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Photosynthetic productivity of the epilithic lichen
Lecanora muralis : Long-term field monitoring of CO_2 exchange
and its physiological interpretation

I. Dependence of photosynthesis on water content, light, temperature, and CO_2 concentration from laboratory measurements

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Summary

CO_2 exchange of the epilithic, green algal lichen *Lecanora muralis* was monitored continuously for 15 months by means of an automatic cuvette in its natural habitat in the Botanical Garden, Würzburg (Bavaria, Germany). As a first stage in the interpretation of the results, identically treated parallel samples were used, under controlled laboratory conditions, to determine the dependence of net photosynthesis (NP) and dark respiration (DR) on light, CO_2 concentration, thallus hydration and temperature. Results of these measurements are communicated in the present, first part of a series of publications.

The lichen showed an extremely large and extended suprasaturation depression of its CO_2 assimilation. NP at high hydration was reduced almost to the compensation point. Maximal NP was only possible in a very small window of thallus water content (WC). Thallus water relations dominated the lichen's responses to the other environmental factors and the combination of 'optimal' moisture and light conditions was a rare event and lasted only for short times under natural conditions.

Light response curves showed typical saturation kinetics with 'sun-plant' characteristics. Maximal NP, light saturation, maximal quantum use efficiency, and light compensation point were highly dependent on WC. Temperature optimum of NP was about 22 °C. But, at 2 °C, NP was still 60% of maximal NP. Under optimal WC, NP became saturated at c 1 000 ppm external CO_2 and, at natural, ambient CO_2, NP was 62% of maximal NP with a CO_2 compensation point of 16 ppm. Suprasaturation depression of NP was not completely removed by 5 000 ppm external CO_2. Seasonal changes in photosynthetic capacity and other photosynthetic parameters were extremely small. However, dark respiratory capacity showed a clear adaptation to low winter temperatures. This resulted in a higher light compensation point for CO_2 exchange in winter than in summer.

The daily and seasonal courses of CO_2 exchange of *L. muralis* under natural conditions will be reported in further communications. The field performance of the lichen will be interpreted and analysed by means of the data presented here.

Key words : Lichen, photosynthesis, water content, light, temperature, *Lecanora muralis*

Introduction

Our knowledge about the photosynthetic performance of lichens has greatly improved during the last decades. Factorial analyses of lichen CO_2 exchange and chlorophyll fluorescence under controlled conditions have revealed the physiological peculiarities of these poikilo-hydrous organisms and, in numerous field studies, lichen performance under natural conditions has been measured in many different climates. It has been shown that laboratory studies are, in general, able to analyse, to interpret and to predict extremely well the behaviour of lichens in their natural habitat (Lange et al. 2001). This prior work has resulted in a wealth of important infor-

mation which, however, is usually restricted to specific situations and to relatively short episodes in the long life of a lichen.

In contrast, long-term studies of lichen photosynthetic production in nature are relatively rare. This is certainly due, primarily, to the technical difficulties which are involved in making field measurements that must be continuous for long periods of time. On the other hand, such studies are necessary in order to analyse the annual photosynthetic primary production of lichens. Several attempts have been made to estimate long-term productivity by extrapolation from spot measurements of lichen CO_2 exchange (e.g., LANGE et al. 1994; see review by KAPPEN 1988) which were often repeated at the same site under specific climatic situations and during different seasons of the year (e.g., LANGE et al. 1998; LANGE 2000). Modelling of lichen metabolism from its dependency on the environmental variables supported such projections (e.g., KAPPEN et al. 1979; SUNDBERG et al. 1997b). Although this work has been extremely useful to generate apparently reasonable estimates of annual carbon gain, inherent uncertainties continue to exist. These not only concern the precise numbers for primary production *per se* but also the problem of quantifying the occurrence of specific functional features in terms of their ecological relevance for lichen productivity. For instance, questions such as: how long is a lichen metabolically active and how long is it inactivated through desiccation? What is the impact of thallus suprasaturation with water on lichen photosynthetic carbon gain? Which is the main growing season (in terms of carbon gain) for a lichen? In recent times, chlorophyll fluorescence measurement has opened the door for automatic long-term monitoring of photosystem II activity and this method has been very successfully applied to some of these problems, e.g. for many years under antarctic conditions (SCHROETER et al. 2000; INSAROV & SCHROETER 2001), for epiphytes (RENHORN et al. 1997; GREEN et al. 2001), and for temperate soil lichens (LEISNER et al. 1996). However, how to translate fluorescence data into carbon assimilation is a continuing problem which often is both critical and, sometimes, almost impossible for lichens (LEISNER et al. 1997; SUNDBERG et al. 1997a; GREEN et al. 1998; LANGE et al. 1999b).

We have tried to avoid the difficulties of extrapolation and of interpretation by the continuous and direct measurement of CO_2 exchange in the field at least for one lichen species (one individual sample of *Lecanora muralis*) for a period of 15 months (462 diel time courses). Measurement took place with an especially constructed 'klapp cuvette' (LANGE et al. 1997b), which delivered one measurement of CO_2 exchange and environmental factors every 30 minutes. More than 22,000 data sets (each with at least 12 parameters for CO_2

exchange and microclimate measurement, in addition chlorophyll fluorescence data) are available for evaluation.

We will be reporting the results of this study in a series of articles. This first communication describes laboratory experiments under controlled conditions to determine the dependence of photosynthesis and respiration of *L. muralis* on thallus water content, light, temperature, and ambient CO_2 partial pressure. These data are necessary for understanding and physiological interpretation of the field measurements of the lichen. A selection from an extensive body of results is presented which will serve as a basis for parameter estimation in subsequent modelling efforts. In subsequent communications, daily and seasonal patterns of net photosynthesis and respiration of *L. muralis* will be described, seasonal and annual carbon balance will be discussed, chlorophyll fluorescence will be compared with concomitant CO_2 exchange, and the natural CO_2 environment of the lichen in the field will be analysed. In a concluding publication, a mathematical model is planned for photosynthetic production of *L. muralis* as dependent on environmental conditions. It is hoped that this extensive case study for one lichen species in one habitat can serve as a general model for lichen photosynthesis ecophysiology.

Material and methods

The experimental lichen

Lecanora muralis (SCHREBER) RABENH. [syn. *L. saxicola* (POLLICH) ACH., *Placodium s.* (POLLICH) KÖRBER, *Protoparmeliopsis muralis* (SCHREBER) M. CHOISY] is a green algal, placodioid lichen which forms circular patches or rosettes closely attached to its substrate at the centre, the thallus becoming lobate at its outer margin. As discussed in detail by SEAWARD (1976), this taxonomically polymorphic taxon is geographically ubiquitous and it is found throughout the temperate latitudes of the northern hemisphere. The species is chiefly saxicolous on calcareous and non-calcareous, then nutrient-enriched, rocks but occasionally corticolous, lignicolous, or muscicolous. The lichen is also reported as a member of biological soil crust communities in North America (ROSENTRETER & BELNAP 2001). In central Europe, *L. muralis* belongs to the group of very common lichens on man-made substrates, such as concrete, asbestos-cement, asphalt, and tiles, and on different types of prepared natural stone surfaces, such as rock walls, kerbs, and monuments. It is one of the more pollution-resistant species and often occurs in the midst of large cities (see SEAWARD 1982).

The experimental samples (*L. muralis* s. str.: 'var. *muralis*', see POELT 1969) fitted the description given by SEAWARD (1976) and were collected from a wall in the Spessart region (Frammersbach, 48 km northwest of Würzburg). The lichen was growing on thin sandstone slices which were cut to fit the
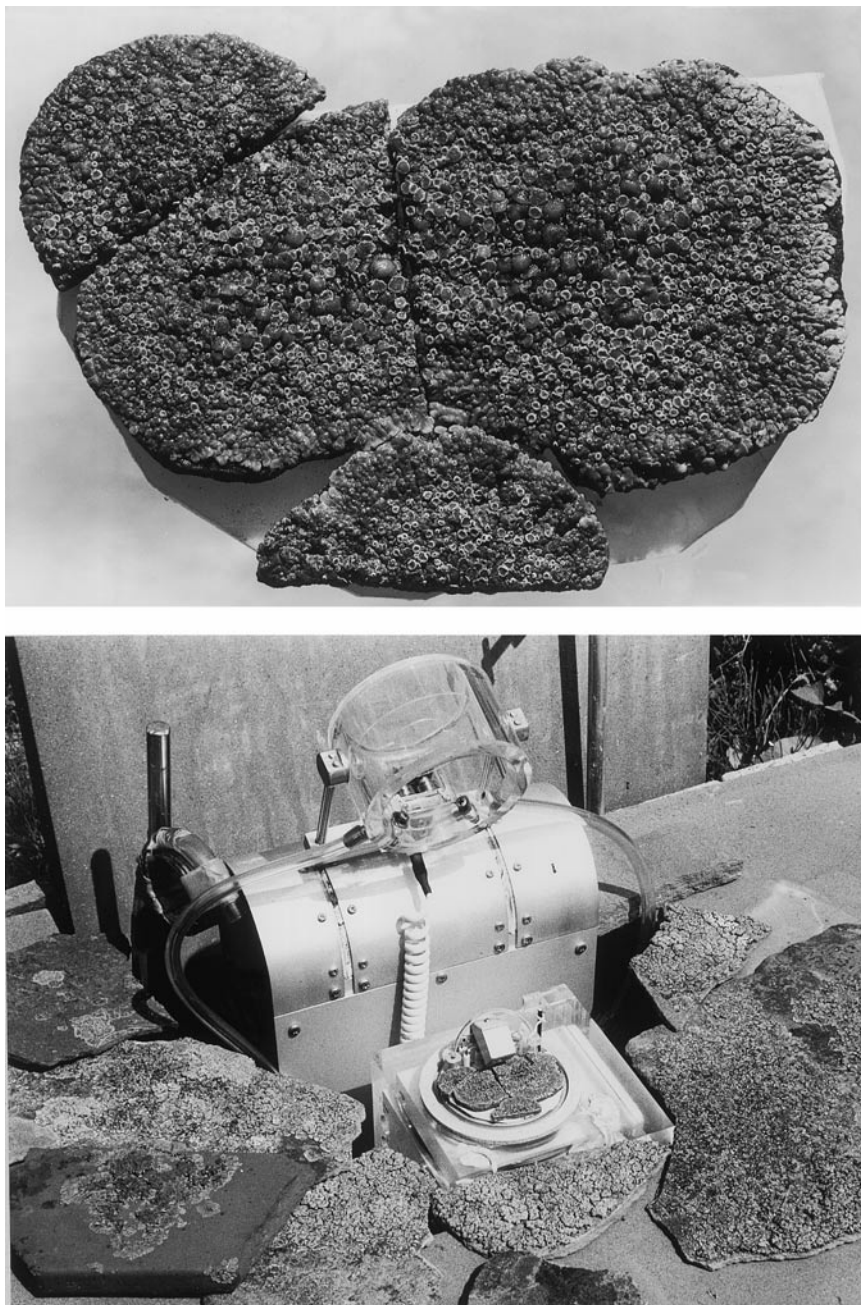
Fig. 1. Top: The sample of *Lecanora muralis* (A) used for the field measurements after ending the long-term monitoring (largest diameter c 6.5 cm). Bottom: Cuvette during field work, built into a brick wall; the lid is in the process of descending. The lichen in the cuvette is surrounded by stone slabs covered by the same species on the top of the wall.

measuring cuvette. The material was transferred to the Botanical Garden, Würzburg and exposed for about six months before the experiments so that it could become adapted to the local conditions.

The study presented is based upon two, almost identical samples of the experimental lichen each totalling about 16 cm² projected thallus area. Both samples were composed of several sectors of circular thalli with a vegetative outer rim and crowded apothecia in the centre (for photosynthetic performance of lecanorine ascomata see DEL-PRADO et al. 2001). Figure 1

(top) shows one of the samples (A, see below) at the end of the measuring period.

Initial CO_2 exchange measurements under controlled conditions had shown the photosynthetic capacity of the two samples to be almost identical. Both samples were exposed for the complete study period, i.e. for about 15 months from June 23, 1995 to September 29, 1996, side by side on the top of a wall (see below). Sample A was included in a 'klapp cuvette' and its performance was followed under natural conditions without removal for the total time. Sample B was removed from

time to time and brought to the laboratory for CO_2 exchange measurements under controlled conditions. Its responses were studied in order to enable physiological interpretation of the lichen A's performance under field conditions. These measurements had to be repeated at different times throughout the year in order to evaluate possible seasonal changes. After each laboratory experiment, during which the sample was handled with greatest care, the lichen was replaced in its field site so that it continued to experience the normal, natural environment. Before and immediately after the long-time measurements, CO_2 exchange of both samples was checked under controlled standard conditions (WC-response curves at saturating PPFD, see Fig. 14). Area-related photosynthetic capacity proved to have not altered over the 15 months of experimentation, and both samples showed a remarkable growth rate (see the following communications).

Water content (WC) of *L. muralis* was expressed as mm 'precipitation-equivalent' which relates WC to amount of water taken up by the lichens (one mm equals one liter m^{-2}; see LANGE et al. 1997a). Similarly, CO_2 exchange of the lichen was related to (projected) surface area. After completion of the long-term measurements, the lichen thalli were carefully removed from their stone substrate, thallus dry weight, thallus total chlorophyll (determined after RONEN & GALUN 1984) and carbon content (elemental analyzer, CHNO-Rapid, Foss Heraeus, Hanau, Germany) were determined, resulting in 103.91 g carbon and 563.6 mg total chlorophyll per m^2 thallus area. The dry mass of the lichen contained $32.9 \pm 4.4\%$ of carbon.

CO_2 exchange measurements under controlled laboratory conditions

The instrumentation for CO_2 exchange measurements in the laboratory was essentially identical to those of LANGE et al. (1996). A 'minicuvette system' was used (Walz Company, Effeltrich, Germany) operating under fully controlled conditions of temperature, light, humidity, and external CO_2. Sample B (lichen thallus on its thin sandstone slab) was temporarily transferred from the Botanical Garden to the laboratory for measurement of net photosynthesis (NP) and dark respiration (DR). All measurements were conducted at 350 ppm external CO_2 if not otherwise stated.

Two types of gas exchange experiments were conducted. First, the dependence of NP and DR on thallus WC was determined. The sample was maximally hydrated by first spraying and then, after a period of time, submerging it in water for several minutes (see SEAWARD 1976 for time sequence of water uptake by the species), followed by shaking to remove adhering water drops. Comparisons have shown that this treatment produces the degree of hydration of *L. muralis* which occurs in nature after a strong rain shower. The water saturated sample was then enclosed in the cuvette and gas exchange was recorded as the sample slowly dried. Sample water content was obtained by removing and quickly weighing the lichens on an electronic digital balance and then calculated as the difference from the sample dry weight (24 h drying over silica gel). One drying cycle could last longer than 10 hours.

The routine was repeated at different, constant levels of photosynthetically active photon flux density (PPFD) and at different temperatures. In addition, the dependence of NP on WC at specific light levels was derived from the light response curves at different WC (see below). In addition to drying-down curves, special experiments were made in which the dry lichen sample had its WC increased stepwise by addition of water. This gave identical WC-dependencies of NP showing that no hysteresis effect complicated the interpretation of the results.

Dependence of NP on WC and PPFD was also determined at single, selected CO_2 partial pressures between 11 and 5000 ppm. The required CO_2 concentrations were generated using a gas-mixing system (Walz Company, Effeltrich, Germany) in which CO_2 was first removed from the ambient air supply and then either pure CO_2 or a 10% CO_2 mixture added using mass-flow controllers. Adjustments were made until the exact, required CO_2 concentration was obtained as indicated by an absolute CO_2 IRGA (see BEYSCHLAG et al. 1986). Interpolation from these drying down curves, each obtained at a single fixed CO_2 concentration, allowed photosynthetic response to CO_2 to be calculated for different thallus water contents. The WC used were chosen as follows: first the WC was found for maximal NP on the drying curve obtained at 350 ppm CO_2, then eight more WCs were chosen, four spaced approximately evenly above and four below that value. The NP at each of the 9 WCs was then found and these values were plotted against CO_2 partial pressure to obtain the final CO_2 response curve. By this means a suite of CO_2 response curves could be generated. The optimised response curve was then obtained by taking the maximal NP at any chosen CO_2 partial pressure regardless of WC.

Secondly, NP responses to light were determined by changing incident PPFD in steps from darkness to 1750 μmol m^{-2} s^{-1} (which was above saturation level) at different WC and at different temperatures. The light response curves were fitted to the data points by non-linear regression (SYSTAT Statistic Program for the Macintosh, SYSTAT Inc. Evanston IL., USA) using the 'SMITH-function' (SMITH 1938; see LANGE et al. 1991). Coefficients of determination (r^2, see SOKAL & ROHLF 1995) for all of the regressions were better than 0.94 and, in many cases, they reached 0.99. This model expresses NP as a function of PPFD, DR, GPmax$_{th}$ (theoretical maximal gross photosynthesis at saturating PPFD), and α (initial slope of the light response curve which is identical to the apparent maximal quantum yield of CO_2 fixation, Φ). Two additional parameters were also calculated from the SMITH-equation: PPFD$_{95\%}$, the light intensity which gave 95% of NPmax$_{th}$ (the theoretical maximal net photosynthesis at saturating PPFD, as derived from GPmax$_{th}$ minus DR) and which was considered to be a reasonable estimate for light saturation of the lichens and LCP, the light compensation point of CO_2 exchange. Generation of one response curve run, which always proceeded from low to high PPFD, required 30 to 45 min, and some water loss could not be avoided during this time. Each of these curves, therefore, is for a hydration range although an average WC is given for each. For comparison purposes, Φ was taken to have been generated at the initial WC during generation of each light response curve, i.e.: at low PPFD, whilst GPmax$_{th}$ and NPmax$_{th}$ were allocated to the final WC, i.e.: the highest PPFD used. PPFD$_{95\%}$, was related to the average WC during generation of the light response curve.

Monitoring of CO_2 exchange in the field

CO_2 exchange of lichen samples in the field was recorded using an automatic cuvette system (Walz Company, Effeltrich, Germany). The technical details of this 'klapp cuvette' are described by LANGE et al. (1997b). The lichen sample was positioned on a basal part of the cuvette where it was fully exposed (with c 5° inclination to the south) when the cuvette was open, and experienced the microclimatic environment and moistening by dew, fog, or rain as if it was growing naturally. At regular intervals an upper lid automatically enclosed the lichen in a plexiglas cuvette of c 190 cm³ volume which was stirred by a transparent vibrator. Outside air was pumped through the cuvette and the CO_2 exchange of the sample and absolute ambient CO_2 partial pressure were measured by using two different infrared gas analyzers. The analyzers were calibrated at regular intervals using gas mixtures of known CO_2 concentrations in cylinders and which had been checked by means of Wösthoff pumps. The same two cylinders were used which allowed calibration both of absolute CO_2 concentration as well as CO_2 differential over the entire measuring period in the field and in the laboratory. In addition, PPFD, air temperature (ventilated sensor), air humidity (c 10 cm distant from the lichen sample), and lichen thallus temperature (non-contact, infrared thermometer) were recorded. A thin fibre optic (1.5 mm in diameter) was mounted above the lichen in order to record chlorophyll fluorescence signals from the lichen thallus during gas exchange measurements using a Mini-PAM fluorometer (Walz Company, Effeltrich, Germany). Also attached to the fluorometer was a thermocouple that could be inserted in the lichen thallus and a 'Micro Quantum Sensor' (c 3 mm² sensor area: Walz, Type 2060; spectral sensitivity identical to a LiCor quantum sensor) that could be placed in the cuvette to record PPFD immediately above the thallus. A raingauge (Tipping Bucket Raingauge DRG 3, Campbell Scientific Inc., Logan, Utah, USA) measured rainfall (resolution 0.2 mm) at a distance of about 2 m from the sample. It was not possible to determine water content of sample A during the automatic CO_2 exchange monitoring in the field because the lichens were never disturbed. Measurements were made on a 30 min cycle during which the cuvette was 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 disturbance to the lichen sample from too frequent closure of the cuvette.

The klapp cuvette for measurements with *L. muralis* was built into a low, 40-cm-high brick wall, covered by sandstone slabs (Fig. 1, bottom). The wall was located at an open site in the Botanical Garden Würzburg (Bavaria, Germany) and was surrounded by other stonewalls, rocks and pavement, all covered for decades with several epilithic lichens including *L. muralis.* Thus, measurements took place under close to natural environmental conditions for this lichen. Würzburg represents a relatively dry form of the temperate, central European climate with high sunshine duration (1 600 h a⁻¹), annual mean temperature of 9 °C, and an annual rain fall of c 600 mm (for full details see following communications).

In addition to this cuvette in the wall habitat we also installed a second instrument nearby on the ground where the ex- perimental lichens in the cuvette were exposed at the level of the soil surface. This instrument was surrounded by soil, stones and rocks with attached lichens in a quasi-natural arrangement similar to the open, local steppe formation where the soil lichens had been collected. Photosynthetic performance of these lichens (such as *Cladonia convoluta, Collema cristatum, Diploschistes muscorum, Fulgensia fulgens, Squamarina lentigera*) is reported elsewhere in detail (e.g., LANGE 2000). The data set from this second site offers the possibility to compare the responses of *L. muralis* with that of other lichen life forms, studied simultaneously under similar environmental conditions.

Results

Dependence of lichen photosynthesis on light and hydration: general overview

Thallus hydration and light are the predominant factors that determine the instantaneous rate of net photosynthesis for *Lecanora muralis* with a characteristic interaction pattern. The species belongs to those lichens (type D, LANGE et al. 1993) which suffer from an extremely strong depression of CO_2 fixation when the thallus is suprasaturated with water. This is very clear in Fig. 2, where light response curves of NP (only positive rates given) are plotted for different thallus water contents. The broken line at 1 800 μmol m⁻² s⁻¹ is the NP response to WC at saturating PPFD. There is only a narrow peak of maximal photosynthesis at optimal WC. Photosynthesis of the drier as well as the suprasaturated lichen is zero or close to zero. This response pattern reflects the interplay between increasing activation of the metabolic processes as hydration increases from an initially dry state followed by increasing inhibition of CO_2 fixation due to water-induced thallus diffusion resistances at supraoptimal hydration.

In the following Sections, these dependencies are analysed in detail. A selection of typical responses will be presented from a much larger body of material which was generated for later modelling work.

Response of net photosynthesis and dark respiration to degree of hydration

Maximal water holding capacity of the lichen after experimental moistening was about 1.6 mm 'precipitation equivalent', a value which was frequently reached in nature after rain showers and which is about 310% on a thallus dry weight (dw) basis. This is a much higher value than the 150–180% dw reported by SEAWARD (1976) for *L. muralis* and this is almost certainly due to his definition of maximal water-holding capacity as
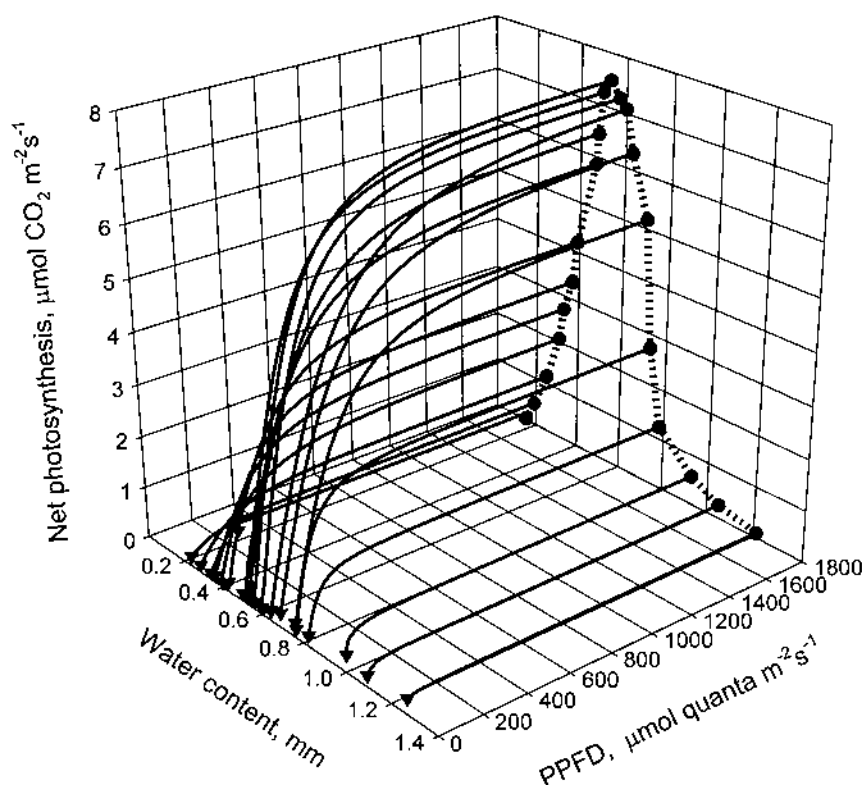
Fig. 2. Response of net photosynthesis (NP) to PPFD (photosynthetic photon flux density) at several thallus water contents for *Lecanora muralis* (winter 1995/96, 12 °C). Only NP rates >0 are plotted, filled triangles indicate light compensation points.

water content after careful blotting of the thalli with absorbent paper. Moisture compensation point of CO_2 exchange of *L. muralis* at 17 °C was at about 0.15 mm WC (29% dw). Dark respiration seemed to be activated at slightly lower WC. Under a natural ambient CO_2 concentration of about 350 ppm and saturating light (Fig. 3; bold curve; 17 °C, spring 1996), NP increased almost linearly with water content at 2.25 µmol CO_2 m^{-2} s^{-1} per 0.1 mm WC, reaching its maximum at around 0.55 mm WC. The range of WC for maximal NP was extremely narrow: rates more than 90% of maximal NP occurred only between 0.44 and 0.64 mm WC. Outside this small window, i.e. at lower as well as higher degrees of hydration (i.e. at subsaturation and at suprasaturation), decline in photosynthetic gain was substantial. At about 0.8 mm WC, less than 10% of maximal photosynthesis remained and still higher water contents reduced NP almost to the compensation point.

Hydration dependence of dark respiration of *L. muralis* followed saturation-type kinetics (Fig. 3). Maximal rates were reached at slightly higher WC than for net photosynthesis and it remained essentially constant with increasing hydration.

The general pattern of the WC response curves remained similar at ambient CO_2 concentrations lower than natural (Fig. 3) and maximal NP as well as the steep drop in CO_2 uptake at suprasaturation always occurred over the same range of WC. Even at external CO_2 concentration as low as 22 ppm, suprasaturation resulted in a depression of NP so that the compensation point was reached at c 0.8 mm WC, and higher hydration resulted in a small respiratory CO_2 release.

CO_2 saturation of NP at optimal WC occurred at about 1 000 ppm (see Section 3.5) and further increase in external CO_2 up to 5 025 ppm, the highest concentration used in these experiments, produced no further gain (Fig. 3). However, there was a pronounced effect on NP rates at WC above 0.8 mm. The suprasaturation depression was ameliorated with increase in external CO_2 from 1 200 to 2 500 and, finally, 5 025 ppm, but even the latter CO_2 concentration did not cause its total removal. The lack of response of NP to extremely high external CO_2 concentrations at optimal hydration in contrast to the clear increases at supraoptimal WC shows convincingly that the suprasaturation depression of this lichen is due to very large thallus diffusion resistances.

The suprasaturation depression of *L. muralis* proved to be independent of incident PPFD. At a CO_2 concentration of 350 ppm, maximal NP declined in step with decreasing light but the overall WC-response remained similar (Fig. 4; 12 °C, fall 1995). The WC-range for optimal NP broadened as light became more and more limiting but, even at 50 µmol m^{-2} s^{-1} PPFD, the maxi-
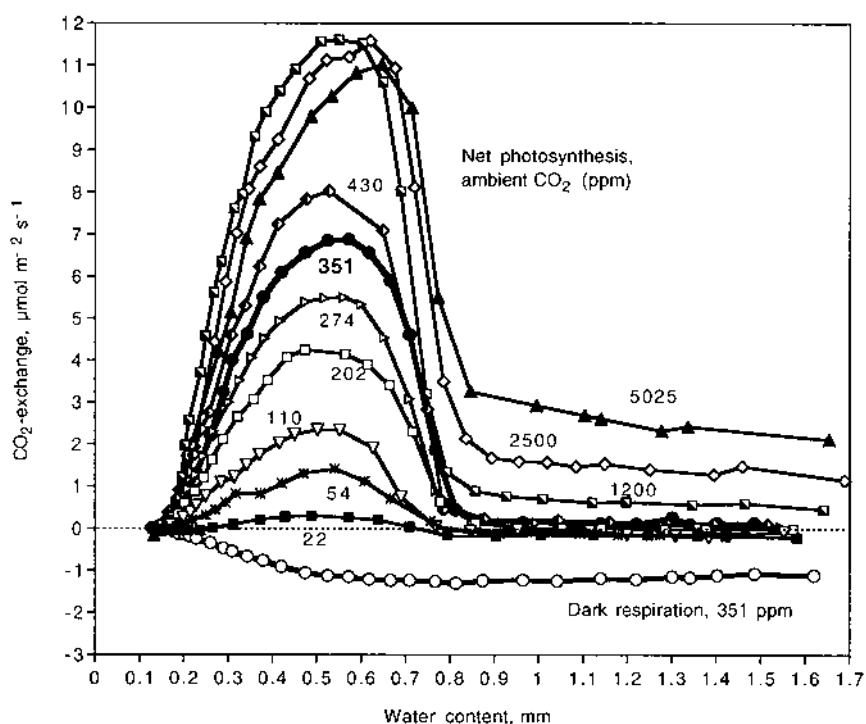
Fig. 3. Response of net photosynthesis (at saturating PPFD) and dark respiration (open circles) to thallus water content at different external CO_2 concentrations (from 22 to 5025 ppm, as indicated on each curve) for *Lecanora muralis* (spring 1996, 17 °C).
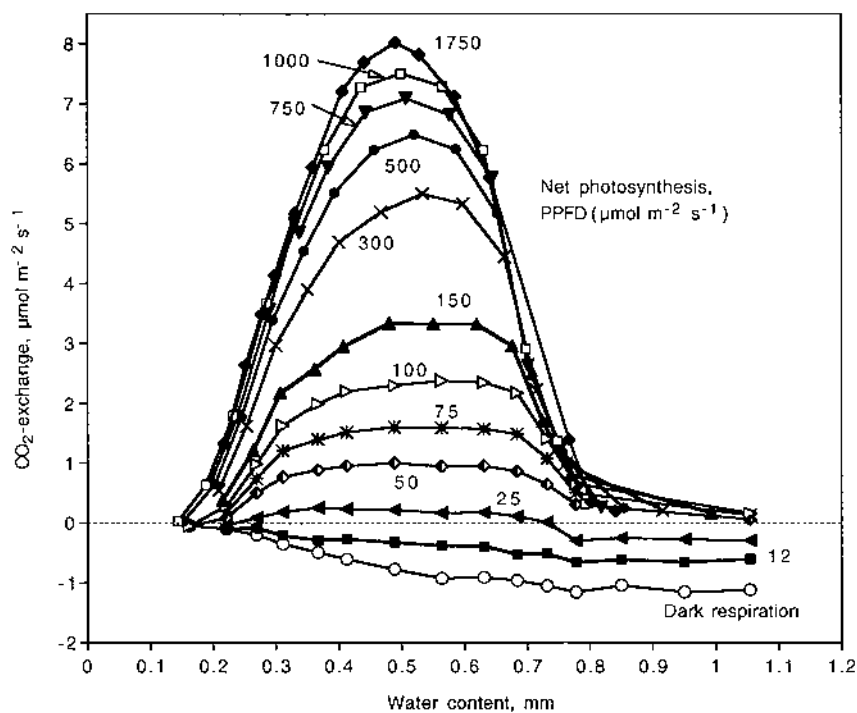

Fig. 4. Response of net photosynthesis to thallus water content (WC) at different PPFD (from 12 to 1750 μmol m^{-2} s^{-1}, as indicated on each curve) and of dark respiration (open circles) for *Lecanora muralis* (fall 1995, 12 °C, 350 ppm ambient CO_2 concentration).

mal NP of about 1 μmol CO_2 m^{-2} s^{-1} at optimal WC was still depressed to almost zero at suprasaturation. At still lower PPFD, such as 25 μmol m^{-2} s^{-1}, an upper moisture compensation point occurred and the lichen released small rates of CO_2 at WC greater than c 0.72 mm.

Light response of photosynthesis

Net photosynthesis of *L. muralis* showed a typical saturation type light response (Fig. 5; 7 °C, fall 1995) with 'sun-plant' characteristics. There was no indication of
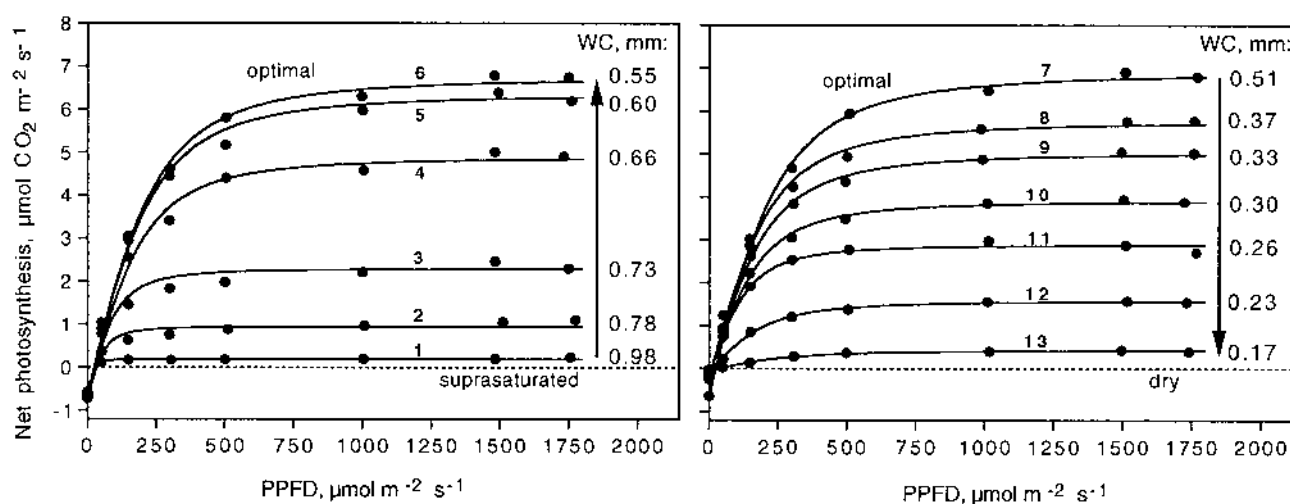
Fig. 5. Response of net photosynthesis to incident PPFD of *Lecanora muralis* at different water content (WC) at 7 °C (fall 1995). Curves were fitted by the SMITH-function, all the response curves have a similar level of fit ($r^2 > 0.94$). Each response curve is annotated with the average WC during its experimental production. The arrows and numbers indicate decreasing values for WC, from suprasaturated to optimal conditions with increasing NP (left panel) and from optimal to dry conditions with decreasing rates of NP (right panel).
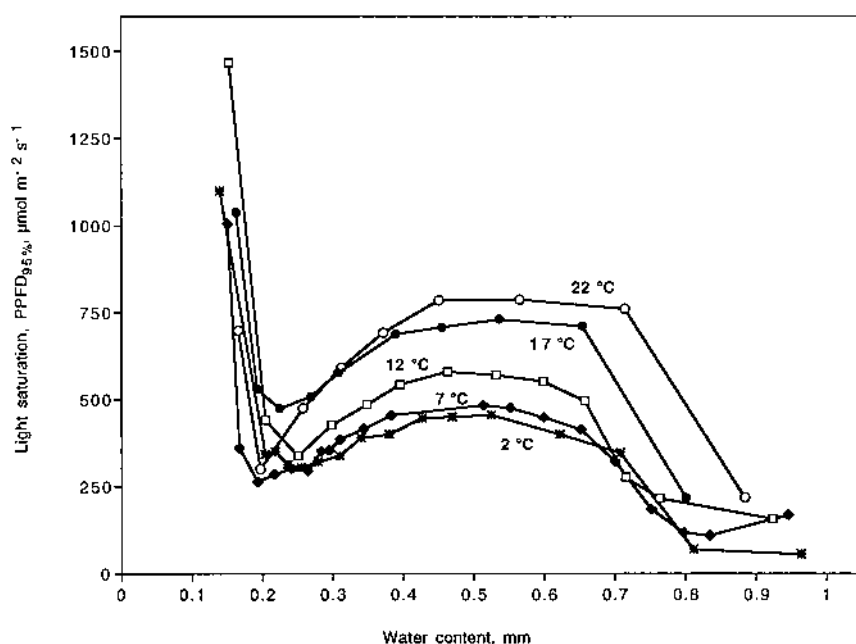
Fig. 6. Light saturation of photosynthesis (defined as lowest PPFD which gives 95% of theoretical maximal net photosynthesis) for *Lecanora muralis* as dependent on thallus water content at different, indicated temperatures (fall 1995).

photoinhibition, even at the highest PPFD tested. As described in the previous Section, the maximal values for light saturated NP were dependant on thallus hydration. At the highest WC tested, 0.98 mm, NP of the suprasaturated lichen was low at all light intensities (Fig. 5, curve number 1). As WC decreased, light saturated NP increased (left panel) and maximal rates of NP were achieved at WC of 0.55 and 0.51 mm, respectively (curve numbers 6 and 7, see sequence of response curves shown by the arrows). The subsequent decrease in light saturated NP as WC declined further was very obvious (sequence of curves, Fig. 4, right panel) until, at 0.17 mm WC, the highly desiccated thallus had almost totally lost its photosynthetic capacity. Similar response patterns occurred at other temperatures tested between 2 and 27 °C (not shown in detail).

The PPFD required to saturate NP ($PPFD_{95\%}$) was also strongly dependent on thallus hydration with a cha-

racteristic pattern in which values were temperature dependent (Fig. 6; fall 1995). Light saturation occurred at very low PPFD, as low as around 60 μmol m^{-2} s^{-1} at 2 °C, when the lichen was suprasaturated (compare also Fig. 7, curve for WC of 1.054 mm). Under these conditions, increased thallus diffusion resistances prevented high rates of photosynthesis. With decrease in WC, and consequently improving internal CO_2 availability, more quanta could be used for photosynthesis, and PPFD$_{95\%}$ increased. Light for saturation was high in the WC range optimal for NP (Fig. 4) and temperature-dependency of photosynthetic capacity then determined the value. When low temperatures limited photosynthetic metabolism, PPFD$_{95\%}$ was lower (around 460 μmol m^{-2} s^{-1} PPFD at 2 °C), and increased to c 790 μmol m^{-2} s^{-1} at more favourable temperature conditions (22 °C). Obviously, suboptimal WC decreased biochemical photosynthetic capacity so that the photosynthetic apparatus became saturated at progressively lower PPFD; a minimum occurred in the range between 0.2 and 0.3 mm. At very low WC, near the lichen moisture compensation point, PPFD$_{95\%}$ increased dramatically as photosynthetic activity became more strongly depressed than respiratory processes.

The responses of NP to low PPFD are depicted at higher resolution for selected WCs in Fig. 7 (12 °C, fall 1995). Maximal apparent quantum use efficiency, i.e. the initial slope of the response curves (Φ) was almost identical at all WC from suprasaturation to those opti-
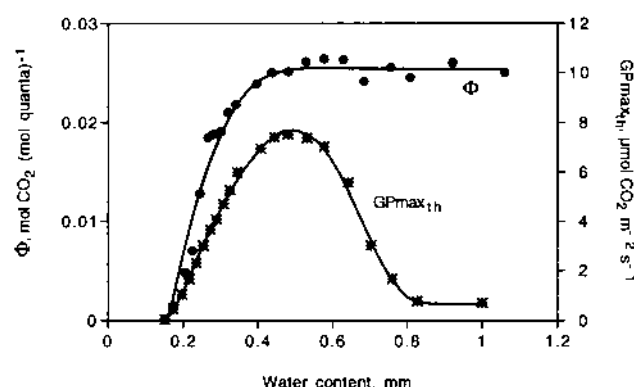
Fig. 8. The dependence of maximal apparent quantum use efficiency (Φ, initial slope from light response curves) and of GPmax$_{th}$ (theoretical maximal gross photosynthesis at saturating PPFD and optimal WC) of *Lecanora muralis* on thallus water content (7 °C, fall 1995).

mal for NP. This was especially impressive at the highest WC, 1.054 mm, when, as long as internally provided respiratory CO_2 was available for the phycobionts below the light compensation point, photosynthetic performance, and Φ, of the extremely suprasaturated lichen did not differ from that at optimal WC (0.564 mm). However, as soon as the LCP was surpassed and uptake of external CO_2 was required, the curve flattened and light saturation occurred. In contrast, at suboptimal WC (0.269 and 0.221 mm), NP was higher although Φ was smaller. This is also clear in Fig. 8 (7 °C, fall 1995) where one example is given of the dependence on WC of both Φ and the theoretical maximum of gross photosynthesis. Initially, GPmax$_{th}$ and Φ rose as photosynthetic activity became activated by increasing hydration. However, suprasaturation resulted in a steep fall in GPmax$_{th}$ whilst Φ remained almost unaffected. This again confirmed that potential photosynthetic activity of the photobionts was not affected by high water contents and that the depressed rates of NP were due to lack of the substrate CO_2 as a result of high diffusion resistances.

Light compensation point of CO_2 assimilation of *L. muralis* was also influenced by degree of hydration. The lowest LCP was at about 0.3 mm WC (Fig. 9; 12 °C, fall 1995). With increasing WC, LCP rose almost linearly from less than 20 to c 45 μmol m^{-2} s^{-1} PPFD. This is most probably due to increasing mitochondrial respiration in combination with slowly rising thallus diffusion resistances although it is possible that changes in optical properties of the upper cortex also contributed. As soon as photosynthesis was depressed at suprasaturation, LCP increased substantially to about 180 μmol m^{-2} s^{-1} at maximal WC. Another increase in LCP also occured near the moisture compensation point of the lichen.
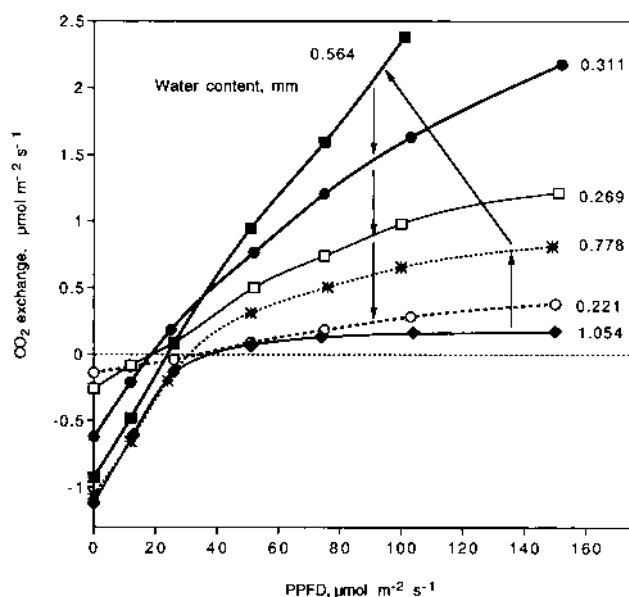

Fig. 7. Response of net photosynthesis to incident PPFD of *Lecanora muralis* for selected thallus water contents (mm WC, see indicated figures) at high resolution near the light compensation point (12 °C, fall 1995). Arrows indicate the shape changes of the curves when WC decreases.

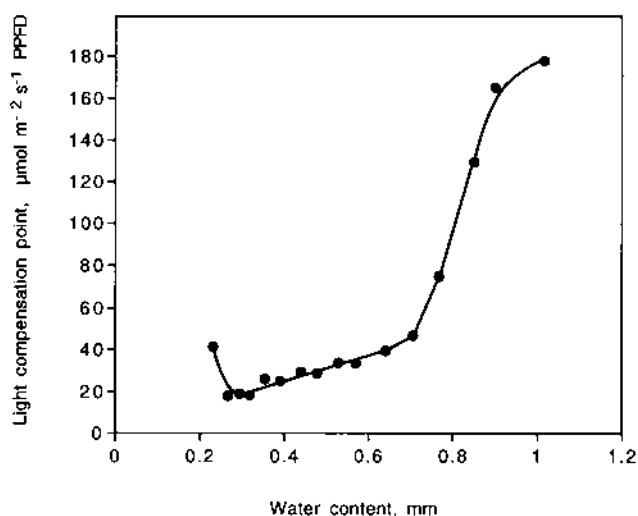Fig. 9. The dependence of the light compensation point of CO_2 exchange for *Lecanora muralis* on thallus water content (12 °C, fall 1995).

Temperature response of photosynthesis and respiration

Experimental determination of the temperature-dependency of CO_2 exchange of *L. muralis* proved to be difficult due to the high sensitivity of this lichen to its water content. It was impossible to subject the sample in the measuring cuvette to stepwise changes in temperature without changing its hydration at the same time. Therefore, we first produced a suite of WC and light response curves at a series of constant temperatures. In Fig. 17A light-responses of NP at optimal WC and three different temperatures are overlaid on field measurements (conditions summer 1996). We then extracted temperature-dependencies at selected WC from these response curves and Fig. 10 shows the dependency on temperature of $GPmax_{th}$, NP, and DR at saturating PPFD and optimal WC. There was a clear and relatively high temperature optimum for photosynthesis at 22 °C. However, decline in activity at lower temperatures was relatively small so
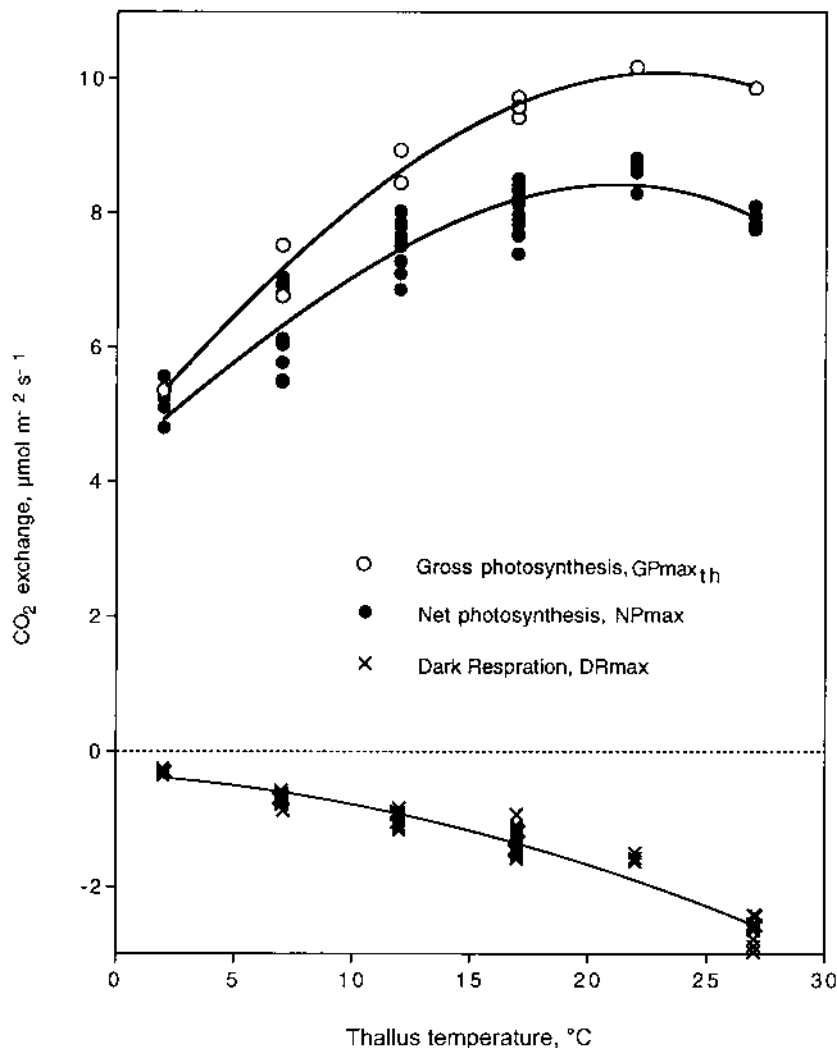

Fig. 10. The dependence of maximal gross photosynthesis ($GPmax_{th}$, theoretical maximal gross photosynthesis at saturating PPFD and optimal WC), maximal net photosynthesis (NPmax, highest measured rates at saturating PPFD and optimal WC), and maximal dark respiration (DRmax, highest measured rates at high WC) on thallus temperature for *Lecanora muralis* (fall 1995). Generated from light-response curves at different temperatures and WC.
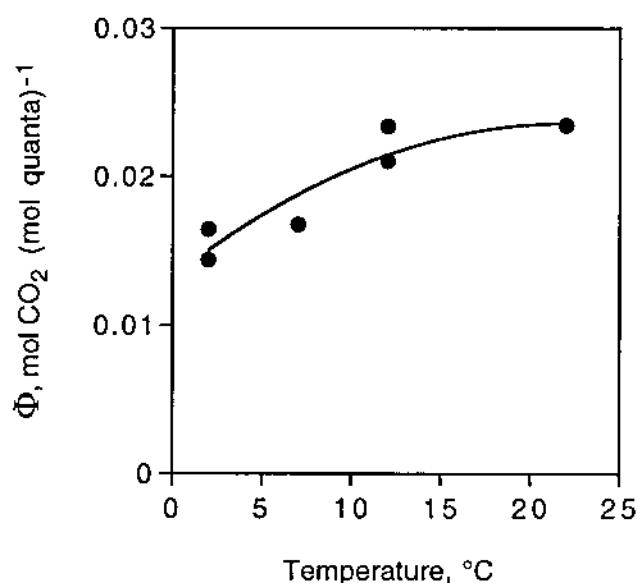
Fig. 11. The dependence of maximal apparent quantum use efficiency (Φ, initial slope from light response curves) on thallus temperature at optimal WC (range between 0.4 and 0.77 mm) for *Lecanora muralis* (winter 1995/96 and summer 1996).
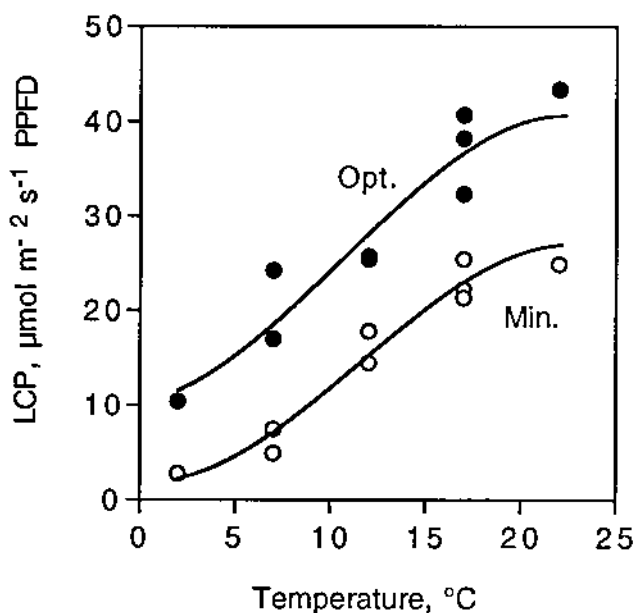

Fig. 12. The dependence of the light compensation point of CO_2 exchange (LCP) on thallus temperature for *Lecanora muralis* (fall 1995). Min: lowest LCP with respect to WC; Opt.: average LCP for range of WC which gave optimal NP (0.45–0.65 mm; compare Fig. 9).

that, at 2 °C, rates were still about 60% of maximal NP. As expected, temperature optimum of NP and $GPmax_{th}$ shifted to lower temperatures with decreasing PPFD (not shown).

Most of the photosynthetic parameters of the lichen were affected by temperature and two different examples are given. Maximal apparent quantum use efficiency (expressed as the average of Φ at optimal WC) characteristically rose with increasing temperature (Fig. 11). In Fig. 12 two measures of light compensation point are given, minimal LCP as well as average LCP at WC optimal for NP, and both increased with temperature. This was most likely due to increase in DR with temperature which could not be fully compensated by concomitant increased quantum use efficiency.

Response of photosynthesis to external CO_2 concentration

Photosynthetic response to CO_2 could be constructed for any chosen WC from the drying-down curves at different ambient CO_2 partial pressures, as outlined in the methods Section (see Fig. 3). A selection of such responses is given in Fig. 13 (spring 1996, 17 °C, saturating PPFD). As expected (centre panel), a saturation-type response occurred at optimal WC (with slight variations for the different CO_2 concentrations, see methods Section and discussion in LANGE et al. 1999a). CO_2 saturation at optimal WC (defined as lowest concentration which allowed 95% of maximal NP) was 1009 ppm. At 350 ppm (normal natural CO_2), NP was 62% of maximal NP, so that the lichen was at the upper end of the linear portion of its response curve with NP still being highly sensitive to CO_2 changes. CO_2 compensation value was as low as 16 ppm, much lower than for normal C3 plants and indicating the presence of a carbon concentration mechanism (PALMQVIST 2000).

At suboptimal water contents (Fig. 13, upper panel) CO_2 saturation occurred at progressively lower NP whilst carboxylation efficiency (the initial slope of the response curves) also declined due to dehydration. At supraoptimal WC (lower panel), NP at saturation also progressively declined but much higher external CO_2 was required for saturation. At the highest WC NP became almost linearly related to CO_2 concentration. These results again indicate the presence of extremely high thallus diffusion resistances at suprasaturation for *L. muralis*.

Seasonal changes of photosynthetic capacity and possible acclimation

Large seasonal changes of photosynthetic capacity and substantial acclimation of photosynthetic metabolism to prevailing temperature and light regimes are reported for many lichens under different climatic conditions
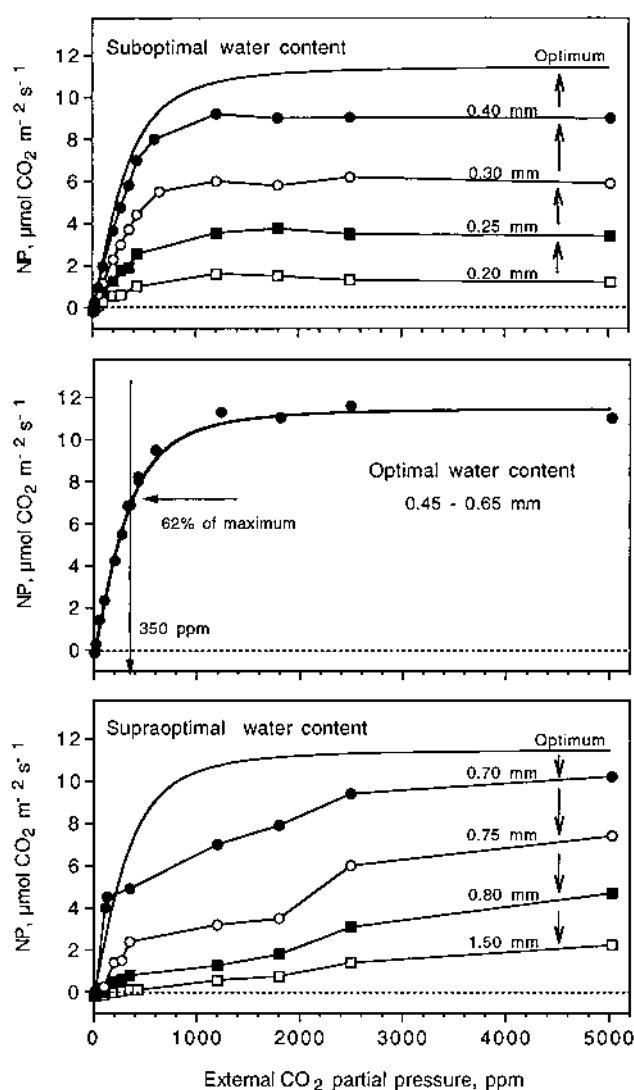
Fig. 13. Net photosynthesis as a function of external CO_2 concentration at selected thallus water contents (see number by each curve; arrows indicate increasing WC). The curves have been generated from those in Fig. 3 as described in methods. Center: optimal WC, top: dry lichen to optimal WC; bottom: optimal WC to suprasaturated lichen.

(review: KERSHAW 1985). In order to study such seasonal responses for *L. muralis*, the experimental sample (B) that was exposed to natural field conditions was measured according to a standard protocol on several occasions over the 15 month period. The use of a single sample had the advantage that possible seasonal changes would not be hidden through the biological variability if several specimens had been used. It was a surprising fact, that time- and season-dependent variations in photosynthetic performance proved to be relatively small for *L. muralis*.

Most of the photosynthetic characteristics were remarkably stable throughout the entire measuring period. This is illustrated for the dependence of area-related $GPmax_{th}$ on WC (Fig. 14) derived from suites of light response curves run at the beginning and at the end of the experiment as well as the intervening winter. Not only did the general form of the response patterns agree almost totally but, in this case, the absolute values were also almost identical.

The statistical analyses show that there were some, but only small, seasonal differences in maximal net photosynthetic capacity (maximal rates achieved at optimal WC, saturating PPFD) and especially in maximal dark respiration capacity (Fig. 15). At all three temperatures tested, the tendency was for NPmax to be higher in fall than in winter and in summer (18, 13, and 12% and 11, 2, and 11% at 2, 12, and 22 °C, respectively). However, this difference was not always statistically significant. On the other hand, at all temperatures maximal dark respiratory capacity was highest in winter, and the differences to the average rates in summer and fall were statistically significant in most of the cases. Apparently due to this increased mitochontrial respiration during the cold season, light compensation point was the only photosynthetic parameter that showed a distinct seasonal fluctuation. At all temperatures and at all WC, LCP was higher in winter than in summer, and this difference became greater at higher temperatures (Fig. 16).

Limitation of photosynthesis in nature

In the laboratory it was possible to construct a set of conditions for PPFD, temperature and water content which produced maximal NP for *L. muralis*, and 'optima' for the different factors could be defined. In nature the photosynthetic response of the lichen is the result of its interaction with changing external parameters, and it appears that optimal combinations of factors are rare. This is exemplified in Fig. 17A in which NP of the lichen on its wall-top habitat (sample A) is presented for the summer months May through September (1996). All the readings (one every 30 min) are for times when PPFD was > 1 μmol m^{-2} s^{-1} on days during which moistening allowed at least some metabolic activity. Also plotted are the light response curves (SMITH regressions) of *L. muralis* from measurements under controlled conditions (sample B) for the summer season and for 7, 12 and 22 °C. Only a small number of the NP measurements lie on the envelope curves which delineate the optimal response of NP to PPFD at the temperatures noted. Many measurements were at high PPFD but most have very low or zero NP and indicate that the lichen could not respond to the available light because it was too dry, suprasaturated (see LANGE et al. 2000, 2001) or,
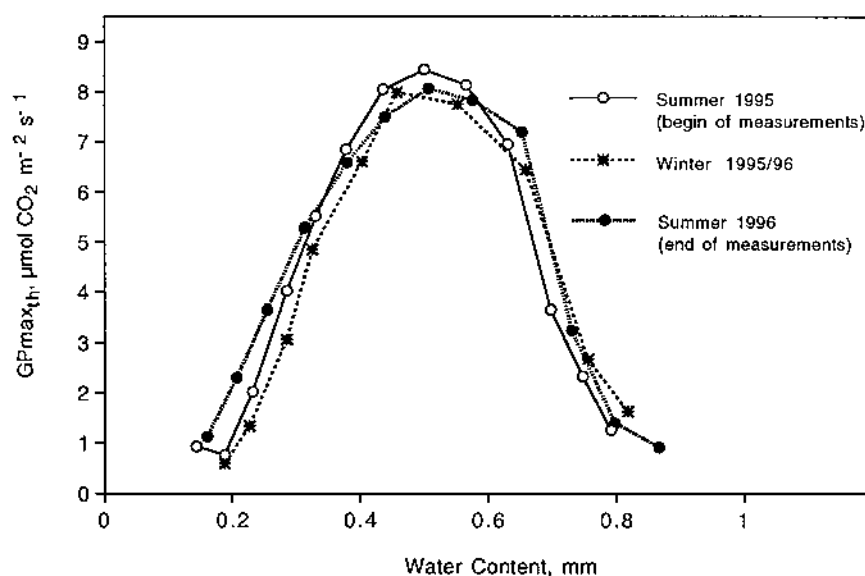
Fig. 14. The dependence of $GPmax_{th}$ (theoretical maximal gross photosynthesis at saturating PPFD and optimal WC) of *Lecanora muralis* on thallus water content at 12°C in summer 1995, winter 1995/96, and summer 1996. Generated from light response curves at different WC.
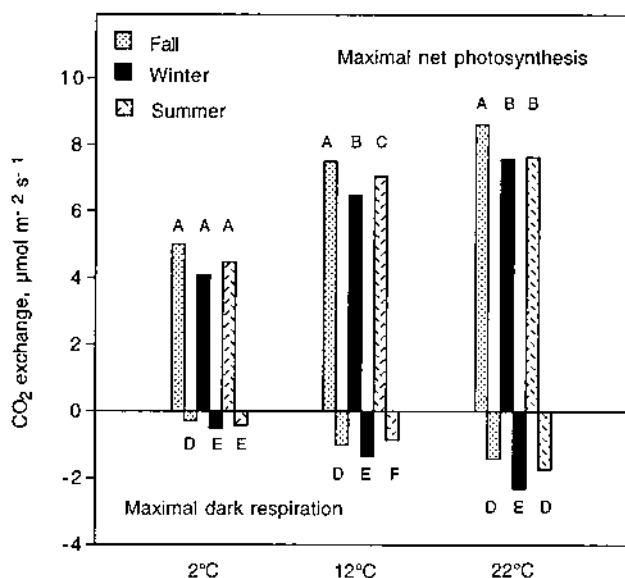

Fig. 15. Seasonal changes in photosynthetic and respiratory capacity of *Lecanora muralis* at different thallus temperatures: Averages of measured maximal rates of net photosynthesis and dark respiration in fall (1995), winter (1995/96), and summer (1996). Significant differences within temperature steps are indicated by different letters (t-test, $P < 0.05$).
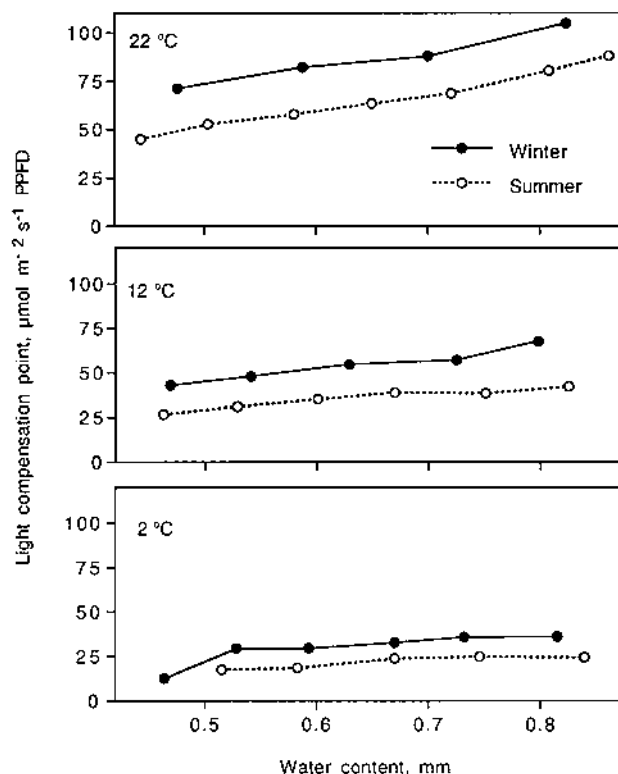

Fig. 16. Seasonal differences in water-content dependent light compensation point of CO_2 exchange at three different temperatures for *Lecanora muralis* (winter 1995/96, summer 1996).

in very rare cases, warmer than 22°C. When NP was related to ETR (relative electron transport rate), only those measurements are presented where positive quantum yield of the lichen indicated sufficient hydration for metabolic activity, i.e. all NP values when the lichen was dry are excluded (Fig. 17B). Even then, the huge majority of NP data were lower than the potential rates which were possible for a particular ETR (envelope lines).

There are many measurements with NP close to zero but with high ETR and this is exactly what would be expected if the lichen was suprasaturated. The optimal combinations of light and hydration required for maximal rates
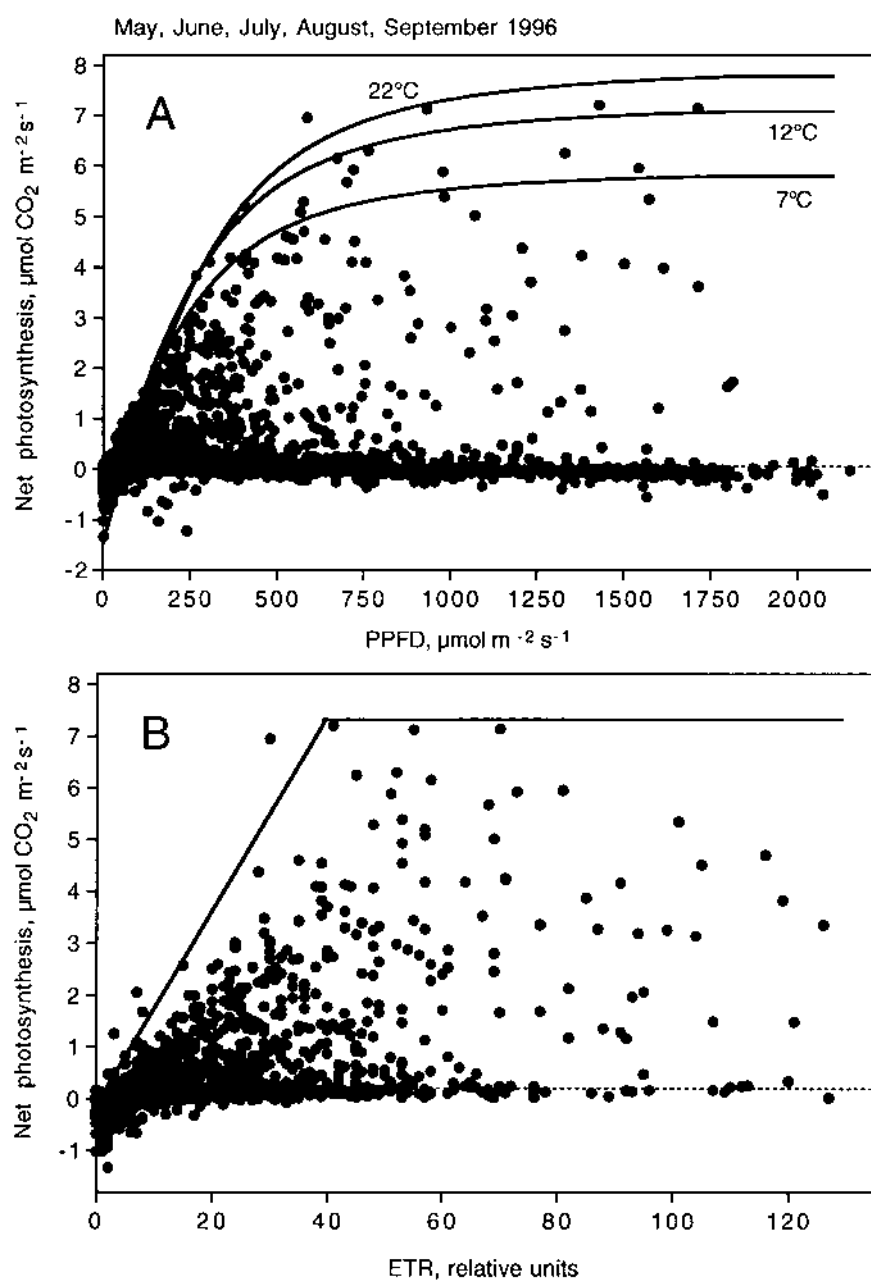
May, June, July, August, September 1996

Fig. 17. A: The dependence of net photosynthesis on incident photon flux density (PPFD) for *Lecanora muralis*. Plotted (dots) are all measurements which took place under natural conditions every 30 min (top-wall, Botanical Garden) during daylight hours (PPFD > 1 μmol m^{-2} s^{-1}) when metabolic activity of the lichen occurred (May through September 1996). The lines are light-response curves (SMITH-function) at three different temperatures produced under controlled conditions at the same time. B: As (A) however, NP (dots) is shown in relation to calculated relative electron transport rate. A fitted envelope line is drawn.

of NP occurred rarely. In addition to desiccation and suboptimal WC, suprasaturation was the main factor preventing the lichen from making optimal use of the available light.

Discussion

Area-related maximal rates of NP for *Lecanora muralis* proved to be remarkably high even when compared to leaves of C3 crop plants which have an average maximum NP between 20 and 40 μmol CO_2 m^{-2} s^{-1} (LAR-CHER 1994). Both under controlled conditions and in nature, NPs around 8 μmol m^{-2} s^{-1} were reached under natural external CO_2 (the absolute highest rate measured being 8.82 μmol m^{-2} s^{-1}). Maximal NP increased to almost 12 μmol m^{-2} s^{-1} when external CO_2 was saturating. However, this high photosynthetic potential, which required saturating light, optimal temperatures and optimal WC, was achieved only rarely under field conditions. Water content proved to be the most critical limiting factor because of the extremely small window of optimal hydration which allowed maximal net photosynthesis. Optimal WC was bounded by the opposing

processes of (1) activation of the biochemical mechanisms of the photosynthetic apparatus through increasing hydration in the suboptimal range and (2) limitation of CO_2 supply caused by increasing thallus diffusion resistances when hydration became supraoptimal. Two lines of evidence suggest that these two processes might actually overlap so that, under natural external CO_2 concentration and saturating light, resistance-induced depression of photosynthesis had already started at WC when hydration had not yet fully activated the biochemical processes of CO_2 assimilation. First, as hydration increased net photosynthesis was already decreasing when dark respiration had still not reached its maximal rates (see Fig. 4) suggesting that metabolic activation was still occurring even as CO_2 uptake was already becoming diffusion limited. Second, the optimum for NP shifted to higher WC as external CO_2 concentrations increased (see Fig. 3), an indication that photosynthetic potential was higher at those WC but could not be realised at normal CO_2 levels because of diffusion resistances. This interaction would explain why, for *L. muralis* under non-limiting light conditions, 'optimal WC' is one specific WC or, at most, a very narrow window of WC rather than a broad range of water contents. The exact position of this optimum depends to some extent on the other environmental conditions and, even at the same WC, on the momentary distribution of water and its exact site within the thallus (GREEN et al. 1985). It was also clear, that the range of optimal WC became broader when other factors, i.e. light, were limiting for photosynthesis (see Fig. 4).

There are other lichen species, such as *Fulgensia fulgens*, that behave in a very similar manner to *L. muralis*, and these contrast with lichens such as *Pseudocyphellaria murrayi* with a much broader range of optimal WC or *Diploschistes muscorum* without any depression of NP at high WC (e.g., DEL-PRADO & SANCHO 2000; GREEN et al. 1994; LANGE et al. 1993, 1999a; see also VESTE et al. 2001).

An extremely high depression of NP at suprasaturation was another feature of *L. muralis*. The 'sealing' of the thallus in terms of CO_2 diffusion resistances was so great at high WC that it prevented almost all net CO_2 assimilation under natural ambient CO_2 concentrations. The depression could only be partially removed when external CO_2 was increased to more than 5000 ppm, i.e., the gradient for CO_2 supply was increased by the factor of about 14 (see Fig. 3). If we assume the highest possible water holding capacity of suprasaturated *L. muralis* was 1.6 mm, the lichen had to lose 50% of its water in order to begin substantial carbon gain and about 60% before optimal photosynthesis became possible.

Under natural conditions, high irradiance increases water loss and drying of a lichen thallus so that, for a lichen like *L. muralis*, optimal water content occurs only for very brief periods of time. This explains why maximal rates of NP are rare events in the life of this lichen and why, for most of the time, its CO_2 assimilation is limited by suboptimal or supraoptimal hydration (see Fig. 17).

Laboratory studies on photosynthesis of *L. muralis* were greatly impeded by its special water relations. It was very difficult to keep its water content constant for a longer period of time when it was illuminated in a measuring cuvette, and it was almost impossible to produce conditions which maintained its optimal degree of hydration. Therefore, in this study, we mainly ran drying-down curves to investigate the influence of different environmental parameters on lichen metabolism (see methods Section). This was a valid procedure because many repeats and also wetting rather than drying runs showed no hysteresis effects. It became clear by the measurements that most of the photosynthetic parameters, such as light dependence of CO_2 exchange, maximal quantum use efficiency, light saturation of NP, and light compensation point were dependent on thallus water content in a complex manner. In addition, these responses were moderated by temperature but, in general, the influence of temperature on photosynthetic productivity was slight.

Since the pioneering studies by STÅLFELT (1939) it has been known that, under natural conditions, lichens can show seasonal changes in their photosynthetic capacity which could, at least partly, be interpreted as acclimation to prevailing weather conditions (LARSON 1980). The occurrence of such changes in photosynthetic activity has been confirmed by HAHN et al. (1989) for soil lichens growing in local xerothermic steppe formations near Würzburg in Franconia. Maximal NP of *Peltigera rufescens* and *Cladonia convoluta* was three and two times higher, respectively, in summer than in fall under similar environmental conditions. Such large differences were not found for *L. muralis* growing in the same area. The greatest change in NP capacity was 12%, being higher in fall than in winter at 22 °C. There was no clear difference between summer and winter but a trend existed of higher potential rates in fall than in summer (see Fig. 15). In contrast, dark respiratory capacity showed a clear seasonal adaptation: it was largest in winter, especially at the higher temperatures tested. This influenced the light compensation point of the experimental lichen which was also higher in winter than in summer. Nevertheless, the extremely small responses of photosynthetic capacity of *L. muralis* to seasonal weather conditions were surprising.

Daily and seasonal courses of CO_2 exchange of *L. muralis* under natural conditions will be reported in a subsequent paper. Field performance of the lichen will be interpreted and analysed by means of the data presented here.

Acknowledgements

References

BEYSCHLAG, W.; LANGE, O. L. & TENHUNEN, J. D. (1986): Photosynthese und Wasserhaushalt der immergrünen mediterranen Hartlaubpflanze *Arbutus unedo* L. im Jahreslauf am Freilandstandort in Portugal. I. Tagesläufe von CO_2-Gaswechsel und Transpiration unter natürlichen Bedingungen. – Flora **178**: 409–444.

DEL-PRADO, R. & SANCHO, L. G. (2000): Water relations and photosynthetic performance of fruticose lichens from the semiarid Southeast of Spain. – Flora **195**: 51–60.

DEL-PRADO, R.; SANCHO, L. G. & KAPPEN, L. (2001): Photosynthetic performance of photosymbiotic ascomata in the lichen *Teloschistes lacounosus*. – Flora **196**: 261–168.

GREEN, T. G. A.; SNELGAR, W. P. & WILKINS, A. L. (1985): Photosynthesis, water relations and thallus structure of Stictaceae lichens. In: BROWN, D. H. (ed.): Lichen physiology and cell biology, 57–75. Plenum Press, New York.

GREEN, T. G. A.; LANGE, O. L. & COWAN, I. R. (1994): Ecophysiology of lichen photosynthesis, the role of water status and thallus diffusion resistances. – Crypt. Bot. **4**: 166–178.

GREEN, T. G. A.; SCHROETER, B.; MASEYK, K. S.; SEPPELT, R. D. & KAPPEN, L. (1998): An assessment of the relationship between carbon dioxide exchange and chlorophyll *a* fluorescence in an antarctic moss and lichen. – Planta **206**: 611–618

GREEN, T. G. A.; SCHLENSOG, M.; SANCHO, L. G.; WINKLER, J. B.; BROOM, F. D. & SCHROETER, B. (2001): The photobiont determines the pattern of photosynthetic activity within a single lichen thallus containing cyanobacterial and green algal sectors (photosymbiodeme). – Oecologia **130**: 191–198.

HAHN, S.; SPEER, D.; MEYER, A. & LANGE, O. L. (1989): Photosynthetische Primärproduktion von epigäischen Flechten im "Mainfränkischen Trockenrasen". I. Tagesläufe von Mikroklima, Wassergehalt und CO_2-Gaswechsel zu den verschiedenen Jahreszeiten. – Flora **182**: 313–339.

INSAROV, G. & SCHROETER, B. (2001): Lichen monitoring and climate change. In: NIMIS P. L.; SCHEIDEGGER, C. & WOL-SELEY, P. A. (eds.): Monitoring with lichens – monitoring lichens, 83–201. Kluwer Academic Publishers, Dordrecht.

KAPPEN, L. (1988): Ecophysiological relationships in different climatic regions. In: GALUN, M. (ed.): Handbook of lichenology, Vol. 2, 37–100. CRC-Press, Boca Raton, Florida.

KAPPEN, L.; LANGE, O. L.; SCHULZE, E.-D.; EVENARI, M. & BUSCHBOM, U. (1979): Ecophysiological investigations on lichens of the Negev Desert. VI. Annual course of the photosynthetic production of *Ramalina maciformis* (DEL.) BORY. – Flora **168**: 216–229.

KERSHAW, K. A. (1985): Physiological ecology of lichens. Cambridge University Press, Cambridge.

LANGE, O. L. (2000): Photosynthetic performance of a gelatinous lichen under temperate habitat conditions: long-term monitoring of CO_2 exchange of *Collema cristatum*. – Bibl. Lichenol. **75**: 307–332.

LANGE, O. L.; MEYER, A.; ULLMANN, I. & ZELLNER, H. (1991): Mikroklima, Wassergehalt und Photosynthese von Flechten in der küstennahen Nebelzone der Namib-Wüste: Messungen während der herbstlichen Witterungsperiode. – Flora **185**: 233–266.

LANGE, O. L.; BÜDEL, B.; HEBER, U.; MEYER, A.; ZELLNER, H. & GREEN, T. G. A. (1993): Temperate rainforest lichens in New Zealand: high thallus water content can severely limit photosynthetic CO_2 exchange. – Oecologia **95**: 303–313.

LANGE, O. L.; MEYER, A.; ZELLNER, H. & HEBER, U. (1994): Photosynthesis and water relations of lichen soil-crusts: field measurements in the coastal fog zone of the Namib Desert. – Functional Ecology **8**: 253–264.

LANGE, O. L.; GREEN, T. G. A.; REICHENBERGER, H. & MEYER, A. (1996): Photosynthetic depression at high thallus water content in lichens: concurrent use of gas exchange and fluorescence techniques with a cyanobacterial and a green algal *Peltigera* species. – Bot. Acta **109**: 43–50.

LANGE, O. L.; BELNAP, J.; REICHENBERGER, H. & MEYER, A. (1997a): Photosynthesis of green algal soil crust lichens from arid lands in southern Utah, USA: role of water content on light and temperature responses of CO_2 exchange. – Flora **192**: 1–15.

LANGE, O. L.; REICHENBERGER, H. & WALZ, H. (1997b): Continuous monitoring of CO_2 exchange of lichens in the field: short-term enclosure with an automatically operating cuvette. – Lichenologist **29**: 259–274.

LANGE, O. L.; HAHN, S. C.; MEYER, A. & TENHUNEN, J. D. (1998): Upland tundra in the foothills of the Brooks Range, Alaska, U.S.A.: lichen long-term photosynthetic CO_2 uptake and net carbon gain. – Arctic Alpine Res. **30**: 252–261.

LANGE, O. L.; GREEN, T. G. A. & REICHENBERGER, H. (1999a): The response of lichen photosynthesis to external CO_2 concentration and its interaction with thallus water-status. – J. Plant Physiol. **154**: 157–166.

LANGE, O. L.; LEISNER, M. R. L. & BILGER, W. (1999b): Chlorophyll fluorescence characteristics of the cyanobacterial lichen *Peltigera rufescens* under field conditions. II. Diel and annual distribution of metabolic activity and pos-

sible mechanisms to avoid photoinhibition. – Flora **194:** 413–430.

LANGE, O. L.; BÜDEL, B.; MEYER, A.; ZELLNER, H. & ZOTZ, G. (2000): Lichen carbon gain under tropical conditions: water relations and CO_2 exchange of three *Leptogium* species of a lower montane rainforest in Panama. – Flora **195:** 172–190.

LANGE, O. L.; GREEN, T. G. A. & HEBER, U. (2001): Hydration-dependent photosynthetic production of lichens: what do laboratory studies tell us about field performance? – J. Exp. Bot. **52:** 2033–2042.

LARCHER, W. (1994): Ökophysiologie der Pflanzen, 5. Aufl., Verlag Eugen Ulmer, Stuttgart.

LARSON, D. W. (1980): Seasonal change in the pattern of net CO_2 exchange in *Umbilicaria* lichens. – New Phytol. **84:** 349–369.

LEISNER, J. M. R.; BILGER, W. & LANGE, O. L. (1996): Chlorophyll fluorescence characteristics of the cyanobacterial lichen *Peltigera rufescens* under field conditions. I. Seasonal patterns of photochemical activity and the occurrence of photosystem II inhibition. – Flora **191:** 261–273.

LEISNER, J. M. R.; GREEN, T. G. A. & LANGE, O. L. (1997): Photobiont activity of a temperate crustose lichen: long-term chlorophyll fluorescence and CO_2 exchange measurements in the field. – Symbiosis **23:** 165–182.

PALMQVIST, K. (2000): Carbon economy in lichens. – New Phytol. **148:** 11–36.

POELT, J. (1969): Bestimmungsschlüssel europäischer Flechten. Cramer-Verlag, Lehre.

RENHORN, K.-E.; ESSEEN, P.-A.; PALMQVIST, K. & SUNDBERG, B. (1997): Growth and vitality of epiphytic lichens. I. Responses to microclimate along a forest edge-interior gradient. – Oecologia **109:** 1–9.

RONEN, R. & GALUN, M. (1984): Pigment extraction from lichens with dimethylsulfoxide (DMSO) and estimation of chlorophyll degradation. – Environ. Exp. Bot. **24:** 239–245.

ROSENTRETER, R. & BELNAP, J. (2001): Biological soil crusts of North America. In: BELNAP, J. & LANGE, O. L. (eds.): Biological soil crusts: structure, function, and management. Ecological Studies **150,** 31–50. Springer-Verlag, Berlin Heidelberg.

SEAWARD, M. R. D. (1976): Performance of *Lecanora muralis* in an urban environment. In: BROWN, D. H.; HAWKSWORTH, D. L. & BAILEY, R. H. (eds.): Lichenology: progress and problems, 323–357. Academic Press, London.

SEAWARD, M. R. D. (1982): Lichen ecology of changing urban environments. In: BORNKAMM, R.; LEE, J. A. & SEAWARD, M. R. D. (eds.): Urban ecology, 181–189. Blackwell Scientific Publications, Oxford.

SCHROETER, B.; KAPPEN, L.; SCHULZ, F. & SANCHO, L. G. (2000): Seasonal variation in the carbon balance of lichens in the maritime Antarctic: long-term measurements of photosynthetic activity in *Usnea aurantiacoatra*. In: DAVISON, W.; HOWARD-WILLIAMS, C. & BROADY, P. (eds.): Antarctic ecosystems: models for wider ecological understanding, 258–262. The Caxton Press, Christchurch, NZ.

SMITH, E. L. (1938): Limiting factors in photosynthesis: light and carbon dioxide. – J. Gen. Physiol. **22:** 21–35.

SOKAL, R. R. & ROHLF, F. J. (1995): Biometry. Freeman and Co., New York.

STÅLFELT, M. G. (1939): Der Gasaustausch der Flechten. – Planta **29:** 11–31.

SUNDBERG, B.; CAMPBELL, D. & PALMQVIST, K. (1997a): Predicting CO_2 gain and photosynthetic light acclimation from fluorescence yield and quenching in cyano-lichens. – Planta **201:** 138–145.

SUNDBERG, B.; PALMQVIST, K.; ESSEEN, P.-A. & RENHORN, K.-E. (1997b): Growth and vitality of epiphytic lichens. II. Modelling of carbon gain using field and laboratory data. – Oecologia **109:** 10–18.

VESTE, M.; LITTMANN, T.; FRIEDRICH, H. & BRECKLE, S.-W. (2001): Microclimatic boundary conditions for activity of soil lichen crusts in sand dunes of the north-western Negev desert, Israel. – Flora **196:** 465–474.