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Field measurements of carbon dioxide exchange of the Antarctic lichen *Usnea sphacelata* in the frozen state

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Abstract: Field measurements of CO_2 exchange were made with an infra-red gas analyser system on lichens at Bailey Peninsula, Wilkes Land, continental Antarctica. It has been demonstrated that *Usnea sphacelata*, a prominent element of the cryptogamic vegetation of this area, became photosynthetically active at temperatures below 0°C when the thalli were covered by drifted snow. Carbon dioxide uptake was detected down to –10°C. The carbon production during such a 'frost' day was considerable for a slow-growing Antarctic lichen. The importance of snow for production in lichens is emphasized. The mechanism of water uptake when the thalli are frozen needs further investigation.

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Introduction

Low temperatures are the main limiting factor for life in Antarctica. Even during the austral summer season when sufficient light is present to enable photosynthetic activity of plants, temperatures frequently remain below 0°C. Earlier literature reports that CO_2 assimilation in lichens was possible at –20 to –40°C (see Atanasiu 1971). To a lesser extent this has been confirmed by more modern CO_2 exchange measurements (Lange 1965, Lange & Metzner 1965, Lange & Kappen 1972). According to these more recent experiments, the lower temperature limit for net photosynthesis was between –7 and –13°C, and in two species reached even –24°C. Active respiration has also been recorded at temperatures down to –10°C in arctic lichens (Kallio & Heinonen 1971). In these laboratory experiments the lichens were subjected to the low temperatures for about 1 h.

Only a few studies have been carried out in winter in the field (Schulze & Lange 1968, Atanasiu 1969, 1971). As the lichens were exposed to subzero temperatures above –10°C for short periods of time, the possibility cannot be excluded that the thalli were not totally frozen or that water had melted near the surface of the lichen or between the hyphae under the influence of solar radiation even in the presence of clouds (Kappen 1985*a*). At lower temperatures (–10 to –14°C) it is more likely that the lichens were frozen. However, Atanasiu (1971) who found assimilatory activity within this temperature range in winter, did not give any information about the water or ice status of his lichens. Gannutz (1970) stated that water-soaked Antarctic lichens remain unfrozen at –10°C. It is reported (Ahmadjian 1970) that Gannutz and Lange have measured significant CO_2 uptake at –18°C in *Neuropogon* near Hallett station, Victoria Land.

In most habitats on the Antarctic continent, snow or ice is the only source of moisture for the lichen (Kappen 1985*a*). Field measurements were carried out to determine whether, after a cold, dry period, snow and ice enable lichens to resume photosynthesis as they can after being soaked by rain.

Material and methods

A field station was established *c.* 1 km south-west of Casey station (Budd Coast, Windmill Islands, Wilkes Land, 66°17'S, 100°32'E) on the top of a hill (46 m asl). The equipment for the measurement of CO_2 exchange in the lichens was described in detail by Kappen *et al.* (1986) and is based on an open-flow IRGA system. The control and measuring units of the system were mounted in a wooden hut, and the two CO_2 exchange cuvettes were installed at a distance of 15 m east of the hut. They were mounted on the ground close to a lichen-colonized granitic boulder. One cuvette was facing east, the other west. The measurements under consideration here were made in the west-exposed cuvette. This was the direction of the rock face where the selected lichen species was most abundant. The cuvettes were made of plexiglass and contained a temperature-conditioning unit and a fan. The air humidity in the cuvette was not controlled, and so water vapour exchange of the lichens could not be measured. Quantum flux density was measured by a Licor quantum sensor inside the cuvette.

Usnea sphacelata R. Br. is one of the dominant macrolichens in this area, and in Greater Antarctica in general. The fruticose, blackish thalli were about 3–4 cm high. Twelve thalli were fixed with their holdfast on a 6 × 10 cm plexiglass tray. Four such trays were placed at the west-exposed side of the rock in the open, so that the lichens were under natural conditions. Depending on the weather conditions, every few hours another tray was placed in the CO_2 exchange cuvette.

The temperature in the cuvette was kept at that of the ambient air by a feed-back control for the first two hours of 7 December and during the time period after 14.00 h. Between 11.00 and 13.00 h the temperatures were artificially reduced. The data presented in this study illustrate the coldest of a series of about 15 diurnal courses measured with *U. sphacelata* during November and December 1985. In order to confirm this finding a duplicate experiment at −10°C was carried out on 15 December with *Usnea* thalli which had been sprayed with water before freezing.

After the whole series of measurements the lichens were removed from the trays, air-dried and were later transported at about −18°C in freezing containers to the laboratory of the Botanical Institute of Kiel. Here, dry weight (105°C) of the samples was determined. Carbon dioxide exchange was calculated in terms of the dry weight.

Results

Fig. 1 illustrates the diurnal courses of the CO_2 exchange of *U. sphacelata* during 7 and 8 December. There was no precipitation for a period of two days before the measurements. According to hourly recordings between 05.00 and 20.00 h the lichen thalli were always dry and rigid. Air relative humidity measured in the vicinity of our site ranged between 51 and 70% during the period from 18.00 h (6 December) to 08.30 h (7 December). Therefore it was unlikely that the lichens had taken up water vapour sufficient for significant photosynthetic activity. The temperatures were between −4 and −6°C during the last six hours before the beginning of the CO_2 exchange measurements. In the early morning of 7 December easterly winds started to blow and reached a velocity of 12 m s^{-1} between 07.00 and 09.00 h. Under these conditions snow was lifted from the ground as in a blizzard, and as a result the lichens became covered with snow crystals. Snow also accumulated loosely between the branches of the thalli.

In this state *U. sphacelata* was placed in the CO_2 exchange cuvette. The water content of the thalli could only be determined tentatively. The fresh weight of a parallel series of such thalli (in this case shaken, so that most of the snow was removed) as an average of five replicate samples was 163% of d wt. The water content was simply taken to be 63% of d wt. Such a water content would be near the optimum for net photosynthesis (cf. Kappen 1983). The net photosynthetic rate was initially around 0.05 mg CO_2 g d $wt^{-1} h^{-1}$. This rate was maintained at thallus temperatures between −4.9 and −6°C.

When the temperature in the cuvette dropped to −7°C the net photosynthetic rate decreased to 0.03 mg CO_2 g d wt^{-1} h^{-1} and did not cease even at −10.2°C. It immediately

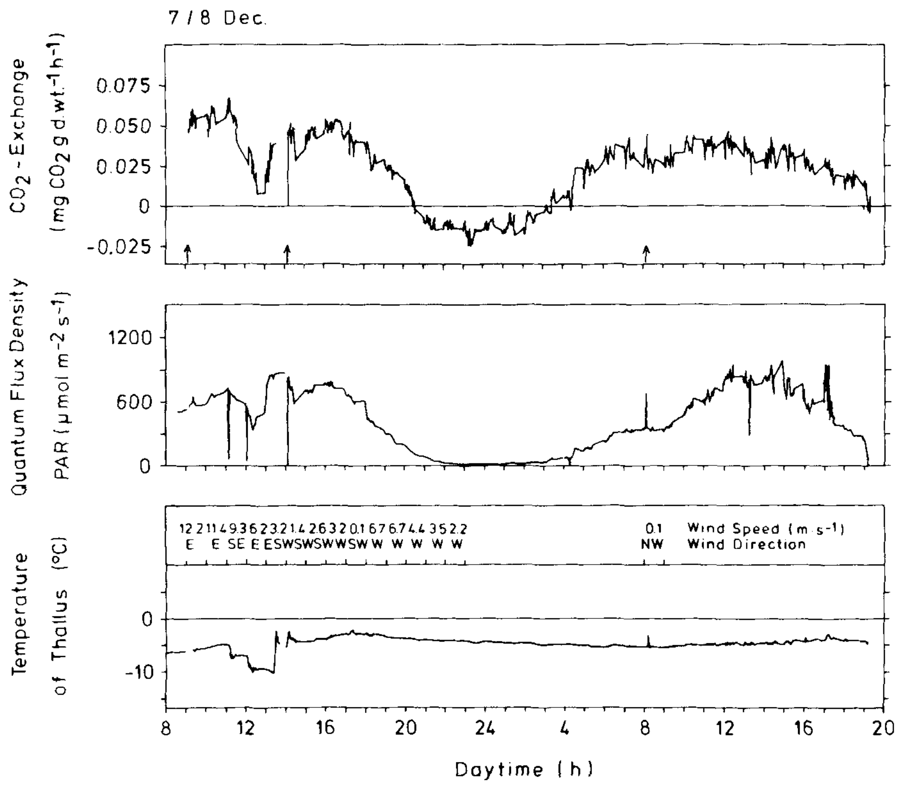

Fig. 1. Diurnal course (7 and 8 December 1985) of thallus temperatures, wind direction (E = east etc.), wind speed, quantum flux densities (photosynthetically active radiation) and CO_2 exchange of *Usnea sphacelata* in the field. Arrows indicate the replacement of a new tray with lichen thalli.

increased with increasing temperature although the thalli were apparently permanently frozen. Quantum flux density during this measuring period was moderate, varying between 400 and 800 µmol $m^{-2} s^{-1}$.

A duplicate experiment at temperatures within minima at –10°C was carried out on 15 December. In this case, however, the thalli were initially sprayed with water. The photosynthetic response was almost identical (0.008 mg CO_2 g d wt^{-1} h^{-1} at –10°C).

At about 14.00 h (7 December, Fig. 1, arrow) another tray with *U. sphacelata* was placed in the CO_2 exchange cuvette. In the meantime the wind had decreased and changed its direction, as it usually does after a blizzard. Snow had accumulated on the lichens as a consequence of light snowfall from *c.* 10.00 to 14.00 h. This sample of 12 thalli with a *c.* 5-mm deep snow cover was about as active as the former sample. The temperature in the cuvette followed that in the field and varied only between –3 and –5°C. During this and the subsequent day the quantum flux density varied between a maximum at about 800 and a minimum at 20 µmol $m^{-2}s^{-1}$ in the cuvette. Maximum photosynthetic rates were around 0.060 mg CO_2 g d wt^{-1}on 7 December and only 0.050 mg CO_2 g d wt^{-1} h^{-1} on 8 December. Since temperatures varied little, the photosynthetic rates were mostly closely correlated with the irradiance level. Net photosynthesis became negative at less than 100 µmol $m^{-2}s^{-1}$ quantum flux density. In the early morning the threshold irradiance was lower than this.

There was no total darkness. However, dark respiration took place for a period of about 7 h. The respiratory rate was up to 0.020 mg CO_2 g d $wt^{-1}h^{-1}$at 5°C. This was the first time that significant dark respiration has been demonstrated in continental Antarctic lichens under natural conditions.

Discussion

The measurements clearly show that the thalli of *U. sphacelata*, after staying dry at temperatures below 0°C, are able to begin metabolic activity when covered by snow crystals. Slight, but not visible, melting at the thallus surfaces may be assumed to take place during the light phase of the first day. However, there was no external energy for melting during the dark phase. The lichens appeared frozen hard and stayed brittle as in the dry state. Under the same temperature conditions in the cuvette the thalli released CO_2 by respiratory activity. As soon as the irradiance was sufficient to pass the compensation point the frozen thalli showed positive net photosynthesis. The rapid response to light in the early morning leads to the assumption that apparent melting was not necessary to enable photosynthetic activity. The fact that two condensated phases of water can exist at temperatures below 0°C and that unfrozen water can be present either in narrow capillaries or as thin absorbed layers has been demonstrated with soils by Banin & Anderson (1975). However, we have no information about any gradient of water potential between the ice crust and the algal and fungal cells.

On the second day the thick snow cover did not expose the thalli either inside or outside the cuvette. A light-filtering effect of the snow may be the reason why, at the same temperatures and even slightly more ambient light, the net photosynthetic rate was lower than in the first phase of the day before, when the thalli looked like plants in a strong hoar frost.

The fresh weight/dry weight ratio of the frozen thalli was close to the range of thallus water contents which allow maximum photosynthetic rates. The optimum water content of *U. sphacelata* from northern Victoria Land was reached at *c.* 75% of d wt (Kappen 1983). The net photosynthetic rates of those thalli, which were sprayed prior to freezing in the laboratory, were significantly lower at –5°C than those measured in the present study. Since it is always difficult to carry out measurements at subzero temperatures in the laboratory, the field measurements here may give a more realistic figure of the performance of frozen lichens. It is interesting to note that the net photosynthetic rate of *U. sphacelata* at –6°C was about the same fraction of the maximum rate measured under optimum light and temperature conditions as it was in *Hypogymnia physodes* (Schulze & Lange 1968) which was briefly subjected to this temperature during measurements on a European winter's day.

The diurnal course of photosynthetic activity shown in this study are characteristic of a situation which is quite typical of 'moist', i.e. productive, days during the summer season in the area of the Windmill Islands. In the early season (October–November) winds are stronger and cause real blizzards. Fog is very rare in this region. Consequently, days with snowdrift and snowfall are important periods of production and growth for the Antarctic lichens. During the periods of investigation the estimated photosynthetic gain was 0.843 mg CO_2 g d wt^{-1} and the respiratory loss 0.073 mg CO_2 g d wt^{-1}. The CO_2 balance of these two days was consequently 0.770 mg CO_2 g d wt^{-1}. At a carbon content of 41% of the thallus d wt (Kappen 1985*b*) the carbon gain of *U. sphacelata* would be 0.051%. The data show that lichens can be productive under permafrost conditions in the presence of snow and confirm the earlier findings of Atanasiu (1969, 1971) who has measured the CO_2 exchange of lichens in winter by $Ba(OH)_2$ titration. They indicate also that when modelling photosynthetic productivity of lichens one has to consider particularly the periods during which thalli are covered by snow.

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