

Photosynthesis of the cyanobacterial soil-crust lichen *Collema tenax* from arid lands in southern Utah, USA: role of water content on light and temperature responses of CO₂ exchange

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Summary

1. The gelatinous cyanobacterial *Collema tenax* is a dominant lichen of biotic soil crusts in the western United States. In laboratory experiments, we studied CO₂ exchange of this species as dependent on water content (WC), light and temperature. Results are compared with performance of green-algal lichens of the same site investigated earlier.

2. As compared with published data, photosynthetic capacity of *C. tenax* is higher than that of other cyanobacterial and green-algal soil-crust species studied. At all temperatures and photon flux densities of ecological relevance, net photosynthesis (NP) shows a strong depression at high degrees of hydration; maximal apparent quantum-use efficiency of CO₂ fixation is also reduced. Water requirements (moisture compensation point, WC for maximal NP) are higher than that of the green-algal lichens. *Collema tenax* exhibits extreme 'sun plant' features and is adapted to high thallus temperatures.

3. Erratic rain showers are the main source of moisture for soil crusts on the Colorado Plateau, quickly saturating the lichens with liquid water. High water-holding capacity of *C. tenax* ensures extended phases of favourable hydration at conditions of high light and temperature after the rain for substantial photosynthetic production. Under such conditions the cyanobacterial lichen appears superior over its green-algal competitors, which seem better adapted to habitats with high air humidity, dew or fog as prevailing source of moisture.

Key-words: Carbon fixation, cryptobiotic crust, cryptogamic crust, water relations

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Introduction

Biotic soil crusts are communities composed of bacteria, cyanobacteria, algae, mosses, liverworts, fungi and lichens. They are a common phenomenon in arid and semiarid lands, and they play an important role in ecosystem functioning. Crust structure and composition increases stability of soil surfaces and influences rain interception, water infiltration, surface evaporation and moisture storage in soils (Harper & Marble 1988). Nutrient cycling in large areas with a low cover of phanerogamous vegetation can be decisively determined by the metabolism of crust microphytes, especially nitrogen and carbon budgets (Beymer & Klopatek 1991; Evans & Ehleringer 1993; Belnap & Harper 1995). On the other hand, soil crusts are very sensitive to surface disturbance, such as fire, livestock

grazing, trampling or vehicles (Belnap & Gardner 1993; Belnap, Harper & Warren 1994; Belnap 1995; see Williams *et al.* 1995). Managers of semiarid regions have become increasingly concerned with aspects of soil-crust protection and re-establishment (Belnap 1993, 1994).

Owing to its importance, scientific interest in soil-crust biology has increased greatly in the last decade (reviews by Harper & Marble 1988; West 1990; Johansen 1993). However, work with soil crusts has focused mainly on structure, distribution and taxonomic composition, including the role of cyanobacterial species as nitrogen fixers. Our knowledge about ecophysiological functioning of the members of soil-crust communities is very limited.

Lichens are an important component of soil-crust biota. We have begun the analysis of the photosynthetic metabolism of soil-crust lichens in the field and under controlled conditions with species from the Negev desert (Lange, Schulze & Koch 1970; see Lange *et al.* 1992), the Namib desert (Lange *et al.* 1994), and a local steppe formation in Franconia, Germany (Lange, Reichenberger & Meyer 1995). Throughout the intermountain area of the western United States, there is a high diversity of lichens in crust communities of semi-arid shrublands, pinyon-juniper woodlands, sagebrush communities and different types of steppe formations; more than 30 different species have been listed by St. Clair, Johannsen & Rushforth (1993). Most of them are green-algal lichens and in preceding work we studied CO₂ exchange of a selection of this group from southern UT (Lange *et al.* 1997). In the present article, we report measurements with one of the few cyanobacterial species, the gelatinous *Collema tenax* (Swartz) Ach. Performance of this lichen is of special interest, because it is the most abundant and the fastest growing one of all of the soil-crust lichens of the area. It dominates regrowth of lichen cover after disturbance of the crusts (West 1990; Belnap 1993) and it is one of the most active nitrogen-fixing organisms of the community (Belnap 1996). With laboratory experiments under controlled conditions, we analysed the features which allow this lichen successful productivity under extreme habitat conditions. Because all metabolic activity of soil-crust lichens in their natural environment is dominated by quick and drastic changes in moisture availability, with only short periods of favourable hydration, we studied the effects of water content on photosynthetic and respiratory responses under different temperature and light regimes. The results compare differences in performance between cyanobacterial and green-algal lichens and contribute to the understanding of ecology of soil-crust functioning.

Materials and methods

Air-dry lichen samples of *C. tenax* were collected 15 km south of Moab, UT, USA, situated in the Colorado Plateau biogeographic province. The site is dominated by sparse vegetation of *Coleogyne ramosissima*, *Pinus edulis* and *Juniperus utahensis*. Soils are Rizzo fine sandy loams. Rainfall is \approx 200 mm annually, with 30% as late summer monsoons. Soil crusts cover about 60% of the ground. The material was transported by courier to Würzburg, Germany, and either used immediately or stored dry at -18 °C until use.

Collema tenax is one of the most common terricolous lichen in the inter-mountain area of the USA (St. Clair *et al.* 1993). It mainly occurs on calcareous or gypsiferous soils and demonstrates high ecological amplitude and substantial morphological variation. The species is not only common throughout North America (Fink 1935) but it is the most widely distributed terricolous species of the *Collema* genus in

Europe and adjacent parts of Asia and Africa (Degelius 1954). The foliose or squamulose, initially rounded but later rather irregular gelatinous thalli of about 1–3 cm in diameter, consist of dark olive-green to brownish or blackish lobes. They are covered by small globular isidia and are attached to soil by white rhizinae; apothecia were rare in the experimental site. As characteristic for the total genus, the thalli have no cortex. They absorb great quantities of water, swelling strongly under moist conditions and shrinking when dry. The photobiont is a cyanobacterial *Nostoc* species (Tschermak-Woess 1988).

The experimental methods used and the mode of treatment of the lichens were identical to those of Lange *et al.* (1997; see Lange *et al.* 1995). Gas-exchange measurements were conducted using a 'minicuvette system' (Walz Company, Effeltrich, Germany) operated under fully controlled temperature, light, humidity and external CO₂. For determination of photosynthetic and respiratory CO₂ exchange, lichens were fixed in wire-mesh baskets which were exposed in the cuvette. Thalli were cleaned and one sample consisted of more than 10 individual lobes from different thalli, having a total thallus area of \approx 10 cm². Thus, response of each sample represents an average performance over a variety of specimens of the population. For analysis of typical lichen responses, performance of one of these samples is depicted. Quantitative numbers for gas-exchange parameters, such as maximal rates, light and moisture-compensation points, were derived from ($n =$) five to 12 sets of experiments, and averages \pm standard deviation are given.

Net photosynthesis (NP) and dark respiration (DR) of the samples were related to (projected) thallus surface area of the lichen. Average dry mass of the experimental material was 1187 g m⁻² and average chlorophyll content (determined according to Ronen & Galun 1984) was 90.8 mg m⁻².

Dependence of NP on water content (WC) of the lichen thalli was determined at constant PPFD (photosynthetic photon flux density) of 1000 μ mol m⁻² s⁻¹ and 17 °C or 26 °C. Samples were maximally hydrated by initially spraying and subsequently submerging them in water for several min, followed by shaking to remove adhering water droplets. CO₂ exchange of these initially maximally hydrated samples was recorded in alternating light and darkness, as they slowly dried. One drying cycle lasted about 9–12 h. During the gas-exchange measurement, WC was determined by removing the samples from the cuvette and weighing them. For convenience of comparison with published data about soil-crust performance, WC was expressed in mm 'precipitation equivalent' (indicated on an area basis as litre m⁻²). This unit is ecologically relevant because it relates WC to amount of precipitation taken up by the lichen. Depending on the individual sample, 1 mm of precipitation equivalent resulted in a water content of 80–85% of thallus dry mass. However, cleaning all adherent soil particles

from *C. tenax* was not possible, so thallus dry mass are estimates.

NP responses to light were determined by changing PPFD in steps from darkness to incident light intensity of $1500 \mu\text{mol m}^{-2} \text{s}^{-1}$ at given ranges of WC and at two constant temperatures of 17 and 26 °C. The data points of light response curves were fitted by the 'Smith-function' (Smith 1937; see Lange *et al.* 1991, 1997; non-linear regression). This model makes it possible to calculate apparent maximum quantum yield of CO_2 fixation (Φ , initial linear slope of light response curve), NP_{max} (the theoretical maximal rate of NP at saturating PPFD), PPFD_{sat} (the light intensity allowing 95% of NP_{max} which represents a realistic estimate for light saturation of the lichen, see Lange *et al.* 1997), and $\text{PPFD}_{\text{comp}}$ (the light compensation point of CO_2 exchange).

For determining temperature dependence of NP with poikilohydric lichens, thallus WC is a critical factor, because it is very difficult and often impossible to keep WC constant during the course of experimental temperature changes. Water loss unavoidably impacts response characteristics of the lichen. To overcome this technical problem, we performed WC response curves at different, constant temperatures and then pooled data for similar degree of hydration to determine temperature dependence of photosynthesis and respiration.

Results

RESPONSE OF NET PHOTOSYNTHESIS AND DARK RESPIRATION TO DEGREE OF HYDRATION

Dependence of photosynthetic performance on WC in four sets of experiments are displayed in Fig. 1. As

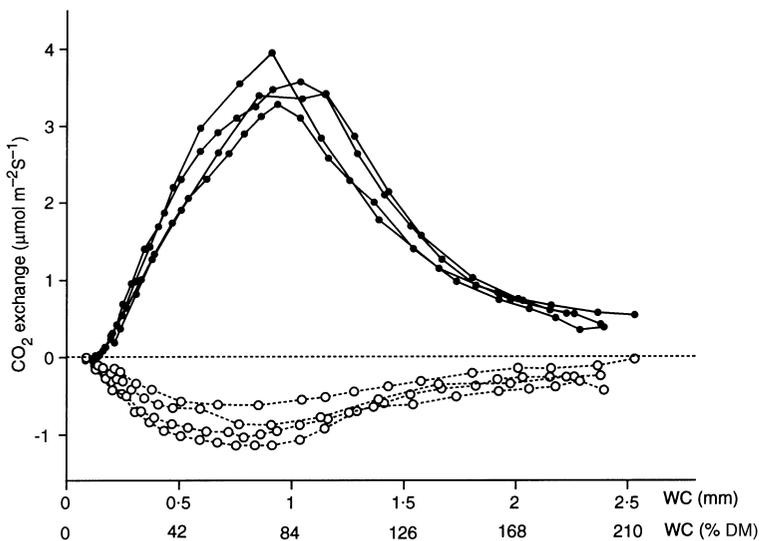


Fig. 1. Dependence of net photosynthesis (closed symbols) and dark respiration (open symbols) on thallus water content (WC, as mm precipitation equivalent and as estimated percentage of thallus dry mass) for *Collema tenax* (four sets of experiments). The highest WC indicated equals the maximal water-holding capacity of the samples; CO_2 exchange rates are related to projected thallus area. Experiments were conducted at 17 °C and $1000 \mu\text{mol m}^{-2} \text{s}^{-1}$ PPFD.

found in other species, photosynthetic activity of *C. tenax* was strongly influenced by WC of the thallus with a clear optimum for NP present in the response curve. Both desiccation and high degree of hydration negatively impacted rates of CO_2 fixation. The maximally hydrated lichen (WC of ≈ 2.5 mm precipitation equivalent, corresponding to $\approx 210\%$ of thallus dry mass) was at less than 15% of its photosynthetic maximal activity. Declining WC initially had little effect on CO_2 exchange and only after having lost about a quarter of its water-holding capacity did the lichen show a steep increase in NP. A narrow peak of CO_2 uptake occurred when the sample had lost $\approx 60\%$ of its maximal hydration. For 12 of such drying cycles (involving four different samples, each consisting of ≈ 10 lichen subsamples), average of optimal WC amounted to 1.06 ± 0.12 mm. Further dehydration resulted in a rapid fall of NP until the lower moisture compensation point was reached at 0.22 ± 0.6 mm WC ($n = 10$).

The response of DR to WC differed from performance of other lichens, especially from green-algal soil-crust species found at the same site (Lange *et al.* 1997). These green-algal species showed saturation type response. Dark respiration of *C. tenax* (Fig. 1), however, increased to optimal rates when or even before NP attained highest values and subsequently decreased to a fraction of its maximum when the thalli became suprasaturated. This may be characteristic of homoimerous gelatinous lichens in contrast to heteromerous species.

LIGHT RESPONSE OF NET PHOTOSYNTHESIS

Net photosynthesis of *C. tenax* showed saturation-type light responses. There was no indication of photoinhibition, even at the highest irradiance levels tested. However, as shown by the above results, highest rates achieved at various PPFDs depended on hydration level of the thalli. At maximal water holding capacity (WC between 2.53 and 2.32 mm) maximal NP was strongly suppressed (Fig. 2, curve number 1). Suprasaturation of the lichen thallus with water (i.e. WC higher than necessary for optimal photosynthesis rates) impacted NP at both saturating light intensities and limiting PPFD, even near the light-compensation point. Decreasing WC increased the level of NP (curves number 2, 3) and maximal rates were achieved at WC between 1.30 and 1.09 mm (curve number 4). The subsequent decrease of NP as WC declined was very obvious (see sequence of curve numbers 5–7) until the fully desiccated thalli lost total photosynthetic capacity. Similar response patterns occurred at other temperatures (not shown in detail).

Light saturation of *C. tenax* was also strongly dependent on thallus hydration (Fig. 3). At low and high WC, photosynthetic CO_2 uptake of the lichen was already light saturated at very low levels of irradiance. At a mid-range, optimal WC, the highest light

levels were necessary for maximal NP. At 26 °C, saturation was not obtained until the extreme PPF_{D_{sat}} value of more than 1600 μmol m⁻² s⁻¹. At still higher optimal temperatures around 30 °C, light saturation of the optimally hydrated lichen was not yet fully attained even around 2000 μmol m⁻² s⁻¹.

In contrast to PPF_{D_{sat}}, the light compensation point of CO₂ exchange proved to be rather insensitive

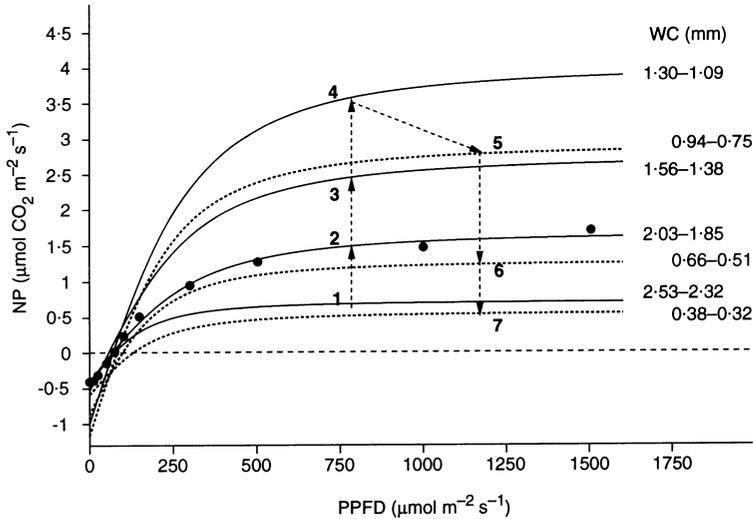


Fig. 2. Response of net photosynthesis (NP, related to thallus area) to incident photon flux density (PPFD) of *Collema tenax* at different water contents and 17 °C. Curves are fitted by the Smith-function (see Materials and methods for explanation); actual data points are given for one example only (curve 2; all the other data points fit their regression lines in a similar fashion). Generation of one response curve required 30–45 min, and some water loss of the lichen thallus could not be avoided during this period. Each of these curves is therefore representative of the hydration range within which it was generated. This range is delineated with the initial and final water content (WC, mm precipitation equivalent) during the experiment. Sequence of numbers and arrows indicate decreasing steps of WC of the thallus. Curve number 1 is characteristic of the performance of the lichen at high WC, near maximum water holding capacity. Solid curves (1–4) indicate range of increasing NP during drying, dotted curves (5–7) indicate range of decreasing NP of drying of the same sample.

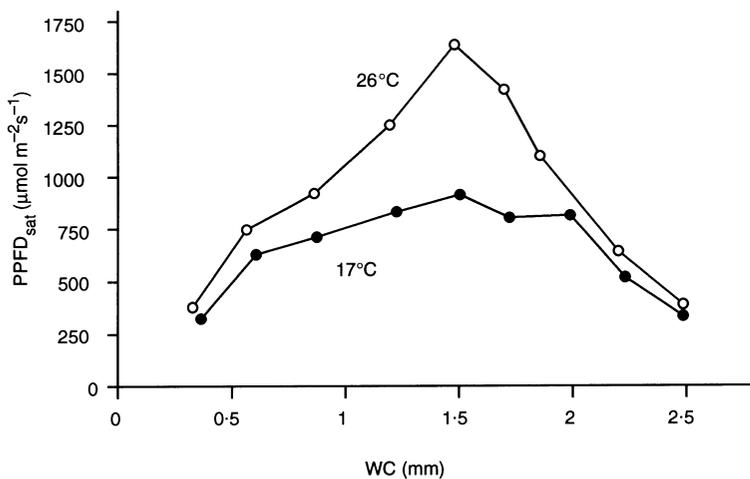


Fig. 3. Dependence of photon flux density, which allows 95% of (theoretical) maximal net photosynthesis (PPFD_{sat}, light saturation, see Materials and methods for explanation) for *Collema tenax* on thallus water content (WC, as mm precipitation equivalent) at 17 °C and 26 °C.

on degree of hydration of the lichen over a large range of WC (from 60% to maximal water holding capacity): PPF_{D_{comp}} was 70 ± 7 μmol m⁻² s⁻¹ (*n* = 7) at 17 °C and increased with temperature. At 26 °C, PPF_{D_{comp}} was 86 ± 6 μmol m⁻² s⁻¹ (*n* = 5). Only at very low WC did PPF_{D_{comp}} increase to more than 120 μmol m⁻² s⁻¹.

Hydration-dependent maximal apparent Φ as represented by the initial slope of light response curves was derived for two different temperatures (Fig. 4). In both cases, Φ initially increased with increasing WC, indicating activation of the desiccated photosynthetic apparatus. However, after high values between 1 and 1.5 mm WC, i.e. at a similar range as found for optimal rates of NP (see Fig. 1), there was a definite drop in Φ when the lichen became suprasaturated. This was a regular phenomenon also under other combinations of experimental conditions as well.

TEMPERATURE RESPONSE OF PHOTOSYNTHESIS AND RESPIRATION

Single WC response curves of the lichen samples were generated for different temperatures in darkness and at 1000 μmol m⁻² s⁻¹ PPF_D. A selection of these curves is displayed in Fig. 5 and shows the large range of potential photosynthetic productivity of this lichen from near freezing to thallus temperatures higher than 41 °C. General characteristics of dependence of CO₂ fixation on WC was not altered by ecologically relevant temperatures; peak NP was maintained at similar optimal WC. Strong depression of CO₂ fixation at suprasaturation occurred at all temperature levels studied.

Impact of temperature on NP decreased when photosynthetic CO₂ fixation was increasingly limited by either desiccation or suprasaturation. Sensitivity of NP to temperature became highest when WC was optimal. Temperature dependence of NP and DR for *C. tenax* at optimal WC is depicted in Fig. 6. There was a steep, fivefold increase of NP between 2 °C and the maximum value, which was attained at temperatures slightly above 30 °C. Substantial rates of NP are still possible at temperatures higher than 40 °C. Dark respiration of *C. tenax* proved to be relatively small: until 41 °C it did not show the excessive increase which is known from many other lichen species at temperatures higher than 30 °C.

Discussion

Average area-related maximum NP of *C. tenax* at near saturating light and in optimal hydration and temperature ranges amounted to 5.3 ± 0.9 μmol CO₂ m⁻² s⁻¹ (six sets of experiments). This corresponded to 59.0 nmol CO₂ (mg chl)⁻¹ s⁻¹ and 4.47 nmol CO₂ (g DW)⁻¹ s⁻¹. The absolute maximum was 7.0 μmol CO₂ m⁻² s⁻¹. These rates are as high or higher than the most active of the green-algal soil-crust lichens from

the same site, the Namib desert or from local steppe formations around Würzburg, as listed by Lange *et al.* (1997). Thus, *C. tenax* has the highest photosynthetic capacity of any soil lichen measured from semiarid or arid regions. The N-fixing capability of its cyanobiont might decisively contribute to this feature (see Hahn *et al.* 1996). In addition, we found that a strong carbon dioxide concentrating mechanism (CCM) is operational in *C. tenax* (see Badger *et al.* 1993; Palmqvist *et al.* 1994) which might contribute to increasing photosynthetic capacity of this species.

Photosynthetic rates of *C. tenax* are well in the upper range of or even higher than the maximal area-related leaf NP rates of the plants characterizing the phanerogamous vegetation of the collection site. According to field measurements conducted in a similar woodland community in UT, the dominant shrub *Coleogyne ramosissima* showed maximal rates of diurnal NP of 8.1–8.7 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ in May, dropping down to 1.57–5.1 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ during the summer dry period in August (S. Phillips, unpublished data). Maximal rates of net photosynthesis of *Juniperus osteosperma* attained 4–9 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ and that of the needles of *Pinus edulis* were only 1–5 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ (D. Williams, unpublished data). However, in contrast to these homoiohydric phanerogamous leaves, photosynthetic productivity of poikilohydric lichens in the field is restricted to short periods of moistening by sporadic precipitation which only temporarily interrupts the dormancy of the desiccated thalli.

In comparison with other plant types, photosynthetic carbon gain of *C. tenax* is activated by small amounts of moisture, as NP becomes positive after hydration by only 0.22 mm of precipitation equivalent. However, this moisture requirement is high in comparison to green-algal soil-crust lichens from the same site (Lange *et al.* 1997). This is in agreement

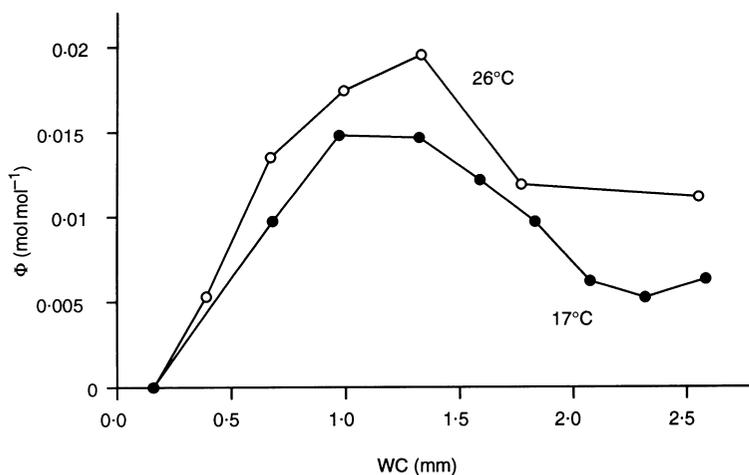


Fig. 4. Dependence of maximal apparent quantum yield of CO₂ fixation (Φ) for *Collema tenax* on thallus water content (WC, as mm precipitation equivalent). Φ was calculated from the light response curves (see Materials and methods for explanation). Experiments were conducted at 17 °C and 26 °C.

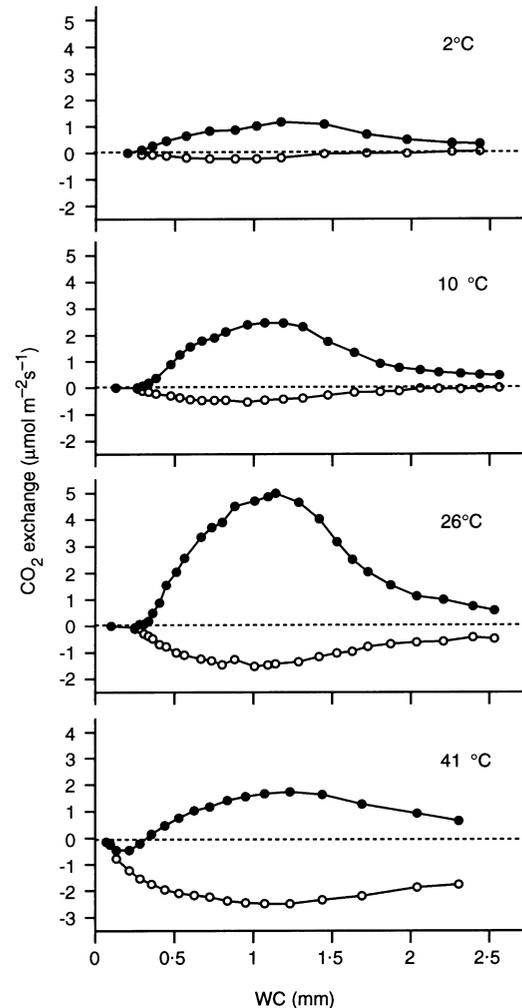


Fig. 5. Dependence of net photosynthesis (filled symbols) and dark respiration (open symbols) on thallus water content (WC, mm precipitation equivalent) for *Collema tenax* at different, indicated temperatures. The highest WC indicated equals the maximal water holding capacity of the samples; CO₂ exchange rates are related to projected thallus area. Experiments were conducted at 1000 $\mu\text{mol m}^{-2} \text{ s}^{-1}$ PPFD.

with the general fact that cyanobionts need considerably more water for onset of net photosynthesis than phycobionts (Lange *et al.* 1993; see Green, Lange & Cowan 1994), possibly owing to requirements of their CCM. With respect to field performance, this would mean that green-algal soil-crust lichens would be favoured in terms of carbon gain when moistening is very low, e.g. by dew. This disadvantage to *Collema* may be compensated by the larger water holding capacity of its gelatinous thallus, which allows prolonged phases of favourable hydration for active photosynthetic metabolism after heavier precipitation.

A high water requirement for NP was observed for both the moisture compensation point and maximal rates of photosynthesis for the cyanobionts of *C. tenax*. Optimal WC was attained at 1.06 mm of precipitation equivalent, whereas the green-algal species from the same site needed much lower degrees of hydration for maximal NP (ranging from 0.35 to

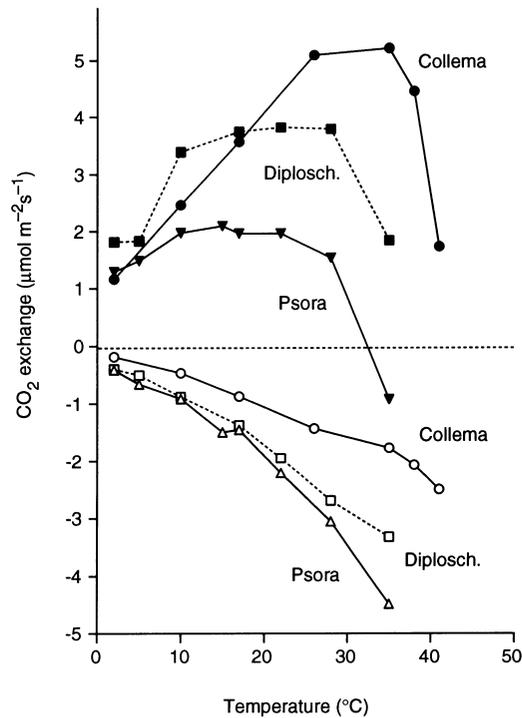


Fig. 6. Dependence of net photosynthesis (closed symbols) and dark respiration (open symbols) on temperature at optimal water content and $1000 \mu\text{mol m}^{-2} \text{s}^{-1}$ PPFD for cyanobacterial *Collema tenax*, for green-algal *Psora cerebriformis* and *Diploschistes diacapsis* (see Lange *et al.* 1997). CO_2 exchange rates are related to thallus area. Data were extracted from WC response curves at different temperatures (see Fig. 5).

0.94 mm). The lowest WC optimum of a green-algal soil-crust lichen was found for *Fulgensia fulgens*, which needed only 0.25 mm of precipitation equivalent for attaining highest rates of NP (Lange *et al.* 1995). On the other hand, maximal water holding capacity of *F. fulgens* is less than one half that of *C. tenax*.

At supraoptimal water content, *C. tenax* showed a strong reduction of NP. The species belongs to reaction type C (as defined by Lange *et al.* 1993) characterized by an extended depression in NP at high WC, with an inflection point in the response curve. The depression is substantial at all ecologically relevant temperatures (2–41 °C) and it occurs not only at saturating light intensities but also under conditions of limiting PPFD. Depression of photosynthesis at a high degree of hydration is a common phenomenon for many lichens (see Green *et al.* 1994). It was shown that the reduction in NP is caused through increased thallus resistance owing to CO_2 diffusion pathway blockage. Supporting this interpretation is the fact that maximal quantum yield of CO_2 fixation (Φ) was not affected by high WC (Lange *et al.* 1996). This indicated unchanged potential photosynthetic activity of the photobionts. However, all of the lichens studied so far have been heteromerous species. The gelatinous, homoiomerous *C. tenax* behaved differently. Φ became depressed in the

same range of WC which also depressed NP. The photosynthetic depression at high WC in this species may indicate intrinsic efficiency of the photosynthetic apparatus for CO_2 assimilation is affected by suprasaturation. This phenomenon, for which we do not yet have a definite explanation, may also be a result of nitrogen fixation of the cyanobionts of *C. tenax* or photorespiratory processes functioning as additional consumers of electrons.

Light requirement of *C. tenax* is higher than that found for the green-algal soil-crust lichens of the same habitat (Lange *et al.* 1997). When hydrated optimally, *C. tenax* showed extreme 'sun plant' characteristics. This characterization must be applied to the intact lichen, as we do not know how much light is penetrating to the active sites of the cyanobionts. Under optimal temperature conditions, the lichen does not seem to be totally light saturated even at $2000 \mu\text{mol m}^{-2} \text{s}^{-1}$ PPFD. Light requirements of NP are much lower when NP is depressed at high WC. However, even then, about $250 \mu\text{mol m}^{-2} \text{s}^{-1}$ are necessary for saturation. With values between 70 and $86 \mu\text{mol m}^{-2} \text{s}^{-1}$ PPFD, the light compensation point of *C. tenax* is rather high and agrees with 'sun plant' photosynthetic features while extreme shade lichens saturate at $30 \mu\text{mol m}^{-2} \text{s}^{-1}$ PPFD and light compensation of CO_2 exchange is at or even below $1 \mu\text{mol m}^{-2} \text{s}^{-1}$ PPFD (Green, Kilian & Lange 1991).

Photosynthesis of *C. tenax* is adapted to higher temperatures than that of the green-algal soil-crust lichens studied from the same habitat (Fig. 6). Temperature optimum of NP lies above 30 °C, substantially higher than for *Diploschistes diacapsis* and for *Psora cerebriformis*. In contrast to *C. tenax*, both of these species have a much flatter temperature response curve. This allows almost optimal rates of NP for *P. cerebriformis* down to 10 °C, whereas NP of *C. tenax* is already strongly reduced. At 41 °C, NP of *C. tenax* is still at 30% of the optimal rate. This is an exceptional performance, because lichen photosynthetic metabolism usually tends to work most efficiently at much lower temperatures (Kappen 1988; Nash 1996). The cyanobacterial nature of the photobiont might contribute to this special characteristic, as adaptation to high temperatures are known from other cyanobacterial lichens, such as the tropical *Dictyonema glabratum* (Coxson 1987; Lange, Büdel *et al.* 1994) and the epilithic *Peltula capensis*, from the Karoo area, an inland semi-desert in South Africa (Wessels & Kappen 1993).

In many deserts of the world, e.g. the Negev and the Namib, dew and fog are the main source of water for the soil-crust lichens. Green algal species, which are able to activate their photosynthetic metabolism with the smallest amounts of precipitation or even by water vapour uptake at high air humidity, are favoured under such conditions. In contrast, cyanobacterial lichens, such as *C. tenax*, need stronger hydration and rely on

liquid water (see Lange 1993). In fact, there are no or almost no cyanobacterial lichens in the otherwise rich soil-crust vegetation of the Namib fog desert (Lange *et al.* 1991). On the Colorado Plateau, dew fall and fog are rare events. Here, erratic rain showers are the main source of water. Cyanobacterial species seem to be well suited for these conditions and *C. tenax* is the most abundant species (Belnap 1993). Even if the green-algal soil-crust lichens begin photosynthetic production earlier after the onset of rain owing to their lower moisture-compensation point, the cyanobacterial *C. tenax* is able to store much more water in its gelatinous thallus. Therefore, time available for photosynthesis before desiccation will be longer compared with the other soil-crust species. Generally, this lichen is able to stay moist until occurrence of higher illumination after the rain storms (J. Belnap, personal observation). Its extreme 'sun plant' character ensures effective use of extensive sun radiation. Adaptation to high temperatures allows photosynthetic production even when high sun radiation is warming up the dark thalli, and its photobionts seem to be well protected against photoinhibition (see Leisner, Bilger & Lange 1995). Thus, *C. tenax* can make use of its enormous photosynthetic potential, which is much higher than that of its green-algal competitors.

Experiments under controlled conditions in the laboratory have described and analysed physiological performance of *C. tenax*. Combined with field experiments, these data will assist our understanding of inter-relationships between photosynthetic carbon gain, water relations and the environmental factors of light and temperature in soil lichens under natural conditions.

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