

Patterns of CO₂ gas-exchange and thallus water content in Arctic lichens along a ridge profile near Ny Ålesund, Svalbard

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Two abundant and partly dominating lichen species, *Cetraria nivalis* and *Cetraria delisei*, were compared with respect to their thallus water content and their gas-exchange response to light, temperature and moisture in the field and in the laboratory. *C. nivalis* had higher net photosynthetic rates than *C. delisei*. The differences between the species were more pronounced when photosynthesis was related to dry weight than to chlorophyll content. Light compensation and light saturation of photosynthesis increased with increasing temperature. Higher light compensation and saturation values were found in *C. delisei* than in *C. nivalis*. The chionophobic *C. nivalis* showed moisture compensation and optimum water content for net photosynthesis at higher thallus water contents than the chionophilous *C. delisei*. Depression of net photosynthesis at thallus saturation, found in both species, is thought to be due to the increased internal CO₂ diffusive resistance at high thallus water content. The maximum thallus water contents of *C. nivalis* were higher than those of *C. delisei*. The lower drying rate, found in *C. delisei* in comparison with that of *C. nivalis*, is attributed to the more sheltered position of its habitat and to morphological characteristics.

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Introduction

The objective of this study was to analyse relationships between snow cover and productivity of lichens. The CO₂ gas-exchange, i.e. photosynthesis and respiration respectively, is suited for the investigation of productivity as a measure of plant growth rate (net dry weight gain per unit time) (Osmond et al. 1980) and also as a measure of fitness and adaptedness of plants to the habitat conditions (Mooney 1972). *Cetraria nivalis* and *Cetraria delisei* were chosen in this investigation because they are abundant and partly dominating in Arctic ecosystems.

In Arctic areas there are complex vegetation patterns not only on larger topographic scales, such as along altitudinal gradients, but also on smaller scales, such as on ridges or frost structured grounds (Polunin 1945; Rønning 1969; Brossard et al. 1984). The patchiness of vegetation is mainly the result of meso- or microtopographic variations, which cause uneven distribution of snow and thus differences in soil moisture, heat exchange and protection against windblast (Billings 1973). The snow cover is one of the most important ecological factors influencing the vegetation in Arctic areas. Both snow depths and duration of snow cover have an influence on distribution of vegetation and growth, mainly by determining the length of the growing season (e.g. Dahl 1956; Billings 1973; Lewis & Callaghan 1974; Gjaerevoll & Rønning 1980).

Chionophobic ridge top plants have a longer growing season than chionophilous snow bed plants. The environmental conditions of exposed habitats, especially wind speed, temperature and water availability, are harsher and more changeable than those of more sheltered habitats, where the growing season is restricted to the warm season. Thus, chionophobic species should

Abbreviations:

H _C	= moisture compensation
H _{max}	= maximum thallus hydration
H _{opt}	= optimum thallus hydration (at which P _{max} is reached)
I _C	= light compensation
I _{sat}	= light saturation
PAR	= photosynthetic active radiation
P _{max}	= maximum net photosynthetic rate
T _C	= temperature compensation
T _{opt}	= optimum temperature (at which P _{max} is reached)
TWC	= thallus water content.

show a wider tolerance to climatic fluctuations and harsh habitat conditions than chionophilous species.

Chionophobic lichens are thought to have a lower water compensation point for photosynthesis, maximum net photosynthesis at lower thallus water contents (Kershaw 1972), higher light compensation and light saturation levels (Larson & Kershaw 1975a) and a wider temperature optimum, whereas chionophilous lichens are thought to have a higher water compensation point, a wider range of optimum hydration, maximum net photosynthesis at higher thallus water content (Blum 1973; Matthes & Feige 1983), lower light compensation and saturation levels (in adaptation to the snow cover) (Kappen et al. 1989) and a higher temperature optimum.

Species description and distribution

Cetraria nivalis and *Cetraria delisei* are fruticose terricolous macrolichens with an erect, irregularly branched thallus. They grow in small stands, tussocks, cushions, or larger mats formed of several individual thalli, but also in singular thallus lobes (Dahl & Krog 1973; Thomson 1984). *C. delisei* is dull, pale brown; the basal parts are yellowish brown. The thallus lobes are weakly canaliculate. The thallus of *C. nivalis* is dull straw yellow to yellow-green; the basal parts are bright yellow or brown, when dying. The lobes are almost flattened, often undulate and reticulate (Thomson 1984).

C. delisei has an Arctic-circumpolar distribution, with some extra-Arctic localities in mountainous areas and bogs in Scandinavia, Iceland, Scotland and Eastern Europe, and even on the Southern Hemisphere (Hasselrot 1953). One find is also reported from the Austrian Alps (Daniels & Sipman 1976). *C. delisei* is a chionophilous or hydrophilous species and grows typically in periodically water logged localities, such as snow beds and mires (Lyngé 1938; Hasselrot 1953; Dahl 1956; Kärnefelt 1979).

C. nivalis is a chionophobic lichen species with an Arctic-alpine distribution only in the Northern Hemisphere (Hasselrot 1953). Outside of the Arctic zone it is found in the alpine belts of many European, Asian and American mountains, further as glacial relict in some European lowland heath areas, mostly on islands in the North Sea and Baltic Sea (Hasselrot 1953). *C. nivalis* typi-

cally grows on exposed sites which have no or shallow snow cover in winter (Hasselrot 1953; Dahl 1956).

On Svalbard these two species belong to the commonest and most widespread lichens (Lyngé 1938). In the area of Ny Ålesund, on Brøggerhalvøya, *C. delisei* is a dominating species in the *Saxifraga oppositifolia*-*Cetraria delisei*-community of strandflats and in low depressions, where the snow melts late (Lyngé 1938; Polunin 1945). It also grows between rocks on gentle slopes (Elvebakk 1979, 1985).

Cetraria nivalis grows on the top of hillocks and on exposed raised mounds and ridges in *Dryas*-communities (Polunin 1945; Hartmann 1980; Brossard et al. 1984). According to Lyngé (1938), Polunin (1945) and Elvebakk (1985) this species was also very common in Brøggerhalvøya before 1977. In 1977 a small group of reindeer was introduced to Brøggerhalvøya by the Norwegian MAB programme (Man and the Biosphere) (Elvebakk 1985). Due to the high grazing pressure by the reindeer, populations of *C. nivalis* in the area of Ny Ålesund were sparse in 1990 for the present investigations. This species is preferred by reindeer as winter forage because it can be easily reached.

Material and methods

The two different lichen species *Cetraria nivalis* and *Cetraria delisei* were compared with respect to their thallus water content and gas-exchange response to light, temperature and moisture both in the field and in the laboratory.

Sampling. – Lichen cushions (ca. 500 mg dry weight (DW)) were collected at two field sites, on top of and on the lower slope of a raised terrace near Ny Ålesund, and put into small nylon baskets (7 × 7 cm). These baskets were covered with a thin nylon net to avoid material loss. They were then replaced in the original field site for the period of investigations and were fixed at the ground with metal-pins. For each species five replicate baskets were used. All replicates were covered with a fishing net to prevent reindeer from eating the lichens.

Gas-exchange measurements in the field (1990). – The CO₂ gas-exchange measurements in the field were carried out with a portable CO₂/H₂O-

porometer (ADC Ltd., Hoddesdon, England). The instrumental arrangement consisted of an air supply unit (type ASUM2), an open system infrared gas analyser (type LCA2) and a Parkinson leaf-chamber (cuvette).

The ASU acts as source for reference air, which is sucked in by a pump, and controls air-flow through the cuvette. To provide dry ambient air, the air passes through absorber columns containing the drying agent silica gel.

The Parkinson leaf-chamber is supplied with a fan for mixing the air in the chamber. Further, it contains a photocell to check incoming photosynthetic active radiation (PAR), a thermistor (placed to the lichen samples as close as possible) to measure the temperature in the chamber, and a Coreci-element to measure the humidity of outgoing air. The chamber window is an interference filter with a sharp cut-off at 700 nm. The tubing from the leaf-chamber to the analyser had to be supplied with a small container filled with silica gel to dry the outgoing air before it reached the infrared gas analyser.

For gas-exchange measurements, lichen samples were put into the leaf-chamber and left there until the reading was constant (5–10 min). The samples were then replaced at the site until the next measurement. Before and after each measurement the samples were weighed on a battery-powered balance (Sartorius PT 120).

As far as possible the measurements were carried out under natural environmental conditions. However, because the lichens were dry and inactive during warm and sunny weather, they were sprayed with distilled water for some measurements to obtain a higher total number of different combinations of moisture, temperature and light conditions. When all the measurements had been concluded, the lichen samples were transported air dry to Abisko Naturvetenskapliga Station, Sweden. Here they were kept in a freezer (at –18°C) until measurements of dry weight and chlorophyll content were made.

After evaluation of the field gas-exchange data, it was apparent that the porometer, which had not been used before for gas-exchange measurements with cryptogams, showed some deficiencies. Difficulties in the measurements occurred especially when the environmental conditions for the lichens' gas-exchange were suboptimal. Therefore, in addition to the field measurements, gas-exchange was also measured in the laboratory under controlled conditions of light, temperature

and thallus water content using freshly collected lichen material from the field sites.

Gas-exchange measurements in the laboratory (1991). – These measurements were carried out at Abisko, Sweden with an infrared gas analyser (model 225-MK, ADC Ltd., Hoddesdon, UK) in the open system. Before the measurements were started, the lichens were kept in controlled conditions of temperature (5°/10°C), light (0/175 $\mu\text{mol m}^{-2}\text{s}^{-1}$) and humidity (daily spraying with distilled water) in a growth chamber. For a detailed description of the infrared gas analyser-system and the instrumental design see Sonesson (1989).

Micrometeorological measurements. – At the field site a micrometeorological station was set up for the period of gas-exchange measurements (7–18 August 1990) and water content measurements (11–23 July 1991). An anemometer (Didcot Instruments, Ltd., Alvingdon, Oxon, UK; type DWR/201 G), a ventilated miniature psychrometer (Delta-T Devices, Burwell, Cambridge, UK; type WVU/2), a silicon-sensor (Delta-T Devices, type ES) and a rain gauge were installed at about 30 cm above the ground. All instruments, except the rain gauge, were connected to Squirrel-Dataloggers (Grant Instruments, Ltd., Cambridge, UK; type SQ8-4U and SQ8-1V1/3V2). The interval for the readings was set at 15 minutes. The psychrometer was ventilated by a battery-powered (6 V) fan, which was started 1 minute before each reading.

Thallus water content measurements in the field (1991). – Collection of lichen material and preparation for the measurements were carried out as in 1990. Two different sets of replicates were prepared: five nylon baskets filled with lichen cushions (3.5 cm in diameter), and seven single thallus pieces, because those are mostly found in areas with high grazing pressure by reindeer. The thallus water content (TWC) was measured gravimetrically and expressed as percentage of thallus dry weight (% of DW). At both lichen sites several diurnal courses of thallus water content (in 1990 parallel to the gas exchange measurements) and some series of desiccation were measured under different weather conditions. Parallel to the weighings, air temperature, relative air humidity, wind speed and incoming light intensity (PAR), were recorded at the *C. nivalis* site.

Dry weight and chlorophyll determination. – The dry weight of the lichen samples used for the gas-exchange measurements in the field was determined after keeping the samples for at least 24 hours in a freeze dryer. This method, recommended by Sestak et al. (1971) and Hansson (1988), was chosen to prevent destruction of chlorophyll by drying the samples in an oven. A comparative test showed that the freeze dry weight corresponds to the oven dry weight at 80°C after 24 hours. The dry weight of the other samples was determined by drying them in an oven for 24 hours at 100°C. The samples used in the laboratory measurements were divided in two parts, one part was used for chlorophyll extraction, the other for determination of dry weight.

Extraction of chlorophyll was carried out using 85% acetone in weak light. The air dry lichen material (about 300 mg) was ground in a mortar. A small amount of quartz sand and $MgCO_3$ was added, to avoid destruction of chlorophyll by lichen acids, and about 10 ml of acetone. The acetone-chlorophyll mixture was centrifuged in

the cold for 10 min at 3,000 rpm and the supernatant decanted into a 25 ml flask. Then the residue was washed with acetone and centrifuged again. This procedure was repeated until no more chlorophyll could be extracted from the material. The extract was made up to a volume of 25 ml with acetone and kept for about one hour in the dark at 0°C. Absorbance was measured using a spectrophotometer (Perkin Elmer, Model 124) against 80% acetone at wavelengths of 750, 645 and 663 nm. Calculation of chlorophylls *a*, *b* and *a* + *b* were made according to Arnon (1949).

Results

CO₂ gas-exchange in the field

Generally, a large number of data points must be taken in field studies to obtain satisfactory response curves in relation to light, temperature and water content. In the present investigation a sufficient number of measurements was obtained

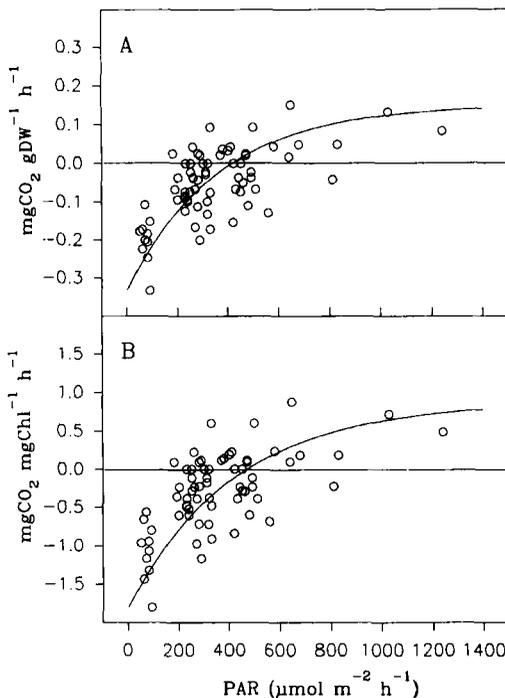


Fig. 1. *C. nivalis*, light response (field). CO_2 gas exchange response to light at about optimum thallus water content (100–200% of DW) and in the temperature range of 7.5 to 12.5°C (curve fitted by exponential function). A = related to dry weight; B = related to chlorophyll content.

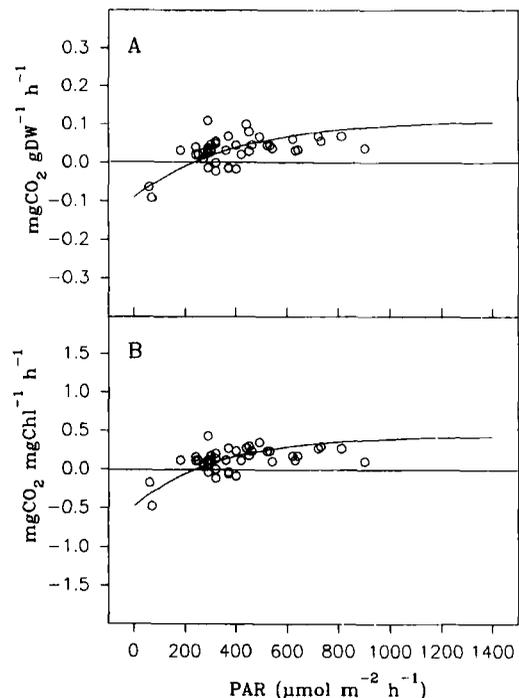


Fig. 2. *C. delisei*, light-response field. CO_2 gas exchange response to light at about optimum thallus water content (100–200% of DW) and in the temperature range of 7.5 to 12.5°C (curve fitted by exponential function). A = related to dry weight; B = related to chlorophyll content.

only in the temperature range between 5 and 13°C and at light intensities up to approximately 800 μmol m⁻²s⁻¹.

Response to light (Figs. 1 and 2). – The photosynthetic response to light followed a saturation type curve. The most reliable results were obtained in the temperature range between 7.5 and 12.5°C and at about optimum thallus hydration (100–200% of DW).

C. nivalis needed higher irradiances for light compensation (>200 μmol m⁻²s⁻¹) and light saturation of photosynthesis (>400 μmol m⁻²s⁻¹) than *C. delisei*, where light compensation (I_C) was found at about 100 μmol m⁻²s⁻¹, and light saturation (I_{sat}) at about 200 μmol m⁻²s⁻¹.

The maximum net photosynthetic rate (P_{max}) on dry weight-basis, reached in this temperature range was about the same in both species (0.12 versus 0.10 mgCO₂ gDW⁻¹h⁻¹). On chlorophyll basis P_{max} was almost three times higher in *C. nivalis* than in *C. delisei* (0.60 versus 0.21 mgChl⁻¹h⁻¹).

Response to thallus water content (Figs. 3 and 4). – The photosynthetic response to TWC followed an optimum type curve. The photosynthetic response to TWC is presented in the temperature range between 5 and 10°C and with saturating PAR (>400 μmol m⁻²s⁻¹). The optimum thallus hydration (H_{opt}), i.e. the water content at which the highest net photosynthetic rate (P_{max}) is obtained, was between 100 and 150% of thallus dry weight (% of DW) in *C. delisei* and somewhat higher (between 150 and 200% of DW) in *C. nivalis*.

P_{max}, related to dry weight, was slightly higher in *C. nivalis* than in *C. delisei* (0.12 versus 0.08 mgCO₂ gDW⁻¹h⁻¹). When related to the chlorophyll content P_{max} was about three times higher in *C. nivalis* (0.70 versus 0.25 mgCO₂ gChl⁻¹h⁻¹ in *C. delisei*). Minimum hydration level needed to reach compensation (H_C) was at about 40–50% of DW in both species. Maximum hydration (H_{max}), measured after long lasting rain and snowfall, was 300% of DW in *C. delisei* and 350% of DW in *C. nivalis*.

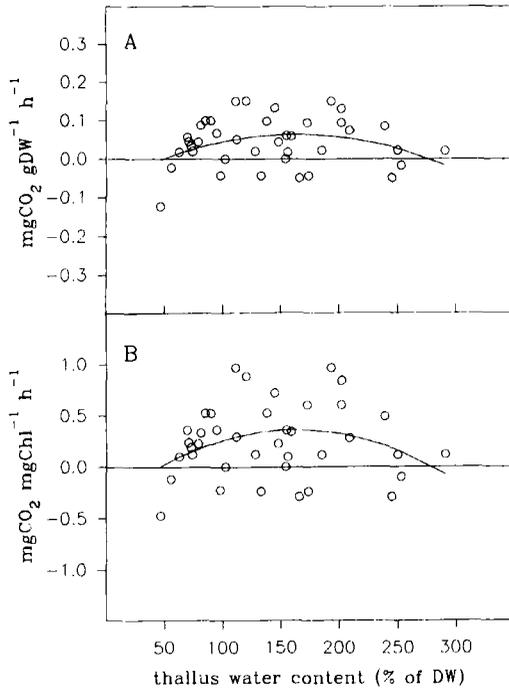


Fig. 3. *C. nivalis*, response to thallus water content (field). CO₂ gas exchange response to thallus water content at saturating photosynthetic active radiation and in the temperature range 5 to 10°C (curve fitted by polynomial regression). See Figs. 1 and 2 for explanation.

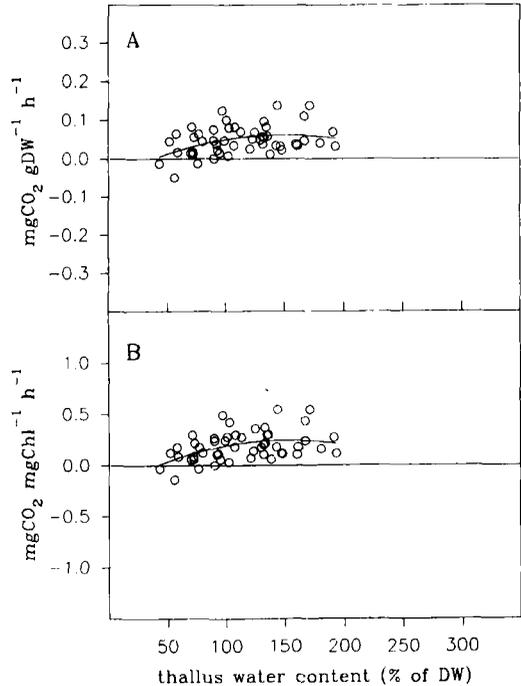


Fig. 4. *C. delisei*, response to thallus water content (field). CO₂ gas exchange response to thallus water content at photosynthetic active radiation and in the temperature range 5 to 10°C (curve fitted by polynomial regression). See Figs. 1 and 2 for explanation.

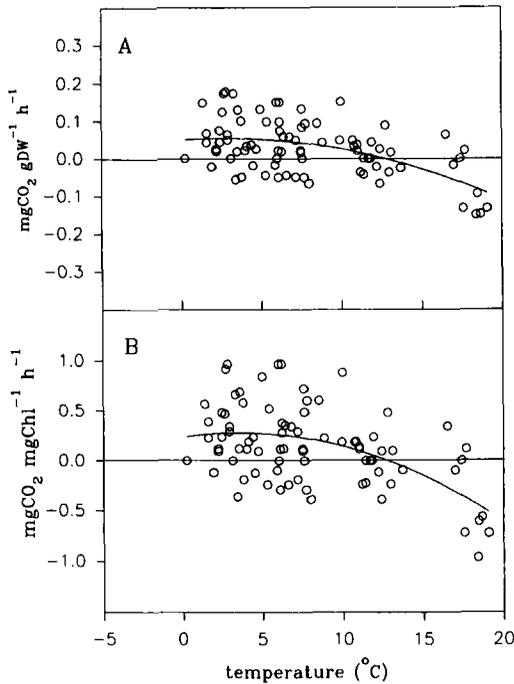


Fig. 5. *C. nivalis*, temperature-response (field). CO₂ gas exchange response to temperature (inside the cuvette, close to the lichen samples) at about optimum thallus water content and at saturating PAR (curve fitted by polynomial regression). See Figs. 1 and 2 for explanation.

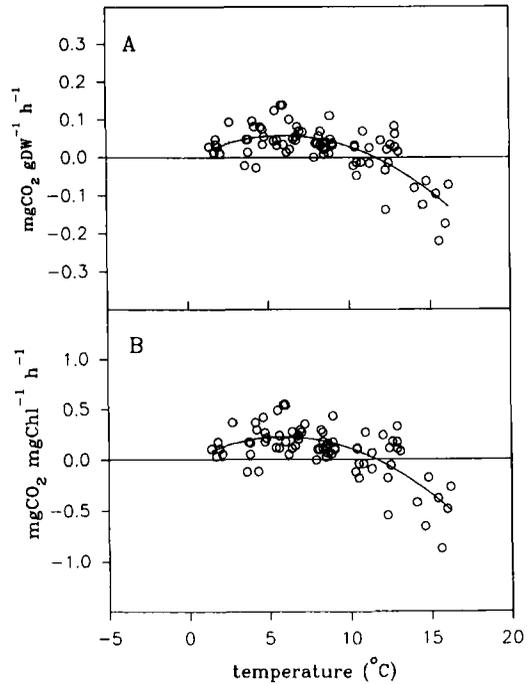


Fig. 6. *C. delisei*, temperature-response (field). CO₂ gas exchange response to temperature (inside the cuvette, close to the lichen samples) at about optimum thallus water content and at saturating PAR (curve fitted by polynomial regression). See Figs. 1–2 for explanation.

Response to temperature (Figs. 5 and 6). – The gas-exchange response to temperature (inside the cuvette close to the lichen samples) followed an optimum type curve. The optimum temperature (T_{opt}), where P_{max} is reached, measured at saturating PAR and about optimum thallus hydration, was between 5 and 7.5°C in *C. delisei* and between 2.5 and 5°C in *C. nivalis*. The slope of the temperature curve was steeper in *C. delisei*. Respiration dominated under the chosen light and hydration conditions at temperatures above 12.5–15°C, thus in these ranges there was no net gain of carbon.

CO₂ gas-exchange in the laboratory

Response to light (Figs. 7 and 8). – P_{max} was greatest at around 10°C in both species. At this temperature, related to dry weight, P_{max} was about twice as high in *C. nivalis* (0.50 mgCO₂ gDW⁻¹h⁻¹) than in *C. delisei* (0.25 mgCO₂ gDW⁻¹h⁻¹). On the basis of chlorophyll content P_{max} was only slightly higher in *C. nivalis* (1.80 versus 1.20 mgCO₂ mgChl⁻¹h⁻¹ in *C. delisei*).

The light compensation point (I_c) and light saturation (I_{sat}) increased with increasing temperature towards higher PAR in both species. At all temperatures I_c and I_{sat} were found at higher PAR in *C. delisei* than in *C. nivalis*. At 30°C no positive net photosynthesis occurred in either species.

At high PAR (1200 and 1500 $\mu\text{mol m}^{-2}\text{s}^{-1}$), together with temperatures of 25 and 30°C, a slight decrease of net photosynthesis indicating a tendency of photoinhibition, was shown by *C. delisei* (only at 25°C) and *C. nivalis*.

Response to thallus water content (Figs. 9 and 10). – The maximum hydration (H_{max}), reached after 30 minutes of soaking in water, was higher in *C. nivalis* (340–440% of DW) than in *C. delisei* (250–280% of DW). Also, the range of optimum hydration (H_{opt}) was wider and at higher TWC in *C. nivalis* (150–300% of DW) than in *C. delisei* (150–250% of DW). With increasing temperature H_{opt} shifted to higher TWC.

P_{max} , related to dry weight, was higher in *C. nivalis* than in *C. delisei* at all temperatures. When

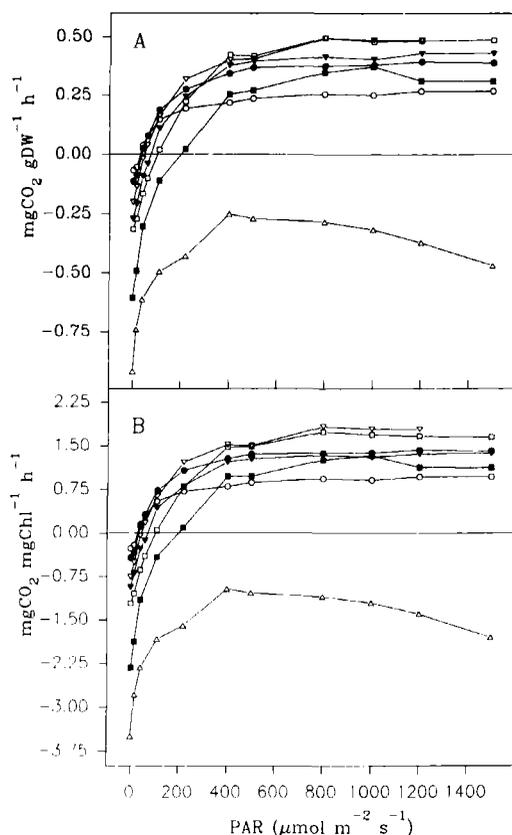


Fig. 7. *C. nivalis*, light response (laboratory). CO₂ gas exchange response to light (PAR) at about optimum thallus water content (100–200% of DW) and at different temperatures (0–30°C) (curve fitted by exponential function). Each point represents the mean of five replicates. A = related to dry weight (ranges of SE: 0.0050–0.0908); B = related to chlorophyll content (ranges of SE: 0.0062–0.4840). Symbols: ○ = 0°, ● = 5°, ▽ = 10°, ▼ = 15°, □ = 20°, ■ = 25°, △ = 30°C.

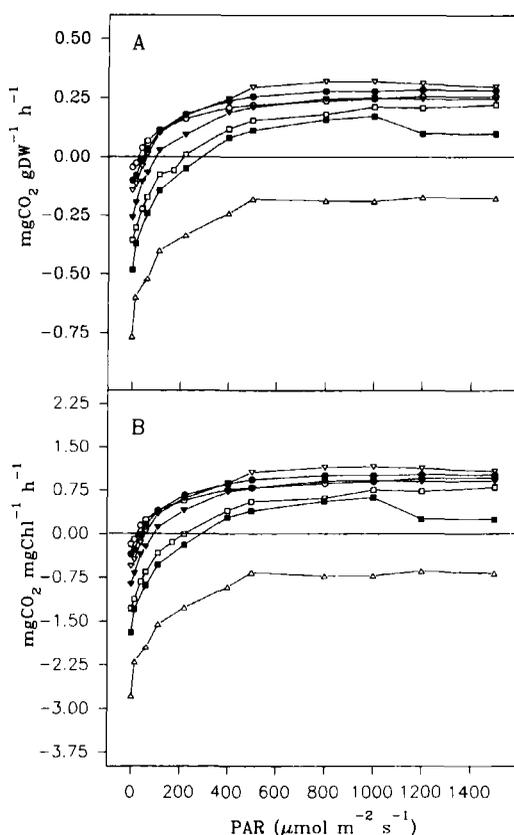


Fig. 8. *C. delisei*, light response (laboratory). CO₂ gas exchange response to light (PAR) at about optimum thallus water content (100–200% of DW) and at different temperatures (0–30°C) (curve fitted by exponential function). Each point represents the mean of five replicates. A = related to dry weight (ranges of SE: 0.0017–0.0905); B = related to chlorophyll content (ranges of SE: 0.0049–0.4387). Symbols: ○ = 0°, ● = 5°, ▽ = 10°, ▼ = 15°, □ = 20°, ■ = 25°, △ = 30°C.

related to chlorophyll, the net photosynthetic rates were about twice as high as in *C. nivalis* as in *C. delisei*.

The compensation point for photosynthesis (H_C) was at somewhat lower TWC in *C. delisei* (15–40% of DW) than in *C. nivalis* (20–50% of DW). At 30°C neither species reached compensation.

Maximum dark respiration rates (R_{max}) were measured near thallus saturation. These increased with temperature in both species. Up to 15°C no difference was found in respiration rates of the two species. At higher temperatures R_{max} was higher in *C. nivalis* than in *C. delisei*. Respiration ceased at water contents below 50% of DW.

Response to temperature (Figs. 11 and 12). – *C. delisei* showed a lower range of T_{opt} (5–10°C) than *C. nivalis* (10–20°C). T_{opt} shifted with increasing PAR to higher temperatures (from 5°C at $<110 \mu\text{mol m}^{-2}\text{s}^{-1}$ to 10–15°C at I_{sat}). Net photosynthetic rates, related to dry weight and chlorophyll, were about twice as high in *C. nivalis* at all temperatures. With increasing temperature the temperature compensation point (T_C) shifted to higher PAR (from $40 \mu\text{mol m}^{-2}\text{s}^{-1}$ at 0°C to $>400 \mu\text{mol m}^{-2}\text{s}^{-1}$ at 25°C). Neither species reached T_C at 30°C, *C. delisei* not even at 25°C.

Dark respiration rates were about the same or only slightly higher in *C. nivalis* than in *C. delisei* in the temperature range between 0 and 20°C. At

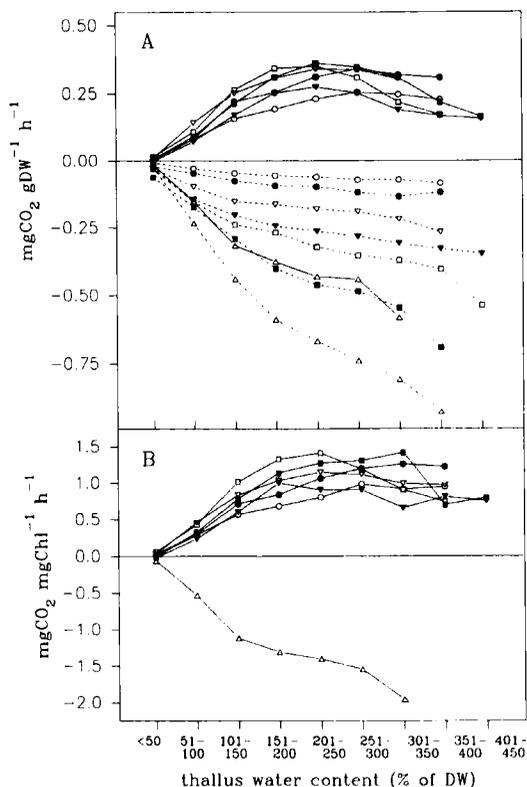


Fig. 9. *C. nivalis*, response to thallus water content (laboratory). CO₂ gas-exchange response to thallus water content (classes to each 50%) at saturating PAR (>500 $\mu\text{mol m}^{-2}\text{s}^{-1}$) and at different temperatures (0–30°C). A = related to dry weight (ranges of SE: 0.0031–0.0808 (NP), 0.0015–0.1304 (RD)), B = related to chlorophyll content (ranges of SE: 0.0103–0.5924 (NP)). — = net photosynthesis (NP), --- = dark respiration (RD). Symbols: ○ = 0°, ● = 5°, ▽ = 10°, ▾ = 15°, □ = 20°, ■ = 25°, △ = 30°C.

higher temperatures (25 and 30°C) there was a sharper increase in respiration in *C. nivalis*.

Chlorophyll content (Table 1). – The chlorophyll content (Chla, Chlb, Chla + b, each per g DW) and also the ratio Chla:Chlb was higher in *C. delisei* than in *C. nivalis*.

Microclimate of the field site (Fig. 13)

Continuous recordings of precipitation, light (PAR), air temperature, relative air humidity and wind speed were undertaken during the periods 7–18 August 1990 and 11–23 July 1991 at the *Cetraria nivalis* field-site on the top of the terrace.

The recorded precipitation (10.2 mm in 7–18

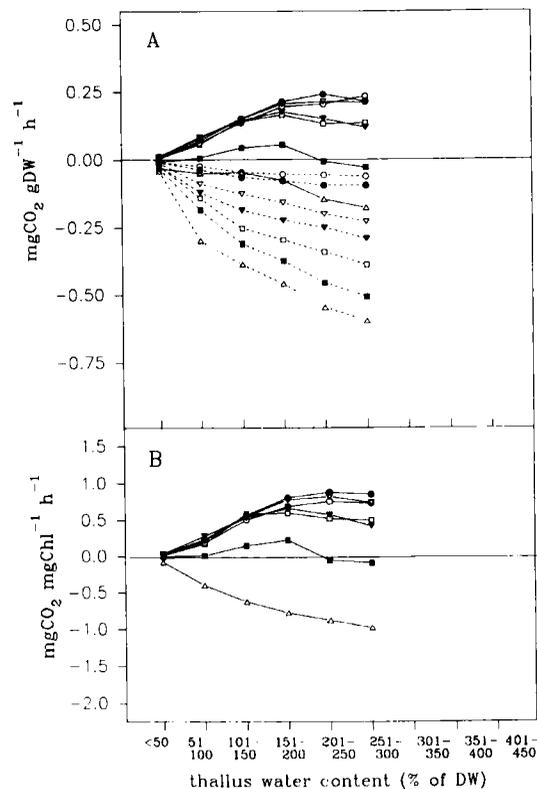


Fig. 10. *C. delisei*, response to thallus water content (laboratory). CO₂ gas-exchange response to thallus water content (classes to each 50%) at saturating PAR (>500 $\mu\text{mol m}^{-2}\text{s}^{-1}$) and at different temperatures (0–30°C). A = related to dry weight (ranges of SE: 0.0017–0.0294 (NP), 0.0012–0.0669 (RD)), B = related to chlorophyll content (ranges of SE: 0.0097–0.1507 (NP)). — = net photosynthesis (NP), --- = dark respiration (RD). Symbols: ○ = 0°, ● = 5°, ▽ = 10°, ▾ = 15°, □ = 20°, ■ = 25°, △ = 30°C.

August 1990 and 2.0 mm in 11–23 July 1991) probably underestimates the real amounts, because in Ny Ålesund nearly all precipitation events (mostly snow) during these periods were connected with strong wind.

PAR between 20 and 1363 $\mu\text{mol m}^{-2}\text{s}^{-1}$ PAR were recorded. Values between 50 and 150 $\mu\text{mol m}^{-2}\text{s}^{-1}$ were most frequent, values higher than 500 $\mu\text{mol m}^{-2}\text{s}^{-1}$ were rare.

The minimum temperatures measured were -1.0°C (1990) and -0.5°C (1991), the maximum temperatures 14.2°C and 15.4°C respectively. The daily course of temperature showed relatively small variations: the mean daily amplitudes were 4.7°K (1990) and 5.9°K (1991), the maximum daily amplitudes were 8.4°K (1990) and 10.0°K

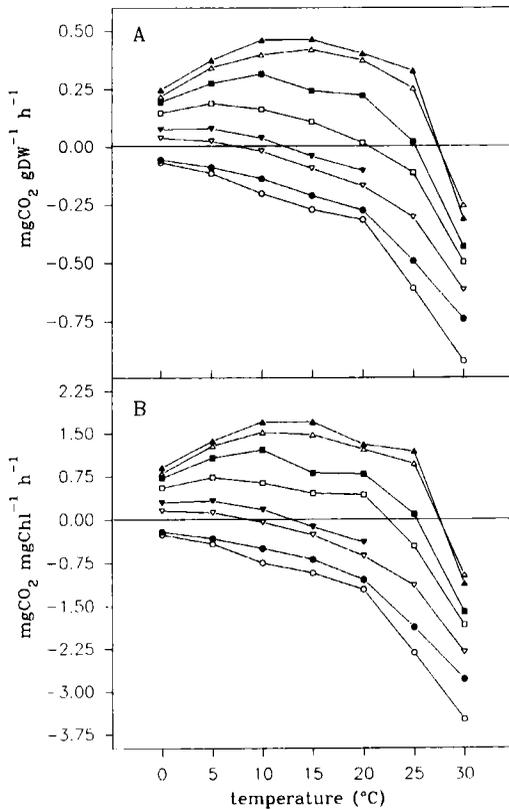


Fig. 11. *C. nivalis*, temperature response (laboratory). CO₂ gas-exchange response to temperature (inside the cuvette, close to the lichen samples) at about optimum thallus water content and at different PAR (symbols: ○ = 0, ● = 15, ▽ = 40, ▼ = 60, □ = 110, ■ = 220, △ = 400, ▲ = >500 μmol s⁻²m⁻¹). A = related to dry weight (ranges of SE: 0.0050–0.0908), B = related to chlorophyll content (ranges of SE: 0.0062–0.4840).

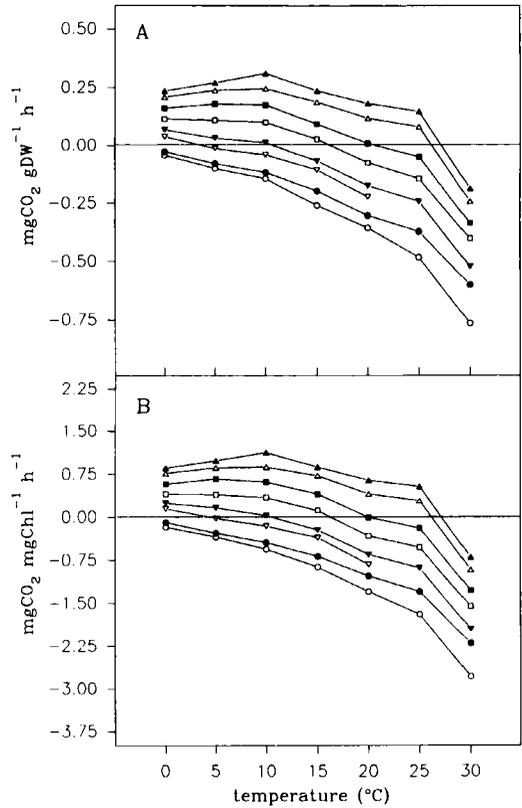


Fig. 12. *C. delisei*, temperature response (laboratory). CO₂ gas-exchange response to temperature (inside the cuvette, close to the lichen samples) at about optimum thallus water content and at different PAR (symbols: ○ = 0, ● = 15, ▽ = 40, ▼ = 60, □ = 110, ■ = 220, △ = 400, ▲ = >500 μmol s⁻²m⁻¹). A = related to dry weight (ranges of SE: 0.0017–0.0905), B = related to chlorophyll content (ranges of SE: 0.0049–0.4387).

(1991). Frost occurred on some days during both measuring periods. Temperatures between 0 and 2.5°C and 7.5 and 10°C were most frequent in 1990, between 5 and 7.5°C in 1991.

Minimum values of relative air humidity were 46% (1990) and 26% (1991), maximum values were 100% in both periods. The maximal diurnal amplitudes were 40% and 64% respectively, the mean diurnal variations were 45% (1990) and 25% (1991). Most frequently relative air humidity values > 90% were obtained (almost as frequent was the range between 60 and 90%) in 1990. In 1991 RH% between 50–60% and 100% were most frequent. Values lower than 60% were rare.

In the recording period 1990 wind speeds between 1–3 m/s were most frequent. Periods of

calm weather (wind speed 0–1 m/s) dominated in 1991. The maximum wind speed measured in 1990 was 7.9 m/s, in 1991 10.7 m/s.

At the *C. delisei* site on the lower slope of the terrace no instrumentation for microclimatic recordings was available. It is assumed that at this site wind speed, duration of sunshine due to shading by the slope and temperature fluctuations will be less, and that water availability will be higher than on the top of the terrace (Geiger 1971; Kershaw & Larson 1974).

Thallus water content and desiccation

Diurnal courses of thallus water content. – In 1990 one diurnal course (9–10 August 1990) of TWC

Table 1. Literature review of ecophysiological works on *C. nivalis*.

Reference	Locality	Lichen part used	P_{max} ($mg\ CO_2\ g^{-1}h^{-1}$)	T_{opt} ($^{\circ}C$)	I_{sat}	H_{opt} (%TDW)	H_{max} (%TDW)
Bliss & Hadley 1964	Mt. Washington/ New Hampshire (North America)	total specimen	0.3–0.38	15–20	ca 1600 ft. c. (~300 μmol)	—	—
Kallio & Heinonen 1971	Kevo (North Finland)	—	0.3	ca 10	10–20 klx (~190–380 μmol)	—	296–413
Kallio & Kärenlampi 1975	Kevo (North Finland)	total specimen	0.3–0.4	ca 10	10–20 klx (~190–380 μmol)	100–200	—
Larson & Kershaw 1975a, b	East Pen Island (North America)	top parts (1 cm)	0.8–1.0	7–14	—	150	400
Türk 1981, 1983 (Austria)	Eastern Alps	upper 1.5 cm	0.68–1.2	5–10	20–30 klx (~380–550 μmol)	150–250	410

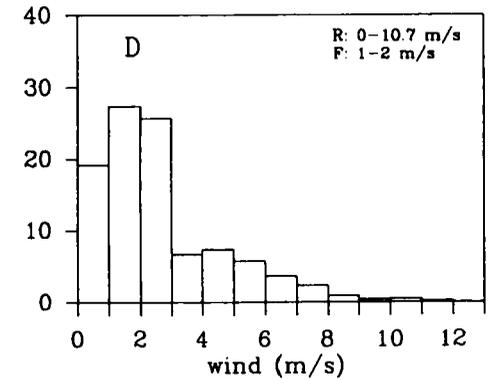
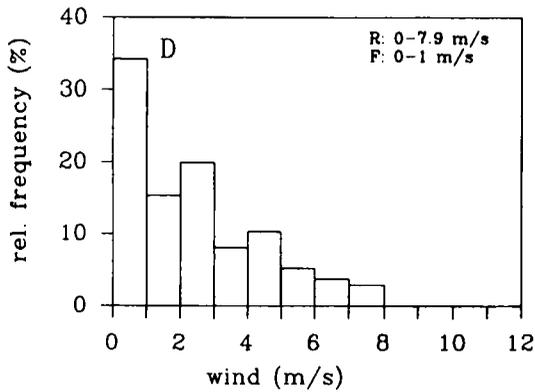
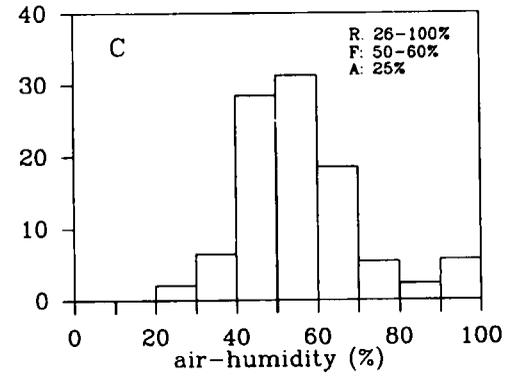
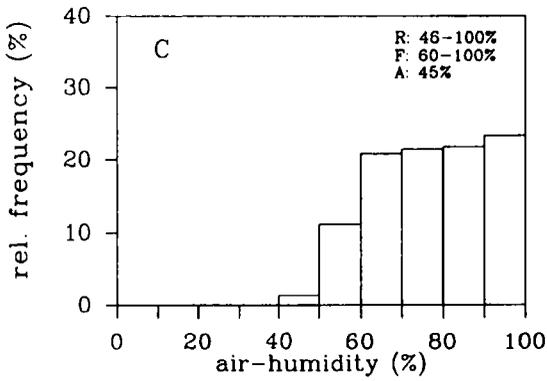
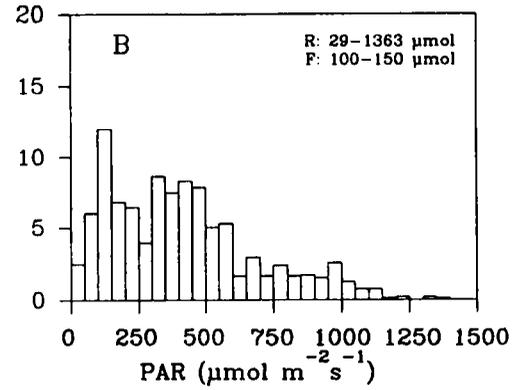
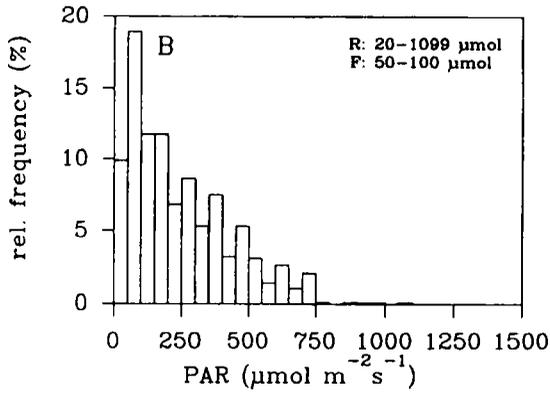
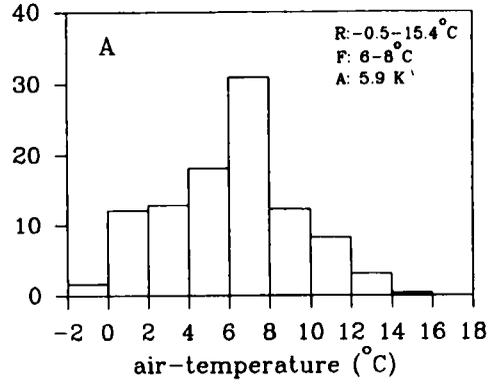
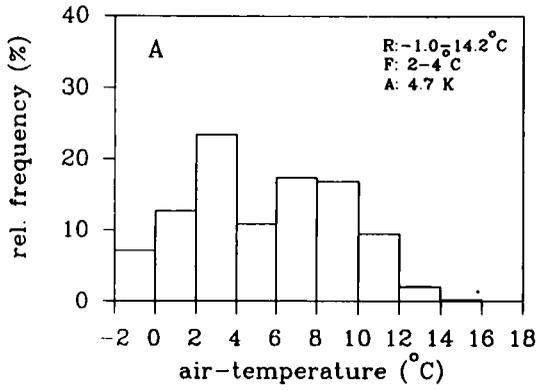
was measured, under cold and mostly wet conditions (Fig. 14). Because it snowed or rained during most of the previous day, the lichens were nearly saturated when the measurements started at 10.00 a.m. on 9 August. At this time the snow and rain had ceased, but the sky was still overcast. Between 11.30 a.m. and 5.00 p.m. there were rapid and frequent changes of snow showers, sunshine and gusty wind, followed by a dry, but windy and mostly overcast period for some hours. From about 8.00 p.m. until the morning of 10 August more or less heavy snow, sleet or rain showers prevailed, together with strong wind. For some time the lichens were covered with snow.

The TWC curves of both species run parallel, following the humidity conditions of the 24-hour period. TWC of *C. nivalis* was higher than that of *C. delisei*. The TWC of *C. nivalis* decreased faster (during the afternoon of 9 August), possibly due to the more wind-sheltered position of the *C. delisei* site. The TWC decreased from near saturation (*C. nivalis* 321% of DW, *C. delisei* 150% of DW) to about 60 and 50% of DW respectively towards the evening, before the next wet period caused a steep increase of TWC up to high saturation again (*C. nivalis* 250–300% of DW, *C. delisei* 200–240% of DW).

In 1991, two diurnal courses of lichen water content were examined, the first on 12–13 July under cold, windy and snowy conditions, the second on 16–17 July under mostly sunny and quite warm weather conditions.

12–13 July 1991 (Fig. 15): After some weeks of rainy weather it became colder during the night of 11 July and it began to snow. From early morning until 10.00 a.m. of 12 July a thin layer of snow covered the entire area around Ny Ålesund. TWC measurements were started at 11.00 a.m. under slight snowfall and strong wind. The lichens were already moist (*C. nivalis* 133% of DW, *C. delisei* 180% of DW), but not saturated and not covered with snow anymore. In the early afternoon there were some hours with only periodic snow showers, thus the lichens dried out to a

Fig. 13. Frequency distribution of microclimatic parameters 1990 (left) and 1991 (right). A = Air-temperature, classes of 2.5 $^{\circ}C$; B = PAR, classes of 50 $\mu mol\ m^{-2}s^{-1}$; C = RH%, classes of 10%; D = Wind, classes of 1 m/s. R = absolute range, F = highest frequency, A = mean daily amplitude.



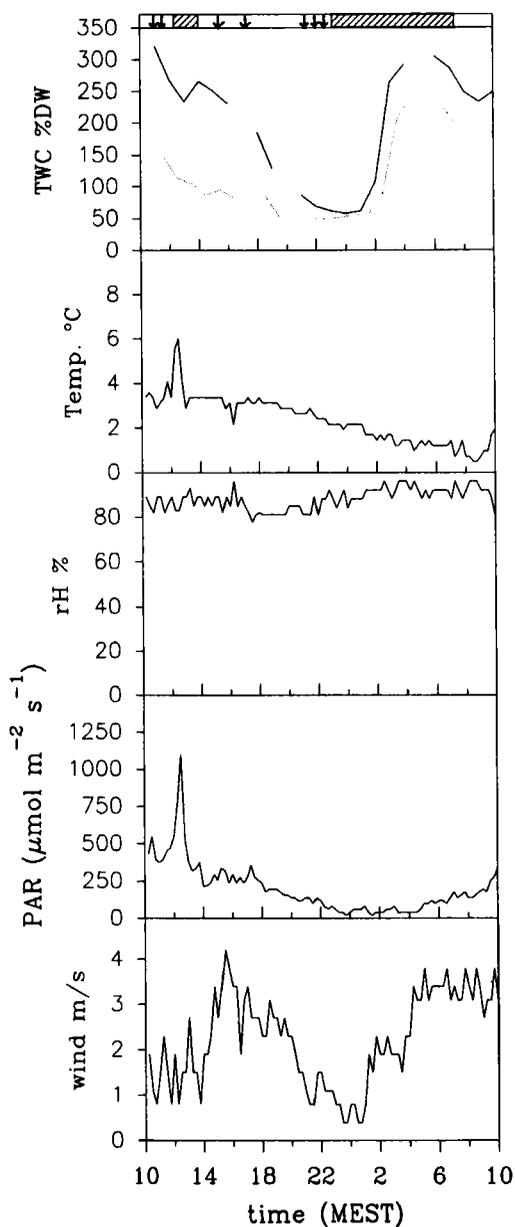


Fig. 14. Diurnal courses of thallus water content (% of DW) of *C. nivalis* (solid line) and *C. delisei* (dashed line) and microclimatic parameters on 9–10 August, 1990. Arrows and // - bars indicate precipitation events. MEST = Middle European Summer Time.

TWC of about 39 and 47% respectively. In late afternoon snowfall set in again and wind grew stronger. There was a sharp increase of TWC during the night, when the snow did not melt from the ground and the lichen samples became more and more snow-covered. Due to the heavy

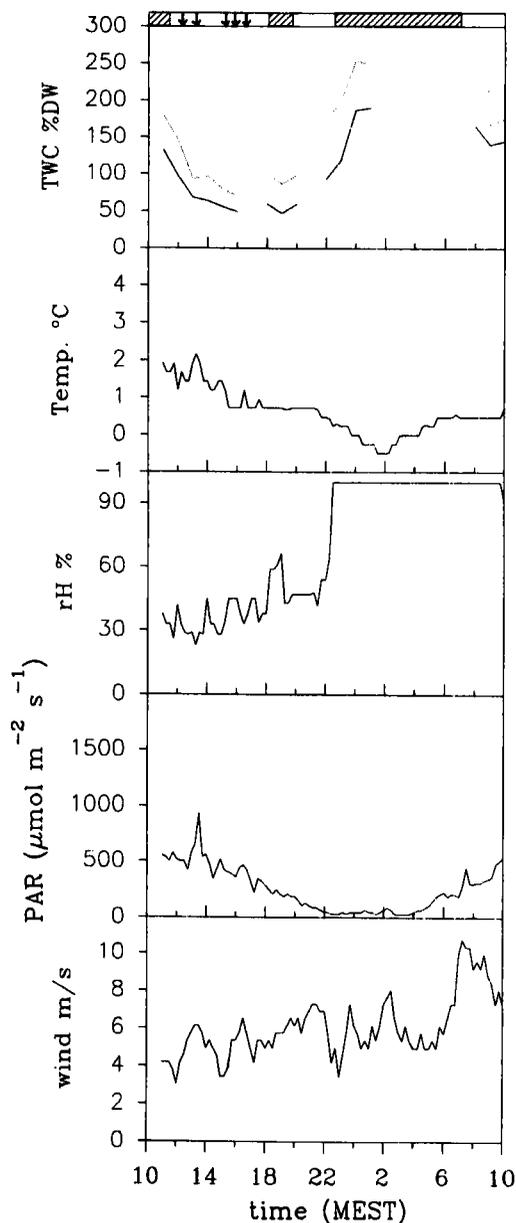


Fig. 15. Diurnal courses of thallus water content (% of DW) of *C. nivalis* (solid line) and *C. delisei* (dashed line) and microclimatic parameters on 12–13 July, 1991. Arrows and // - bars indicate precipitation events. MEST = Middle European Summer Time.

snowfall and the resulting high snow cover (about 5 cm above the samples), it was not possible to remove the samples for weighing without disrupting the lichens because they were frozen on the ground. Therefore there is a break of some hours in the measurements. In the morning of 13

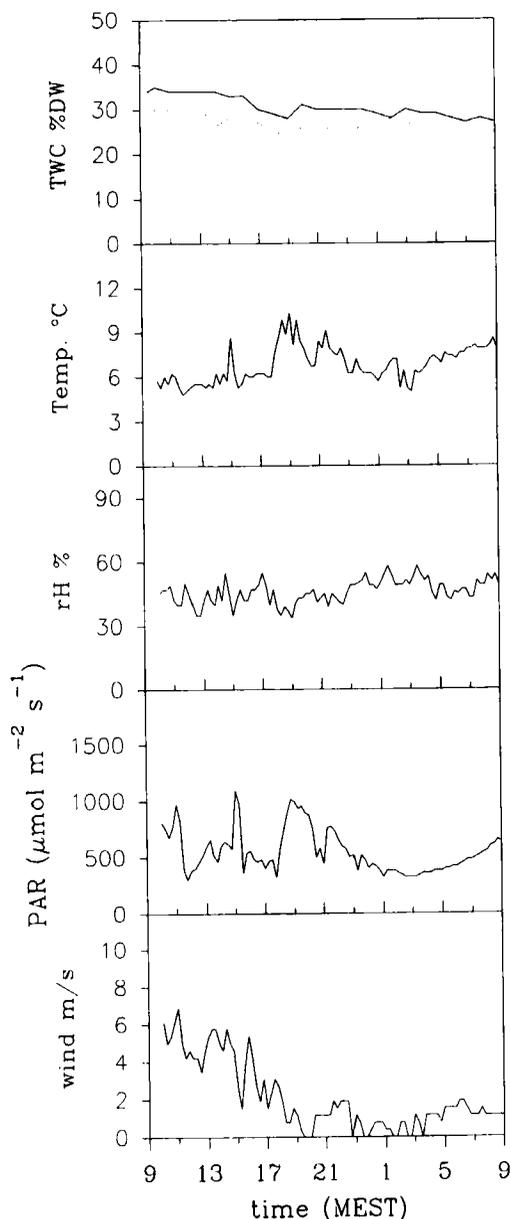


Fig. 16. Diurnal courses of thallus water content (% of DW) of *C. nivalis* (solid line) and *C. delisei* (dashed line) and microclimatic parameters on 16–17 July, 1991. Arrows and // - bars indicate precipitation events. MEST = Middle European Summer Time.

July, when snowfall changed to sleet and the snow had melted from the ground, the TWC was still high (*C. nivalis* 145% of DW, *C. delisei* 175% of DW). The extremely high TWC of the single thalli during the night (up to 389% of DW and 438% of DW respectively) may not show the real saturated

TWC. This may partly be due to small frozen snow and ice clumps on the thalli or between the thallus branches.

Under these weather conditions the TWC of *C. delisei* was higher than that of *C. nivalis*. The course of the water content curve of both species, however, was rather parallel, and followed the course of precipitation.

16–17 July 1991 (Fig. 16): Measurements started at 9.30 a.m. on 16 July. This day was dry with some overcast periods and some hours of rather strong wind in the early afternoon. From late evening (22.00 p.m.) until the end of measurement on the morning of 17 July (9.00 a.m.), the sky was cloudless and the measuring site was in full sunlight. Partial shading of the *C. delisei* site occurred, however, for some hours during the night.

Under these weather conditions the TWC of *C. nivalis* was higher than that of *C. delisei*. The variation in TWC over the entire day was low in both species. The maximum TWC, reached between 10.00 p.m. and 4.00 a.m. on 16 July was around 30% of DW, minimum TWC around 20% of DW. There was no marked increase of weight during the night because the sun was shining high above the horizon and no dew formation occurred. Comparing the lichen cushions and single lichen thalli respectively, generally the cushions showed higher TWC than the single thalli except the daily course measurement in snow and ice (Fig. 15). Here the TWC of single pieces were higher.

Desiccation experiments (Fig. 17 and 18). – Four desiccation experiments were carried out: one under natural conditions (after nightly rain showers) in the beginning of the dry weather period (15 July); the others after artificial watering, simulating the effect of brief rain showers (19, 20 and 22 July).

The absolute TWC (% of DW) of *C. nivalis* was higher than that of *C. delisei*, except in the experiment on 15 July with the naturally moistened lichens, where TWC was about the same in both species. Also the relative TWC (% of H_{max}) was the same in the two species. The single thalli showed a steeper decrease in water content. The single thalli reached their “air-dry” weight (weight in balance to the prevailing air humidity) after 1–1.5 hours (after artificial watering), whereas the cushions needed about 5–6 hours to become “air-dry”.

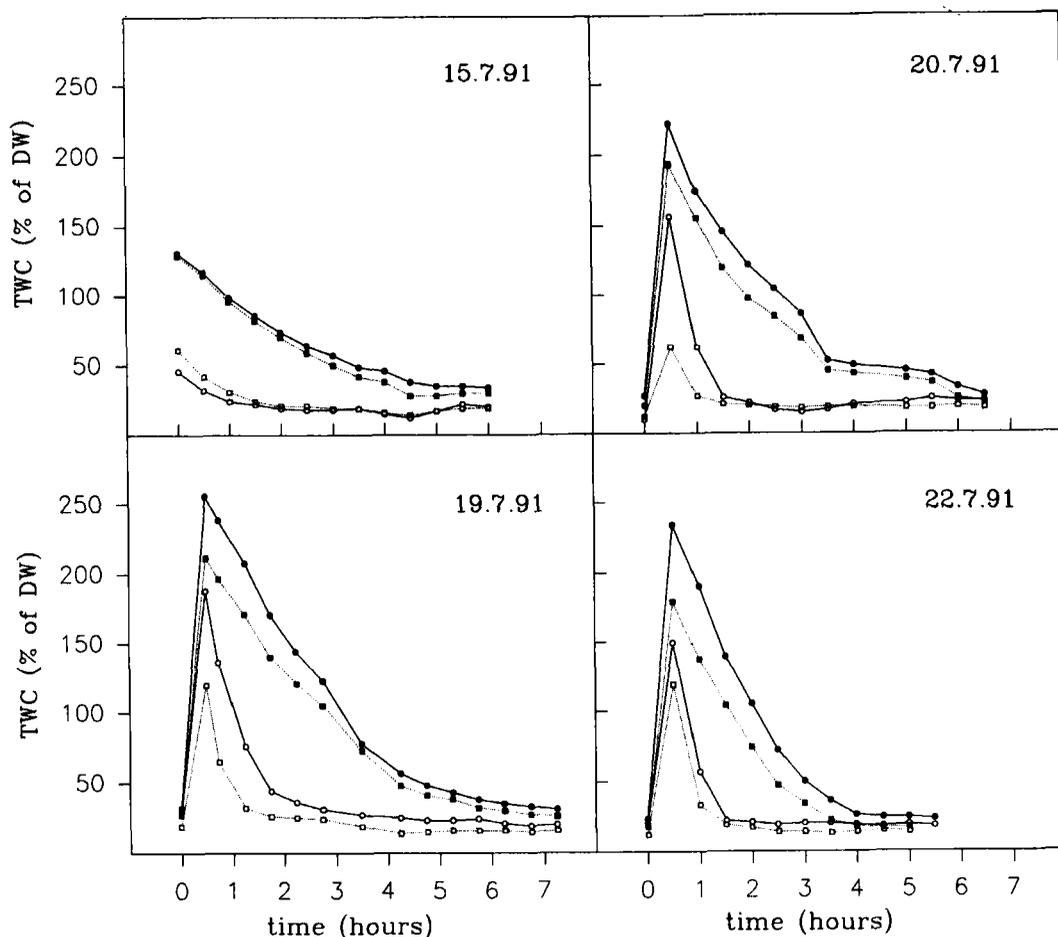


Fig. 17. Desiccation curves of *C. nivalis* (solid line: ○ = single thalli, ● = cushions) and *C. delisei* (dashed line: □ = single thalli, ■ = cushions), expressed as % of thallus dry weight (TWC% of DW).

Discussion

CO₂ gas-exchange in the field and in the laboratory

The response curves to light (saturation-curve), temperature and thallus water content (optimum-curves) obtained both in the field and in the laboratory correspond to those reported for most lichens and other plants (e.g. Ried 1960; Larcher 1975; Türk 1981, 1983; Kershaw 1985).

The photosynthetic rates measured in *C. nivalis* correspond with that reported for *C. nivalis* (e.g. Bliss & Hadley 1964; Kallio & Kärenlampi 1975; Larson & Kershaw 1975a; see Table 1). With respect to *C. delisei* no relevant references have

been found. Differences in gas-exchange responses (with respect to the parameters P_{max} , I_C , I_{sat} , T_C , T_{opt} , H_C , H_{max} , H_{opt}) were found between the two species, between field and laboratory data and between the data related to dry weight and chlorophyll content respectively (Table 2).

The differences between the laboratory and field data may be due to the conditions experienced by the lichens prior to the measurements. The lichens in the laboratory were kept at constant conditions in a growth chamber, whereas the lichens in the field have experienced highly variable conditions. The results of the field measurements showed a high degree of scattering compared with the laboratory measurements.

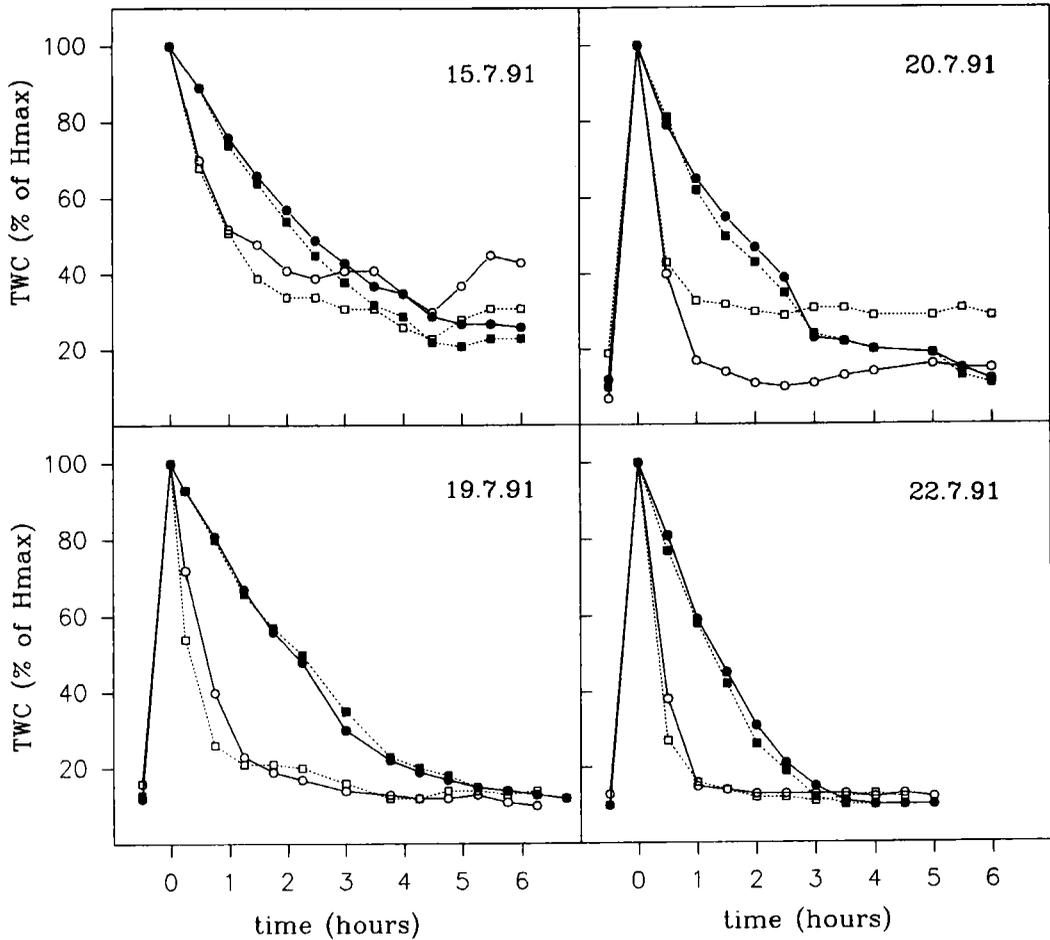


Fig. 18. Desiccation curves of *C. nivalis* (solid line: ○ = single thalli, ● = cushions) and *C. delisei* (dashed line: □ = single thalli, ■ = cushions), expressed as % of maximum water content (TWC% of H_{max}).

Differences between individual thalli may also play an important role. Attempts to reduce this source of variation were made by random sampling and random distribution of lichen thalli into the nets. Another reason for the large variation is the rapid change of factors influencing the gas-exchange (especially light, temperature and thallus water content), which occurs under natural conditions. Also the mode of hydration, by snow, rain, humid air or spraying, may influence the photosynthetic response of lichens (Schroeter 1991). Similar variation of field data was obtained in other studies concerning gas-exchange measurements in situ (e.g. Hahn et al. 1988; Schroeter 1991). However, in the present investigation scattering and resulting uncertainties are

also obviously dependent on some technical deficiencies of the field infrared gas analyser instruments when used with cryptogams. The problem of high humidity values inside the leaf chamber and in the outgoing air, caused by evaporation of well-moistened lichen samples, was overcome by leading the outgoing air stream through a container filled with a drying agent (silica gel). However, the limited operation range of the LCA2 analyser with respect to air humidity (up to 85% relative humidity) and temperature (+5 to +40°C) can lead to erratic readings and unreliable results when the instrument is used during humid or cold conditions, as experienced on Svalbard. In addition, overheating in bright sunshine might have occurred due to "cuvette-effects", since the

Table 2. Comparison of gas-exchange data obtained in the laboratory and in the field.

	<i>Nivalis</i>		<i>C. delisei</i>	
	Laboratory	Field	Laboratory	Field
R_{\max} (at 10°C) (mgCO ₂ gDW ⁻¹ h ⁻¹)	-0.30	—	-0.25	—
P_{\max} (at 10°C) mgCO ₂ gDW ⁻¹ h ⁻¹	0.50	0.12	0.25	0.10
mgCO ₂ mgChl ⁻¹ h ⁻¹	1.80	0.70	1.20	0.25
I_{sat} (μmol m ⁻² s ⁻¹)	>350	>400	>400	>200
I_C (μmol m ⁻² s ⁻¹)	ca. 50	ca. 200	ca. 50	ca. 100
photoinhibition	+	—	+	—
H_{\max} (% of DW)	ca. 340	ca. 300	ca. 260	ca. 250
H_{opt} (% of DW)	150–350	150–200	150–250	100–150
H_C (% of DW)	20–50	40–50	20–40	40–50
T_{opt} (°C)	10–15	2.5–5	10	5–7.5
T_C (lower) (°C)	—	<1–1.5	—	<1–1.5
(upper) (°C)	ca. 26	>13–15	ca. 22	>13–15
Chlorophyll				
Chla (mg gDW ⁻¹)	0.125		0.154	
Chlb (mg gDW ⁻¹)	0.066		0.078	
Chla + b (mg gDW ⁻¹)	0.191		0.232	
Chla:b	2.00		2.57	

temperature in the leaf chamber could not be controlled.

Response to light. – The position of I_C increased markedly with increasing temperature because of strongly increasing respiration rates. I_C (at about T_{opt}) measured in the field was rather high (200 μmol m⁻²s⁻¹ in *C. nivalis* and 100 μmol m⁻²s⁻¹ in *C. delisei*) compared with the results of the laboratory measurements (50 and 70 μmol m⁻²s⁻¹ respectively). High I_C of 10 Klux (200 μmol m⁻²s⁻¹) was reported for *Buellia frigida* and *Neuropogon acromelanus* (at 12°C) from the Antarctic (Lange & Kappen 1972) and also for *Usnea antarctica* of 100 μmol m⁻²s⁻¹ (at 9°C, Schroeter 1991). Species from open, exposed habitats are supposed to have I_C at higher PAR than species growing in shaded habitats or in depressions (Larson & Kershaw 1975a). This is in agreement with the field measurements, which showed a higher I_C in *C. nivalis* than in *C. delisei*.

Some evidence of photoinhibition was found in both species at PAR of 1500 μmol m⁻²s⁻¹ together with high temperatures (25° and/or 30°C) during laboratory measurements (Figs. 7 and 8). However, this decrease in photosynthetic rates may probably be an artefact caused by variations in thallus water content, because the lichens dried out very quickly under conditions of high

irradiance and high temperature. Photoinhibition has seldom been reported from laboratory measurements of lichen gas-exchange before, but lower maximum light levels were used in previous investigations (e.g. Türk (1981) ca. 650 μmol m⁻²s⁻¹, Kappen (1985) ca. 800 μmol m⁻²s⁻¹, Schroeter (1991) 750 μmol m⁻²s⁻¹). Coxson (1987), however, found photoinhibition in some *Stereocaulon*-species at PAR of 1500 μmol m⁻²s⁻¹ and temperatures of 30°C or higher. For higher plants, photoinhibition induced by high temperatures is also reported (see review by Ludlow 1987). In contrast to some recent reports about CO₂ gas-exchange of cryptogams in the field (Adamson et al. 1988, 1989; Kappen et al. 1989), neither *C. nivalis* nor *C. delisei* showed any evidence of photoinhibition at high PAR in the field (range of temperature 7.5–12°C). Circumstances which reduce the dark reactions of photosynthesis, for example low temperatures or other environmental stress factors, lower the quantum flux density required for photosynthesis and hence increase the sensitivity to photoinhibition (Adamson et al. 1988). However, even at temperatures less than 5°C no photo-inhibition was found in the present field data. Situations with high PAR together with low temperatures and high thallus water content will be rare in the Arctic. Precipitation is mostly snow which is combined with

rather low temperatures at low light levels. In addition, due to the low solar angle at the high latitude of Ny Ålesund (78°N), even in summer the incoming radiation is not as high as it may be in Antarctica, from where photoinhibition of cryptogam photosynthesis was reported (at about 66°S; Adamson et al. 1988, 1989; Kappen et al. 1989).

Response to thallus water content. – The response of lichen gas-exchange to TWC is a function of physiological, morphological and anatomical features of the thallus and often also of the characteristics of the habitat (e.g. Ried 1960; Rundel 1988). *C. delisei*, as a chionophilous inhabitant of snow beds and other wet habitats, could be assumed to show higher H_{\max} , H_C and H_{opt} than the chionophobic lichen *C. nivalis*, which grows in more xeric habitats (Blum 1973; Matthes & Feige 1983). The results of the present study are in contrast to this hypothesis, since higher values of TWC were found in *C. nivalis*, both in the field and in the laboratory. This might be explained by morphological and/or anatomical differences between the two species. Further, the habitats of *C. delisei* on the Arctic tundra of Svalbard are not permanently wet like localities of *C. delisei* in mires or “alpine” snow beds in the subarctic (Gjaerevoll 1956; Dahl 1956). In Svalbard *C. delisei* is dominant on strandflats and early snow beds on lower slopes of terraces, which are wet only in spring when meltwater is stagnating upon the permafrost soil (Elvebakk 1979, 1985). In late summer these habitats are almost as dry as the exposed ridges (personal observations). On the other hand, also *C. nivalis* may occur under less chionophobic habitat conditions (DuRietz 1925; Dahl 1956). Larson & Kershaw (1974, 1975a, b) found a higher abundance of *C. nivalis* on the lower slopes of raised beach ridges with a prolonged snow cover than on the exposed ridge tops in Arctic N-America. Also Richardson & Finegan (1977) described *C. nivalis* as preferring more moist and less exposed habitats. However, findings of *C. nivalis* in the moderate snow beds on ridge slopes and in depressions in Svalbard are explained by transport of fragments by wind; these thalli are reported to survive only for short periods (Elvebakk 1984).

Depression of net photosynthesis at thallus saturation was found in both species, but less extreme than in a number of other species (Lechowicz et al. 1974; Lange & Matthes 1981;

Türk 1983), especially at low temperatures. This depression is thought to be due to increased internal CO₂ diffusive resistance at high TWC, which depends partly on thallus structure (Kershaw 1972; Lange & Tenhunen 1981; Matthes & Feige 1983; Türk 1983; Kappen & Redon 1987; Rundel 1988; Sancho & Kappen 1989). According to Matthes & Feige (1983) species growing in wet habitats show lower depressions of photosynthesis at high TWC than species growing in xeric habitats. Türk (1983) postulates a lower depression for species with a high capacity for water uptake. He describes two lichen types with respect to photosynthetic response to TWC, i.e. lichens with a low and with a high potential for water uptake respectively. According to this classification, *C. nivalis* with a water uptake potential of more than 300% (Türk 1983) belongs to the second type. The high degree of maximum hydration of *C. nivalis* and the low depression of photosynthesis at supraoptimal TWC, obtained in the present investigation, are in agreement with Türk's statements.

Comparing field and laboratory data, H_{\max} in the field was not or was only slightly lower (292% of DW, (SE 4.969) in *C. nivalis* and 249% of DW (SE 2.258) in *C. delisei*) than in the laboratory (*C. nivalis*: 336% of DW, SE 14.541; *C. delisei*: 258% of DW, SE 11.249), whereas H_{opt} showed a wider range in the laboratory (span of about 100–150% than in the field (span of ca. 50%).

Response to temperature. – At saturating light intensity T_{opt} in the field (ca. 5°C) was lower than that obtained in the laboratory (between 10 and 15°C). The position of T_{opt} in the laboratory corresponds to that reported for many other Arctic-alpine and temperate lichen species (i.e. 5–15°C, e.g. Kallio & Kärenlampi 1975; Larcher 1975; Larson & Kershaw 1975a; Türk 1981). In general, plants of cold climatic regions tend to have T_{opt} similar to, or slightly above the mean temperature in their habitat. The same may be true for the lichens from Svalbard, where temperatures of 15°C or more are rather the exception (Table 3). A lower T_{opt} indicated in the field as well as the higher T_{opt} in the laboratory may reflect an acclimatisation to the actual conditions due to physiological plasticity. Shifts of T_{opt} (from 14°C in summer to 7°C in autumn) at PAR of 150 $\mu\text{mol m}^{-2}\text{s}^{-1}$ for *C. nivalis* were reported by Larson & Kershaw (1975a).

Photosynthetic adaptation of plants from cold

Table 3. Macroclimatic conditions at Ny Ålesund (Svalbard). Data from weather station at Ny Ålesund (78°55'N, 11°56'E, 8 m.a.s.l.) (Steffensen 1982); Det Norske Meteorologiske Institutt (Klimaavdelingen), Oslo.

Month	Mean temperature (°C)			Mean precipitation (mm)			Mean rel. air-humidity (%)		
	1990	1991	Period 1971–1980	1990	1991	Period 1971–1980	1990	1991	Period 1971–1980
Jan.	-6.4	-10.8	-12.8	28	43	31	72	73	77
Feb.	-9.9	-10.1	-13.9	3	114	34	70	81	79
Mar.	-15.5	-8.0	-13.1	42	73	39	80	74	79
April	-8.7	-11.0	-11.1	105	28	19	84	70	78
May	-4.9	-3.4	-3.8	27	29	22	79	77	81
June	2.1	2.6	2.1	20	3	13	87	80	85
July	5.2	3.9	5.2	7	37	33	82	90	87
Aug.	4.1	5.1	4.1	31		42	81	81	87
Sept.	4.7	-0.7	0.1	145		39	80	79	85
Oct.	-3.2	-5.7	-5.5	38		47	73	73	71
Nov.	-11.5	-11.5	-9.7	6		35	66	69	68
Dec.	-8.1	-12.6	-11.7	35		31	70	77	69
Year	-4.4	-4.8	-5.8	496		385	77	77	79

climates generally involves high rates of dark respiration. Hence, a rise of temperature is followed by a particularly large increase in respiration (Billings & Mooney 1968; Lange & Kappen 1972; Larcher 1975; Friend & Woodward 1990; and others). Thus, at high temperatures respiration will dominate and determine the position of the upper T_C , which was reached at lower temperature in the field (above ca. 15°C) than in the laboratory (above ca. 22°C in *C. delisei*, and ca. 26°C in *C. nivalis*). Türk (1981) reports the temperature maximum of net photosynthesis for alpine *Cetraria*-species to be between 22 and 27°C, which corresponds well with the present laboratory results. The dominating role of respiration becomes evident in the laboratory in the sharp increase of respiration at temperatures above 15°C (Figs. 11 and 12).

Lichens are known to have positive net photosynthesis at very low temperatures (e.g. Lange 1962, 1965; Atanasiu 1971; Lange & Kappen 1972). In *C. nivalis* photosynthetic CO₂-uptake occurred at -14°C (Kallio & Heinonen 1971). Thus a lower T_C , indicated in *C. delisei* in the field (<ca. 1°C), which was also not confirmed in the laboratory, may be an artefact due to instrumental deficiencies. That means that both species are able to be photosynthetically active at temperatures below the freezing point.

With respect to dark respiration no differences between *C. nivalis* and *C. delisei* were obtained at temperatures up to 15°C. The dark respiration

rates were comparable with those reported for *C. nivalis* and other Arctic and alpine lichen species (Bliss & Hadley 1964; Kallio & Heinonen 1971; Larson & Kershaw 1974, 1975a).

Results based on dry weight and chlorophyll content. – Since variations in photosynthetic rates occurring in different lichen species may be partly attributed to different proportions of algal and fungal material associated with different thallus structures (Harris 1971; Matthes & Feige 1983; Sancho & Kappen 1989), photosynthesis per dry weight is not the best method when comparing different species. Therefore, photosynthesis is also expressed per chlorophyll content, which gives information about the photosynthetic efficiency of the phycobiont (Richardson 1973; Nash III et al. 1980; Kershaw 1985).

C. nivalis had higher net photosynthetic rates than *C. delisei*, both in relation to dry weight and to chlorophyll content, but the difference was more pronounced when photosynthesis was given per dry weight (twice as high) than when related to chlorophyll (one and a half times as high), at least in the laboratory measurements. The higher chlorophyll content of *C. delisei* could support the hypothesis that a similar relationship may exist between lichens of exposed sites and depressions as exists between sun and shade plants, where the photosynthetic capacity related to dry weight is higher in the sun plants and differences in photosynthetic capacity can be eliminated or

diminished if chlorophyll content is used as relation basis for photosynthesis (Björkman 1981).

Thallus water content of C. nivalis and C. delisei

Maximum hydration. – In 1990 H_{\max} obtained in the field was not different from the values obtained in the laboratory. In 1991 H_{\max} in the field was not as high. The highest TWCs measured in Ny Ålesund (especially in 1991) probably do not correspond to full thallus hydration, because precipitation was mostly falling as snow combined with strong wind. Even a snow cover of some cm deep (as in 1991) consisting of dry snow did not hydrate the lichen thalli fully, whereas wet snow, sleet and rain (as in 1990) lead eventually to saturation. The TWC of the snow-covered lichens ranged between 119 and 187% of DW in *C. nivalis* and between 146 and 198% of DW in *C. delisei*. This is approximately 37 to 58% and 63 to 85% respectively of the maximum thallus hydration. Kappen & Breuer (1991) showed that TWC of snow-covered thalli of *Usnea sphacelata* in the Antarctic ranged between 49 and 115% of DW, which is equivalent to about 28 to 66% of the maximum hydration (=175% of DW) of *U. sphacelata*. The higher TWC of *C. delisei*, obtained only under the snowy conditions in 1991, may be a consequence of its more sheltered site, where snow could accumulate not only upon the cushions but also between the thallus branches and could not be removed without destroying the thalli. However, in general there may be some overestimations of the maximum hydration values in both species, because not all fastened water could be removed in the tight lichen cushions by shaking or blotting.

Desiccation. – *C. nivalis* dried out faster than *C. delisei* after a precipitation event or artificial irrigation. Desiccation of lichens is dependent on thallus-morphology and the microtopography of their habitat (Larson & Kershaw 1976; Kershaw 1985). Denser mats and more finely branched thalli, like *C. delisei*, will have a higher surface to weight ratio (A/W-ratio) and hence a greater evaporation resistance and water holding capacity (Larson & Kershaw 1976; Larson 1981). *C. nivalis* appears to be more wetttable than *C. delisei*. It takes up and loses water quicker and may be able to use short rain showers more efficiently for

photosynthesis than a species of sheltered, wetter habitats, such as *C. delisei*. Further, a rapid desiccation may increase the mechanical resistance to wind (Kappen 1973). These characteristics are important for lichens growing in exposed and dry habitats.

The different treatments, i.e. using both cushions and single thalli, showed the expected differences with respect to drying rate and TWC. The cushions showed higher TWC with exception of the measurements in snow and ice. Here the very high TWC of the single thalli can be explained with a frozen, unremovable water film on the surface of the thalli. The lichen cushions dried slower than the single thallus pieces, again due to the higher water holding capacity and higher evaporation resistance of cushions compared with that of single thalli. Larson & Kershaw (1976) showed the contribution of area to weight ratio, thallus shape and degree of clumping in the control of evaporation rate in lichens. For example, the area to weight ratio (cm²/gDW) of the loosely growing cushions of *C. nivalis* (345–370) was less than that of *Cladonia stellaris* (420–625), which grows in denser clumps.

Thallus colour

According to Larson & Kershaw 1974; Kershaw 1985; Kappen 1988, species of exposed habitats are often darkly pigmented (e.g. *Alectoria nigricans*, *A. nitidula*, *Sphaerophorus globosus*, *Cornicularia divergens*), whereas chionophilous species (e.g. *Cladina alpestris*, *Stereocaulon paschale*, *S. alpinum*) often are light-coloured or greenish. The thallus colour of the investigated species, i.e. pale greenish yellow (*C. nivalis*) and olive-dark brown (*C. delisei*) is opposite to these observations. The dark pigmentation is thought to be an adaptation to protect against high irradiance in open habitats (Kappen 1983, 1988). In addition a dark thallus can be advantageous because it absorbs heat more readily, increasing thallus temperatures above 0°C and permitting photosynthesis even under a thin snow cover. Further the warming of the thalli initiates and accelerates snow melt (Larson & Kershaw 1974; Kershaw 1975). These advantages of a dark pigmentation may also be favourable for a chionophilous species such as *C. delisei*, especially in summer, by aiding the thawing of freshly fallen snow. The lichen could possibly then use the meltwater for carbon gain. On the other hand, a

light-coloured lichen can avoid overheating by reflection of radiation (albedo-effect) and thus decrease evaporative water loss from the thallus and the soil (Larson 1979; Kershaw 1978). A light coloured thallus must therefore not be disadvantageous in an exposed habitat. The function of dark pigmentation as radiation screen may be overtaken in *C. nivalis* by the lichen substance usnic acid, which is assumed to protect against high radiation (Rundel 1969). However, there are also a great number of other light-coloured chionophobic lichens, e.g. *Thamnolia vermicularis* and *Alectoria ochroleuca*. Since in the present study no comparative measurements of thallus temperature or reflectance of visible and infrared radiation in *C. nivalis* and *C. delisei* were made, the discussion of relationships between thallus colour and habitat conditions is rather speculative.

Conclusions

Although light and temperature are important factors influencing the gas-exchange of lichens, the thallus water content appears to be a major limiting factor for productivity. The poikilohydrous nature of the lichens allows no active control of their water status. Thus, in spite of continuous light in the Arctic summer and adaptations to low temperatures, they are often metabolically inactive. The ability of *C. nivalis* or other chionophobic lichens to take up water rapidly and to assimilate CO₂ at very low temperatures (Kallio & Heinonen 1971) appears to be advantageous for lichens growing in exposed and drier habitats. This ability, combined with higher photosynthetic rates (in comparison with *C. delisei*), may enable *C. nivalis* to profit from short precipitation events. This species may also make use of periods of hydration in early spring, when light is already present, but the more sheltered sites are still dark because of a thick snow layer. The thickness and density of the mats of *C. delisei* may be significant in maintaining water balance, as well as regulating the microclimate of its habitat, e.g. by buffering fluctuations at the soil surface and thus extending the favourable periods of growth.

Some of the lichens' responses were unexpected, that means in contrast to the hypotheses that lichens growing in wet habitats have (1) higher H_{max}, H_C and P_{max} at higher TWC (Kershaw 1972;

Blum 1973; Matthes & Feige 1983) and (2) require lower PAR for I_C and I_{sat} (Larson & Kershaw 1975a; Kappen et al. 1989) than lichens growing in drier and exposed habitats. Therefore, future investigations should explore (1) whether *C. delisei* populations of wet subarctic mires responded similarly to Arctic populations with respect to water uptake capacity or photosynthetic response to thallus water content, and (2) whether *C. delisei* is able to assimilate CO₂ even under a snow cover, with high water availability and low irradiances, as do other lichens (e.g. *Usnea sphacelata*, Kappen et al. 1991), or whether it is inactive until snow has completely melted.

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