UNAM

Functional Ecology 1994
8, 253–264

Photosynthesis and water relations of lichen soil crusts: field measurements in the coastal fog zone of the Namib Desert

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Summary

1. Although the coastal fog zone of the Namib Desert has negligible rainfall, large parts may be covered by soil-crust lichens with chlorophyll contents and photosynthetic rates (under optimal conditions of hydration and light), on an area basis, almost equal to the leaves of typical higher plants.

2. The photosynthetic and respiratory CO_2 exchange rates of three soil-crust lichens, *Acarospora* cf. *schleicheri, Caloplaca volkii* and *Lecidella crystallina* were measured in the field (September 1990). The three species responded in a similar fashion to changing environmental conditions. Nocturnal hydration, by fog and/or dew, activated dark respiration which was followed after sunrise by a short period of positive net photosynthesis that continued until metabolic inactivation occurred from desiccation. Light compensation point for CO_2 exchange was relatively high (28–43 μmol m^{-2} s^{-1} photon flux density), and apparent quantum yield was low. This most probably was due to light interception by non-photosynthetic pigments in the lichens' cortex. Maximal water uptake by the biological soil crusts after heavy fog was 0·49–0·73 mm (precipitation equivalent). The moisture compensation point, i.e. the minimum water content allowing positive net photosynthesis, was very low (0·13–0·26 mm).

3. Area-related, maximal, daily net photosynthetic carbon gain of the three species under natural conditions was 158–290 mg C m^{-2} day^{-1}. A very rough, first estimate of the annual carbon balance of the soil-crust lichens (photosynthetic gain minus repiratory losses) was 16 g C m^{-2} $year^{-1}$.

Key-words: Biological crust, dew, fog

Functional Ecology (1994) **8,** 253–264

Introduction

Soil crusts, generated by microphytes, are important components of ecosystems in arid and semi-arid landscapes. They influence rain interception, water infiltration into the soil, surface evaporation and moisture storage. By aggregating and stabilizing the uppermost layers of the soil, these biological crusts not only help to avoid soil erosion by water or wind, but they also affect the germination and establishment of phanerogams. Furthermore, in arid ecosystems characterized by low total biomass, soil-crust organisms can cover the soil surface with a thin, often almost continuous, chlorophyll-containing layer and can also substantially influence nutrient cycling, such as nitrogen balance and carbon gain. The different physical, chemical and biological aspects of soil crusts are described in recent reviews by West (1990), St Clair & Johansen (1993) and Johansen (1993); but see also Cameron & Blank (1966) and Friedmann & Galun (1974) for the older literature.

Interest is growing in the structure and function of biological soil crusts in view of world-wide efforts to both preserve these fragile ecosystems and to control the impact of human activity on landscapes in arid regions (see Wessels & van Vuuren 1986). Taxonomic analyses have shown that many different types of microphytes can be involved in the formation of soil crusts, including mosses, lichens, fungi, green and blue–green algae (cyanobacteria) as well as bacteria, resulting in complex plant communities. Recent publications on soil crust biology cover topics such as run-off generation in semi-arid, sand-dune ecosystems (Yair 1990), soil microstructure as determined by the cyanobacterium *Microcoleus vaginatus* (Belnap & Gardner 1993), lichen communities (St Clair, Johansen & Rushforth 1993), bryophyte communities

(Downing & Selkirk 1993), life strategies of soil mosses (Frey & Kürschner 1991), potential contribution of carbon (Beymer & Klopatek 1991), drought tolerance of cyanobacteria (de Winder 1990), and hydration-dependent CO_2 exchange of the systems (Lange *et al.* 1992, 1994). However, efforts have been mainly concentrated on floristics and distribution of various crust components rather than on the ecology and functioning of the intact, microbiotic soil crusts. Almost all studies on crust metabolism have been conducted under controlled conditions in the laboratory, and we are not aware of any publication which reports the metabolic performance of soil crusts in their natural environment. On the other hand, we believe that such investigations are essential in order to understand the ecological features of soil-crust functioning.

Here, we report field measurements, made in the coastal fog zone of the Namib Desert, on water relations and CO_2 exchange of soil crusts composed of crustose lichens. The metabolic activity of the lichens is correlated with microclimatic conditions, and we show how short periods of primary production occurred because of nocturnal hydration by fog and dew which are the main sources of water in a region almost devoid of rainfall. The study was part of a larger programme, investigating lichen existence and lichen productivity in the Namib Desert, which began with measurements in autumn (April) 1988 (see Lange *et al.* 1990, 1991) and was continued in spring (September) 1990.

Materials and methods

HABITAT DESCRIPTION

The field research site was located on the coastal plain between Wlotzkasbaken and Cape Cross (Henties Bay), 40 km north of Swakopmund (Namibia) and about 1500 m east (inland) from the coast. This area belongs to that part of the Namib fog zone which seems to be well suited for lichen growth. A rich assemblage of saxicolous and terricolous species is present there. Rainfall is extremely irregular (see Walter & Breckle 1984) and records at Swakopmund indicate an annual mean precipitation of not more than 13 mm (Logan 1960; see Wessels & van Vuuren 1986) falling on 1–5 days per year. In contrast, fog is frequent along the coast, and overcast and foggy days, or days with dew-fall, total 202–295 per year (see Walter 1937).

The experimental site is located in a flat or slightly undulating plain dissected by sandy washes and interrupted by rock outcrops; it belongs to 'lichen field III' (Schieferstein & Loris 1992) or 'Flechtenfeld 4' (Schieferstein 1989). Perennial phanerogams, such as *Arthraerua leubnitziae* and *Zygophyllum stapfii*, are very scarce and widely scattered. The vegetation consists mainly of a fruticose–foliose lichen community (see Schieferstein 1989) dominated by *Teloschistes capensis* and *Xanthoparmelia walteri*, together with other fruticose lichens such as *Santessonia hereroensis, Ramalina* and *Alectoria* species. Thalli of the vagrant lichen, *Xanthomaculina convoluta*, are interspaced. The soil surface, between the stones and lichen cushions, is densely covered by soil-crust lichens amongst which *Lecidella crystallina* is the most important species. Other crustose species are present at much lower coverage. This mosaic of soil-crust lichens and fruticose species is characteristic of the more humid region adjacent to the coast. The impact of frequent fog declines further inland and the presence of fruticose species decreases so that, in the outer areas of the lichen fields, biological soil crusts dominated by lichens remain the only vegetation over large areas (see Schieferstein & Loris 1992).

SOIL CRUST EXPERIMENTAL MATERIAL

Three crustose lichen species were selected for our experimental work to characterize the metabolic performance of the biological soil crusts:

1. *Acarospora* cf. *schleicheri* (Ach.) Mass. (material was determined by the specialist for this group, Professor Dr N. S. Golubkova, St Petersburg, Russia, but a firm identification of sterile specimens is still not possible). The lichen thallus consists of small (< 1 mm) yellow or greenish (sometimes dirty white), separate areoles which can coalesce to cover almost completely the ground surface for areas of a few square centimetres. The individual thallus squamules are tightly attached to the soil. This conspicuous, soil-crust lichen is relatively rare and grows scattered between the other species of the soil-crust community of the lichen field around the measuring site.

Caloplaca volkii Wirth et Vězda was first collected by Professor O. H. Volk near our experimental site in the early 1970s. The lichen was described by Wirth & Vézda (1975) and named in honour of the collector.[1] It grows as a continuous, cracked crust with irregular, wrinkled or verrucose areoles, dirty ochraceus or brownish in colour and covered with soil particles and crystals. Almost scutiform apothecia, 1–2 (occasionally 4) mm in diameter, with a reddish-brown disc, are frequent and characteristic for this lichen. In contrast

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[1] Professor Volk (Julius-von-Sachs-Institut für Biowissenschaften der Universität Würzburg) has devoted much of his scientific work to the investigation of epigeic cryptogams, especially bryophytes of arid regions, including South Africa and Namibia. In his publication on 'Schaumböden' (foam-structured soils), soils in desert areas with a vesicular appearance, he described an important phenomenon of soil-crust physics and its impact on plant growth (Volk & Geyger 1970). We dedicate this paper to Professor Volk to celebrate his ninetieth birthday and in appreciation of his pioneering work. Appropriately much of this paper deals with the performance of 'his' species *C. volkii* which we studied in Namibia.

to the thallus, the apothecia contain parietin. Individual specimens of this lichen may reach a diameter of 5 cm, with edges that are sometimes lobate but are usually indistinct. The crust is closely attached to the ground and the lower parts of the thallus are densely interspersed with soil particles. The species is found with *L. crystallina* and is a typical member of the soil-crust community, especially on soils rich in gypsum.

Lecidella crystallina Vézda et Wirth was also described for the first time from the vicinity of our measuring site (Wirth & Vézda 1975). It consists of thick (about 2 mm), continuous crusts with indistinct edges, which individually can cover more than several square decimetres. The often dirty, brownish-ochre, angularly areolate and wrinkled surface of the lichen is covered by many gypsum crystals which are also interspersed in the cortex and the medulla of the thallus. Apothecia (up to 1·5–2 mm in diameter) with a black, whitish-pruinose disc are irregularly distributed, occasionally crowded or missing on some parts of the thallus. The crustose thallus is closely attached to the ground and the hyphae of the lower part of the medulla penetrate into the upper layers of the soil. Sometimes, the centre of a crust loses contact with the ground and arches up like a large bubble. This species is the most abundant of the soil-crust lichens in the area and grows frequently between the foliose and fruticose species. Along with *C. volkii,* it dominates the soil-crust microphyte community in the outer areas of lichen fields where other lichen life-forms become rare (Schieferstein 1989; Schieferstein & Loris 1992).

CO_2 EXCHANGE MEASUREMENTS

Photosynthetic and respiratory CO_2 exchange were measured with H_2O/CO_2 porometers (Walz-Company, Effeltrich, Germany) using infrared gas analysers (BINOS, Rosemount, Hanau, Germany); see Lange *et al.* (1984, 1990) for a detailed description of the measuring systems. For ease of handling, soil-crust samples were fixed horizontally in small wire-mesh baskets about 40 mm in diameter. Three types of experiments were conducted.

1. The CO_2 exchange of the soil crusts was studied under natural conditions. The specimens in their baskets were exposed at their normal growth site. This was done so that their hydration state depended on the natural balance between wetting from dew, fog, or high air humidity, and desiccation due to heat and light. At chosen intervals, and taken in order, the trays containing the soil-crust material were enclosed in the porometer cuvette for a short time-period sufficient for gas-exchange measurement (1 to at most 2 min). For these measurements, the porometer measuring head was automatically controlled to ambient conditions and was attached to a stand close to the ground and adjacent to the growth site of the soil crusts. Concurrently, records were made of environmental parameters such as photosynthetically active photon flux density (PFD), air humidity and temperature. After each gas-exchange measurement and before placement back in their growth site, the samples, with baskets, were weighed on an electronic balance. Diel courses of hydration and CO_2 exchange of the soil crusts were obtained from these measurements.

2. On some days soil-crust samples were sprayed with water during the night, before sunrise. The samples, wetted to near maximal hydration, were then exposed to natural, ambient conditions in order to study the time–course of photosynthesis as they dried.

3. In a third set of experiments, the gas exchange of drying soil-crust samples was measured under controlled conditions. Soil-crust lichens were first hydrated to maximal water-holding capacity by submerging them for 5 min in water and then briefly shaking them in order to remove loosely attached water. The samples were then exposed in a porometer cuvette at constant temperature (19·6–20·8 °C), high light (*c.* 1000 µmol m^{-2} s^{-1} PFD) and a relative humidity that decreased from 80 to 70%. The lichens lost water and were air dry after about 150 min. CO_2 exchange was recorded during drying at 30-s intervals.

Two different types of Walz porometers were used for these measurements. The normal CO_2/H_2O porometer, with a measurement 'head' originally designed for work with leaves of higher plants, was taken for short-term measurements of lichen samples (see Hahn *et al.* 1989; Lange *et al.* 1990, 1991). In addition, a second porometer was used which had a measurement 'head' that had been specially developed for lichens and soil crusts (see Lange 1992). The measurement 'head' has three parts: the handle, the body and the cover (also called the cuvette); these are labelled A, B, and C, respectively in Fig. 1. Air enters and leaves through the handle and is kept well stirred by a fan inside the body. The internal air temperature can be maintained at ambient air temperature (measured by an external probe), even during the opening and closing of the cover, by a Peltier-temperature controller placed in the handle. The cooling capacity is such that samples can also be held at constant temperatures for long periods, even under desert conditions. The top of the body is open and is covered by a grid on which the soil-crust sample is placed in its basket. The sample is enclosed by the transparent lid which consists of a plexiglass cylinder covered at one end by plastic film. An air-tight seal is then produced by means of a ring-shaped electromagnet at the top of the body which attracts another metal ring at the base of the cover. When the electromagnet is activated a reassuring 'click' announces air-tight closing of this 'click–cuvette'. For a critical discussion of the methods used, as well as possible errors, see Bruns-Strenge & Lange (1991) and Hahn *et al.* (1989, 1993).

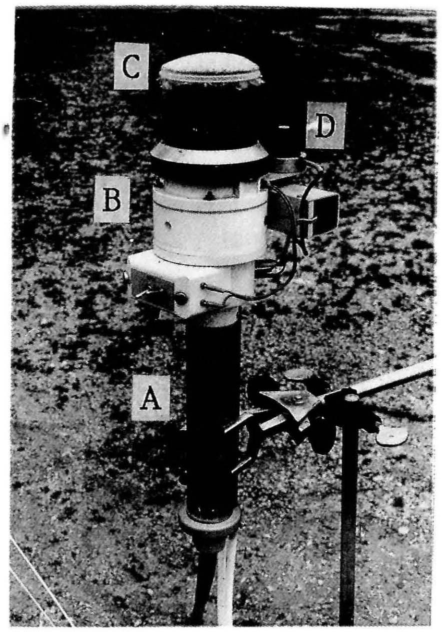

Fig. 1. Conditioned porometer head of the 'click cuvette', which is mounted near the ground, where the dense lichen vegetation can be recognized. (A) Handle with the electronic and the pneumatic connections and with part of the temperature and humidity control inside; (B) body with ventilating fan inside; (C) transparent cover of the cuvette chamber in which a fruticose lichen sample can be seen; (D) quantum sensor.

Soil-crust samples were collected which were entirely covered by one of the three lichen species and had a total area of 8–11 cm^2. The samples were composed of the surface lichen together with underlying soil of such a thickness that all lichen rhizinae were included. After the measurements, the surface area of the samples was measured and their total chlorophyll (*a*+*b*) content determined according to Ronen & Galun (1984). Net photosynthesis (NP) and dark respiration (DR) were related to crust surface area as well as to chlorophyll content. Water content (WC) of the soil-crust samples was expressed as mm 'precipitation-equivalent'; it was determined for any particular time during the measurements as the difference between the sample weight at that time and the weight at 'zero' water content. This was defined as the weight of the sample at its driest conditions during the measurements (a situation where the absolute water content of a lichen thallus usually still has an amount of water of about 10% of its oven dry weight).

The field measurements took place between 11 and 25 September 1990. Eleven or 12 diel courses of water content and CO$_2$ exchange for each of the three experimental species were completed, in addition to the experiments with artificial moistening. It was our objective to follow CO$_2$ exchange of an identical sample of each species for the total measuring period so that the day-to-day responses could be compared and analysed. Limitations of man-power and time did not permit substantial replication needed for statistical treatment [see discussion of representative samples by Hahn *et al.* (1993)]. However, each measuring sample was made up of different pieces of soil crusts of the same species, so the results do represent the average response of several subsamples. We are convinced, therefore, that these measurements characterize the general features of the metabolic performance of soil-crust lichens during typical Namib weather conditions. In addition, the experiments involving artificial hydration and the drying cycles were designed to help the interpretation of the diel cycles.

Results

DIEL COURSES OF SOIL-CRUST LICHEN CO$_2$ EXCHANGE

The soil-crust lichens responded similarly to nocturnal hydration by dew and fog as fruticose and foliose lichens which had been studied 2 years earlier in autumn at the same site (see Lange *et al.* 1990, 1991). Carbon dioxide exchange, on a day when samples became very wet (24 September), is depicted in Fig. 2A for all three species. The previous afternoon was dry and hot; all soil crusts had become very dry so that their metabolism was inactivated. Just after midnight, fog began to drift over the coastal plain from the sea and dew condensation took place. The lichen crusts absorbed water and, by the first measurement (about 02.20 h), WC had increased to between 0·25 mm (*L. crystallina*) and 0·42 mm (*C. volkii*). Two of the crusts were respiring at an air temperature of about 11 °C. As the water content of the crusts rose the respiration of all species increased to a maximum of CO$_2$ release at 06.50 h, the time of sunrise. Well-hydrated lichens then started to carry out photosynthesis. Because of the dense fog cover, radiation levels increased only slowly, water uptake by the lichens continued until 08.30 h and water content between 0·48 mm and 0·73 mm were attained. The light compensation point was reached at 07.40 h, and then CO$_2$ uptake rose steeply to a maximum at about 10.00 h. PFD was then about 520 μmol m^{-2} s^{-1} and the fog had almost disappeared. The higher radiation, the increasing temperatures and decreasing air humidity rapidly dried the soil-crust lichens and photosynthetic CO$_2$ uptake quickly declined. The compensation point was reached about 45 min after the CO$_2$ uptake maximum; a short phase of minor CO$_2$ release followed and then the soil crusts became so dry again that no CO$_2$ exchange could be detected for the remainder of the day. The heavy fog had not only strongly hydrated the soil crusts but also delayed the occurrence of full sun radiation. As a result, the time until the thalli were desiccated was extended and positive net photosynthesis could take place for a relatively long time, about 3 h 20 min. All three species responded in an

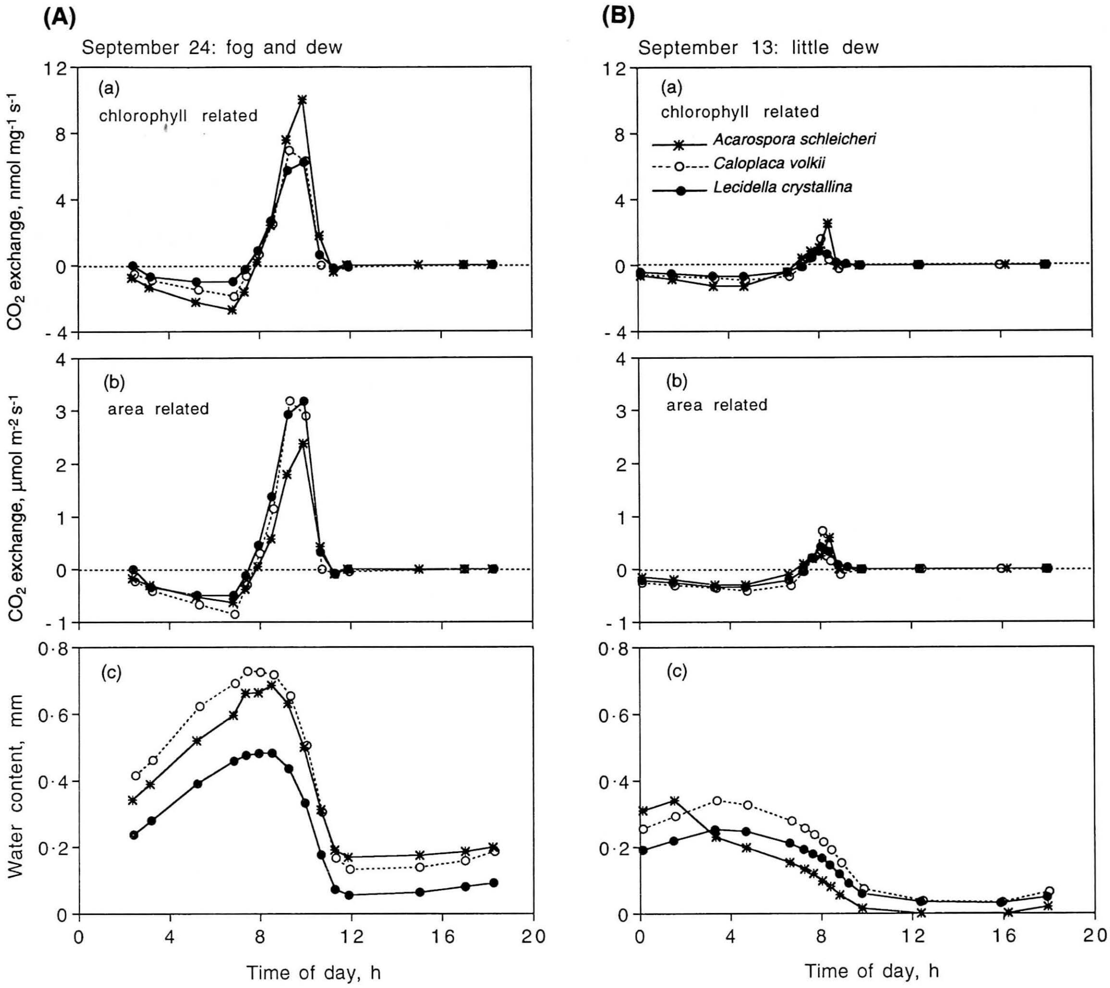

Fig. 2. Daily time–courses of CO_2 exchange (CO_2 uptake positive) related to chlorophyll content (a) and surface area (b) and daily time–courses of water content (c) (for definition see text) for the three experimental soil-crust lichens. (A) Day with heavy nocturnal fog and dew; (B) day with little dew-fall.

almost identical fashion. *Acarospora schleicheri* had the highest chlorophyll-related rate of NP, whereas *L. crystallina* was best if CO_2 uptake was related to thallus area. The lichens attained a net carbon gain under these conditions, i.e. carbon loss due to nocturnal respiration was more than compensated by photosynthetic carbon gain after dawn.

A different situation is illustrated in Fig. 2B (13 September). There was no fog but a light dew-fall occurred before midnight. This activated respiratory CO_2 loss by all three species during the night. Water loss started to occur between 02.00 and 04.00 h as a result of declining air humidity. Finally, water content was so low at sunrise, that photosynthesis reached only a small peak before desiccation again stopped all metabolic activity. Positive net photosynthesis lasted less than 60 min and photosynthetic carbon gain was not sufficient to compensate the respiratory losses which occurred after midnight.

The photosynthetic activity of the Namib soil crusts therefore differed from day to day according to the weather and the degree of hydration. As an example, Fig. 3 shows the performance of *L. crystallina* over 12 days from 11 September to 24 September (no measurements 21 and 22 September). Dew, in combination with fog of varying intensity, was measured on 6 days and resulted in pronounced morning peaks of photosynthesis. On 2 days dew occurred without fog; photosynthesis took place on both days but on one, 17 September, a pre-dawn water content of more than 0·3 mm was reached and this allowed high rates of photosynthesis. Four days were so dry that no photosynthetic activity was measurable.

All data sets under conditions of nocturnal wetting, a total of 23 diel courses, are pooled for all three lichen species in Fig. 4. Although some individual differences occurred, for instance *L. crystallina* tended to have lower water content than *Acarospora schleicheri* the three soil crusts showed striking similarities in performance. Their pattern of hydration was the same whenever wetting took place from fog and/or dew. Water content increased during the second half of the night to a maximum between 06.00 and 09.30 h which was followed by rapid drying. At the same time three

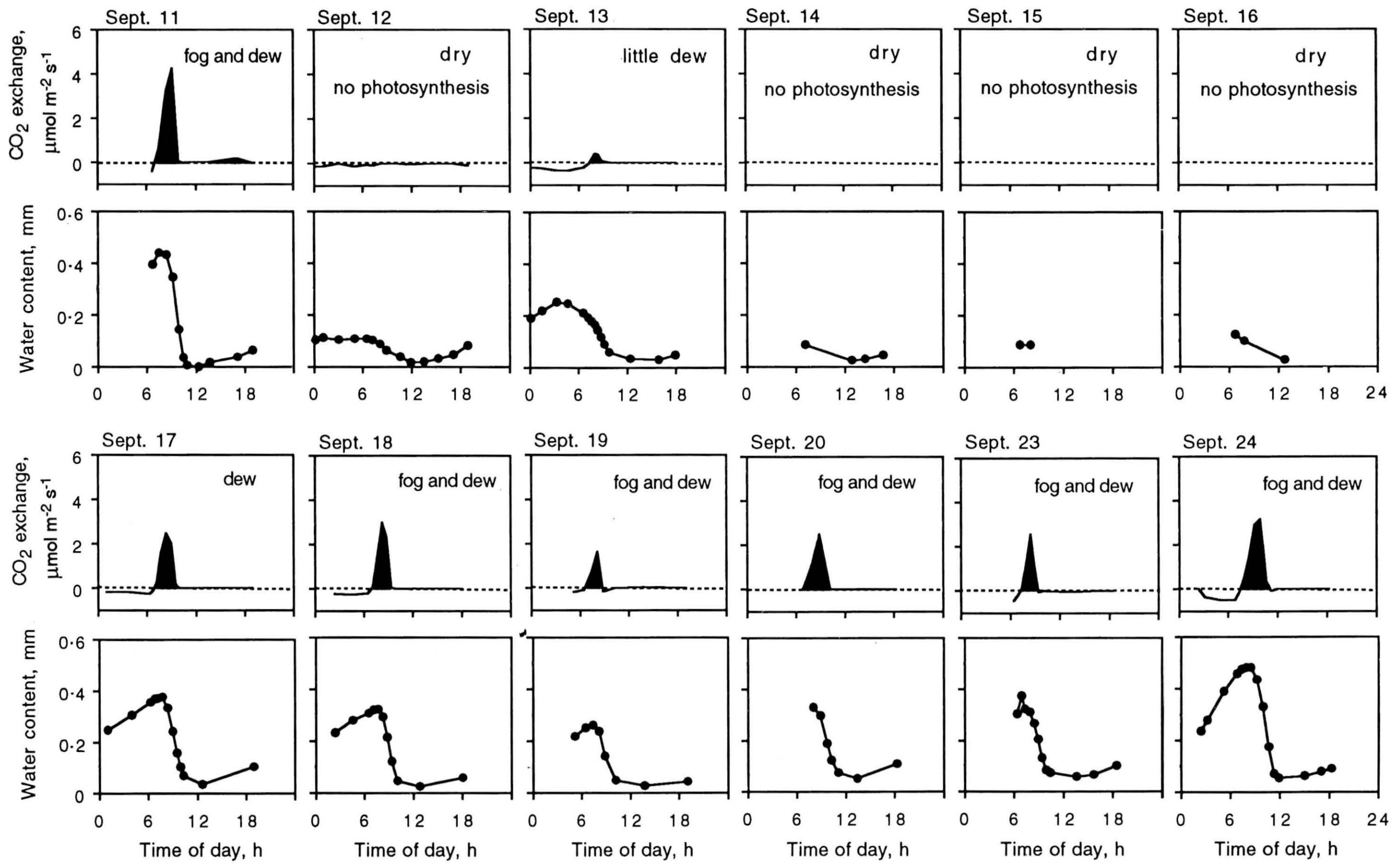

Fig. 3. Daily time–courses of area-related CO_2 exchange and of water content for *Lecidella crystallina* during the period from 11 to 24 September 1990 (no data are available for 21 and 22 September).

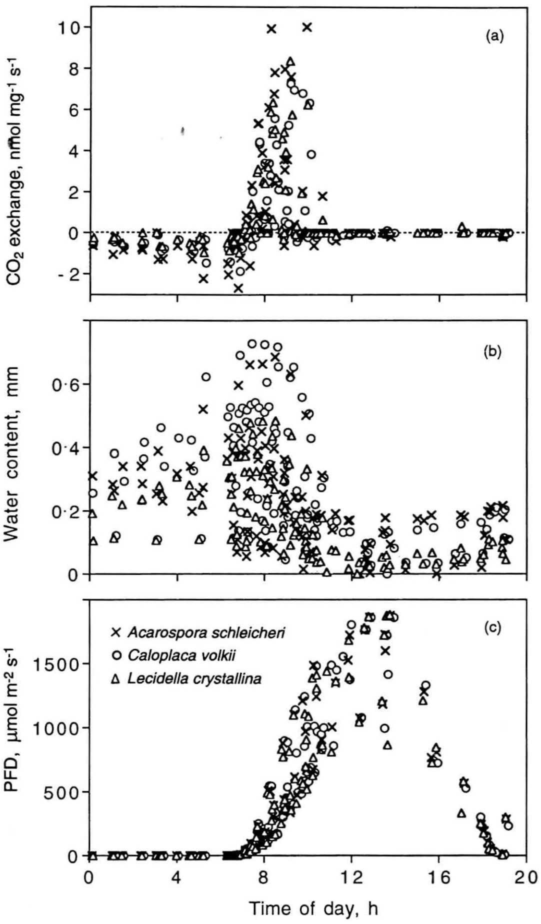

Fig. 4. Daily time–courses of chlorophyll-related CO_2 exchange (a), water content (b) and incident photosynthetic active photon flux density (PFD) (c). The data for all three soil-crust lichens from days with nocturnal fog and/or dew hydration, have been pooled (see text).

phases of CO_2 exchange could be recognized. First, respiratory CO_2 loss increased between 05.00 and 07.00 h, the hours just before sunrise; second, substantial rates of positive net photosynthesis were possible only immediately after sunrise from 07.30 to 10.30 h; third, the lichens dried and were almost completely inactive until dusk. In the third phase there was a tendency for hydration to increase later in the afternoon due to water vapour uptake at higher air humidity. On some days this increased hydration allowed a short period of very low rates of photosynthesis just before sunset (see Fig. 3, 11 September). However, this reactivation through water vapour uptake was much less for soil crusts than for fruticose species growing in the same site. The larger surface area of fruticose lichens appears to allow more rapid exchange of moisture with the atmosphere.

PHOTOSYNTHETIC RESPONSES TO LIGHT AND HYDRATION

As shown with other lichen species (Lange *et al.* 1990) and for the studied species photosynthetic rates are light determined immediately after dawn, whereas the decrease after the maximum is caused by progressive drying of the thalli. All lichens pass first through a light compensation point as positive net photosynthesis starts, and then through a moisture compensation point as it ends.

The last data points for CO_2 exchange before sunrise and the very first data points after sunrise can be used to obtain the initial, linear response of CO_2 exchange to light. Data for the three soil-crust lichens and for every diel course where initial water contents had been higher than 0·25 mm are included in Fig. 5 (closed circles). The scatter of the data points was high because air temperature varied in the range between 7 and 12 °C and water contents were also not constant. Nevertheless, linear regressions gave reasonable estimates of light compensation points (see discussion by Lange *et al.* 1991). The compensation

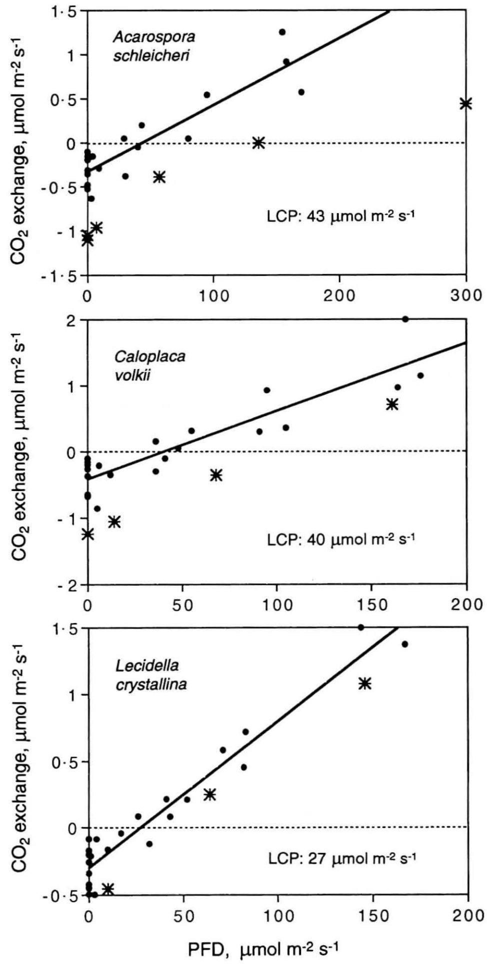

Fig. 5. Light compensation points (LCP) of the three soil-crust lichens determined by linear regression. The first CO_2 exchange points (CO_2 uptake positive) from mornings with natural hydration (●) are plotted against photosynthetically active photon flux density (PFD). Thalli that have been artificially and copiously moistened (*) are not included in the regression.

points were all relatively high (Table 1) with a maximum of 43 µmol m^{-2} s^{-1} PFD for *Acarospora schleicheri*. Figure 5 (asterisks) also shows the initial light response of the same samples after their water content had been increased two to three times, compared to natural hydration, by pre-dawn spraying. The higher water content increased the dark respiration for all three species and resulted in an obvious increase in their light compensation point. The initial slope of the light–response curves (Fig. 5) gave the apparent quantum yield as related to incident radiation (Table 1). As for the light compensation point, *L. crystallina* had the highest efficiency and *Acarospora schleicheri* the lowest; however, the difference between all three species was very low.

Exact values for the moisture compensation point were difficult to obtain from field measurements because drying of the soil crusts after the morning peak of photosynthesis took place so quickly (see discussion by Lange *et al.* 1991). In Fig. 6, data points for the three species are plotted for the last phase of their morning peak of CO_2 uptake. The regression lines show the moisture compensation points to be 0·26 mm (*C. volkii*), 0·14 mm (*Acarospora schleicheri*) and 0·125 mm (*L. crystallina*).

It is known from many other lichens (e.g. Lange *et al.* 1993), and also for soil-crust species that rates of CO_2 exchange at favourable light and temperature conditions can be limited by both low and high thallus hydration. The depression of CO_2 exchange at high hydration was exceptionally strong for *L. crystallina*. If this lichen was experimentally saturated to maximal water-holding capacity (i.e. at the start of the drying cycle depicted in Fig. 7), only CO_2 release was possible, even when light and temperature conditions were favourable for high rates of net photosynthesis. Some water loss was necessary to reach the upper moisture compensation point and then, with further

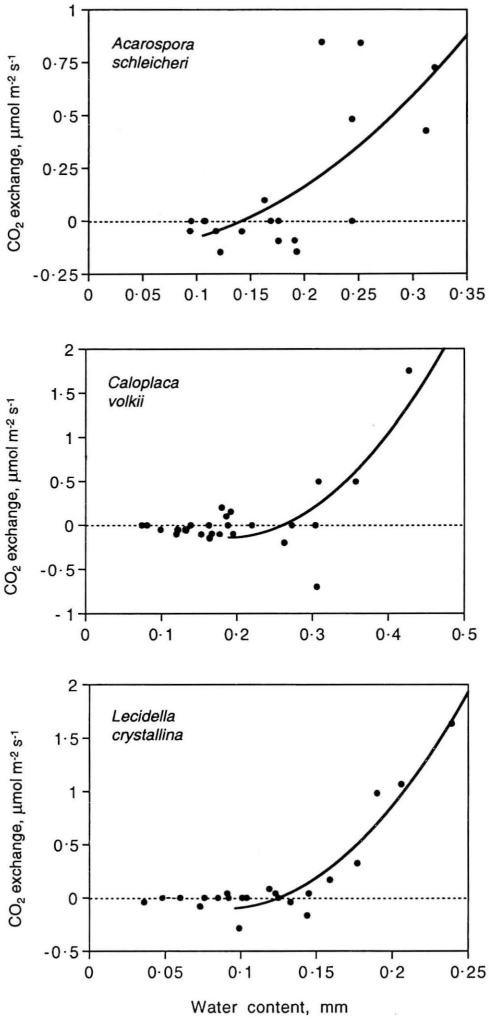

Fig. 6. CO_2 exchange (CO_2 uptake positive) as a function of water content for the three soil-crust lichens during the last phase of the drying period in the late morning after natural, nocturnal hydration. The data are fitted with quadratic regressions to estimate the moisture compensation points.

Table 1. Total chlorophyll content per soil-crust area; maximal rates of area and of chlorophyll-related net photosynthesis under natural conditions; average and maximal area and chlorophyll-related (chl) daily carbon gain (related to all days with fog and/or dew); estimates of light and moisture compensation points and of apparent quantum yield of carbon fixation (related to incident radiation). Data are from one sample for each soil-crust lichen species (composed of several subsamples) from the measuring period 11–25 September

	Chlorophyll (area basis) (mg m^{-2})	Maximal NP (area basis) (µmol CO_2 m^{-2} s^{-1})	Maximal NP (chlorophyll basis) (nmol CO_2 mg^{-1} s^{-1})	Average (and maximal) daily carbon gain (mg C day^{-1})		Light compensation point (µmol m^{-2} s^{-1})	Apparent quantum yield (mol CO_2 mol^{-1} quanta)	Moisture compensation point—after drying (mm)
				m^{-2}	mg^{-1}			
Acarospora schleicheri	236	2·4	10·0	92 (158)	0·391 (0·669)	43	0·0076	0·14
Caloplaca volkii	457	3·3	7·3	130 (226)	0·285 (0·493)	40	0·0103	0·26
Lecidella crystallina	508	4·3	8·8	155 (290)	0·306 (0·570)	28	0·0111	0·13

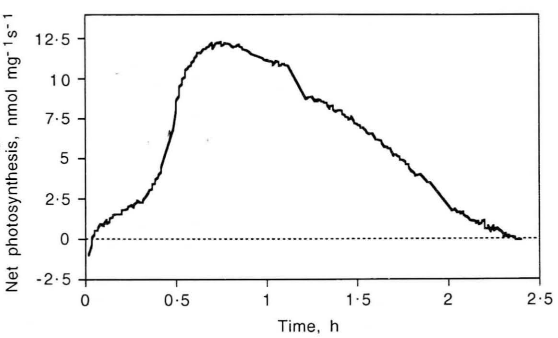

Fig. 7. Time–course of chlorophyll-related net photosynthesis of *Lecidella crystallina* during a drying cycle at constant temperature (19·6–20·8 °C) and light conditions (*c.* 1000 µmol m^{-2} s^{-1} PFD). The experiment began after wetting the samples to maximal water-holding capacity; they became dry after 2·4 h.

drying, net photosynthesis increased steeply. This is a typical response as CO_2 diffusion resistances decreased within the lichen thallus (see Cowan, Lange & Green 1992). An optimal hydration was reached where rates of net photosynthesis were considerably higher than the maxima found under natural conditions. Then, as drying continued, water became limiting for CO_2 uptake, and photosynthesis declined and eventually ceased 2·4 h after initial exposure of the wet samples in the gas-exchange cuvette. The actual soil-crust water content was not measured in this experiment; but we know that the maximal water-holding capacity of the samples, after experimental moistening, exceeded the water content that was reached naturally from fog and dew by a factor of 3–4.

SOIL-CRUST CARBON BALANCE

After natural wetting, the three soil-crust species had very similar, maximal carbon gains during the daylight hours. It made no difference if the gain was related to chlorophyll content or to surface area (Table 1). The same was true for daily carbon gains averaged over all measurement days with nocturnal fog and/or dew. The mean daily carbon gain for the three lichen species was 126 mg C m^{-2} day^{-1}. Extrapolation from 12 or 13 days to the whole year requires great care, but we can now make a first, very rough estimate of the soil-crust carbon balance. We know that fruticose and foliose lichens at the same research site had a pattern of photosynthesis, after nocturnal wetting, that was similar in both autumn and spring suggesting that photosynthetic production was independent of season. As a first approach we can suggest that each fog event results in the same average amount of photosynthetic gain. Assuming that our measurements were typical for the soil-crust lichens, we can combine the mean, daily carbon gain that we found, with the annual average of 250 foggy days, and obtain an annual gross productivity of about 32 g C m^{-2} soil crust (100% covered with lichens). In this calculation we have not taken into consideration the extra carbon gain during the few days each year when rain and more extended periods of lichen hydration occurred; at the moment we have no information on lichen performance under these weather conditions. Nor do we yet have sufficient information to calculate accurately total nocturnal carbon loss of the lichens in the Namib habitat. An approximation is possible: based on the rates of nocturnal CO_2 release that we measured after hydration of soil crusts by dew and fog, and including experiences with fruticose species of the same site (see Lange *et al.* 1990), we arrive at a respiratory loss equal to about half the total carbon gain, a proportion similar to the estimate of annual carbon loss for the fruticose lichen *R. maciformis* in the Negev desert (Kappen *et al.* 1979). The calculated annual net input (diurnal net photosynthesis less nocturnal respiration) is 16 g C m^{-2} (again assuming 100% lichen cover). Certainly this number is no more than a very rough approximation. It is, however, an indicator of the magnitude of the contribution by soil-crust lichens to the photosynthetic productivity of the desert ecosystem, a system in which they are often the only, or at least the most dominant, primary producers.

Discussion

When experimentally exposed to optimal conditions of light and hydration, the lichen soil crusts in the Namib Desert appear to have a photosynthetic potential almost equal to that of higher plant leaves. Their area-related chlorophyll content (236–508 mg m^{-2}, see Table 1) are not only surprisingly high compared with other biological crusts (see Lange *et al.* 1992) but are similar to the chlorophyll content of typical higher plant leaves. In the textbook by Lawlor (1990) the chlorophyll content for an average leaf of C_3 plants is 500 mg m^{-2}, and according to Björkman (1981; see Gabrielsen 1948) maximum quantum yield of photosynthetic CO_2 uptake for leaves of C_3 species is reached at 500–700 mg chlorophyll m^{-2}. It seems that the ground, in the soil-crust area of the Namib Desert, is covered by a continuous sheet of photosynthetic machinery equivalent to a layer of phanerogamous leaves. On a chlorophyll basis, photosynthetic rates of soil-crust lichens moistened naturally by fog or dew were similar to those of fruticose and foliose lichens in the same habitat (Lange *et al.* 1990, 1991). Maximal chlorophyll-related CO_2 fixation by *L. crystallina* when experimentally exposed to optimal light and hydration (12·8 nmol mg^{-1} s^{-1}) was also similar to maximal rates for Negev soil crusts in our laboratory experiments (14·8–35·2 nmol mg^{-1} s^{-1}).

On an area basis, however, the maximal CO_2 uptake rate of *L. crystallina* under optimal conditions of the experiment, 5·9 µmol m^{-2} s^{-1}, was higher than the Negev soil crusts and was almost similar to maximal rates for higher plant leaves. Lüttge, Kluge & Bauer (1988) gave 10–20 µmol CO_2 m^{-2} s^{-1}, at normal ambient CO_2 partial pressure, as typical for light-saturated net photosynthesis of sun plants. Certainly this number is much smaller than maximal rates of CO_2 fixation achieved by rapidly photosynthesizing crop species. In the classification of Larcher (1980) *L. crystallina* falls near the groups 'sclerophylls of predominantly dry regions' (7·9– 23·8 µmol m^{-2} s^{-1}) and 'desert shrubs' (9·5–31·7 µmol m^{-2} s^{-1}). The soil crusts of the Namib Desert not only contain a similar amount of chlorophyll as leaves but also achieve comparable maximal photosynthetic rates under optimal conditions.

However, in contrast to higher plants, the soil-crust microphytes are poikilohydrous organisms which are desiccated and inactive for most of the day. As a result, both the actual photosynthetic rates and the duration of CO_2 fixation are greatly reduced. Under natural conditions *L. crystallina* reached only two-thirds of its potential maximal photosynthetic rate and then only for a brief time (see Table 1). Under conditions of favourable light, photosynthetic activity was always limited by thallus desiccation. The daily carbon gain of the three soil-crust lichens, even after extensive nocturnal wetting, was only 158–290 mg C m^{-2} day^{-1}, orders of magnitude less than carbon gain by higher plant leaves. However, considering the hostility of the Namib environment with its virtual absence of rain, the net carbon gain of the soil-crust system, 16 g C m^{-2} $year^{-1}$, is remarkable and an important contribution to the desert ecosystem.

Although desiccation is a disadvantage of poikilohydry, it is counterbalanced by the ability of the soil-crust lichens to use small amounts of water from fog, dew and even humid air. Many factors could affect the moisture yield and length of the hydrated period of the lichen crusts; these include structure, colour and thermal properties. Unfortunately we have insufficient data at present to allow any comparison to be made between the different lichen species. There were certainly differences in water content after nocturnal wetting; the maximal values attained being 0·49 mm (*L. crystallina*), 0·69 mm (*Acarospora schleicheri*) and 0·73 mm (*C. volkii*). *Lecidella crystallina* maintained positive net photosynthesis to a very low water content of 0·125 mm. According to our laboratory experiments, this was similar to cyanobacteria-dominated soil crusts from sand-dunes of the western Negev Desert. Those crusts had a moisture compensation point of 0·1 mm (Lange *et al.* 1992), which is lower than the average dew-fall in the highlands of the central Negev (0·16 mm, Avdat experimental farm, Evenari, Shanan & Tadmor 1982; see Lange, Schulze & Koch 1970).

In all our CO_2-exchange measurements on soil crusts made to date, the moisture compensation point was determined as the samples dried. A gradient in water content within the crusts might have occurred especially in field experiments where the crusts were exposed to the direct sun. Under such conditions the lichen photobiont could have become more desiccated than the lower portions of the soil crust and the overall water content of the crust might not have been representative of the site of photosynthesis. Photosynthesis could, in principle, be possible at lower overall water content than found during the drying experiments. This seems to be true. On some days, when relative air humidities were above 90%, water vapour uptake occurred in the afternoon. The hydration of the soil-crust lichens increased but only to very small values, 0·038 mm for *L. crystallina*; however, low rates of net photosynthesis were detected. This agrees with the known ability of many green algal lichens to attain positive photosynthesis by taking up moisture from the atmosphere even when water potentials are lower than –200 bar, possibly as low as –380 bar (Lange 1988). However, in contrast to fruticose lichens in some desert environments (e.g. in the 'fog oases' of the southern Atacama Desert; see Lange & Redon 1983), this ability was of little ecological importance to soil-crust lichens in the Namib Desert. Their compact structure meant that water vapour uptake was slow and, because there was only a brief period in the late afternoon when high air humidity coincided with sufficient light, the photosynthetic gain was small.

Desiccation was the major limitation to carbon gain, but the soil-crust lichens also had relatively high light requirements for photosynthesis. Their light compensation points were between 28 and 43 µmol m^{-2} s^{-1} PFD, far higher than the low 1 µmol m^{-2} s^{-1} PFD for deep-shade lichens (Green, Kilian & Lange 1991). Their apparent quantum yield (related to incident light), 0·0076–0·0111 mol CO_2 (mol quanta)$^{-1}$, was much lower than values for the leaves of higher plants (around 0·06 mol mol^{-1}, with around 0·052 mol CO_2 mol^{-1} absorbed quanta; Osmond, Björkman & Anderson 1980; Björkman 1981; Lawlor 1990) and for other lichens (e.g. species from the temperate rain forest; B. Büdel, T. G. A. Green, U. Heber, O. L. Lange, A. Meyer & H. Zellner, unpublished data). The inefficient use of incident light is almost certainly a result of the thick, pigmented cortex which appears to be characteristic for soil lichens (see Starck 1992). The cortex probably absorbs a substantial portion of the photosynthetic active radiation before it can reach the photobionts. Light absorption by the cortex would increase the light compensation point and would decrease the apparent quantum yield. In *Peltula* species, the cortex reduces the incident photon flux density to less than 10% at the algal layer (Büdel & Lange 1994). The pigmented cortex may be a necessary adaptation of the soil-crust lichens to the bright desert environment. It may protect the green algal photobionts from excessive radiation and thus avoid photoinhibition of the photosynthetic apparatus (see Demmig-Adams *et al.* 1990).

Our information about the ecological functioning of biological soil crusts in their desert environment remains very limited and the present study is only a first step towards an understanding of their photosynthetic performance. It does appear that much of our knowledge about the ecophysiology of fruticose and foliose lichens can also be applied to soil-crust lichens. However, soil crusts have many special properties. These include the tight contact between thalli and the porous ground that influences the water relations of the crusts, the leaching of assimilates from the thalli into the ground, and the interactions with other organisms in the soil-crust microphyte communities. There remains a need for further experimental work with soil-crust organisms both in the laboratory and in the field.

Acknowledgements

The work was supported by the Deutsche Forschungsgemeinschaft (Bonn) as a project within the 'Sonderforschungsbereich 251' of the University of Würzburg and by the 'Fonds der Chemischen Industrie' (Frankfurt). Ms B. Melzer participated in the field measurements and her help is gratefully acknowledged. We thank Professor D. Wessels (Sovenga, RSA) and Professor N. S. Golubkova (St Petersburg, Russia) for assistance with determination of the soil-crust lichens. We are grateful to Professor O. H. Volk (Würzburg) for his advice, Ms D. Faltenbacher-Werner and Mr G. Radermacher for their help with evaluation of the data, and Professor A. Green (Hamilton, New Zealand) for critically reading the manuscript.

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Received 15 June 1993; revised 14 September 1993; accepted 28 September 1993