dipped only in distilled water. These treatments were repeated every day, the net photosynthesis was measured every week at +5°C in optimum light conditions, and the rest of the time these mosses were kept in culture cabins at a temperature of +5°C and in the rhythmic light, 12 hours 4000 lux and 12 hours dark.

## 3. Results

### 3. 1. *Rhacomitrium lanuginosum*

The curves in Fig. 1 show the responses of the net photosynthesis of the different strains to the temperature. In Fig. 2 the curves are drawn so that in all the 9 different strains the maximum value is plotted to 100 %, and all the other values are indicated as percentages of this maximum value. It is seen that the optimum temperature is at +5°, the minimum for the compensation near -10°, and the maximum temperature near +30°. At both ends of the curves the time factor is important: at the temperature of +30° the inten-

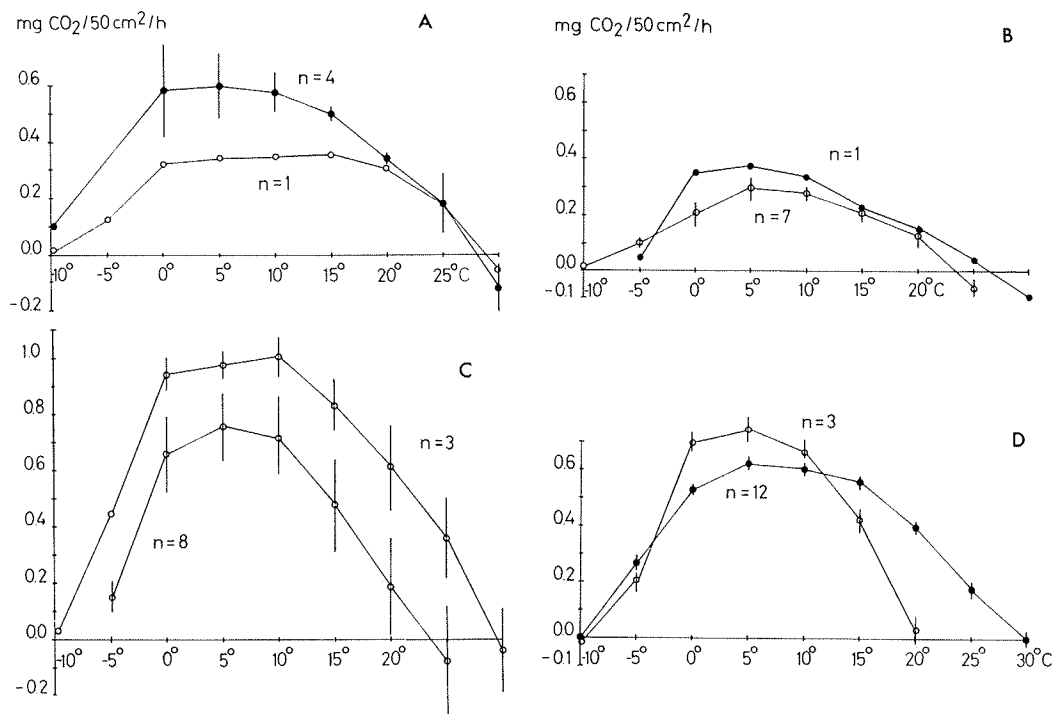


Fig. 1. Temperature response of net photosynthesis in *Rhacomitrium* strains. A = Ny Ålesund (dots, 23. 8.—4. 9. -72) and S Georgia (circles, 28.—30. 9. -72), B = Wales (dots, 27.—31. 10. -72) and Kevo (circles, 11.—26. 11. -71), C = Glenamoy (upper curve, 19.—25. 5. -72) and S Finland (x), D = Bergen (circles, 13.—20. 1. -72) and Piburger See (dots, 29. 4.—9. 5. -72).

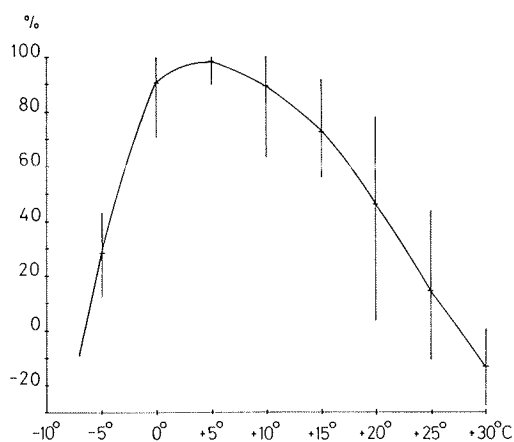


Fig. 2. The curve indicates the mean value of the curves (see Fig. 1.); the maximum value is plotted to 100 % and the other values are given as percentages of this value.

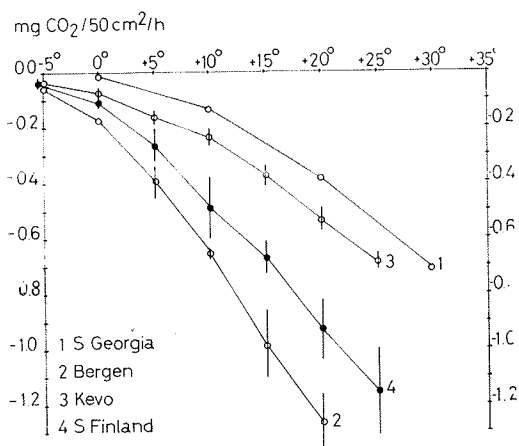


Fig. 3. Respiration as dependent on temperature in some *Rhacomitrium* strains.

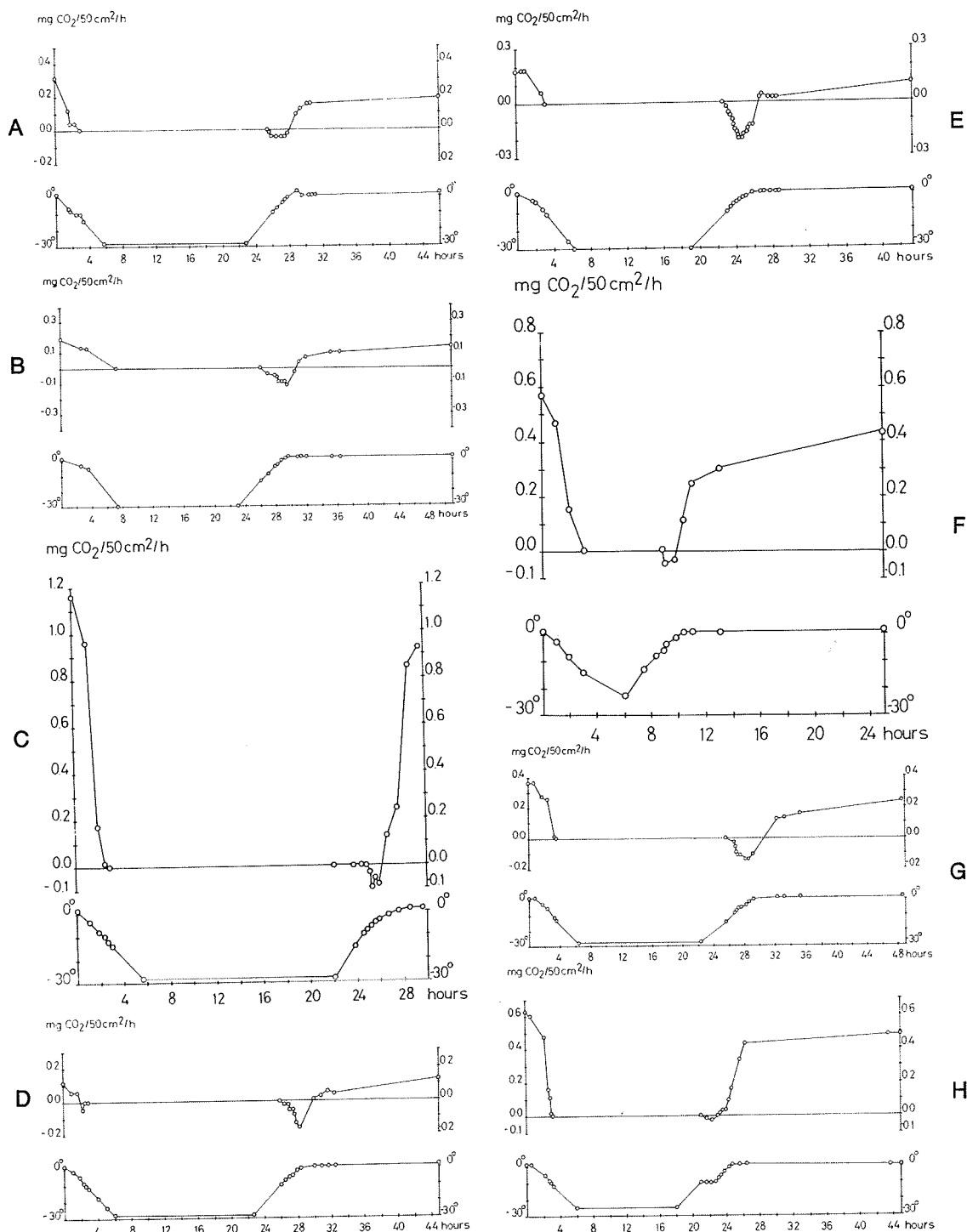


Fig. 4. A—H. Freezing experiments with different strains of *Rhacomitrium lanuginosum*. The lower curve indicates the temperature during freezing. The upper curve indicates the CO<sub>2</sub> consumption before the treatment at 0°C, respiratory surges during the freezing, and the reactivation after freezing. A = Kevo (3.—8. 11. -72), B = Ny Ålesund (6.—9. 10. -72), C = S Finland (13.—14. 10. -72), D = Bergen (25.—27. 10. -72), E = Scotland (28. 9.—1. 10. -72), F = Glenamoy (18.—20. 5. -72), G = Wales (1.—3. 11. -72), H = Piburger See (8.—10. 5. -72).

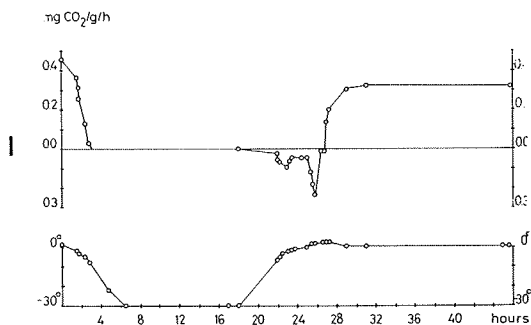
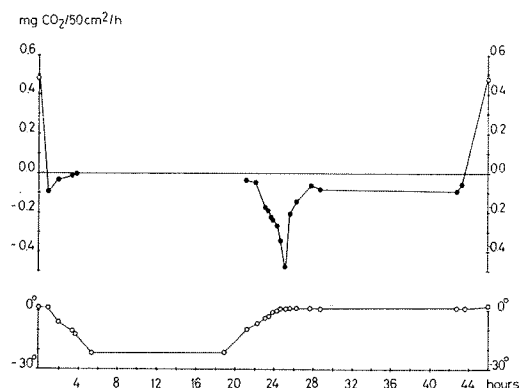


Fig. 4. I (continued page 46). S Georgia (2.—4. 10. -72).


 Fig. 5. Freezing experiment in the dark. *Rhacomitrium* strain from S Finland (18.—22. 12. -72). The light period has started at 44 hours.

sity decreases within a few hours and is irreversible; at  $-10^{\circ}$  the positive assimilation proceeds for many hours. The form of the curve is rather flat in comparison with many other plants. This means that the moss is not sensitive to temperature variations in the wide range between  $-5^{\circ}$  and  $+15^{\circ}$ .

In the respiration curves there are essential differences between the different strains (Fig. 3).

The effect of the low temperature is indicated by the curves in Fig. 4. The lower curve shows the change of the temperature during the experiment and in the upper curve the  $\text{CO}_2$ -content fixed or released, is indicated. When the temperature goes down at the rate of  $6^{\circ}/\text{h}$ , the activity will continue down to ca.  $-10^{\circ}$ . If the air flow to the cuvette is closed, some respiration can be observed in all strains in temperatures between  $-10^{\circ}$  and  $-15^{\circ}$ , too.

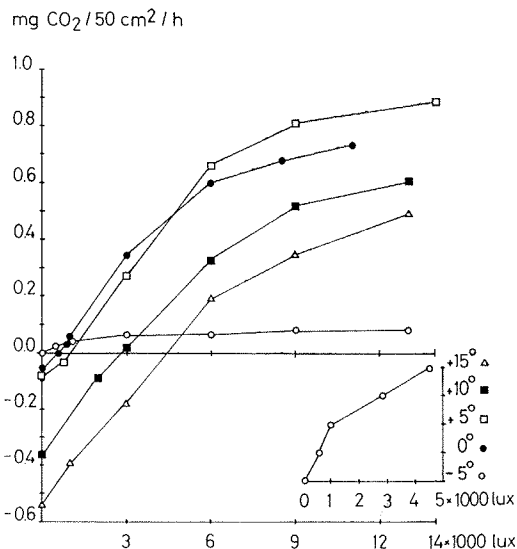
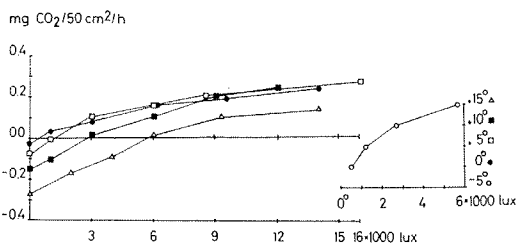


Fig. 6. Dependence of net photosynthesis on light intensity in different temperatures. The compensation points are indicated by the smaller curve. A = Kevo strain, B = S Finland strain.

The absolute lowest limit was not measured, but our normal method (without the continuous air circulation) revealed respiration at  $-15^{\circ}$  in some experiments in both Kevo and Yläne strains.

At  $-30^{\circ}$ , the air having been closed for 15 hours, no accumulation of  $\text{CO}_2$  was observed.

When the temperature goes up, a clear respiration peak, i.e. a release of  $\text{CO}_2$  was always seen in our experiments at the temperature between  $-10^{\circ}$  and  $0^{\circ}$ . The positive net assimilation usually takes place below  $0^{\circ}$ . Also in the dark, the curve of  $\text{CO}_2$  surges has almost the same form (Fig. 5).

When the temperature is made constant at  $0^{\circ}$ ,  $\text{CO}_2$ -consumption increases rapidly during the first three hours. In all strains the recovery of the net photosynthesis was on an average 60 % of the value measured before freezing. In the following hours reactivation goes on,

but on an average only ca. 70 % of the level previous to freezing was reached. The control specimen that was kept in the assimilation chamber in continuous light and at the temperature of  $0^{\circ}$  for the same time as in the freezing experiment also showed a decrease but not in the same degree. That the high light intensity in low temperature conditions is the cause for the decreasing activity in these experiments, is seen in Fig. 5 which shows a moss that has been in the dark during the freezing. The reactivation is total. Thus no "cold damage" in the short-time freezing experiments is observed. There were no significant differences between the strains examined. No differences were found in responses to freezing in autumn and spring experiments. Apparently no seasonal hardening process is needed for the reactivation in the *Rhacomitrium* strains studied.

The response to the light intensity is seen in Fig. 6. The compensation point varies between 5500 and 500 lux in *Rhacomitrium*, and the optimum (during short period) is apparently at the level of 12000–14000 lux in the optimum temperature conditions ( $+5^{\circ}$ ) used in our experiments. The dependence of the light compensation point on temperature is seen in Fig. 6. There are considerable differences in the light response curves when different strains are compared. In continuous low light conditions the compensation point goes down in constant tem-

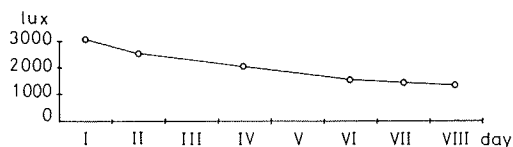


Fig. 7. The change (decrease) of the compensation point in continuous low light conditions and in constant temperature.

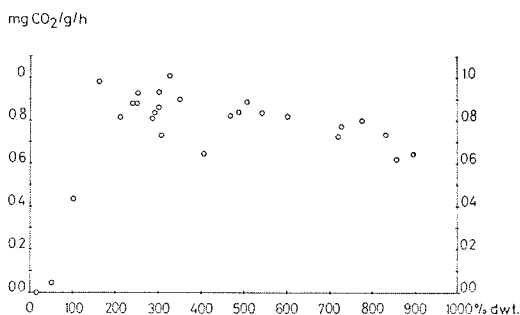


Fig. 8. The effect of moisture on net photosynthesis in *Rhacomitrium* (S Finland strain).

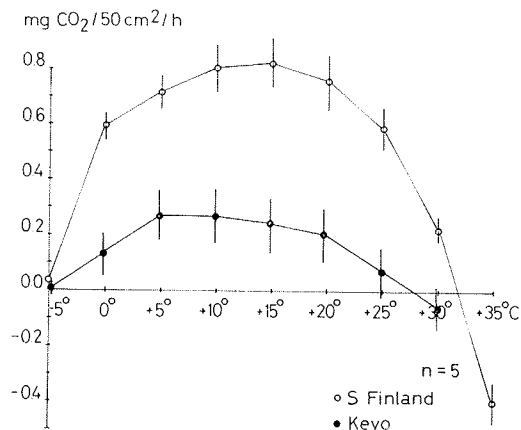


Fig. 9. Dependence of net photosynthesis on temperature in *Pleurozium schreberi*; the upper curve = S Finland strain, the lower curve = Kevo strain.

peratures (Fig. 7). Some acclimation of *Rhacomitrium* to low light conditions is seen particularly in the Scotland strain. The light compensation goes in 4 days down from 2800 lux to 1400 lux at  $+5^{\circ}$  and in optimal moisture conditions (ca. 300 % dwt.).

The effect of the continuous light, in the intensity of ca. 15000 lux was studied with the Scotland, Spitsbergen, Austrian Alps and S Finland strains. A decrease of 50 % in the activity was seen in five days in all other strains but not in the Alps strain, which had only a decrease of 15 %. No changes occur in constant rhythmic light conditions, the light intensity being the same during a period of a week.

The effect of moisture on the net photosynthesis is represented in Fig. 8. Moisture is a very important ecological factor in mosses, and its effect has been studied by TALLIS (1964) in *Rhacomitrium*. The moisture values between 200 % and 400 % were taken as limits in our experiments because the moisture response curve shows rather little variation in this area. The minimum moisture content for the positive net assimilation is around 50 %. There is also a descending part in the curve showing that the water content was too high at that point.

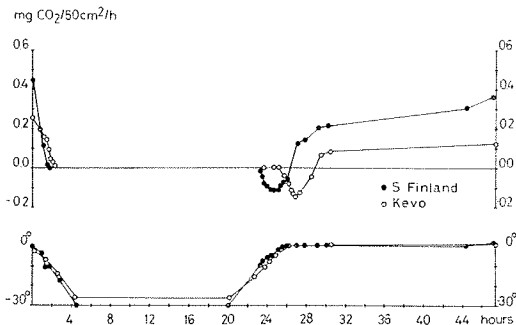
The nitrogen fertilization has no, or a very small, effect on the photosynthesis. A bad damage results in stronger concentrations, but in the concentration of 0.001 %  $\text{KNO}_3$  *Rhacomitrium* still seems to suffer little.

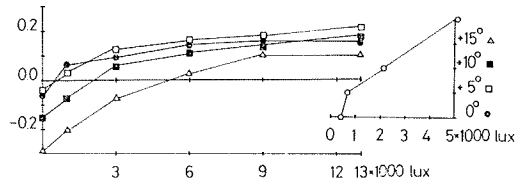
3. 2. *Pleurozium schreberi*

Fig. 9 shows the temperature response of the net assimilation for *Pleurozium schreberi*. When compared with *Rhacomitrium* the cardinal points of the curves reveal some differences. The minimum temperature for net assimilation is about  $-7^{\circ}\text{C}$ , the optimum ca.  $+15^{\circ}\text{C}$  and the maximum  $+32^{\circ}\text{C}$  in the optimal light and moisture conditions. A comparison of the Kevo and S Finland material shows that the northern strain is less active and the temperature range of its net assimilation is narrower.

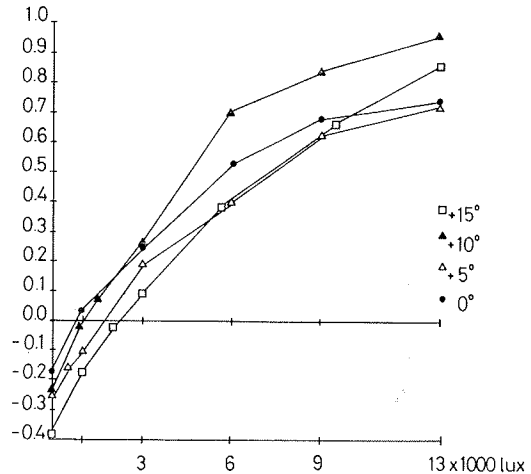
The freezing experiments are demonstrated in Fig. 10. The recovery is slow: in both strains it is only ca. 35 % during the first three hours after exposure and the final reactivation rarely reaches more than the level of 60 %. The  $\text{CO}_2$  surge is almost the same in comparison with *Rhacomitrium*. The light curve of *Pleurozium* for the net photosynthesis is seen in Fig. 11. The compensation values varied between 400—1000 lux at  $0^{\circ}\text{C}$ , and as regards the dependence of light compensation on the temperature, the values are between 400 lux and 5000 lux (in the temperature range  $0^{\circ}$  and  $+15^{\circ}$ ). In the longer experiments the light intensity must not be too high. 15000 lux lowers the activity rapidly, at  $+5^{\circ}$  ca. 50 % in 5 days. In a continuous light of 3000 lux there is also to be seen a decrease in the activity, while in conditions of the rhythmic light, i.e. dark in the night and the light of 6000 lux for 12 hours, the activity is constant. It is hence not only a question of the light intensity but also of the photoperiodic response.

No differences were observed in this respect in the comparison of the Kevo and S Finland strains.

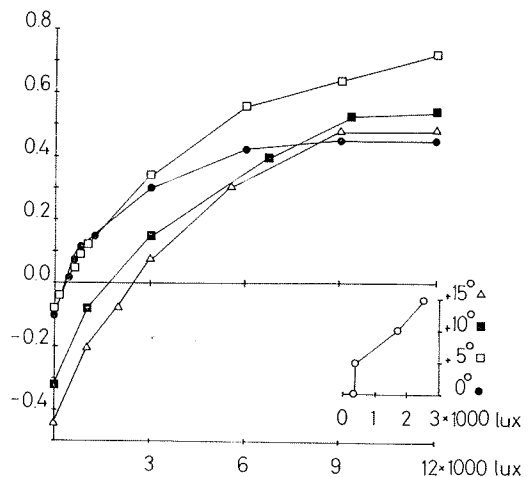

 Fig. 10. *Pleurozium schreberi*, freezing experiments.

 mg  $\text{CO}_2/50\text{cm}^2/\text{h}$ 


A

 mg  $\text{CO}_2/50\text{cm}^2/\text{h}$ 


B

 mg  $\text{CO}_2/50\text{cm}^2/\text{h}$ 


C

 Fig. 11. Light curves for net photosynthesis. A = *Pleurozium schreberi* — Kevo, B = *Pleurozium schreberi* — S Finland, C = *Pytoecium proliferum* — S Finland.

KEVO

 Turun Yliopiston  
Lapin tutkimuslaitos

The optimum moisture is between 200 % and 400 %, and between these limits the variation in the photosynthetic activity is small. The compensation point is ca. 50 % at the temperature of +10° and in the light of 12000 lux; this is thus the lowest moisture value for accumulation of CO<sub>2</sub> in the moss.

The positive effect of nitrogen fertilization is clearly seen in *Pleurozium*, particularly in the Kevo strain. During a period of 8 weeks the photosynthetic activity was increased 25 %. The same trend was also seen in the *Hylocomium proliferum* from Turku.

#### 4. Discussion

Although the variation is high as regards the activity of different strains of *Racomitrium*, responses to the temperature seem to be similar; the optimum temperature for net photosynthesis is ca. +5°C although the curve is flat in shape. All provenances still have a positive net assimilation at temperatures below 0°, and it continues in most cases until -10°, in some experiments until -15°, but no significant differences are seen in compensation points of the low temperatures in the different strains.

The minimum temperature for the net photosynthesis in *Racomitrium lanuginosum* is one of the lowest among the moss species studied. In *Bryum sandbergii* the photosynthesis has been measured at -5° (RASTORFER & HIGINBOTHAM 1968), and ATANASIU (1971) has found a positive net photosynthesis in *Brachythecium gehebi* and *Camptothecium philipceanum* at -9° and in *Isoetecium viviparum* at -8°. The limit is even lower than in the typical antarctic mosses which have the corresponding minimum at -4°C (AHMADJIAN 1970; GANNUTZ 1970; RASTORFER 1972).

The optimum temperature for net photosynthesis in *Racomitrium lanuginosum* is one of the lowest known. In two *Bryum*-species from the Antarctic investigated by RASTORFER (1970), *Bryum argenteum* and *B. antarcticum*, the optimum temperatures were estimated between +15° to +20°C and +5° to +10° respectively, and over +25° in some other species (RASTORFER 1972). BAZZAZ et al. have for *Polypodium juniperinum* a value of +10° to

+15°C, the maximum being over +30°C, which is one of the highest values for the forest mosses; RASTORFER & HIGINBOTHAM (1968) have a value of +24° to +30° for *Bryum sandbergii*, STÄLFELT (1937) +14° to +15° for *Hylocomium squarrosum* and TALLIS (1959) +14° for *Racomitrium lanuginosum*.

*Racomitrium lanuginosum* has a rather wide temperature range for positive CO<sub>2</sub>-balance, mostly near 40°. The curve indicating the temperature response is usually rather flat between 0° and +15°, i.e. changes of temperature have no great effects on the quantity of the CO<sub>2</sub> change in this area.

All strains are able to reactivate rapidly after being in the low temperature of -30° for many hours. This recovery is as rapid as in many plants which are well-adapted to the most severe habitats (LANGE 1962; 1965; AHMADJIAN 1970; GREENE & LONGTON 1970; KALLIO & HEINONEN 1971; KAPPEN & LANGE 1972).

The freezing temperature -30°C in our studies represents an average minimum in many habitats. The surges of respiration, whose quantity is to some extent dependent on the freezing stress (cf. BAUER et al. 1969), also represent the maximum stress occurring in nature; for instance, after a freezing to -15° the surge is a little smaller. This respiration peak occurs very soon after the temperature has reached the normal active range. Mosses are thus as flexible as lichens (KALLIO & HEINONEN 1971), in contrast to slower vascular plants (PISEK & KEMNITZER 1968).

Between different strains there are big differences in quantities of photosynthesis. How much this depends on differences in chlorophyll content, on density of tufts, perhaps on the seasonal differences of the experiments, remains to be discussed. The conditions before the experiments, especially the transportations etc., may also have some effect on the results. There may be some differences between the different strains particularly in the response of photosynthesis to high temperatures.

The strains from Spitsbergen, Turku, Ireland and the Alps are rather similar when compared on the areal basis. On the other hand, the result is quite different when the values are compared on the basis of the dry weight unit. The density of the stands is the main factor responsible for this discrepancy: the stands



Table 1. The maximum and mean photosynthetic values of different *Rhacomitrium* strains and some other mosses.

Species	Locality	t°	mg CO <sub>2</sub> /50 cm <sup>2</sup> /h /g dwt /h	
<i>Rhacomitrium lanuginosum</i>	Ny Ålesund	(+ 5°)	0.95	0.20
	mean		0.60	0.15
	Kevo	(+ 5°)	0.40	0.25
	mean		0.29	0.19
	Kevo (May)	(+10°)	0.83	0.27
	mean		0.78	0.26
	S Finland	(+ 5°)	0.76	0.61
	(Yläne)	(+ 5°)	1.32	0.71
	(Nousiainen)	(+ 5°)	1.17	0.66
	(Uusikaupunki)	(+10°)	0.94	0.46
	(Harvaluoto)	(+ 5°)	0.72	0.52
	Bergen	(+ 5°)	0.86	
	mean		0.74	
	Glenamoy	(+10°)	1.11	0.37
<i>Pleurozium schreberi</i>	Kevo	(+ 5°)	0.28	0.24
	S Finland	(+15°)	1.17	1.13
<i>Hylocomium proliferum</i>	S Finland	(+11°)	1.16	2.46
	S Finland	(+10°)	1.03	1.86
<i>Hypnum cupressiforme</i>	S Finland	(+ 5°)	1.82	1.96
<i>Pohlia drummondii</i>	S Finland	(+ 5-10°)	2.21	1.56
<i>Polyptrichum juniperinum</i>	Kevo	(+ 5°)	0.43	0.34
<i>Dicranum elongatum</i>				

of the strains from Spitsbergen and the Alps are much denser than e.g. the S Finnish strain.

As a whole, *Rhacomitrium lanuginosum* shows a low activity when compared with the other mosses from S Finland. These have almost the same average photosynthetic activity as the average (2.3 mg/g dwt) of the forest mosses studied by STÅLFELT (1937). E.g. the *Hylocomium proliferum* value of STÅLFELT 2.5—3.2 mg/g coincides well. The values given by HOSOKAWA et al. (1964) to epiphytic mosses vary in the range 0.6—1.4 mg/g dwt and are on the average lower than those of the soil mosses. The mean values of four antarctic mosses studied by RASTORFER (1972) is near 2 mg/g dwt.

It seems that *Rhacomitrium lanuginosum* represents a species with a low photosynthetic activity. On the other hand, the adaptation to wide range of ecological variation makes it able to such a yearly growth which apparently is not much lower than the average growth of mosses. Although there are no quite comparable data, the average near 10 mm/year (TALLIS 1964) seems not to be slow when compared with the values given e.g. for the antarctic *Chorisodontium aciphyllum* by BAKER (1972) or with those given by ROMOSE (1940)

for *Homalothecium* (ca. 500 g/m<sup>2</sup>/year) or TAMM (1953) for *Hylocomium*.

These observations contribute to the discussion of the problems of ecology and distribution of the species. TALLIS (1958) excellently dealt with these problems and grouped the factors controlling distribution to latitude, oceanity and biotic pressure. In a later publication (1964) he studied experimentally the effect of two ecological factors, moisture and temperature. The response of photosynthesis to temperature offers an explanation to the preference of *Rhacomitrium lanuginosum* for colder climates. Our experiments fully confirm the main idea that the preference for a colder climate is a reflection of the metabolism of *Rhacomitrium lanuginosum*. It is, however, likely, that the temperature range for growth is not so limited as TALLIS (1964) proposed, evidently owing to too small numbers of experimental data. The climatic conditions, e.g. in the maritime Antarctic, where the temperature is near 0° the whole year (LONGTON 1967), gives the species possibilities for positive energy yield at South Georgia, particularly from October to March (cf. LONGTON 1970, fig. 2). In Great Britain this is possible almost throughout the year. On the other hand, the conditions are more severe at Kevo, where the low humidity in the summer time restricts the growth to the occasional rain periods, to the dew formation and to the autumn, i.e. to seasons with a lower temperature than the average summer temperature; still, the species has been able to survive. The ecological problem is the same as in lichens in the same area (KÄRENLAMPI 1972). In the arctic and subarctic conditions particularly, as well as in the Antarctic, even the most active period for the species is characterized by night frosts and great daily temperature ranges (cf. TKHOMIROV et al. 1960; RUDOLPH 1965; BIEBL 1968; LONGTON 1970; RASTORFER 1970). Therefore adaptation to changing temperature conditions is a prerequisite for the distribution in many localities, e.g. in Kevo and apparently in Spitsbergen. It is important to note that the response of a species to low temperature and to its effects afterwards is not easily deduced from the "oceanity" of the habitat. The adaptation to a night frost of -30° gives no advantage to the strains of *Rhacomitrium* in Glenamoy, or in Wales, but it has no disadvantages, either. In the arctic conditions the distri-

bution is also primarily determined by drainage and air-humidity (cf. TALLIS 1958).

This species has a preadaptation which gives it wide ecological possibilities. In the development of the species the local recent environmental features thus have not functioned as factors of the evolution pressure. In this respect mosses resemble the group of lichens as a whole. It is typical of this group — with many exceptions of course (cf. KAPPEN & LANGE 1972) — that it tolerates low temperatures even though it grows in temperate regions and even in tropics (cf. LANGE 1965; BIEBL 1968).

The preadaptation means that *Rhacomitrium lanuginosum* has not developed any special adaptative mechanism particularly for the arctic conditions alone. This matter has been emphasized by AHMADJIAN (1970) in his study concerning the terrestrial life of the Antarctic as a whole. This means also that in *Rhacomitrium* the primary resistance, as defined by ALEXANDROV et al. (1970), the structure and the genetically controlled "common flexible base without a local adaptation or acclimation are enough for the hardening". In *Rhacomitrium lanuginosum* no good physiological ecotypes are found although this is typical of many cosmopolite plants (cf. GEMMEL 1950). Its adaptation to different altitudes presented by TALLIS (1958) may be explained in terms of phenotypes. This is well in accordance with the previous discussion. *Rhacomitrium lanuginosum* represents an arctic/antarctic species with all the ecological features discussed by the authors of the "polar biologists" (cf. SØRENSEN 1941; TIKHOMIROV et al. 1960; WARREN WILSON 1960; BLISS 1962; LANGE 1965; RUDOLPH 1965; GREENE 1967; BIEBL 1968; BILLINGS & MOONEY 1968).

*Dicranum elongatum* from Kevo and *Drepanocladus uncinatus* from Spitsbergen show almost the same response type as regards the net assimilation curve in different temperatures, as well as the reactivation after the freezing (the authors, unpubl.). The lichens from the subarctic and arctic zones show quite the same adaptational features of "primary resistance".

In addition to the lack of the ecotype formation, *Rhacomitrium lanuginosum* shows no clear short-term acclimation to temperatures as it is e.g. in *Fontinalis* (HARDER 1925) and in

many algae (ALEXANDROV et al. 1970). This lack of the ability to acclimation manifests itself also in the small seasonal differences. The acclimation for different seasons is apparently smaller than in the forest mosses studied by STÅLFELT (1937) ROMOSE (1941), ATANASIU (1971), or in epiphytic mosses (MIYATA & HOSOKAWA 1961). Although our experiments were not designed to elucidate the annual rhythm of activity, they seem to indicate that this is not very important. The values in spring and in autumn do not differ significantly.

*Rhacomitrium* is a heliophilous plant growing on open habitats, its compensation point of the light for net photosynthesis being higher than in most typical forest mosses (cf. STÅLFELT 1937; 1960; TALLIS 1958; PAOLILLO & BAZZAZ 1968, fig. 2). Its light saturation is also one of the highest among mosses. The time factor, however, may affect this species as well as many mosses (cf. RASTORFER 1970). *Rhacomitrium* is sensitive to high continuous light intensity. There seem to be no big differences between the different strains. But when compared with *Pleurozium schreberi* and *Hylocomium splendens*, clear differences are seen also in this respect: the degradation of the chlorophyll in *Rhacomitrium* (cf. TALLIS 1959) is much less sensitive to continuous light than in *Pleurozium*. However, *Rhacomitrium* is particularly sensitive to high light intensities at low temperatures, which conditions are rarely found in nature.

The rhythm of light, which probably has a great significance to the reproductive ecology also among mosses (cf. CLARKE & GREENE 1971), has not been studied thoroughly.

In literature there are, however, examples of a physiological race formation among mosses. BAZZAZ et al. (1970) in their studies with forest and alpine populations of *Polytrichum juniperinum*, found clear differences in the response curves of net photosynthesis to the temperature, the differences reflecting climatic conditions in the habitats of the two species. Adaptation to different light conditions is also seen in these species. CLARKE & GREENE (1971) showed clear adaptations of the reproductive ecology to local climatic conditions in the comparison of *Pohlia nutans* and *P. cruda* from S Georgia and England. In *Hypnum cupressiforme* different response types to moisture are known (LEE & STEWART 1971).

Are there any special features in arctic mosses when compared with those of temperate zones? A very typical moss of forest regions is *Pleurozium schreberi*. This species is adapted to growing at a low temperature, too. One difference is rather clear when compared with *Racomitrium*. The reactivation of *Pleurozium* after the freezing to  $-30^{\circ}$  is slower than in *Racomitrium lanuginosum*. *Pleurozium* in its main distribution area is a forest plant and as regards the habitat strictly chionophilous, and is covered by snow during the winter season: the plant apparently has a main growth (activity) season in autumn (cf. TAMM 1953; 1964; KUJALA 1962). It is also rather a shadow plant, adapted to growing in the canopy effect of trees, like *Hylocomium* (TAMM 1953; 1964). In the tundra and oceanic area there are only habitats without trees; these are suitable for *Racomitrium* but unfavourable to *Pleurozium*. The difference in the nitrogen content may be correlated with the particular differences in the nitrogen content in arctic and temperate regions. It is likely that the susceptibility of *Racomitrium* to the variation in the humidity, and its high demands for moisture, are the decisive reasons for the oceanic distribution.

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