Polar Biol (1983) 1:249–255

Polar Biology

Ecology and Physiology of the Antarctic Fruticose Lichen *Usnea sulphurea* (Koenig) Th. Fries

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Received 12 December 1982; accepted 1 March 1983

Summary. Only a few small areas of the coast of north Victoria Land are free of ice. Such an area is Birthday Ridge, Yule Bay, where a lichen vegetation is developed in the interspaces of granitic rocks of the mountaintop detritus. The largest and most frequent lichen is *Usnea sulphurea,* growing as a "light" form at exposed habitats and as a "shade" form below pebbles. Both forms differ by chlorophyll content and temperature dependency of net photosynthesis, which demonstrates an adaptive response of these forms to their environment. *Usnea sulphurea* is able to take up water from humid air, but in its natural habitat it is moistened mostly by melting snow. CO_2-gas exchange is detectable when the water content of the thalli rises above 30% of the dry weight. A decrease of net photosynthesis at very high water contents (at 6 °C) is not visible. At a CO_2 concentration of the air below 200 ppm the lichens have a negative CO_2 balance; net photosynthesis is still not saturated at 370 ppm CO_2 in the air under the experimental conditions. Like other antarctic lichens, *U. sulphurea* is a moderately productive, slowly growing species.

Introduction

Antarctica as a glaciated continent displays a model for studying ice-age conditions with respect to life conditions for plants. Nonglaciated areas are rare and scattered and usually of limited extent. Climate in coastal regions is even more extreme than in comparable latitudes in the Arctic. For these reasons vegetation on the Antarctic continent consists exclusively of cryptogams and microorganisms. Apart from Palmer Peninsula, vegetation is always scattered and sporadic. Frequently it is only cryptic. Plants must be highly adapted to extreme environmental conditions and therefore exhibit the capabilities and limitations of life in the cold, and also give models for strategies in surviving glacial periods on earth.

The most apparent cryptogams on the continent are lichens and mosses. All growth forms of lichens (crustose, foliose, and fruticose) are present even on the climatically most extreme eastern part of the Antarctic. However, most of the lichens are crustose and small. Wind and ice-blast cause strong deformation of the lichens and make them difficult to define taxonomically. The largest thalli reach 5 cm in height. One very apparent genus is *Usnea (Neuropogon).* In this study we deal with a dominant species of the east Antarctic: *Usnea sulphurea* (Koenig) Th. Fries.

Our knowledge about taxonomy and ecology of lichens in the Antarctic is still restricted. Even the genus *Usnea (Neuropogon)* in Antarctica (Mac Lamb 1939, 1964) is again in the state of revision. Collections are still sporadic. Only after a comprehensive revision of all material our ideas about distribution of lichen species on the continent will become clear. It is therefore still difficult to draw conclusions from ecological and physiological measurements on lichens of one place in the Antarctic and apply these conclusions to other regions on the continent. It is therefore necessary to gather more ecological information in different places to get an idea about the performance of plants in the Antarctic.

Ecological and physiological investigations on lichens in the Antarctic have been carried out with lichens in the maritime Antarctic by a few authors, e.g., Longton and Holdgate (1967), Lindsay (1973, 1975), Hooker (1980 a, b, c), Lewis-Smith (1978), and Gannutz (1970); with high Antarctic lichens such as those from Cape Hallett by Rudolph (1966), Gannutz (1969), and Lange and Kappen (1972); Schofield and Ahmadjian (1972); in Mac-Robertson Land by Seppelt and Ashton (1978); and in the dry valleys by Friedmann (1977, 1982), and by Kappen et al. (1981). Collections of lichens and ecological observations have never before been made from that area of North Victoria Land from which we have collected *U. sulphurea.*

This paper deals with some ecological remarks about the habitat and the dependency of the CO_2 exchange of *U. sulphurea* on light, temperature, CO_2 in the air, and water content of the thallus. These observations may help to illustrate the physiological capacity of the lichen to survive under temporarily bright irradiation and generally cold and dry habitat conditions in the east Antarctic. These data will help to estimate the productivity of the lichen as soon as long term observations of microclimatic parameters of this habitat are available. In a future paper, measurements of environmental conditions and of the lichen vegetation will be discussed.

The Habitat

Only a few mountain slopes or nunataks are ice-free at the coast of North Victoria Land. Such areas are usually no larger than from one to a few square kilometers. Birthday Ridge in Yule Bay (70°47'S, 167°E) is a northerly exposed, steep slope with a mountaintop detritus field in front, which gradually runs into an almost horizontal level approximately 100 m above sea level and finally borders the frozen sea by a steeper rock face. The rock material is formed of coarse granite. Besides some transversal running snowbands and patches in depressions, the granitic slope is free of snow.

Snowfall occurred periodically during our stay (December 11 – 20, 1981). The snow was mostly blown from westerly directions over the block field and was not deposited on the tops of the granitic blocks. However, it accumulated in the space between the blocks at a depth of 20 – 50 cm below the tops. On the bottom of these interspaces and on the rock walls a more or less dense vegetation of lichens has formed.

The density of the lichen cover increases the closer the place is to the coast line. In the most abundant habitats, lichens reach 80% – 90% of the ground cover. Species like *Xanthoria candelaria* (L.) Th. Fr., and *Rhizoplaca melanophthalma* (Ram.) Leuck are restricted to the coastal area. On the more horizontal area of the mountaintop detritus, black or dark taxa of lichens are predominant like *Lecidea physciella* Darb. (very dark form), *Buellia frigida* Darb., *Alectoria minuscula* (Nyl. ex Arn.) Degel., *Umbilicaria decussata* (Vill.) Frey, and particularly *Usnea sulphurea* (Koenig) Th. Fries. These species become rarer on higher ground and *Alectoria minuscula* is the most dominant.

The climate was quite mild during the period of our stay. The air temperature reached a maximum of +6.4 °C, and the minimum did not fall below −4.2 °C. The very intensive solar radiation (more then 2000 μE m^{-2} s^{-1}) heated the rock surfaces, which are colonized by lichens, up to 14 °C. Rain and fog were absent. Under heavy conditions the relative humidity of the air was raised to 80% – 90%. Snow showers were repeatedly recorded. The dark thalli melted the accumulated snow quite rapidly.

Material and Methods

In a restricted area of the almost horizontal level of the mountaintop detritus about 2 km inland, thalli of *U. sulphurea* were collected on December 20, 1981, when the weather was clear and dry. At an air temperature of −2 °C the air-dry thalli were put into a dry dewar vessel and kept there during transport to Kiel until January 16. After arrival at Kiel, the thalli were put immediately into a thermostat at +2 °C, kept under illumination, and intermittently moistened. During the period of most of our measurements (12 weeks) photosynthetic rates did not significantly decrease. Thereafter, rates were decreased by 50%.

The CO_2 gas exchange was measured by means of an infrared gas analyser (Binos, Firma Heraeus). The measuring system (Firma Walz, Effeltrich) consists further of a temperature- and humidity-controlled Plexiglas cuvette (6 dm^3), with fan-operated air circulation, pumps, and flow meters to maintain a constant airstream. The gas exchange was measured in an open system by the difference between CO_2 concentration of the air passed over the lichen and that of another airstream passed through an empty cuvette. The flowrate of the air was 0.5 l/h. The measuring range of the Binos was 50 ppm CO_2 full scale. The CO_2 concentration of the air was always measured in parallel. Humidity was maintained by bubbling the air through a water bottle before it entered the cuvette. Each measured lichen sample had a dry weight of 3 g. The water content of the thalli was intermittently controlled by weighing. These interruptions of the gas exchange measurements took a period of 30 min each. The CO_2 content of the incoming fresh air was controlled by bubbling part of the air through a bottle containing a saturated KOH solution. This airstream and untreated air were dosaged by needle valves in such a way that a range between 155 and 370 ppm (under foggy outdoor conditions) would be kept constant (control by measuring the concentration directly in the Binos).

The chlorophyll content of the thalli was measured photometrically and calculated according to Holden (1965). The thalli were prepared according to the method of Brown (1980) to avoid chlorophyll degeneration by lichen substances. Air-dry thalli (0.4 g) were rinsed first in 10 ml pure acetone, then in 10 ml acetone: water (4: 1) for 30 s each. The thalli were extracted for 20 min in 10 ml pure methanol by adding a spatular tip of Ca CO_3. This was homogenized with sivers of glass in a cooled mortar; the homogenate was put on a suction filter and was rinsed with methanol quantitatively. The green extract was measured at 650 and 665 nm in a Hitachi 100 – 20 Spectrophotometer.

Results

Prior to the experiments, the vitality of the thalli was proved by measuring the gas exchange for 5 days at 5 °C. When the lichen thalli were moistened for the first time after storage in the desiccated state in a dewar vessel (see Methods), they had a negative CO_2 balance in light for some hours (Fig. 1). Such a reversibly increased respiration indicated restoration of the lichen (Kappen and Lange 1972; Farrar and Smith 1976). After about 20 h the lichen had fully recovered, showing then "normal" net photosynthesis rates in light.

The dependency of net photosynthesis (NP) on water content of the thalli is depicted in Fig. 2. At above 30% water content of the dry weight, gas exchange of the thalli is activated. Up to 40% CO_2 is released in dark and in light; then the compensation point is passed. Between 70% and 160% water content, NP is saturated under the given experimental conditions (5 °C, 250 μE m^{-2} s^{-1}) and remains more or less constant. The respiratory rate is comparatively high. A "favorable" relationship between NP and dark respiration results when the water content is between 45% and 70%. Since this experiment was car-

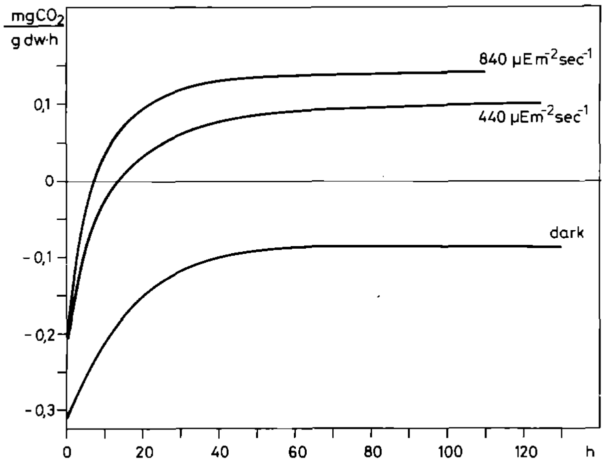

Fig. 1. Restoration of the CO_2 exchange of *U. sulphurea* (*light* form) during a 120-h continuous record 2 days after transport of the thalli to Kiel

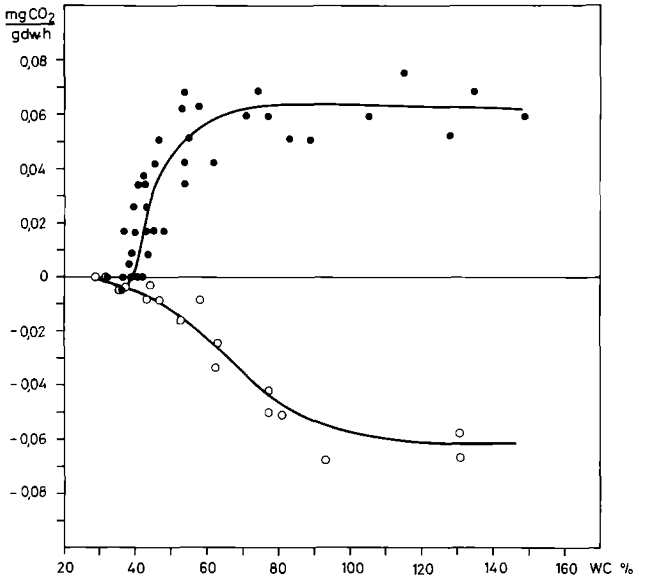

Fig. 2. Dependency of net photosynthesis at 250 µE m^{-2} s^{-1} and dark respiration of *U. sulphurea* on various water contents (*WC*) of the thalli – all measured at 5 °C

ried out 16 weeks after arrival at Kiel, the extremely high respiration here may also indicate reduced vitality of the thalli.

If air-dry thalli of *U. sulphurea* are exposed to air of high humidity, their water content rises consistently within a period of 60 h (Fig. 3). At 6 °C in darkness a maximum water content of 70% of the dry weight is reached. Correspondingly the respiration rate increases strongly. The reduction of the respiratory rate after 36 h may indicate that the rate was at first extremely high due to restoration effects and thereafter normalized. Exposed to light, the water vapor uptake was less intensive; at 360 µE m^{-2} s^{-1} a water content of only 55% was reached, but this water content was sufficient to permit a high photosynthetic rate.

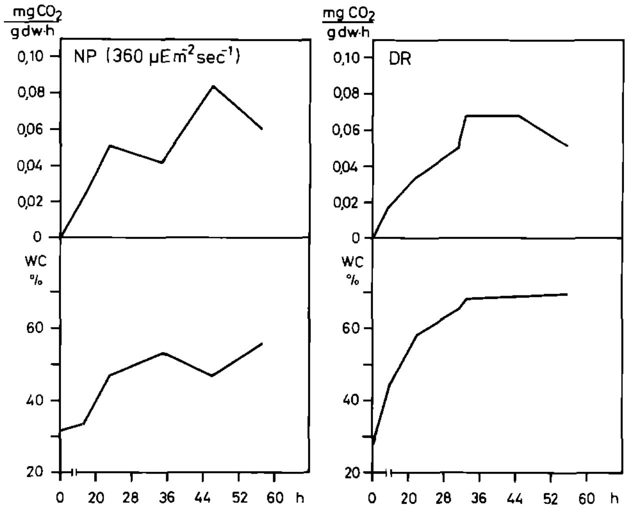

Fig. 3. Increase of net photosynthesis (*NP*) and dark respiration (*DR*) of thalli of *U. sulphurea* with incrasing water content (*WC*) in percentage of dry weight (*WC*) by taking up water from high air humidity (> 96%)

Figure 4 shows the dependency of NP on the CO_2 content of lichen thalli that were highly soaked in water (80% – 120% WC). At a CO_2 concentration of below 200 ppm, the compensation point of net photosynthesis is not surpassed and the thalli lose CO_2 at all quantum flux densities. At higher CO_2 concentrations, NP is increased. At 355 ppm CO_2 in the air, NP is still not maximal. The light compensation point of NP is passed earlier the higher the CO_2 concentration is in the air. At low CO_2 concentrations and low light intensities or darkness, the CO_2 output of the lichen is even higher than the dark respiration rate at normal CO_2 content of the air (340 – 350 ppm). When the CO_2 concentration is between 105 and 150 ppm, light has almost no influence on the gas exchange. When it is 355 ppm, light intensity of only 25 µE m^{-2} s^{-1} is sufficient for net photosynthesis to pass the compensation point.

Usnea sulphurea grows as well on light-exposed rock surfaces as on shaded rock faces or on the underside of hanging pebbles, which only receive reflected light from the ground. Here radiation is only about one-tenth of that in the open. On open faces the thalli are predominantly black (Fig. 5) with only narrow yellowish bands. The basal parts are pale yellow green. Thalli of the permanently shadowed stands are black pigmented only at the outcropping tips of the branches. Thalli below the pebbles are totally pale yellowish green. Thus there is a "shade" form, which lives under reduced light and is never directly insolated under natural conditions, and a "light" form, which is exposed to the open sky and becomes insolated for certain periods of the day. The chlorophyll content of the shade form is 2.25 higher than that of the light form (Table 1).

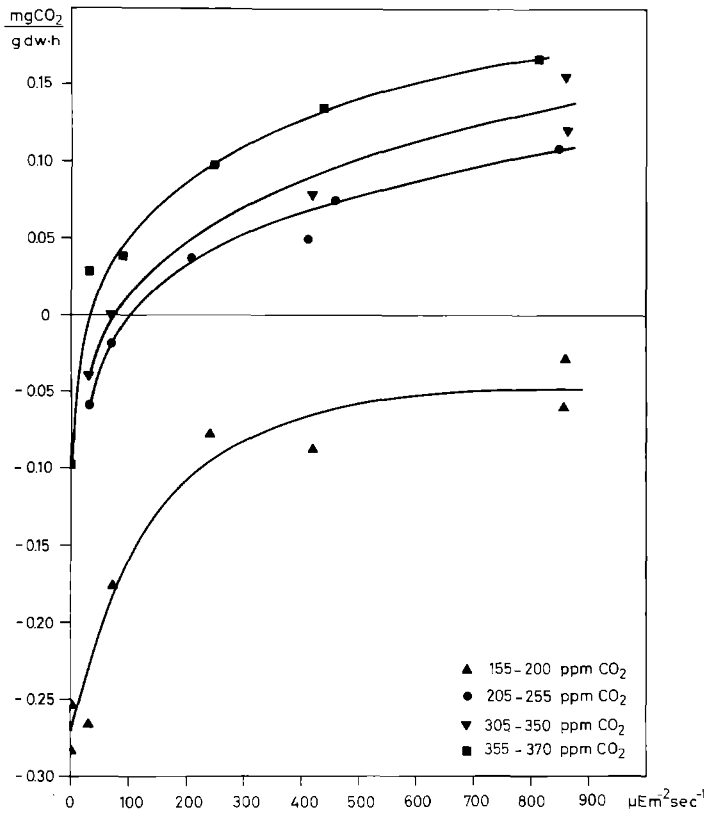

Fig. 4. Light-dependent net photosynthesis of *U. sulphurea* at different concentrations of CO_2 in the air

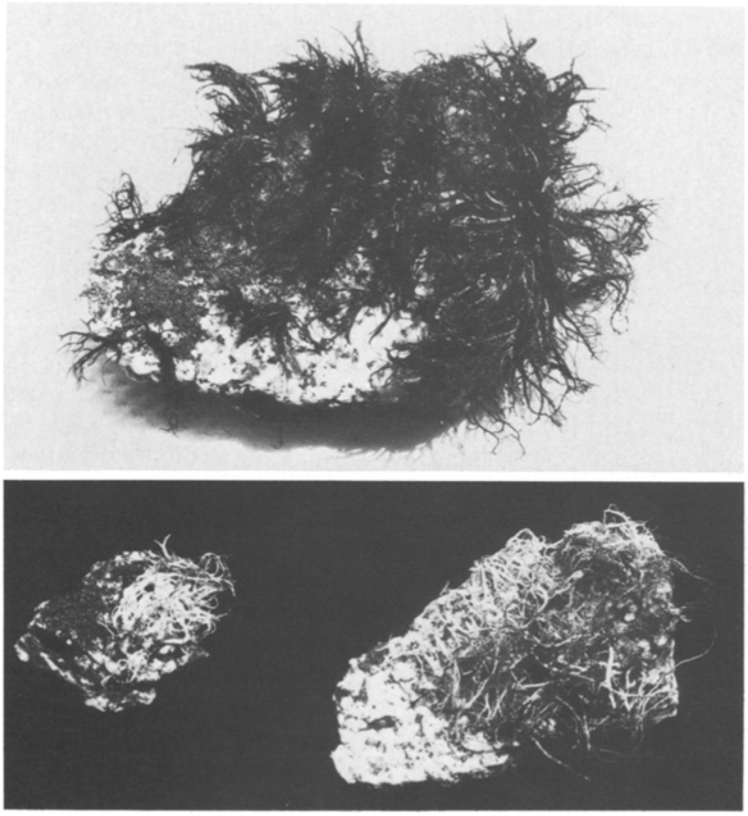

Fig. 5. *Light (above)* and *shade (below)* form of *U. sulphurea* from Birthday Ridge in Yule Bay, NVL, growing on granite rock

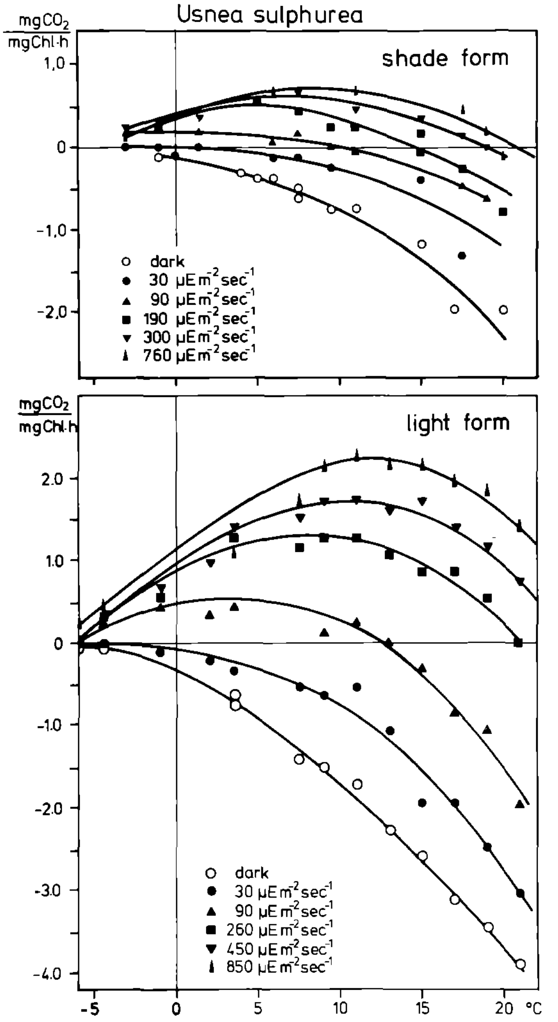

Fig. 6. Temperature-dependence of dark-respiration (○) and net photosynthesis (●) related to chlorophyll content at different light intensities – comparison between *shade* and *light* form of *U. sulphurea*

Table 1. Chlorophyll contents of *Usnea sulphurea*

	Chlorophyll content mg/g TG	Chlorophyll a : b ratio
Light form	0.0821	1.6
Shade form	0.1850	1.6

The net photosynthesis rates of the "shade" form thalli are significantly lower than those of the "light" form if the rates are related to chlorophyll content (Fig. 6). In comparison to those of the "light" form, the optimal net photosynthesis of the "shade" form shifts to the lower temperature range. If NP is related to dry weight of the thalli, the difference between the rates of the "light" and "shade" forms is smaller but the difference between the optimal temperature ranges is more pronounced (Fig. 7). At temperatures below 5 °C the rates of the "shade" form are even higher than those of the "light" form. At about 8 °C the rates of both forms are equal. Above 10 °C the "light" form has increasingly higher NP rates than the "shade" form. This becomes clearly apparent if NP light profiles at these temperatures are depicted (Fig. 8). The adaptation of both forms is obvious by the light dependency of the optima and the upper temperature compensation (C_u) points of NP (Fig. 9), since the C_u of the "light" form reached 27.5 °C under the highest possible quantum flux density of the experiment. C_u of the "shade" form reached only 21 °C. These temperature limits are apparently not much higher at higher light intensities because the slopes of the curves are rather steep.

Discussion

As *U. sulphurea* is one of the more complex growth forms of lichens and one of the largest species in Antarc-

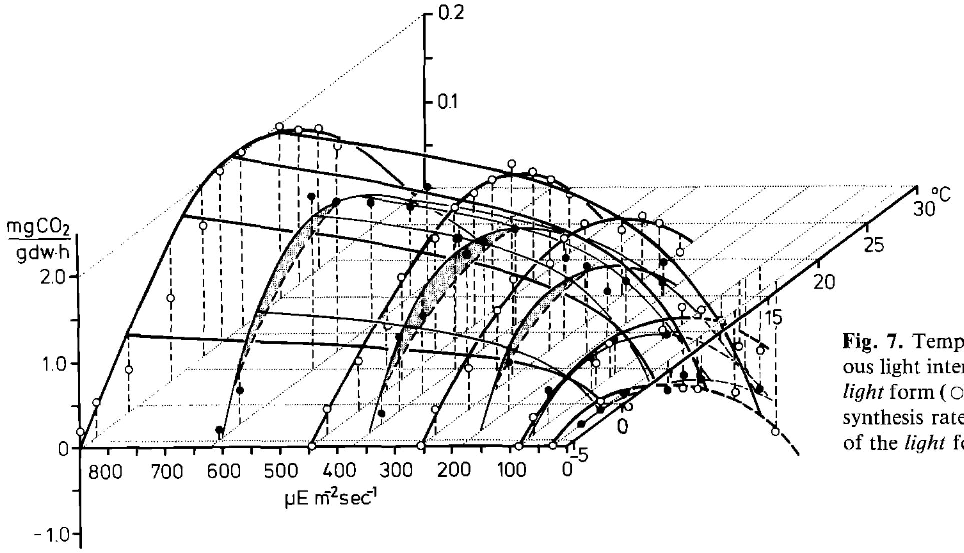

Fig. 7. Temperature-related net photosynthesis at various light intensities in *U. sulphurea* shade form (●) and *light* form (○). The gray area indicates where net photosynthesis rates of the *shade* form are higher than those of the *light* form

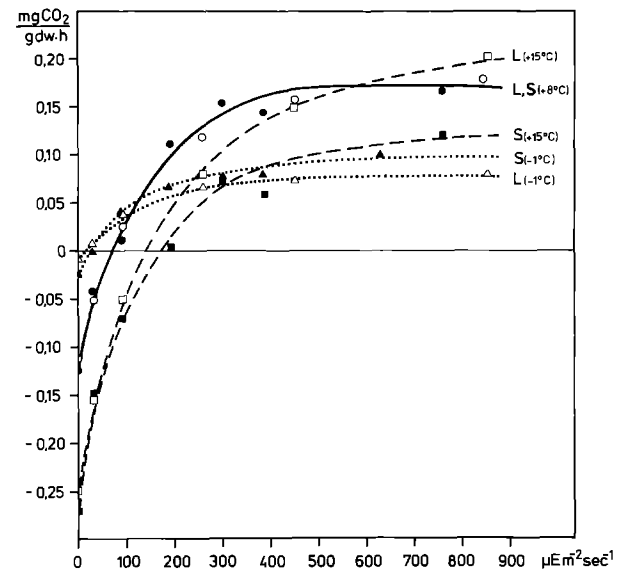

Fig. 8. Light profiles of net photosynthesis of *U. sulphurea light* (o) and *shade* (●) form at different temperatures

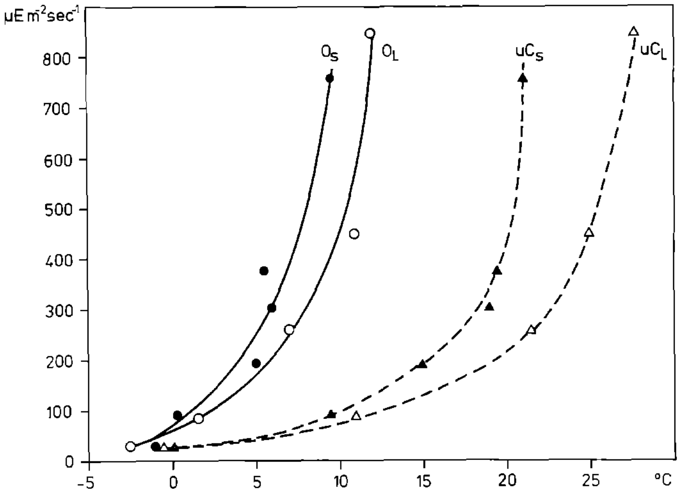

Fig. 9. Comparison of optimum values (O) and upper compensation points (*u*) of *shade* (*S*) and *light* (*L*) forms of *U. sulphurea*

tica, it is an example of the adaptation of plants to the extreme environment of eastern Antarctica. This is also illustrated by its abundance with local biomasses between 70 and 370 g m^{-2}. *U. sulphurea* occurs on the granitic block field with a black "light" form and a pale yellowish green "shade" form. Such different forms or ecotypes of lichens have been described for species from Europe by Ertl (1951). Physiological measurements in "light" and "shade" forms were only rarely done; one example was given with *Cladonia subtenuis* by Rundel (1972). The "light" form has net photosynthesis rates similar to those of *Usnea acromelana* Stirton from Cape Hallett (Lange and Kappen 1972). According to Redon (personal communication) the material from Cape Hallett, which was collected in 1965 from basaltic rocks, may be taxonomically identical with *U. sulphurea*. – The net photosynthesis of the "light" form of *U. sulphurea* extended into warmer temperatures than the Cape Hallett specimens. In comparison with other Antarctic lichens such as *Xanthoria mawsoni* with high NP rates above 4 mg CO_2 dm^{-2} h^{-1} and crustose species like *Rhizoplaca melanophthalma* with maximum rates above 1 mg CO_2 g^{-1} h^{-1} under similar light and temperature conditions (Lange and Kappen 1972), the rates of *U. sulphurea* are moderate. The "shade" form may be a little less productive. Differences in chlorophyll content between "light" and "shade" forms were found in corresponding "sun" and "shade" ecotypes of *Cladonia subtenuis* (Abb.) Evans (Rundel 1972). Thus, the lower chlorophyll-related NP rates of the "shade" form could be compensated for to a wide extent. On the other hand, the shift of the optimum temperatures of the "shade" form into lower temperatures where it has higher rates shows an adaptive response that may enable it to be almost as productive as the "light" form which profits from more light and more heat.

In general, the photosynthetic activity of *U. sulphurea* at subzero temperatures is low and even less than that of other Antarctic and alpine lichen species tested (Lange 1965; Lange and Kappen 1972). In this respect, *U. sulphurea* does not appear to be particularly psychrophilous. Whether this is due to increased diffusion resistance in the frozen thallus or to a higher sensitivity of the photosynthetic apparatus cannot be answered here. The relatively steep increase of dark respiration with temperature in *U. sulphurea* is typical for plants of high latitudes (Larcher 1980). Under natural conditions in the Antarctic, dark respiration must be low or insignificant because in summer light suffices mostly to keep up net photosynthesis (insofar as moisture and temperature do not impose limitations) and in the twilight seasons temperatures are mostly very low, thus reducing the respiratory activity. A low amount of respiratory loss is favorable for the carbon production of the lichen.

Since soil respiration is very insignificant in Antarctic habitats and therefore the CO_2 concentration of the surrounding air is on average lower (less than 320 ppm; Lewis and Callaghan 1976) than in nondesert regions, the question may be relevant whether *U. sulphurea* is highly productive at a relatively low CO_2 content of the air. For a CO_2 gain in light, the lichen needs at least 200 ppm CO_2 in the air. Within all the maximally reached CO_2 concentrations in the experiment (355 – 370 ppm), the net photosynthetic rates were still below saturation. That means that in the natural habitat under higher quantum flux densities, the NP may be still increased by CO_2 concentrations as tested or by higher CO_2 concentrations of the air. Insofar as the Antarctic lichen *U. sulphurea* performs similarly to lichens from other climates (Green and Snelgar 1981; Lange and Tenhunen 1981), there is no specific adaptation of *Usnea* in comparison to, for example, moist forest lichens from New Zealand. Whether lower water contents would have caused higher NP rates at the CO_2 concentrations tested in the air (Lange and Tenhunen 1981) was not proved. However, it is assumed that the NP depression due to high water soaking is less significant in this lichen species and particularly at the low temperature used in these experiments.

With respect to water content of the thalli *U. sulphurea* performs similarly to other desert lichens (Lange 1980). At the low temperature tested, net photosynthesis was maintained at a high level even in highly water-soaked thalli.

Water uptake from humid air was intensive in darkness and resulted in water contents 70% of the dry weight, enabling the lichen to have high photosynthetic rates. Moderate light intensity causes a reduced water uptake, which is not optimal for net photosynthesis. However, there is clear evidence that *U. sulphurea* is capable of absorbing water from the air at low temperatures but above freezing point. According to recent field observations, high air humidity (deep clouds or hazy conditions) was not frequent in the area of Birthday Ridge. Fog seems to be rare in the Yule Bay area. Snow appears to be the main source of moisture for the lichen (Friedmann 1978). Intensive soaking of the thalli by snow-melt was repeatedly observed (Kappen, unpublished). Water repellence, which is typical with species of *Usnea* (s. str.) from temperate forests, was not observed in *U. sulphurea.*

Conclusions about the growth velocity of these lichens are hardly possible from our data, since the length of periods for biomass production (Kappen et al. 1979) is not known. From the maritime Antarctic (Signy Island, 60° S.) another *Usnea* species, *U. antarctica,* is reported to have growth rates ranging between 40 and 150 mg g^{-1} yr^{-1} and may have reached an age of 300 – 600 years (Hooker 1980c). It is assumed that *U. sulphurea* on the Antarctic continent grows more slowly and may reach a higher age.

Acknowledgements. Taxonomical determination of the lichen material by Prof. Dr. J. Redon, Valparaiso, and by Mrs. Joy Walker, British Museum, London, is gratefully acknowledged. I am also indebted to the Deutsche Forschungsgemeinschaft for a research and travel grant and to the BGR, Hannover, for a place in its GANOVEX II expedition.

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