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Influence of short-term low temperature on net photosynthesis in some subarctic lichens

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Abstract

KALLIO, PAAVO & HEINONEN, SAINI. (Botany Dept., Univ., Turku 50, Finland) Influence of short-term low temperature on net photosynthesis in some subarctic lichens. REP KEVO SUBARCTIC RES STAT 8. 63—72. Illus 1971. — Measurements of photosynthesis were made with URAS in laboratory conditions on *Nephroma arcticum, Cetraria nivalis, Parmelia olivacea* and some other species in the surroundings of the Kevo Subarctic Research Station (69° 45'N in Finnish Lapland) and with some lichens from southern Finland. In particular, recovery after chilling to temperatures 20—30°C below zero was followed. In the ascendent phase of the temperature *Nephroma arcticum, Solorina crocea* and *Umbilicaria vellea* exhibited a clear peak of respiration between —10 and 0°. The other species studied (*Cladonia alpestris, Parmelia olivacea, Hypogymnium physodes* and *Xanthoria parietina*) did not have a respiration peak but recovered very rapidly. *Umbilicaria vellea,* although a chionophobous species, is very inactive in the winter and the slowest to recover.

1. Introduction

The adaptation of plants to the thermal environment in northern latitudes has two ecological aspects: adaptation to "inactive" survival during the winter season and adaptation of the "active phase" to ensure the energy input. The annual rhythmic acclimations called hardening and dehardening form part of this system — although some examples may exist even among higher plant groups in the arctic of aperiodic activity changes controlled solely by environmental conditions (cf. SØRENSEN 1941; BLISS 1962). The physiology of these acclimation processes may be split up into (photoperiodic) induction, the problems of protein denaturation, dehydration and changes in the permeability of the plasmalemma, the formation of "protective substances", and the question of the two different levels of low temperature with different effects on the proteins (cf. BRANDTS 1967; LEVITT 1969) and the division into "primary" and general resistance (ALEXANDROV et al. 1970: 419). Much of the mechanism and biochemistry of these processes is understood, as may be seen from the proceedings (ed. by TROSHIN 1967) of the low temperature symposium held in Leningrad 1963.

The ability to harden has gone to the extreme in large groups of arctic, subarctic and alpine plants and poicilothermic animals (WAGER 1938; 1941; SCHOLANDER et al. 1953; TRANQUILLINI 1959; 1964; PISEK 1960; LANGE 1962; 1965; 1966; 1967; BILLINGS & MOONEY 1968; AHMADJIAN 1970). The survival capacity at low temperatures has proved to be unexpectedly great among both vascular plants (PORSILD

et al. 1967) and cryptogams and the ecological niches reflect the great diversity and flexibility of adaptation to conditions during the active phase of the annual cycle.

The adaptation of the photosynthesis to low temperatures in the northern latitudes and at high altitudes is very important to the vegetation, because it enables the plants to compensate for short production period (cf. LARCHER 1969a), the most limiting ecological factor prevailing in these regions (HADLEY & BLISS 1964). In numerous field studies (e.g. MÜLLER 1928; KOSTYTSCHEV et al. 1931; WAGER 1941; WARREN WILSON 1960; PISEK 1960; PISEK & KEMNITZER 1968; PISEK et al. 1969; LANGE 1965; UNGERSON & SCHERDIN 1965; BIEBL 1968; LARCHER 1969b; MOSER 1969; AHMADJIAN 1970) on different plant groups this adaptation has been shown to enable photosynthesis to occur even at temperatures several degrees below 0° (often —6°).

The seasonal transition of the optimum temperature of net assimilation has a similar effect (STÅLFELT 1937; 1938; 1960; PISEK et al. 1969).

The adaptations of plants to differences in the snow cover in the arctic and subarctic zones are correlated not so much with avoidance of the low winter temperature minima as with the differences in the lengths of the productive periods.

Respiration is similarly correlated with the locally and seasonally prevailing temperatures. At higher latitudes and altitudes higher plants tend to have higher respiration rates (FORWARD 1960 and the older literature cited there; BJÖRKMAN & HOLMGREN 1961; MOONEY & BILLINGS 1961; MOONEY & JOHNSON 1965; BILLINGS & GODFREY 1968; MOONEY & WEST 1964; JOHNSON 1969).

The lichens (and mosses), which occupy an increasingly important position in the flora with nearness to the poles, are particularly well adapted to low-temperature conditions (cf. SMITH 1962; HADLEY & BLISS 1964; LANGE 1965; AHMADJIAN 1970). As many lichens in the tropics are also able to withstand unfavorable low temperatures (LANGE 1965; BIEBL 1968), the characteristics seem to have been fixed in this group of plants in the early stages of evolution. SCHOLANDER et al. (1953: 708) have suggested that "the lichens might represent a group which could get along well in the arctic without much need for metabolic adaptation". By this they mean that the lichens are so flexible that with (almost) the same genetic constitution they are able to inhabit wide areas of the globe. Thus adaptation to some factor other than temperature is often key to their ecological versatility. For example, moisture makes the winter the optimum season for the growth of lichens in (Central and West) Europe (SMITH 1962; SCHULZE & LANGE 1968). Although in Lapland the low moisture content may also be the limiting factor for growth (KÄRENLAMPI 1971), the winter cannot be the productive season, owing to the too low temperature and lack of light. The question of how the short, and, as far as growth possibilities are concerned, fragmentary "summer time" is utilized effectively, certainly is one of the main ecological problems of lichenology in the North.

The active production period is the sum of short-term periods of activity and is strongly dependent on the rate at which the net assimilation can recover after chilling (cf. LARCHER 1969a; AHMADJIAN 1970). Among vascular plants, there is typically a recovery period of some hours or even days after exposure to low temperature. This is particularly typical of phanerophytes (cf. BAUER et al. 1968 and the literature cited there; PISEK & KEMNITZER 1968) but is also known in various ecological groups. It is apparently based on fundamental properties of the protoplasm.

The lichens are very flexible in this respect, as indicated long ago by the studies of STOCKER (1927) and STÅLFELT (1937). LANGE (1962) has shown that *Cetraria nivalis* is able to recover within a very short time after chilling; and after long periods at —15°C *Cladonia alcicornis* is able, without a lengthy recovery period, to attain a positive net assimilation. This might be ecologically as important as the very low minima temperatures for net assimilation typical of presumably all northern and alpine lichens (STÅLFELT 1939; LANGE 1962; 1965; SMITH 1962; SCHULZE & LANGE 1968; AHMADJIAN 1970). The adaptational features of arctic and antarctic lichens are not essentially different (AHMADJIAN 1970).

In this paper the response of some subarctic lichens to chilling has been studied in the vicinity of the Kevo Subarctic Research Station of the University of Turku in Finnish Lapland and from southern Finland. The latitude of the Kevo site is 69°45'N and the altitude ca. 100 m. There is normally in winter a snow cover of about 60—80 cm, which lasts 7 months, and the sun does not rise above the horizon at all for a period of 52 days. No possibilities exist for photosynthesis in midwinter. Whether there are any typical adaptations to these subarctic conditions in the ecology of the cryptogams is one the questions to be studied at the Station. The other is to obtain data for measuring production by physiological and microclimatic parameters (cf. LARCHER 1969 b). These studies are connected with the IBP Tundra project at Kevo.

2. Material and methods

Most of the experiments were made with *Nephroma arcticum* (L.) Torss. (syn. *Opisteria arctica* (L) Vain.). Additional subarctic lichen species studied were *Cetraria nivalis* (L.) Ach., *Cladonia alpestris* (L.) Rab., *Parmelia olivacea* (L.) Nyl., *Umbilicaria vellea* (L.) Ach. and *Solorina crocea* (L.) Ach. Some experiments were also made with *Xanthoria parietina* (L.) Th. Fr. and *Hypogymnia physodes* (L.) Ach. from S Finland.

The photosynthesis experiments were partly carried out at Kevo but mostly at the Botanical Laboratory of the University of Turku.

The measurements were made with an infra-red gas analyser (URAS; Hartman & Braun, Hannover). The temperature was stabilized in a water bath with glycol (for the experiments at low temperatures down to —30°C). The temperature was measured on the upper surface of the thallus, where it may be 0.4°C higher than on the lower surface. For the temperature curve of net photosynthesis the temperature was usually changed in steps of 5°. The time at each temperature was one hour. In the chilling experiments lowering and raising of the temperature was regulated with a "Programgeber" (PG; Gebr. Haake, Berlin) and the normal gradient was 6° per hour.

The volumes of the cuvettes were 0.63 dm^3 and 0.49 dm^3 and the air circulation was 10 liters per hour.

The light source was a Philips HBL 1000 W bulb, giving light intensities of up to 20000 lux, as measured at the surface of the lichen.

Water bottles were used to moisten the air but the lichens nevertheless tended dry up in the cuvette. The water loss was measured by weighing, but experience had shown that in experiments lasting only 12 hours the loss did not affect the rate of photosynthesis. This was verified by making the last measurement in the evening under the same temperature and light conditions at which the series had been started in the morning.

The air was taken from a compressed air cylinder to avoid great fluctuations in CO_2 content. The air in Turku is not very polluted as can be seen from the lichen flora of the town (KOVANEN 1961). The lichens were sent by air mail in "freesing boxes" from Kevo to Turku and in winter they were kept under snow between experiments or in the cool room of the laboratory at the temperature near 0°C. In addition, the lichens were grown in culture cabinets in which light and temperature but not moisture could be regulated. After a period of 15 months in these culture cabinets at a temperature of 10°C, *Nephroma* still shows a positive net assimilation, but it has fallen by more than 60 %.

The results are given in mg CO_2 per g dry weight.

3. Results

Nephroma arcticum (L.) Torss. is common in Northern Fennoscandia and has a clear southern limit of distribution in Northern Europe. Apparently, its optimum ecosystem in Finland is the birch forest of the subarctic zone. There, its abundance shows a positive correlation to the moisture gradient (HEIKKI KAUHANEN, private comm.). — In S Finland this lichen is rare and the habitat shady slopes of the forest. One such locality is on Harvaluoto, near Turku. This material was also used in the experiments.

The species has already been used for ecological studies in Abisko, N Sweden by BUTIN (1954: 473—474), who made some field measurements of its photosynthesis in the subarctic night.

Moisture. The thallus is able to retain about 3 times its own dry weight of water. Such saturation leads to a slight fall of assimilation but assimilation is almost constant between water contents of 250 and 150 % relative to the dry weight. When the thallus becomes dryer than this, an abrupt decrease is seen in the net assimilation and the compensation point is reached at water contents between 50 and 100 %. In the experiments the moisture remained at the optimum level for the time

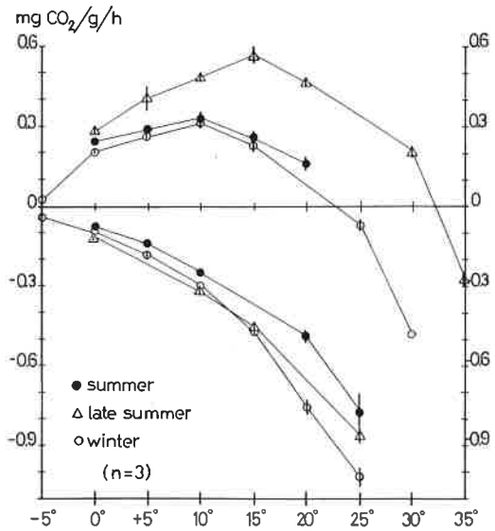

Fig. 1. Nephroma arcticum. — Net photosynthesis as dependent on temperature.

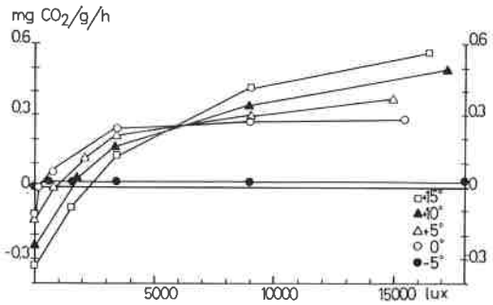

Fig. 2. Nephroma arcticum. — Influence of light on net photosynthesis. One experiment, May 1971.

needed for complete a temperature or light curve of photosynthesis.

Temperature (Fig. 1). The optimum temperature for net assimilation in high light conditions and in the moisture of over 150 % of the dry weight is between +5 and +15°C in winter. In summer (August) it is some 5° higher. The minimum temperature for a positive net assimilation is between —5 and —10°. At still lower temperatures a weak respiration was measured (6. 3. 1969) at —26.6° when the cuvette had been closed for 1 hour. Often, however, no respiration at all could be measured below about —20°. Apparently differences in the moisture at these low temperatures affect the results in some way not analyzed in these experiments.

Light (Fig. 2). In the experiments the highest light intensity used was near 20000 lux. Photosynthesis responds only weakly to differences in light at this level. The light compensation point at 0°C is reached at 400 lux and is near 2000 lux at +15°.

Maximum yield in our experiments in winter was 0.358 ± 0.024 mg CO_2/g/h; in late summer the yield is highest, 0.580 ± 0.052 mg (+15°, 17000 lux).

The effect of chilling (Fig. 3). In these experiments specimens from Kevo and Harvaluoto were used. Net assimilation was first measured at 0°. When this had stabilized the temperature was lowered to —25° to —30° (in some experiments only to —20°). A light intensity of 18000—20000 lux was kept as constant as possible without a rhythm. The CO_2 exchange was also measured during the change of temperature.

In most of the experiments a positive net assimilation was maintained between —5° and —10°, so that it could be measured by the method normally used for measurement of CO_2 assimilation. At temperatures as low as —20°, the CO_2 release was most easily shown by closing the cuvette for one hour. At —25° only rarely a weak respiration could be measured.

When the temperature was raised again after some hours at a rate of 6° per hour, respiration was found to start at a temperature between —12° and —7°, usually near —10°. When the starting temperature of 0° was regained, the peak of respiration sank rapidly and after a period of 1 to 5 hours (Kevo, May 1970) the compensation point was reached. Thereafter recovery took place. There was rather a wide variation even in replicate experiments. The shortest time of recovery was two hours (material taken from Kevo 1. 6. and measurements made 5. 6. 1970). In some experiments the initial level of activity was only reached after some 2 days but mostly on the following

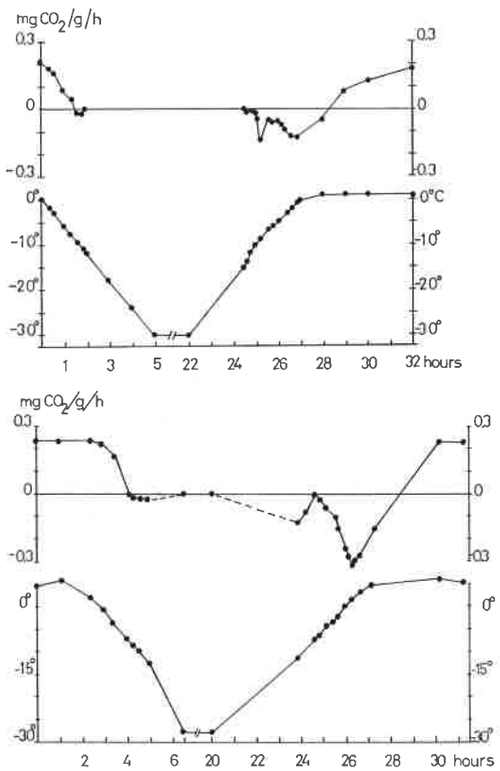

Fig. 3. Nephroma arcticum. — Chilling experiments. Temperature changes indicated by the lower curves, net assimilation by the upper curves.

day. The respiration peak in these experiments was sometimes more than 5 times the average respiration at the temperatures between 0 and —10°.

Even very rapid chilling — to —17° in one hour — did not damage the lichen more than the previous treatment (Harvaluoto 23. 4. 1970): the compensation point was reached in 3 hours and the maximum net assimilation rate after a period of 20 hours.

The formation of the respiration peak takes place also in the dark.

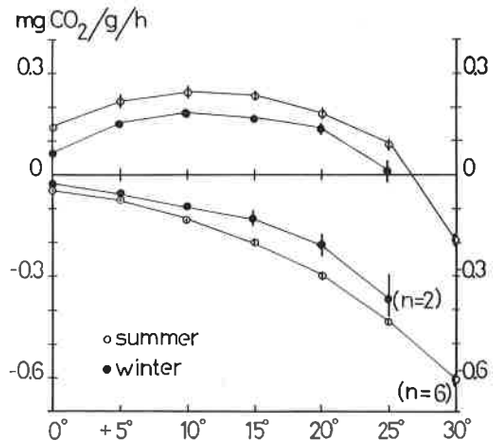

Fig. 4. Cetraria nivalis. — Dependence of net photosynthesis on temperature in different seasons.

Cetraria nivalis (L.) Ach. is also an arctic-alpine species, rare in southern Fennoscandia but one of the most typical lichens in the subarctic mountain region (cf. TRASS 1970). LANGE (1962) has studied the response of this lichen to low temperatures and has shown that recovery after chilling is very rapid. The compensation point is reached after 12 minutes and the normal assimilation rate is resumed in a few hours. HADLEY & BLISS (1964) have also experimented with this species and have noted that the maximal photosynthetic rates (0.30—0.38 mg CO_2/g dry weight/hr) were reached at 15—20°C and at light intensities of 1600 (—3200) ft-c. In the Presidential Range, New Hampshire, where these studies were made, the lichen seems to be well adapted to periods when the surface temperatures are low to moderate and light intensities low — the conditions prevailing in their study area during the

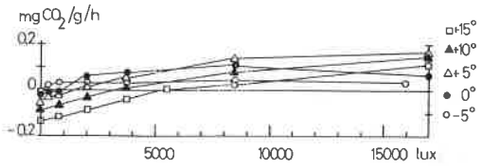

Fig. 5. Cetraria nivalis. — Influence of light on net photosynthesis.

greater part of the summer. In our experiments the temperature optimum for maximal net assimilation was found mostly to be about 10° in winter and the early summer, but in August the optimum was higher (Fig. 4). The maximum yield was 0.3 mg/g/h. Apparently in its response to temperature the strain was as efficient as the strains by HADLEY and BLISS. At —5° the light compensation point was near 100 lux and at +15° 5500 lux (Fig. 5). The moisture content in these experiments range between 296 and 413 % and the difference did not affect the results. A very weak positive net assimilation persisted during the chilling process down to near —20° and after the chilling (—30°) it reappeared when —20° was reached again. Sometimes, however, a slight activation of respiration was seen between —10° and 0°. But a positive net assimilation was reached again below 0°, and at 0° the level prior to the chilling was regained in about 2 hours (Fig. 6). This was one of the most flexible of the lichens studied as regards response to low temperatures.

Cladonia alpestris (L.) Rab. In winter the optimum temperature range for net assimilation of this species was found to be between 10°

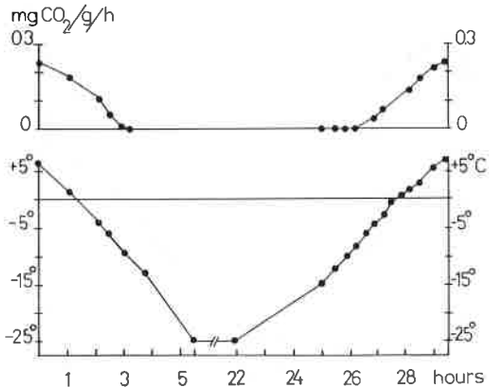

Fig. 6. Cetraria nivalis. — Chilling experiments.

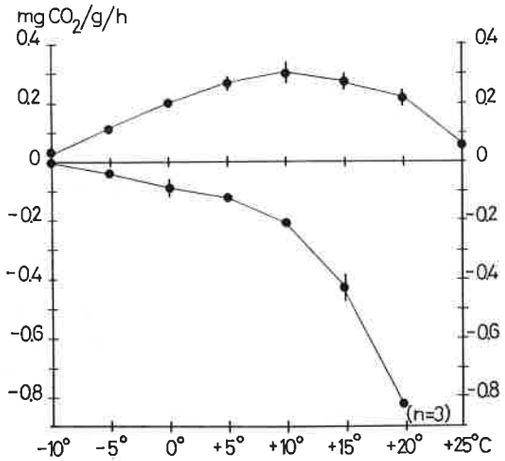

Fig. 7. Parmelia olivacea. — Dependence of net photosynthesis on temperature.

and 18° and in summer between 10° and 25° and the light compensation point from —5° to +15° between 200 and 6000 lux. Net assimilation continued positive until —10° (—15°) and became so again at about —10° as the temperature was raised again. When 0° was reached, the net assimilation was already more than half of the value prior to chilling, and the control level was reached in one hour. That means that no recovery time was needed, because one hour was the time allowed in our technique for lichens to reach the final value after a 5° change in temperature.

In this species no respiration peak was seen as the temperature was raised.

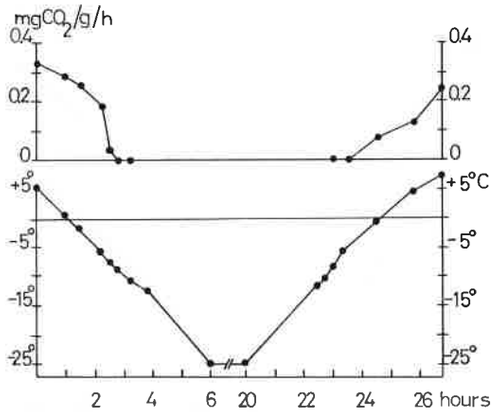

Fig. 8. Parmelia olivacea. — Chilling experiments.

Parmelia olivacea (L.) Nyl. is one of the most typical epiphytes on the subarctic birches, and often occurs also on pine. The species serves as an indicator of the average maximal snow cover, because it normally grows above this limit (cf. AHTI 1966; HÄMET-AHTI 1963).

The temperature curves of the assimilation and dark respiration are presented in Fig. 7. The lower compensation point for net assimilation is between —8 and —10° and the upper over +25° and hence the lichen can not be regarded as a very psychrophilous species (cf. LAMB 1970).

After chilling, positive net assimilation begins at the normal minimum temperature level (—10 to —8) and at 0° maximum activity is reached in one to two hours. No respiration peak is observed (Fig. 8.).

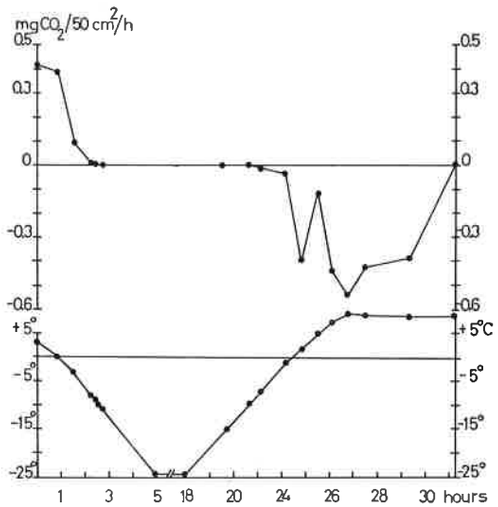

Fig. 9. Umbilicaria vellea. — Chilling experiments.

Umbilicaria vellea (L.) Ach. This is also a northern lichen in Finland, most abundant in the Subarctic, but also common in the arctic-alpine region. The lichen grows on walls of precipies round Kevo and at least in some places is exposed to the influence of the minimum temperatures occurring in the area — i.e. near — 50° as absolute minimum and —30° every year.

Its recovery after chilling to —28° was rather slow (Fig. 9.). It took some hours to reach a positive net assimilation and total recovery had

not taken place after two days. A vigorous respiration peak being much wider than in other species studied is typical of the species.

Solorina crocea (L.) Ach. is in Finland a typical subarctic species growing on barren spots of solifluction soils on the slopes of the mountains, on barren wet paths, round snow patches, etc. The minimum temperature for net assimilation was found to be about —7°. In the chilling experiments in the ascendent phase a surge of respiration started at this same temperature level and reached its maximum at about the time when 0° was reached. The com-

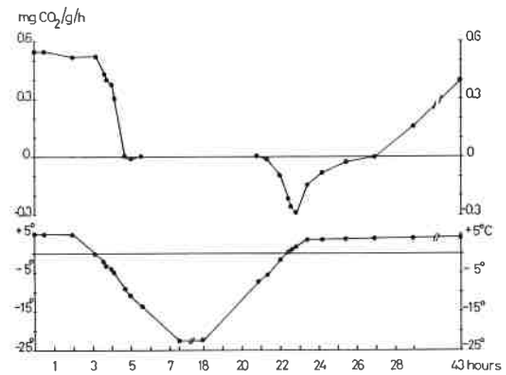

Fig. 10. Solorina crocea. — Chilling experiments.

pensation point was reached after 2—3 hours and reactivation continued for some hours. The level prior to chilling was not reached in one day (but only 80 % at the most — even when the lichen was moistened). *Solorina crocea* and *Nephroma arcticum* belong to the same ecological group as far as recovery after chilling is concerned (Fig. 10.).

Hypogymnia physodes (L.) Ach. is one of the lichens best adapted to low temperature conditions, being a "winter lichen" in Europe (LANGE 1967) but is very rare north of the continuous pine forest limit. Its response to chilling is seen in Fig. 11. After exposure to —25° a positive net assimilation was attained at —10° and the maximum net assimilation was recorded two hours after the thallus reached 0°. In the chilling experiments the lichen often dried too much and the level prior to chilling was only reached after moistening.

Xanthoria parietina (L.) Th. Fr. Three different strains of this lichen have been

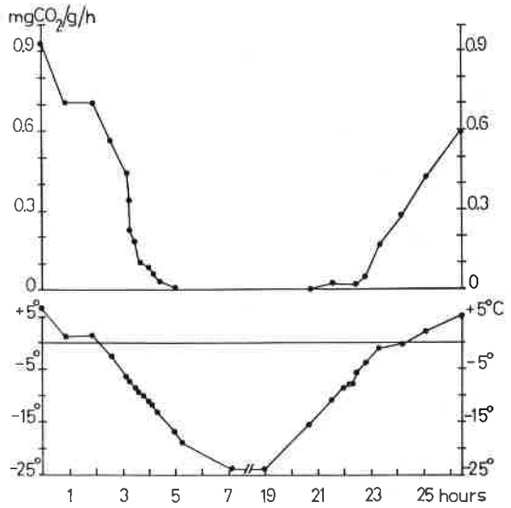

Fig. 11. Hypogymnia physodes. — Chilling experiments.

investigated in our laboratory by ELORANTA (1966): 1) a strain from the trunk of aspens in Ostrobothnia (63° 05'N, 23° 04'E), 2) a strain growing on the cliffs in the archipelago of Turku and 3) a strain growing on the cliffs on the shore of the Arctic Ocean (at 70°N) in Finnmark. These three differ both morphologically and ecologically. In the chilling experiments of the epiphytic strain a positive net assimilation was maintained untill —18° and thereafter weak respiration continued. As the temperature was raised again, positive net assimilation started at about —10 without any peak of respiration and at 0°C the value measured prior to chilling was reached in two hours. This epiphytic lichen seemed to be as flexible

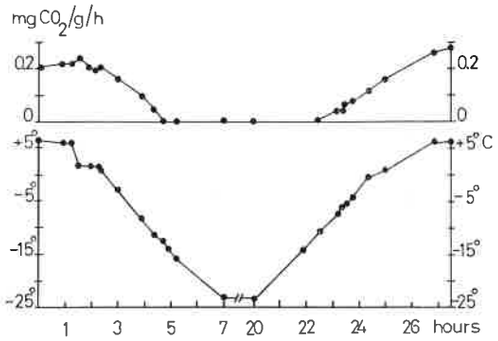

Fig. 12. Xanthoria parietina. — Chilling experiments.

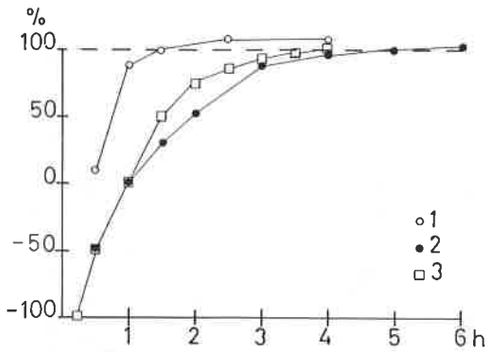

Fig. 13. Xanthoria parietina. — The recovering of three different strains after chilling. 1) epiphytic strain, 2) rock strain from SW Finland, 3) rock strain from Arctic Ocean coast. Acc. to ELORANTA (1966).

as the other even more northern epiphytic lichens studied.

The two other *Xanthorias* growing on the rock recovered somewhat more slowly, but at the optimal temperatures for their net assimilation the control level was regained in a period of 4—5 hours (Fig. 12, 13).

4. Discussion

The most flexible lichen species regarding response to low temperature seem to be the epiphytes growing on trees and *Cladonia alpestris* and *Cetraria nivalis*. These species seem to be almost aperiodic, their activity being controlled solely by environmental conditions. These lichens can hardly have any advantage but equally no disadvantage from this characteristic in the winter in Subarctic because of the weak illumination — the sun is below the horizon for nearly two months. On the other hand, in the rather humid autumn period growth may still continue if the plants are able to recover after the night-chillings (cf. Fig. 14). Among the group of ground species the snow cover reduces the weak light intensity rapidly to the minimum, but the epiphytic species apparently still have their possibilities for photosynthesis. In the spring the epiphytes apparently have a long active period when the ground lichens are covered with snow. This difference may amount to so much as 10 weeks! Whether this accounts for the chionophobia of *Parmelia olivacea* can not be decided from our experiments. The chionophobous feature of this species might equally well be due to differences in the bark surface of the birch or to some mechanical effects of snow on the lichen.

Cetraria nivalis and *Cladonia alpestris* both grow on the tops of the mountains also (eg. IBP site at Jesnalvaara), thus showing at least facultative chionophobia, although *C. alpestris* is also a typical forest lichen. *Nephroma arcticum* and *Solorina crocea* are typical chionophilous species. They also have rather high moisture requirements. The optimal moisture content (between 150 and 250 %), is higher than of the typical epiphytes and of many other lichens (cf. STÅLFELT 1937: 1960; BUTIN 1954; LANGE 1965; SMITH 1962). In Lapland where the low humidity is the most limiting factor, the fall is the most favourable season and these species are able to be active in the thermal conditions of the fall.

A typical feature of *Nephroma* and *Solorina* is the vigorous activation of respiration in the thawing period. This is apparently a common phenomenon among plants (cf. FORWARD 1960; LARCHER 1969a). In vascular plants the process may last some hours or even days, and its maximum intensity may be five times that of the normal dark respiration at the same temperature (BAUER et al. 1969). The height of the peak and its duration have been suggested to be correlated with the degree of the freezing stress and the pronecrotic damage (FORWARD 1960; Pisek & KEMNITZER 1968; BAUER et al. 1969) and resemble recovery after exposure to high temperature (cf. LANGE 1967). In *Nephroma* and *Solorina* this respiratory peak is very sharp and reaches a value which may be several times the normal. Moreover, in some experiments with *Nephroma* and *Solorina* a weak surge of respiration was observed in the descendent phase of chilling (cf. Fig. 3, 10).

Are these two respiration peaks connected with some — as yet physiologically unknown — "fast hardening" and "fast dehardening" processes? A somewhat similar short-term daily acclimation is known to occur in the heat-resistant phanerogams (cf. LANGE 1967).

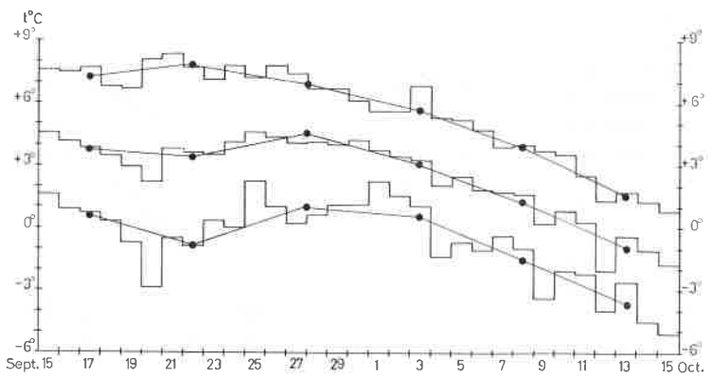

Fig. 14. Mean temperatures between 15. 9 and 15. 10 during 1962—1970 and the corresponding mean maximums and minimums.

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