

Ecophysiology of Lichens in the Dry Valleys of Southern Victoria Land, Antarctica

II. CO₂ Gas Exchange in Cryptoendolithic Lichens

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Summary. CO₂ exchange was measured in three cryptoendolithic lichen samples from the ice-free mountains of Southern Victoria Land. Optimum temperature for net photosynthesis at different light intensities ranged from below 2°C to about 7°C; the upper compensation point ranged from 5°C to 15.7°C, and the lower compensation point could be estimated in two samples as being between –6°C and –8°C. Dark respiration rates were higher than those of net photosynthesis. The results indicate that these cryptoendolithic lichens are not more adapted to low temperatures than are crustose lichens from coastal Antarctica. Calculations show that optimum temperatures for photosynthesis may not be reached in the natural environment. Photosynthetic rates were low, but they increased when samples were split into smaller pieces, permitting gas exchange through broken rock surfaces. In nature, when gas exchange is possible only through the intact rock crust, these apparent rates are probably even lower.

Introduction

In the high mountains of the ice-free desert areas (“dry valleys”) of Southern Victoria Land, Antarctica, the principal substrate for life is porous sandstone, inhabited mostly by the cryptoendolithic lichen community. Cryptoendolithic organisms (Golubić et al. 1981) colonize structural cavities within porous rocks and are covered by a rock crust. Various aspects of the biology of the Antarctic cryptoendolithic ecosystem have been described by Friedmann (1977, 1980, 1982), Friedmann and Ocampo (1976) and Friedmann et al. (1980a, 1980b). The cryptoendolithic microclimate and some biological implications were studied by Friedmann (1977, 1978), Friedmann et al. (1982) and, more extensively, by Kappen et al. (1981) in the first part of this paper.

The present study deals with photosynthesis and respiration of cryptoendolithic lichens under simulated Ant-

arctic conditions. The methods and instrumentation employed are similar to those used by Lange and Kappen (1972) to measure gas exchange in epilithic lichens from Northern Victoria Land, and thus the results of the two studies are comparable.

Experimental work was carried out during a sabbatical stay of E.I.F. in the Laboratory of the Lehrstuhl Botanik II of the University of Würzburg.

Material and Methods

The following samples were investigated:

(1) Sample 789/17, hard quartzitic sandstone, collected on December 20, 1978, in University Valley (77°52'S, 160°39'E, 1650 m alt.). The frozen sample was airmailed from McMurdo Station (Antarctica) in an insulated container to Würzburg, where it arrived at room temperature, stored at –8°C (Rubarth-thermostat) and was investigated in February 1979.

(2) Sample 790/47, soft sandstone, collected on January 18, 1980, on Linnaeus Terrace (77°36'S, 161°05'E, 1600–1650 m alt.) at the site of the microclimate measurements described in the first part of this study (Kappen et al. 1981).

(3) Sample 790/50, soft sandstone, collected January 18, 1980, between Mt. Electra and Mt. Dido (77°30'S, 160°55'E, 1600 m alt.). Both 790 samples were transported in dry ice to Tallahassee, stored at –20°C until April 1980, and then carried in dry ice to Würzburg for examination. Storage at these temperatures had presumably no influence on the vitality of the lichens (cf. Lange and Kappen 1972).

Samples 790/47 and 790/50 were tentatively identified by Dr. Mason E. Hale (personal communication) as *Buellia* sp. Sample 789/17 has not been identified. The cryptoendolithic lichen zone in all samples was covered by a 0.2–0.6 mm thick surface crust and the biologically active zone extended approximately to the upper 5–10 mm in the rock.

Samples were cut into larger (>2 cm thick) and smaller (<2 cm thick) specimens with the upper rock crust intact. CO₂ gas exchange was measured with an infrared gas analyzer in an open (continuous gas flow) system as described by Lange and Kappen (1972). The samples were placed in 4 plexiglass chambers connected in a series (about 20–30 cm² rock surface in each chamber) and immersed in a thermostatically controlled water bath. Illumination was by high-pressure incandescent lamps. Photosynthetically active radiation (PAR) was measured in the chambers in quantum flux density with a Li-Cor 190S quantum meter and temperature was monitored by small copper-con-

Table 1. Chlorophyll, Nitrogen, total organic matter and estimated biomass

Sample	Chlorophyll a/b ratio	Chlorophyll a mg m ⁻²	Organic nitrogen (Kjeldahl) g m ⁻²	Total organic matter from dry combustion g m ⁻²	Estimated biomass g m ⁻²	
					from chlorophyll a ^a	from total N ^b
789/12	2.66	130				
790/47	3.01	66	3.58	119.39–214.16	66	89.5
795/50	1.91	78	4.07	118.53–167.94	89.5	101.8

^a Calculating factor × 1000, derived from relation between lichen dry matter and chlorophyll, based on data from Kärenlampi (1970) and Rundel (1972)

^b Calculating factor × 25, after Friedmann et al. (1980b)

stantane thermocouples inserted into the samples. Humidity was maintained by spraying of the rocks daily with water and by bubbling of the air through a water bottle before it entered the chambers.

Preliminary control experiments showed that in sterilized rocks there was no measurable gas exchange at 8 °C whether illuminated (with up to 500 μE m⁻² s⁻¹) or in the dark.

After the gas exchange measurements, the rock samples were used for analyses. At first, the upper surfaces of the rock pieces were measured by covering the rocks with thin plastic foil and marking the margins of the samples. Chlorophyll was determined spectrophotometrically (Arnon 1949), organic nitrogen was measured according to the Kjeldahl method, and total organic matter was determined from another rock piece and was calculated from weight loss at red heat for 30 min. Since the rocks do not contain calcium carbonate, the latter method was considered reliable (Steubing 1965).

Results

The results of chlorophyll, nitrogen and total carbon determinations are listed in Table 1. Values are calculated per unit area of rock surface (on the assumption that the cryptoendolithic lichen forms a continuous and homogeneous layer in the rock).

Quantities of total biomass, estimated from both organic N content and chlorophyll, were within the range of earlier analyses of Antarctic cryptoendolithic lichens (Friedmann et al. 1980b). Results obtained from carbon loss by dry combustion at 500 °C (total C) were slightly higher. These biomass values include both living and dead organic matter as well as both lichens and other organisms.

Net photosynthesis and dark respiration rates are shown in Figs. 1–3. In sample 790/47 (Fig. 1) the optimum temperature for net photosynthesis rose with increasing quantum flux densities from around 5 °C to about 7 °C. At –4.2 °C (the lowest experimental temperature) there was still substantial net photosynthesis and the lower compensation point can be estimated as being between –6 °C and –8 °C. The upper compensation point was at 9.8 °C at the lowest experimental quantum flux density and rose to 15.7 °C at the highest. In sample 790/50 (Fig. 2), temperature optima were between 2 and 4 °C. The upper compensation point at all quantum flux densities was below 8 °C and the lower appeared to be similar to that of sample 790/47. In both samples, dark respiration rates were generally higher than those of net photosynthesis and increased rapidly at higher temperatures.

In sample 789/17 (Fig. 3) rates of net photosynthesis and dark respiration (measured at a higher quantum flux density) were higher than in the other samples. At the same time, the temperature optimum was much lower, around +1 °C. The upper compensation point was at 15.1 °C; the lower could not be estimated.

In nature, gas exchange takes place through the surface crust of the rock, but in the experiments, free gas exchange was possible through the exposed lateral surface of the samples. To investigate the possible effect of this difference, gas exchange was first measured in four larger rock samples. Then, the samples were split into smaller pieces, thus increasing the surface area open to the atmosphere, and gas exchange rates measured again. Subsequently, the samples were sealed both at the sides and from the bottom with a chemically inert plastic material (“Terostat”). As shown in Table 2, net photosynthesis rose at all quantum flux densities after the rock were split and decreased when the samples were sealed. At the same time, dark respiration rates were less affected.

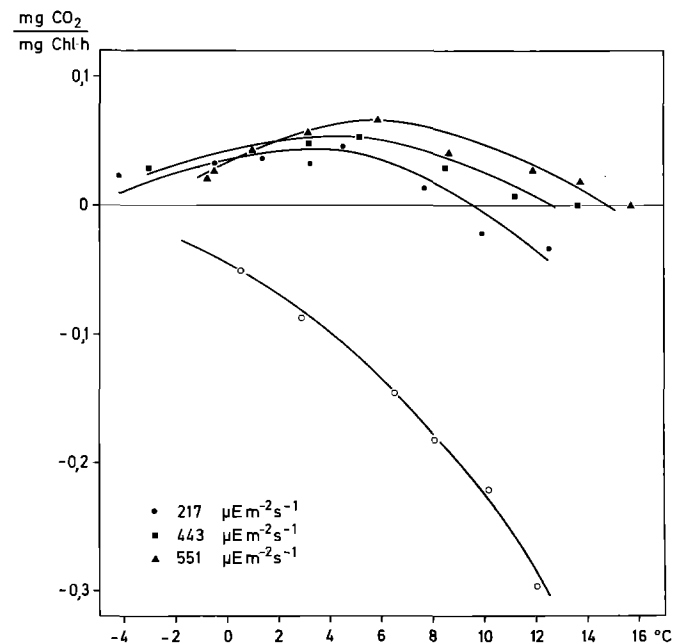


Fig. 1. Net photosynthesis (black symbols) and dark respiration (open symbols) at different quantum flux densities and temperatures. Cryptoendolithic lichen sample 790/47

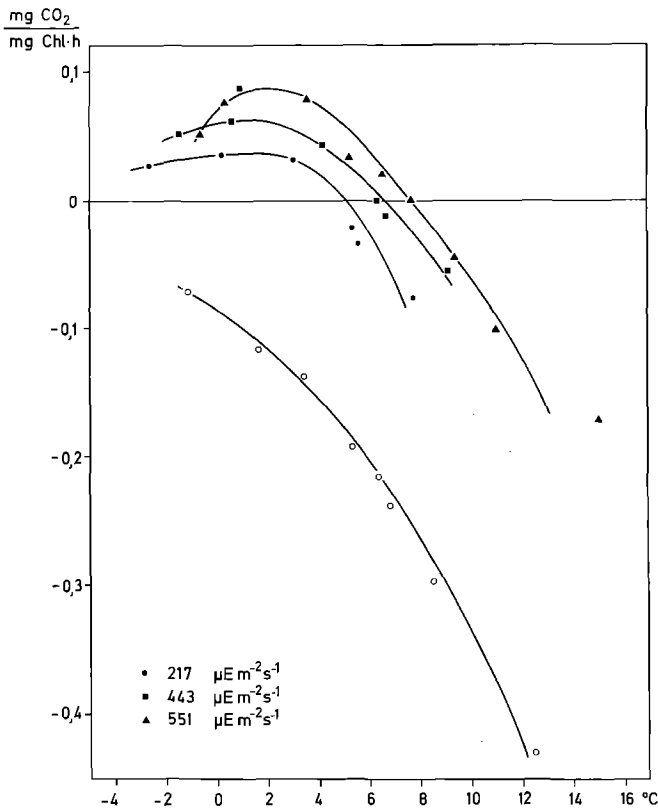


Fig. 2. Net photosynthesis (black symbols) and dark respiration (open symbols) at different quantum flux densities and temperatures. Cryptoendolithic lichen sample 790/50

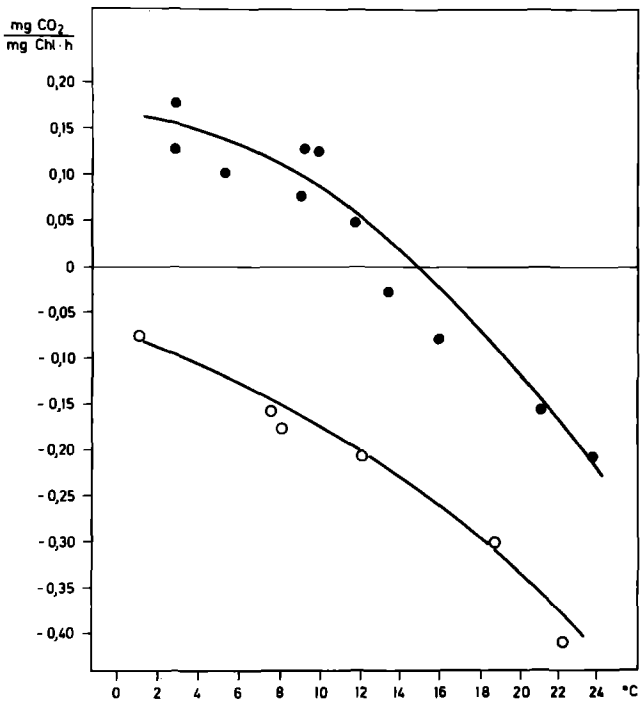


Fig. 3. Net photosynthesis (black symbols) and dark respiration (open symbols) at different temperatures. Quantum flux density: $620 \mu\text{E m}^{-2} \text{sec}^{-1}$. Cryptoendolithic lichen sample 789/17

Table 2. CO_2 exchange rates of cryptoendolithic lichen A790/47 in "open" and "sealed" rock samples (at 0.6°C). A: Four larger rock samples placed in one cuvette. B: Same rock samples cut into several smaller pieces, increasing gas exchange from side and bottom. C: Rock samples as in B, but each piece sealed at side and bottom (for further explanation, see text)

Quantum flux density $\mu\text{E m}^{-2} \text{s}^{-1}$	$\text{mg CO}_2 \times \text{mg}^{-1} \text{chlorophyll} \times \text{h}^{-1}$		
	A	B	C
0	-0.126 ^a	-0.072	-0.075
252	-0.013	0.032	
443	0.0	0.048	
551	0.018	0.054	-0.016

^a Negative values: CO_2 evolution (respiration); positive values: CO_2 consumption (net photosynthesis)

In order to investigate the possible effect of waterlogging (Stocker 1927; Lange 1980) or of drying of the rock substrate on gas exchange, samples were first sprayed with water (see Materials and Methods) and then left without spraying for six days in the experimental chamber. During this time, water content of the rock samples decreased from an initial 3.4% to 1.4%. CO_2 uptake did not increase significantly within 12 h after spraying (which would have been an indication of the effect of waterlogging) and decreased only by one-third when the samples were left without spraying for 43 h. This result suggests that under experimental conditions (daily spraying) the changes in water content did not significantly interfere with the results.

Rapid lowering of temperature to below 0°C during illumination first resulted in a decrease of CO_2 uptake, followed by CO_2 evolution for a period of about 30–45 min, while temperature continued to drop (Fig. 4A). A similar effect, with even more pronounced CO_2 burst, was observed during conditions of dark respiration (Fig. 4B). As CO_2 is largely insoluble in ice, the sudden CO_2 release upon freezing is believed to be due to this physical (rather than a biological) phenomenon.

Discussion

Cryptoendolithic lichens have some unusual features that need to be considered when the experimental results are evaluated. In addition to the phycobiont (*Trebouxia* or *Pseudotrebouxia* sp., Dr. P. Archibald, pers. communication), a non-lichenized green alga is also often present (Tschermak-Woess and Friedmann, in preparation, illustrated in Fig. 6g in Friedmann 1982). These variations in composition and ratio of the algal components may result in differences in the photosynthetic response. Several non-photosynthetic bacteria are also regularly present.

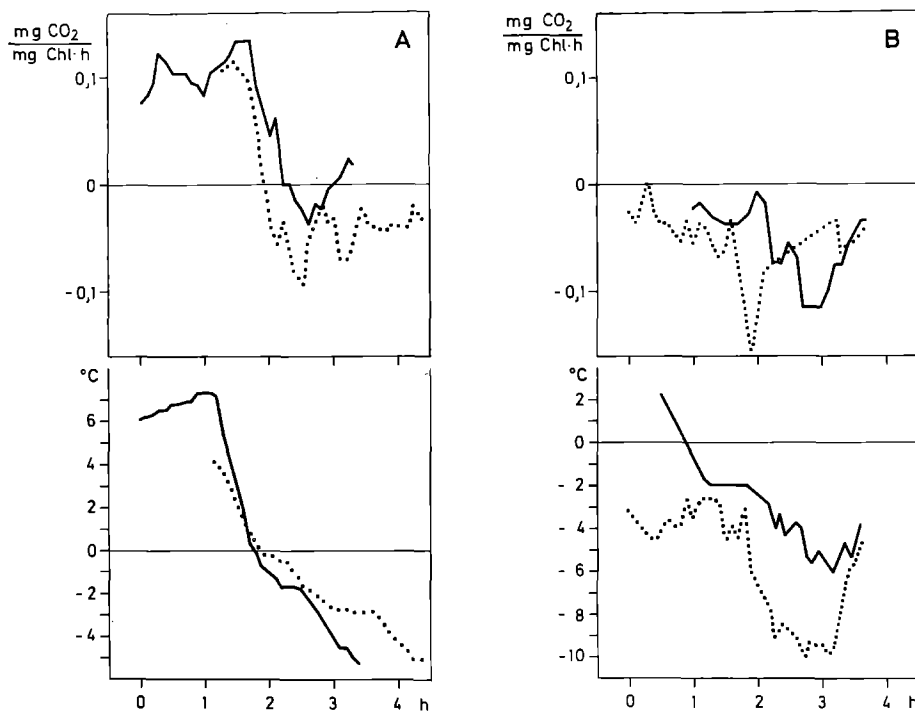


Fig. 4A, B. CO₂ exchange in cryptoendolithic lichen sample 790/47 while temperature drops below 0°C. The dotted and solid lines represent two parallel sets of experiments. **A** Illuminated at 443 μE m⁻² s⁻¹ (photosynthesis). **B** Dark respiration

Despite their unusual characteristics, the physiological responses of cryptoendolithic lichens are comparable to those of other lichen types. Thus, the ratio of chlorophyll a and b (1.9–3.0) was similar to values reported for photophilic epilithic lichens (3.0–4.2, Wilhelmson 1959), *Cladonia* (3.8, Brown 1980) or an isolated *Trebouxia* (2.9, de Nicola and Tomaselli 1961) even though quantum flux densities in the level of the photosynthetic zone in the rock are very low (about 1/100 of ambient quantum flux density, Kappen et al. 1981).

Cold-region lichens are known to have high respiratory rates at elevated temperatures, resulting in a low quotient of maximum CO₂ uptake and dark respiration (Lange and Kappen 1972). For example, the quotients of maximum net photosynthetic rate at 10 klux/dark respiration rate at 20°C for three Antarctic lichens from Cape Hallett (Northern Victoria Land) were between 0.08 and 0.19. In the present study (with a similar light source used for illumination), experimental quantum flux density of 217 μE m⁻² s⁻¹ corresponds to a light intensity slightly higher than 10 klux. Yet, no positive net photosynthesis occurred under these conditions, and even at 10°C, the quotient was only 0.20 for sample A790-47 and 0.11 for A790-50. These values are extremely low compared with lichens from other climates (Kappen 1973, p. 335).

Because of the extreme climate in which they exist, cryptoendolithic lichens of the dry valleys were expected to be adapted to extremely low temperatures. This, however, was not the case: in all three samples, optimum temperatures for net photosynthesis were between 1°C and 6°C or more, a range characteristic for fruticose and foliose lichens of cold climates (Lange 1965), as well as

species from the coastal Antarctic region (Lange and Kappen 1972). For example, in terms of photosynthetic optima, sample A790/47 is comparable to *Buellia frigida* and samples A790/50 and A789/17 to *Lecanora melanophthalma* (Lange and Kappen 1972). The lower compensatory points in cryptoendolithic lichens (about -6°C or -7°C) were also similar to those of *Buellia frigida* and *Lecanora melanophthalma*. These results indicate that cryptoendolithic lichens do not possess special physiological adaptations to cold temperatures: rather, their strategy of survival is to withdraw into the cryptoendolithic niche, where favorable conditions prevail. This withdrawal they achieve by changing their mode of growth from the plectenchymatous to the filamentous, which enables them to colonize the microscopic airspaces inside the porous rock (Friedmann 1982; Friedmann et al. 1982).

Based on micrometeorological observations in the field (Kappen et al. 1981), it is possible to relate laboratory measurements to conditions in the natural environment. As the lower temperature limit of net photosynthesis is around -6°C, it can be estimated that on a mid-summer overcast day (such as December 6/7, 1979) or on a sunny day (such as December 10, 1979) net CO₂ uptake was possible for a period of 13 h. On the sunny but windy day of December 9, 1979, the time for positive net photosynthesis was shorter.

The question arises whether optimum temperatures for photosynthesis are ever reached in this natural antarctic environment. The answer can only be conjecture, as the high levels of radiation that prevail in nature could not be reproduced in the laboratory. Optimum temperatures determined for three quantum flux densities follow

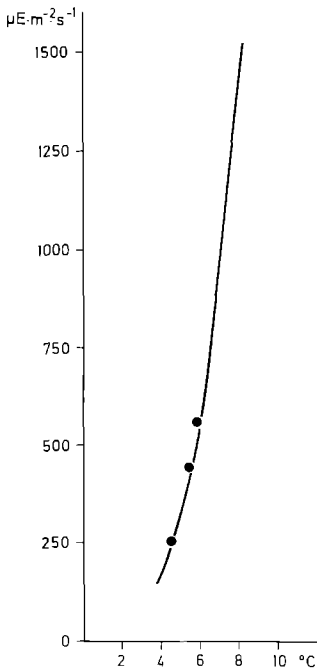


Fig. 5. Extrapolation of optimum temperatures of net photosynthesis to quantum flux densities beyond the range of measurement obtainable under laboratory conditions (black dots). Sample: 790/47

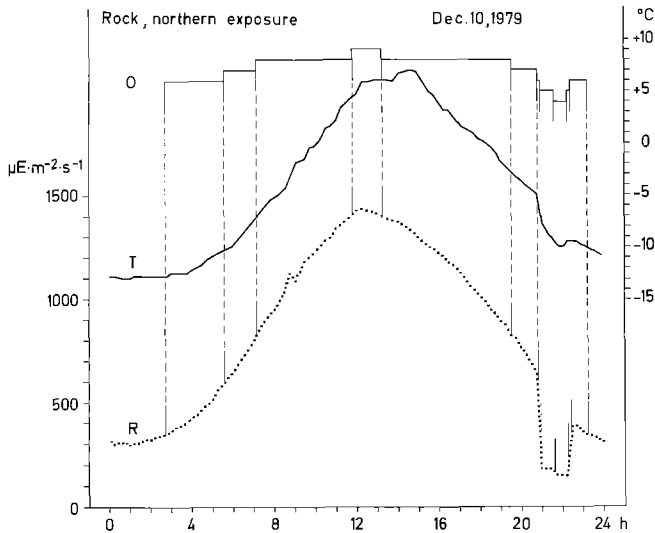


Fig. 6. Comparison of calculated optimum temperatures for photosynthesis and actual temperatures on a clear "warm" day as measured on December 10, 1979, on Linnaeus Terrace. O = Optimum temperatures at different quantum flux densities (from Fig. 5, classes in one-centigrade steps). T = temperature in rock at 2 mm depth. R = natural quantum flux density at rock surface (see Kappen et al. 1981, Fig. 7)

a curve (Fig. 5) that can be formally described by the cubic function $y = 2.75 x^3$. (In this estimate, the upper segment of a cubic function is used rather than a straight line since similar curves for other lichen species such as *Ramalina maciformis* (Lange 1969) also follow a cubic

function. The zero point of this function has no value for the present considerations.) By extrapolation, the estimated optimum temperature at the highest light intensity observed in nature ($1420 \mu\text{E m}^{-2} \text{s}^{-1}$) is 8.1°C . Such a temperature in the rocks was not recorded during field observations either in 1979–80 (Kappen et al. 1981) or in the 1980–81 season (McKay and Friedmann, unpublished). Figure 6 shows the changes in light intensity and rock temperature in a sandstone boulder on Linnaeus Terrace on December 10, 1979, based on data from Kappen et al. (1981) and Fig. 5. On this "warm" midsummer day, the actual temperatures in the rock were at all times at least 1 degree centigrade below the optimum, and for most of the time significantly lower than that. Thus, even during the Antarctic midsummer, temperature seems to be a limiting factor for photosynthetic productivity. Its limiting effect is even more severe in early and late season, as air temperatures are significantly lower (McKay and Friedmann, unpublished) and, because of the lower sun angles, the rocks are not warmed by solar radiation.

It is informative to compare the net photosynthetic rates of cryptoendolithic lichens with those of other lichens. Such a comparison is possible on the basis of the chlorophyll/total organic matter ratio used in the calculations in Table 1 (when this ratio is used, it is assumed that the data reported by Kärenlampi (1979) and Rundel (1972) for other lichens are valid for cryptoendolithic forms as well). Accordingly, maximal rates of net photosynthesis in cryptoendolithic lichens are almost of the order of magnitude of those in *Lecanora melanophthalma* from Cape Hallett, Northern Victoria Land, while corresponding values of the probably more closely related *Buellia frigida* and other Antarctic species are 10 or more times higher (Lange and Kappen 1972). Euendolithic lichens from the Negev desert (Lange et al. 1970) also have much higher rates (per surface area) than cryptoendolithic lichens. However, the reduction of net photosynthesis in "sealed" rock samples (Table 2) suggests that, in nature, rates may be even lower than those measured under laboratory conditions. Thus, CO_2 exchange through the rock surface crust may be very low, while actual photosynthetic activity is higher because an internal CO_2 pool is recycled. Such an extremely low net productivity would not be surprising in a cryptoendolithic community, where the availability of space sets physical limitations to growth.

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