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High thallus water content severely limits photosynthetic carbon gain of central European epilithic lichens under natural conditions

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Abstract Experiments under controlled conditions have shown that net photosynthesis (NP) of many lichens is depressed when their thalli are highly hydrated. In this study we characterise the light and water content (WC) dependency of CO_2 exchange for selected epilithic lichens in the laboratory and match this against samples monitored in their natural habitat by a novel, fully automatic cuvette. Laboratory measurements showed that, at a photosynthetic photon flux density (PPFD) of 1500 μmol m^{-2} s^{-1}, NP of the epilithic foliose lichen *Xanthoria calcicola* was reduced by about 85% (compared to NP at optimal water content) when the thallus was suprasaturated (maximal hydration was defined as WC after spraying, submerging and subsequent removal of adhering water droplets by shaking). Only after loss of about 80% of its maximal WC were the highest rates of NP possible. This depression was still substantial at 50 μmol m^{-2} s^{-1} PPFD. Responses were similar for the crustose epilithic species *Lecanora muralis*. CO_2 exchange of both lichens was monitored under natural conditions by means of the cuvette built into a man-made wall – a common habitat of the species – in the Botanical Garden, Würzburg. For both species, rates of NP were low during and after heavy rain even if incident PPFD and temperature were favourable. This situation occurred frequently and could last through all daylight hours, resulting in a negative carbon balance when nocturnal rates of respiration were high. Often, after rainfall, there was a brief, high peak of NP when optimal WC was transiently attained before metabolic activity finally ceased through desiccation. Other periods with profitable rates of NP occurred after moderate moistening of the lichens by dew, fog or light rain. The lichens were found to perform identically in the field and laboratory. When the two data sets were compared it was clear that the full range of WC produced in the laboratory also occurred in nature and that the productivity of the epilithic lichens was regularly and severely limited by high WC. It is concluded that blockage of diffusive pathways for CO_2 in the thallus through high water contents is an important ecological factor for productivity of these central European epilithic lichens.

Key words Lichen · Water content · Suprasaturation · Photosynthesis · Diffusive Resistance

Introduction

Lichens, being poikilohydric, show reduced and, eventually, zero metabolic activity when the thalli dry out; photosynthetic carbon gain is restricted to periods of sufficient thallus hydration. However, in addition, high hydration can limit CO_2 uptake. More than 100 years ago (Jumelle 1892) it had already been found that a maximally soaked ("suprasaturated") lichen thallus had depressed CO_2 uptake. Since then, laboratory studies have demonstrated that many lichen species show this response, in some cases to such an extent that CO_2 release from the wet lichen can even occur in the light (for review of literature see Lange and Matthes 1981; Kershaw 1985). Following more detailed analysis it is now known that the depression of photosynthesis of the suprasaturated lichens usually is caused by increased CO_2 diffusion resistances through water blockage (Stocker 1927; Cowan et al. 1992; Green et al. 1994; Lange et al. 1996; however, see Honegger and Peter 1994).

The important question, still to be fully addressed, is how good laboratory studies are as indicators of the ecological performance of lichens. Is the depression of net photosynthesis of suprasaturated lichen thalli only a laboratory artefact after excessive experimental moistening,

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or does it also commonly occur under natural conditions? Information on this topic is rare in the literature. Kappen et al. (1996) have shown that, in the arctic winter, *Umbilicaria spodochroa* and *Lasallia pustulata* can suffer from excessive water content after snow melt. However, it seems that in general for lichens of continental Antarctica supraoptimal water contents in the field are the exception rather than the rule (Kappen and Breuer 1991; Kappen et al. 1995). In contrast, in the temperate rain forest of New Zealand, high thallus water content can severely limit photosynthetic carbon gain of foliose lichens (Lange et al. 1993).

In the present paper, we have measured the CO_2 exchange of epilithic lichens both in the laboratory under controlled conditions and also continuously with an automatic cuvette in the field. We showed that lichen performance was similar in both situations and that, under central European climatic conditions, photosynthetic CO_2 uptake of epilithic lichens can be regularly and severely depressed after heavy rainfall.

Materials and methods

Experimental lichens

Most of the experiments were conducted with *Xanthoria calcicola* Oxner [syn. *X. aureola* (Ach.) Erichs.], a foliose lichen of orange-red colour with narrow, contorted lobes loosely attached to the substrate. The centre of the thallus is densely covered in coralloid wart-like isidia with only a few apothecia present. This lichen is typically found on nutrient-rich rocks and man-made substrates in warm dry habitats in southern Germany (Wirth 1995). The experimental samples grew on a roof south of Würzburg. Complete tiles, with undisturbed thalli attached, were transported to the laboratory and then prepared for two different sets of experiments. For laboratory measurements, the thalli were carefully peeled off the stone, spread again to their natural position and fixed on a wire-mesh tray. This allowed easy weighing of the samples for exact determination of thallus water content (WC). For field measurements, small parts of the tile were cut out so that they were more than 90% covered by lichen thalli in their natural, undisturbed position. Additional field measurements were conducted with *Lecanora muralis* (Schreber) Rabenh., a crustose, greenish-grey species with small lobes at the margin. Its thallus is closely attached to the substratum and the centre is covered by numerous apothecia. This lichen is very common on man-made substrates; it is one of the more pollution-resistant species and it is even found near the centre of large towns (Seaward 1976). In the Würzburg Botanical Garden it is one of the more abundant lichens and has high cover on walls, asphalt and pavements. Experimental samples were collected from the horizontal top of a fully exposed sandstone wall in the Spessart area (west of Würzburg). Thin stone layers with thalli remaining attached to their substratum were prepared for the experiments.

CO_2 exchange measurements in the laboratory

The methods used for the CO_2 exchange measurements in the laboratory were essentially identical to those of Lange et al. (1995; and see Lange et al. 1996). They were carried out using a "minicuvette system" (Walz Company, Effeltrich, Germany) operated under fully controlled conditions of temperature, light, humidity and external CO_2, as described by Lange and Tenhunen (1984).

Prior to the actual experiment the lichen material was preincubated for several days in a growth chamber at 15°C under a 12:12 h photoperiod and a photosynthetic photon flux density (PPFD) of about 100 $\mu mol\ m^{-2}\ s^{-1}$. To simulate natural wetting and drying cycles, thalli were sprayed once a day in the morning. The samples with 8–12 cm^2 surface area of lichens (either the removed thalli of *X. calcicola* in wire-mesh baskets or stone layers with the naturally attached lichens from the field experiments) were exposed in the cuvette. Stone substrata were selected with care and thoroughly checked to ensure that there was no production or absorption of any CO_2. Net photosynthesis (NP) and dark respiration (DR) of the samples were related to thallus surface area. For *X. calcicola*, total chlorophyll content (*a+b*, determined according to Ronen and Galun 1984) averaged 1.92 mg per g thallus dry weight or 315 mg per m^2 thallus area. Water content of the detached samples of *X. calcicola* was calculated as the difference between the weight of tray plus lichens (measured on an electronic digital balance during the experiments) and the dry weight determined after drying to a constant weight at 70°C at the conclusion of the experiment. As usual, sample WC was then expressed as percent of thallus dry weight. This was clearly not possible for epilithic lichens which were intimately attached to their substrata. However, for theses samples a relative measure of sample WC, mm "precipitation equivalent" (volume water per projected lichen area) proved satisfactory. This was determined as difference in weight of the total sample (stone substratum together with attached lichen) when hydrated and dry (four days exposure to silica gel). This measure had already proved reasonable for soil crust lichens which cannot be removed from their substrata (see Lange et al. 1994). Comparison of WC between lichens on different substrata can, however, only be done with caution due to differences in the water holding capacity of the materials. For *X. calcicola*, which can easily be detached from its substratum, stone sample WC of 1 mm, precipitation equivalent, was about 600% in relation to thallus dry weight.

Two different types of gas exchange experiments were conducted in order to establish the role of thallus water content in determining the CO_2 exchange of *X. calcicola*.

First, NP responses to light were determined at different levels of hydration at 17° temperature and 350 ppm external CO_2 by stepwise changing incident PPFD from darkness to 1500 $\mu mol\ m^{-2}\ s^{-1}$, which was normally above saturation level. 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, not representative for one, exact WC but rather for a certain hydration range within which it was generated. This range (initial and final WC) is delineated for each measurement run which was always conducted from low to high PPFD.

Second, the dependence of NP and DR on exact levels of WC of the lichen samples was determined at a constant PPFD of 1000 $\mu mol\ m^{-2}\ s^{-1}$, an ambient CO_2 partial pressure of 350 ppm and 17°C. The samples were hydrated by first spraying and subsequently submerging them in water for several min, followed by shaking to remove adhering water droplets, this status was defined as maximum thallus water content. The suprasaturated samples with maximal water content were then enclosed in the cuvette, and their gas exchange was recorded during light/dark changes as they slowly dried in a stepwise decreased ambient air humidity. The water content of the samples was determined by temporary removal from the cuvette and weighing during the measurement of CO_2 exchange. One drying cycle could last longer than 8 h.

In addition, the dependencies of NP on WC at different light levels between 12 and 1500 $\mu mol\ m^{-2}\ s^{-1}$ PPFD were derived from the light response curves. For this, WC had to be interpolated between the initial and final value for each light step of one response curve. This procedure explains the slightly increased scatter of data points in the resulting WC response curves.

A series of additional experiments was carried out to test whether WC of sufficient levels to actually depress NP occurred under natural conditions in the field. Intact stone samples with lichens were exposed at the field measuring site close to the automatic cuvette on the top of the wall. The samples were moistened by rain exactly like the samples in the cuvette and like other epilithic lichens which have grown for decades on nearby walls of the

Botanical Garden. After heavy rain, a wet sample was removed and, within 3 min, brought into the laboratory and transferred to the mini cuvette. It was subsequently kept at constant illumination of 1000 μmol m^{-2} s^{-1} PPFD at similar air temperature as in the field and at a relative humidity which was slowly decreased in steps. Photosynthetic CO_2 uptake of the sample was then recorded automatically every 2 min as it dried out over several hours.

CO_2 exchange measurements in the field

In addition to the laboratory experiments, CO_2 exchange of lichen samples was recorded in the field using a new automatic cuvette system (Walz Company, Effeltrich, Germany) developed from the earlier idea of a "Klapp-Küvette" (Lange 1962). This instrument, which will be described in more technical detail elsewhere, is a fixed form of the hand-operated CO_2 porometer which we designed for field measurements with lichens (Lange et al. 1984; see Schulze et al. 1982). Flat stone samples with 8–16 cm^2 surface area of lichens were positioned on a basal part of the cuvette where they were naturally exposed (with *c.* 5° inclination to the south) to the environment when the cuvette was open. At regular intervals an upper lid automatically enclosed the lichen in a plexiglas cuvette of *c.* 190 cm^3 volume which was stirred by a transparent vibrator. Outside air was pumped through the cuvette and the CO_2 exchange of the sample was measured by a differential infrared gas analyser. In addition, PPFD, air temperature, air humidity and lichen thallus temperature (non-contact, infrared thermometer) were recorded. It was not possible to determine water content of the lichens during the automatic CO_2 exchange monitoring in the field because the lichen was never disturbed. Measurements were made on a 30-min cycle that involved the cuvette being closed for 3 min 20 s and open for the remaining 26 min 40 s. This frequency seemed to be a reasonable compromise between the opposing needs to generate sufficient data points to reveal activity patterns and to minimise the disturbance to the lichen sample from too frequent closure of the cuvette. The cuvette was built into a 40 cm high brick wall, covered by sand stone slabs, so that the lichen samples were at the same level as the wall top and experienced the same microclimatic environment and moistening by dew, fog, rain as if they were growing naturally on the stones of the wall. The wall was located at an open site in the Botanical Garden, Würzburg, surrounded by other stone walls, rocks and pavement covered with other epilithic lichens including *L. muralis.*

Results

Net photosynthesis and dark respiration as influenced by thallus water content

As known from many other species, CO_2 exchange of *X. calcicola* was strongly influenced by the water content of its thallus with a clear optimum for NP present in the response curve (Fig. 1). At maximal water content of *c.* 1.4 mm, NP was strongly depressed to only a fraction of its maximum. As water content declined from the maximal value there was initially little effect on CO_2 exchange; only when more than half the water had been lost did NP increase steeply. A very narrow peak of CO_2 uptake occurred when the sample had lost more than 80% of its water (at 0.25 mm WC), and further dehydration resulted in a rapid fall in NP until the moisture compensation point was reached at about 0.06 mm WC. The response of DR to WC showed an almost perfect saturation response, with CO_2 release highest at WC which were also optimal or above optimal for NP.

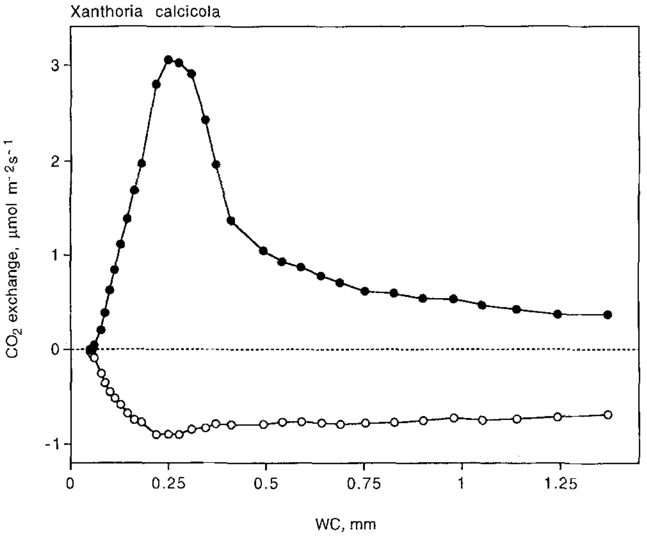

Fig. 1 The dependence of area-related net photosynthesis (*closed symbols*) and dark respiration (*open symbols*) on thallus water content (WC, mm precipitation equivalent) for *Xanthoria calcicola.* The highest WC for which measurements are shown was equal to maximal water holding capacity of the samples; CO_2 exchange rates are related to thallus area; 17°C, 1000 μmol m^{-2} s^{-1} photosynthetic photon flux density (PPFD)

Net photosynthesis showed a characteristic saturation type light-response at all WC (Fig. 2). However, the maximal value for light saturated NP depended on the hydration of the thallus. At maximal water holding capacity, WC between 1.45 and 1.23 mm, NP was low at all light intensities (Fig. 2, upper panel, lowest curve). As WC decreased, light-saturated NP increased and high rates of NP were achieved at WC between 0.36 and 0.27 mm (see sequence of response curves following the arrow, upper panel). The subsequent decrease in maximal NP as WC declined further to values lower than 0.32–0.25 mm was very obvious (see sequence of curves, Fig. 2, lower panel) until photosynthetic activity was totally lost at the lowest WC between 0.10 and 0.04 mm. The initial slopes of all of the light-response curves (maximal quantum yield for CO_2 fixation) were identical for all WC equal or greater than that optimal for NP. A decline in initial PPFD response slope only occurred at WC below that optimal for NP (data not presented in detail). *X. calcicola* behaved in a manner similar to published results for other lichens where the fact that the maximal quantum yield of CO_2 fixation was not affected by even the highest thallus water content contributed to the conclusion that depression of NP of suprasaturated lichen thalli could not have been caused by any loss of photochemical potential of the photosynthetic apparatus but, rather, by reduced CO_2 supply for the photobionts due to increased diffusion resistances (see Lange et al. 1996).

The dependence of NP on WC as extracted from the light response curves is portrayed in Fig. 3 for light intensities between 100 and 1500 μmol m^{-2} s^{-1} PPFD. The limitation by the increased diffusion resistances at high

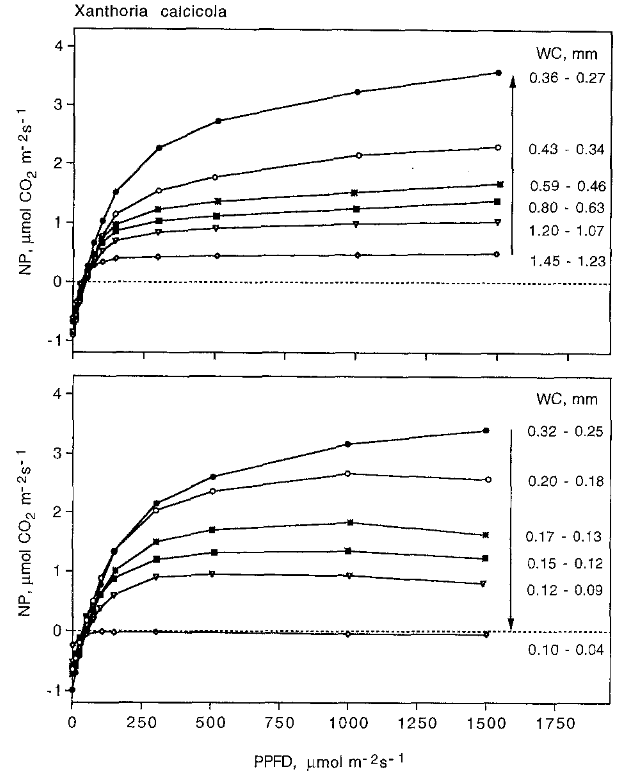

Fig. 2 The response of net photosynthesis (NP, related to thallus area) to incident PPFD of *X. calcicola* at different water content and at 17°C. Each response curve is annotated with the initial and final water content during its experimental generation. The *arrows* indicate decreasing values for WC concurrent with increasing, above optimal (*upper panel*) and decreasing, below optimal (*lower panel*) rates of NP

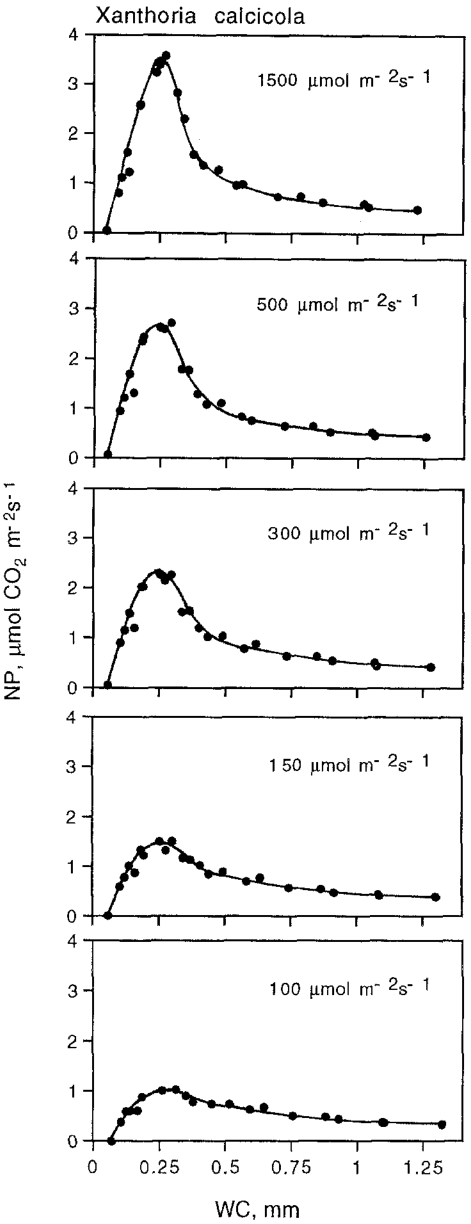

Fig. 3 The dependence of area-related net photosynthesis (NP) on thallus water content for *X. calcicola* at different, indicated light intensities (µmol m^{-2} s^{-1} PPFD). The highest WC at which measurements were made was near the maximal water holding capacity of the samples. The data were extracted from light response curves (see Fig. 2); 17°C. The lines were fitted to the data points by eye

WC was so strong that net photosynthetic rates were virtually unaffected by changes in PPFD. Because NP at optimal WC responded to changes in PPFD, when degree of NP depression at suprasaturation was expressed as a percentage of NP at optimal WC, there was a substantial change in the relative impact of high water content on actual NP (Table 1). This relative depression was 85% at light saturation of 1500 µmol m^{-2} s^{-1} PPFD. However, even at 50 µmol m^{-2} s^{-1} PPFD when NP at optimal WC was reduced to less than one tenth due to low light, there was still a further reduction of 55% at high WC. This demonstrates the ecologically important fact that suprasaturation of the thalli affects photosynthetic carbon gain of these lichens at all PPFD above compensation. CO_2 exchange was not affected by high degrees of hydration below the light compensation point at 25 and 12 µmol m^{-2} s^{-1} PPFD when photosynthetic activity only resulted in a reduction of CO_2 release (Table 1).

Net photosynthesis and dark respiration at high water content in the field

Observations revealed that precipitation could hydrate epilithic lichens to their water saturation capacity. After a rain storm water often covered the horizontal or slightly inclined surfaces of stones and the epilithic lichens on them with a thin film of water, totally imbibing the thalli. This suprasaturation strongly affected CO_2 uptake by the lichens. Figure 4 shows microclimate conditions and CO_2 exchange of *X. calcicola* under natural conditions in the field on a typical day in spring. The night was cool so that the temperature of the dry lichen thallus fell almost to the freezing point. In the early morning, before dawn, there was a very heavy dew fall which, in combination with dampening fog and some rain, completely moistened the experimental lichens. After sunrise, NP of

Table 1. Depression of net photosynthesis through suprasaturation of the thalli for *Xanthoria calcicola* at different light intensities. Depression is expressed as the percentage of maximum of net photosynthesis (NP) at optimal water content (average of the two highest data points recorded) at each photosynthetic photon flux density (PPFD) level. Data extracted from light response curves of the type of Fig. 2 (see Fig. 3); NP at suprasaturation was calculated as the average of all data points with water content (WC) > 1 mm

PPFD (μmol m^{-2} s^{-1})	Maximum net photosynthesis (μmol m^{-2} s^{-1})	Depression of NP at suprasaturation (% of maximum of NP)
12	(–0.49)	no depression
25	(–0.20)	no depression
50	0.33	55
75	0.66	56
100	1.02	65
150	1.51	72
300	2.27	80
500	2.68	82
1000	3.20	84
1500	3.49	85

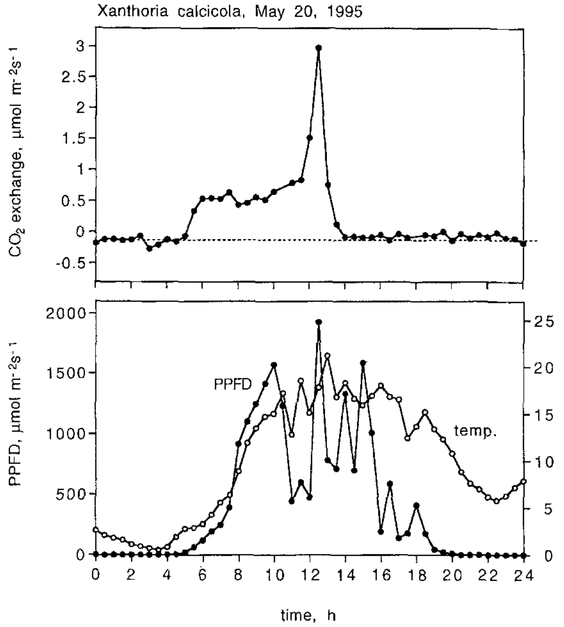

Fig. 4 Diel courses of CO_2 exchange (*upper panel*, CO_2 uptake positive, CO_2 release negative) and (*lower panel*) corresponding PPFD and lichen thallus temperature for *X. calcicola*, 20 May 1995. Measurements were made with an automatic cuvette under natural conditions in the field, Botanical Garden, Würzburg

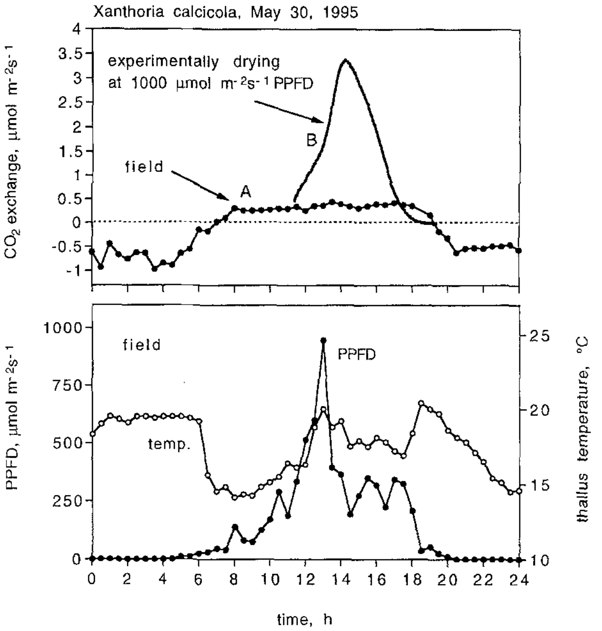

Fig. 5 Diel courses of CO_2 exchange, temperature and PPFD, as Fig. 4, 30 May 1995. Curve of sample A (*line with solid circles*) shows lichen response under natural field conditions, sample B (*line without circles*) was transferred to the laboratory for experimental drying and measurements made every 2 min

the suprasaturated lichen rose with increasing illumination but only until 0600 hours when it had reached a rate of around 0.5 μmol CO_2 m^{-2} s^{-1} at about 120 μmol m^{-2} s^{-1} PPFD. Over the next 4 h, NP remained almost completely insensitive to incident PPFD; the lichen was light-saturated. Even when PPFD reached more than 1500 μmol m^{-2} s^{-1} at 1100 hours, NP of the suprasaturated lichen remained at the initial low level. The thallus, meanwhile, was drying and, at noon, when light intensity was less than 500 μmol m^{-2} s^{-1} PPFD, NP suddenly increased. At that point the WC had obviously reached the optimal value for NP so that peak photosynthesis became possible. A very similar response occurred when suprasaturated thalli were allowed to dry out in the laboratory experiments. Maximal NP, at 1230 hours, was almost identical to maximal NP for this species under controlled conditions (see Fig. 1). As the day went on, at high PPFD, water loss from the thallus continued and, 90 min later, the then completely desiccated thallus had lost all metabolic activity. Reactivation took place the next morning after hydration of the thallus by dew.

A convincing proof that the observed low NP after rain was really due to suprasaturation of the lichen thallus is presented in Fig. 5. 30 May was a day during a period with heavy rain storms. The lichen was water-saturated during the night with substantial rates of dark respiration at relatively high temperatures. At 0600 hours, another heavy rainstorm started with an accompanying drop in temperature and, subsequently, the sky was cloudy with showers of rain interspersed with brighter periods. The suprasaturated lichen (sample A) showed a constant low rate of NP around 0.3 and 0.4 μmol CO_2 m^{-2} s^{-1} during all daylight hours. NP did not respond at all to changes in incident PPFD; even a short period of illumination of almost 1000 μmol m^{-2} s^{-1} had no effect on CO_2 exchange. The combination of such low rates of NP with heavy CO_2 losses during the night meant that the daily carbon balance of the lichen was negative even though it was being continuously hydrated for 24 h. A second stone sample with *X. calcicola* (sample B, see Fig. 5, upper panel) was exposed beside the cuvette lichen (A) and received identical weather conditions.

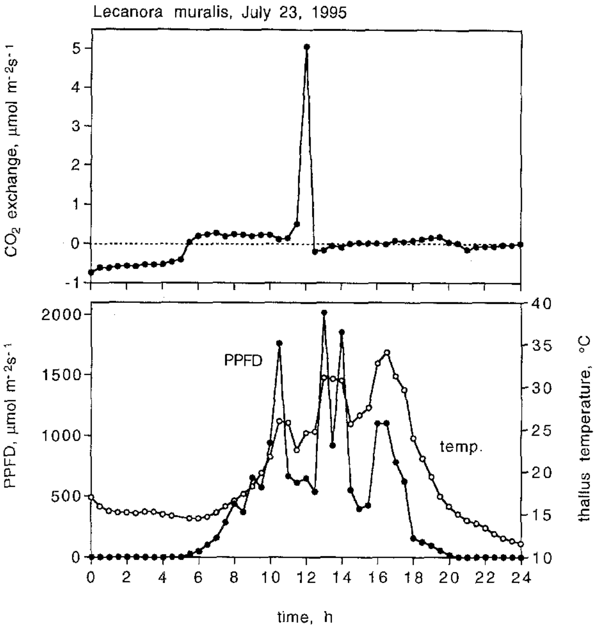

Fig. 6 Diel courses of CO_2 exchange and PPFD, as Fig. 4, for *Lecanora muralis*, 23 July 1995

Sample B was carefully removed at 1120 (WC at that time *c.* 0.9 mm), and its CO_2 exchange was monitored under controlled laboratory conditions at 1000 μmol m^{-2} s^{-1} PPFD whilst it was allowed to dry in the mini-cuvette. Net photosynthesis of this lichen, which was initially identical to the cuvette specimen increased markedly after a period of drying and, after 3 h, reached more than 3 μmol CO_2 m^{-2} s^{-1} before declining to zero through desiccation. Cuvette sample A attained a similar maximal NP a few days later in nature when it dried to optimal water conditions. These results confirm that suprasaturating WC had depressed NP of *X. calcicola* under natural field conditions. The conditions producing suprasaturation, i.e. heavy rain or some equivalent combination of precipitation, occurred on many days during this monitoring period.

The CO_2 exchange of *L. muralis*, the second experimental species, performed similarly to *X. calcicola* with respect to WC. However, the depression of NP through suprasaturation of the thallus proved to be even stronger both during the experimental resaturation and dehydration cycles in the laboratory and during CO_2 exchange measurements in the field. Figure 6 shows a typical diel response pattern for the CO_2 exchange of this lichen in its natural environment. There was a rainstorm during the night of 22/23 July that saturated the lichen which became covered by a thin film of rain water and responded with large respiratory CO_2 release. The weather during the next day, 23 July, was dry and changing cloud cover produced periods of bright sunshine (Fig. 6, lower panel). Light compensation point of the lichen (upper panel) was exceeded at 0530 hours and the wet, suprasaturated lichen then had a low and constant rate of NP for about 5 h. During this time, PPFD increased to 1760 μmol m^{-2} s^{-1} without any impact on NP, which was already light-saturated at about 100–150 μmol m^{-2} s^{-1} PPFD. Just before noon the thallus had dried to such an extend that a very short but extremely high peak of photosynthetic CO_2 uptake at a light intensity of 540 μmol m^{-2} s^{-1} PPFD occurred. There was then a steep fall in NP and a short phase of CO_2 release before CO_2 exchange finally ended. Several hours of inactivity then followed before very low rates of NP occurred again, probably following by water vapour uptake by the thallus due to a large increase in air humidity before sunset.

Discussion

It is now well known that many lichen species have an obvious optimal WC for maximal NP and show substantially depressed NP at higher thallus water contents. What is less well known is just how important this depression at high WC is in nature. In studies of lichen CO_2 exchange under natural conditions the real impact of high levels of hydration might often have been obscured because periods of rain also tended to be times of low light intensities, which would mask the additional effects of suprasaturation (see Wessels and Kappen 1994). With the exception of a small number of field studies (Lange et al. 1993; Kappen et al. 1995, 1996), the vast majority of the response curves have been generated in the laboratory and there has always been the nagging suspicion that unrealistic water regimes could have been imposed. In this study we set out to fully characterise the CO_2 exchange of selected epilithic lichens in the laboratory and then to match this performance against samples that were being monitored in their natural habitat by means of an automatic cuvette. When the two data sets were compared it was clear that the full range of WC produced in the laboratory also occurred in nature and that the productivity of the epilithic lichens was regularly and severely limited by high WC.

The laboratory experiments showed that, for *X. calcicola*, relative depression of NP through suprasaturation was more than 80% (compared with maximal NP at optimal WC) at PPFD levels above 300 μmol m^{-2} s^{-1} (Table 1). The relative impact of high diffusion resistances at high water content became smaller at lower PPFD but was always substantial above the light compensation point of CO_2 exchange still being 55% at 50 μmol m^{-2} s^{-1} PPFD. The overall effect was to make NP almost independent of incident PPFD at WC greater than the equivalent of 0.5 mm precipitation. The same depression was also clearly identifiable in the automatic field monitoring results. After substantial precipitation the NP failed to track incident PPFD and was almost constant (Figs. 4–6). After a period of drying the lichens showed a brief phase of high NP before finally ceasing metabolic activity when completely desiccated. This period of elevated NP was consistent with the thallus drying through the optimal WC range. The NP burst could be readily and consistently duplicated on samples that had been hydrated by precipitation in the field but were allowed to dry under controlled laboratory conditions. The net photosynthetic rates in both the depressed high WC state and at optimal WC were almost identical for the laboratory and field studies (compare Figs. 1 and 3 with Figs. 4 and 5). There seems to be little doubt that the lichen behaved almost identically in the laboratory and field studies. Also, even though the WC could not be monitored, it was clear that periods of high WC were both common and sustained in the field and when thalli were visibly saturated they always showed concurrent depressed NP.

Suprasaturation is clearly not just a laboratory artefact but a real ecological phenomenon for these epilithic lichens. Its occurrence means that there is a steady and high loss of potential photosynthetic yield to the lichens in the field when their thallus water content is high in the light. Such situations occurred on a regular basis for both species during rain and subsequent periods of drying. They were especially obvious following rainfall in the night when, after sun rise, the first hours of illumination could not be used for efficient photosynthesis until sufficient water had been lost (Fig. 6). From a maximally hydrated state over half of the thallus water needs to be lost before the optimal WC zone is reached which spans only about 20% of the total WC range. Over half of the thallus WC is equivalent to about 0.8 mm precipitation and, when it is considered that on normal summer days the total potential evaporation is only a few millimeters equivalent, it can be predicted that long periods of suprasaturation and depressed NP must be inevitable. In contrast, moderate moistening of the thalli by dew, mist and light rain showers result in water contents of the lichens which were small enough to allow substantial rates of NP. It was particularly striking, when the lichen had been optimally wetted and had high NP, that the occurrence of another rain storm led to a dramatic and substantial fall in NP because of the increased WC even though PPFD had not changed. Maximal rates of NP were only a temporary process for these lichens in the field. The lichens spent long periods with depressed NP in the presence of excessive light and, since no negative effects from photodamage were noted, it seems that the thalli possess effective photoprotective systems that have yet to be described.

Leaves of cormophytic higher plants contain diffusion pathways for CO_2 with low gas phase resistances through the unwettable stomatal pore and the airfilled intercellular system of the mesophyll right to the sites of photosynthetic carboxylation. Thallophytic lichens lack such features. Water saturation results in blockage of diffusion pathways and increased diffusive resistances then can cause strong depression of net photosynthetic CO_2 fixation. Temperate rain forest lichens from New Zealand also showed supraoptimal hydration and could be divided into four response types based on the presence, and degree, of depression of net photosynthesis at maximal water contents (Lange et al. 1993). The same groupings could be recognised for European soil crust lichens (Lange et al. 1995). Both of the experimental species, *X. calcicola* and *L. muralis*, belong to response type D, the grouping which shows a large depression in NP at WC above a small range of optimal WC. The response curve of this type has an inflection point so that NP becomes low but almost constant, and never negative, at high WC. As a result, under conditions of suprasaturation the lichens exhibited only low rates of NP, even under high incident PPFD, and their thalli must lose large amounts of water before optimal rates of CO_2 fixation could be attained. However, it is important to note that, although there is a large loss of potential CO_2 fixation, the plant is always gaining carbon when hydrated in the light. As noted for the rain forest lichens (Lange et al. 1993), a little CO_2 fixation over a long period seems to be an effective strategy for lichens, albeit probably an imposed strategy for epilithic lichens where water films form on slow draining surfaces. Epilithic lichens with negative CO_2 fixation at high WC seem unlikely to exist because of the continued carbon losses or they could be confined to habitats where runoff is rapid. Explanations for the differences in lichen responses at high water content are not yet available. The interactions between thallus structure, morphological and chemical features of the diffusive pathways, water content, and CO_2 exchange of the photobionts has become an important field for future functional-anatomical studies.

We are not yet able, in detail, to determine the effect of the various weather situations on total primary production of the lichens. However, we aim to monitor CO_2 exchange of *L. muralis* for an entire annual course. This will then allow quantification of the detrimental effect of thallus suprasaturation on carbon balance. However, the present study leaves no doubt that high thallus water contents are ecologically important for productivity of the epilithic lichens and severely limit their photosynthetic CO_2 fixation.

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