Oecologia (2005) 142: 11–19
DOI 10.1007/s00442-004-1697-x

ECOPHYSIOLOGY

Otto L. Lange · T. G. Allan Green

Lichens show that fungi can acclimate their respiration to seasonal changes in temperature

Received: 20 February 2004 / Accepted: 21 July 2004 / Published online: 19 August 2004

Abstract Five species of lichens, the majority members of a soil-crust community (*Cladonia convoluta*, *Diploschistes muscorum*, *Fulgensia fulgens*, *Lecanora muralis*, *Squamarina lentigera*) showed seasonal changes of temperature sensitivity of their dark respiration (DR) to such an extent that several substantially met the definition of full acclimation, i.e. near identical DR under different nocturnal temperature conditions during the course of the year. *C. convoluta*, for example, had maximal DR at 5°C of −0.42, −1.11 and −0.09 nmol CO_2 g^{-1} s^{-1} in autumn, winter, and summer, respectively, a tenfold range. However, at the mean night temperatures for the same three seasons, 9.7°C, 4.2°C and 13.6°C, maximal DR were almost identical at −1.11, −0.93, and −1.45 nmol CO_2 g^{-1} s^{-1}. The information was extracted from measurements using automatic cuvettes that continuously recorded a sample lichen's gas exchange every 30 min under near-natural conditions. The longest period (for *L. muralis*) covered 15 months and 22,000 data sets whilst, for the other species studied, data blocks were available throughout the calendar year. The acclimation of DR means that maximal net carbon fixation rates remain substantially similar throughout the year and are not depressed by increased carbon loss by respiration in warmer seasons. This is especially important for lichens because of their normally high rate of DR compared to net photosynthesis. We suggest that lichens, especially soil-crust species, could be a suitable model for fungi generally, a group of organisms for which little is known about temperature acclimation because of the great difficulty in separating the organism from its growth medium. Fungi, whether saprophytic, symbiotic or parasitic, including soil lichens, are important components of soil ecosystems and contribute much of the respired CO_2 from these systems. Temperature acclimation by fungi would mean that expected increases in carbon losses caused by global climate warming from soil ecosystems might not be as extensive as first thought. This would ameliorate this positive feedback loop present in some climate models and might substantially lower the predicted warming.

Keywords Adaptation · Soil respiration · Climate change · Soil-crust lichens · Photosynthesis

This work is dedicated to Professor Hubert Ziegler on the occasion of his 80th birthday. We would like to acknowledge his impressive contribution to physiological plant ecology, and to wish him continuing joie de vivre with his scientific interests during a happy retirement.

O. L. Lange (✉)
Julius-von-Sachs-Institut für Biowissenschaften der Universität Würzburg, Lehrstuhl für Botanik II,
Julius-von-Sachs-Platz 3,
97084 Würzburg, Germany
e-mail: ollange@botanik.uni-wuerzburg.de

T. G. A. Green
Biological Sciences, University of Waikato,
Hamilton, New Zealand

Introduction

Fungi are heterotrophic organisms and release CO_2 by respiring substrates obtained from saprophytism, parasitism and symbioses. Cellular respiration rises exponentially with increase in temperature and, because of this, the predicted rise in global temperatures could potentially increase fungal respiration rates with impacts on the carbon balance of organisms and ecosystems. Many fungi are important members of the soil community where they can be free-living and in symbiosis with plant roots forming mycorrhizae. They are major contributors to respiratory CO_2 production from the soil and increased CO_2 release following warming of soil ecosystems is suggested as a positive feedback loop in global climate models (Houghton et al. 2001; Cox et al. 2000). This amplification, because of temperature rise, would be ameliorated if fungi acclimated their respiration rates to temperature as already known for plants (Larcher 2003; Körner 2003). However, fungi are not the easiest organisms to research in their natural environment. They are predominantly hyphal in structure and are highly

integrated into organisms and substrates, especially in soil, and are almost impossible to study without damage to their physical and biological surroundings.

The discrete thalli of lichens offer a solution to these difficulties. Lichens are organisms composed of fungi symbiotic with photosynthetic green algal or cyanobacterial partners. About 19% of all fungi are lichenized (Kirk et al. 2001) and lichens dominate in about 8% of terrestrial ecosystems (Ahmadjian 1995). We suggest that lichens, especially those growing on the soil surface and penetrating the surface of the ground (Belnap et al. 2003), could be a suitable model for understanding fungal response to temperature.

It is known that phanerogamic plants can acclimate to the prevailing temperatures so that their mitochondrial respiratory activity is relatively higher in the cold and lower when warmer (e.g., Arnone and Körner 1997). This results in a better supply of energy at low temperatures whilst preventing increased loss of assimilates at higher temperatures (Larcher 2003). Higher plants have been found to show full acclimation when identical respiration rates occur for plants grown, and measured, at two different temperatures (Körner 2003).

There is almost no information on the ability of fungi to acclimate their metabolic processes under natural conditions, a lack that certainly reflects the difficulties in doing research on these organisms in a natural situation. Possible acclimation to cold temperatures has been reported for a *Fusarium* species and vesicular-arbuscular mycorrhizal hyphae (Robinson and Morris 1984; Addy et al. 1998) whilst a recent review on cold adaptation in Arctic and Antarctic fungi found the situation to still be unclear for the natural environment (Robinson 2001). According to the present literature, the situation for lichens is also not so clear. Differences in respiration rates between seasons were already reported by Stålfelt (1938) for *Ramalina farinacea*. Larson and Kershaw (1975) reported acclimation of net photosynthetic rate for *Cetraria nivalis* measured in the summer and winter whilst Larson (1980) from a larger survey reported that net photosynthesis could both increase and decrease through the year depending on species but that temperature response of respiration did not change substantially. Our present understanding of acclimation by lichens is summarized in Kershaw (1985) and Nash (1996). Although dark respiration (DR) has been shown to correlate with total nitrogen and ergosterol content the source of respiratory CO_2 released from the lichen thallus is still not certain (Sundberg et al. 1999). In most types of heteromerous lichens, the fungus makes up the vast majority of the thallus (Ahmadjian 1993), and it is assumed that the mycobiont contributes the majority of the respiratory CO_2 of a lichen (Quispel 1960). Carbon loss rates through DR can almost equal the net photosynthetic rate and, because respiration has a higher temperature response than photosynthesis, net carbon dioxide exchange can become negative at moderately elevated temperatures under normal light conditions (Green and Lange 1994). It has been suggested that the distribution of lichens in lowland tropical areas is limited by exceptionally poor carbon balance due to increased carbon losses whilst hydrated over warm nights (Zotz and Winter 1994; Zotz 1999; Lange et al. 2000). Thus, lichens and lichen-dominated ecosystems would appear to be particularly at risk if global temperature rises do occur.

We have been studying the carbon balance of mainly soil-crust lichens growing under temperate climate conditions in Würzburg, Germany. A special "klapp cuvette" was used which automatically enclosed an otherwise naturally exposed lichen sample in a 30 min cycle (Lange et al. 1997). Net carbon dioxide exchange and related microclimate parameters were measured whilst the cuvette was closed. The lichen sample was not disturbed at any time during the measurement periods which, for individual lichens, could last for months to over a year. The size and period of the data bases differ for each lichen but the largest data base was for *Lecanora muralis* and extended over 15 months. We have been able to extract information from these large databases that suggests that lichens can dramatically acclimate to habitat temperature.

Materials and methods

The experimental lichens

The measurements were conducted with lichens of different life forms which were collected from a site in a local xerothermic steppe formation north-west of Würzburg (Ammerfeld near Aschfeld). They grow there on calcareous soil together with other lichens and mosses and form a biological soil-crust community known as "Bunte Erdflechtengesellschaft" (community of coloured lichens) described as Fulgensietum fulgentis Gams 1938 and Cladonietum convolutae Müller 1951 (Klement 1955). The experimental species *Cladonia convoluta* (Lam.) P. Cout. forms foliose-fruticose tufts of erect basal squamules that are recurved under dry conditions. *Diploschistes muscorum* (Scop.) R.Sant. has a crustose, continuous, not areolated whitish to dark-grey thallus. *Fulgensia fulgens* (Swarz) Elenk. is a crustose-placodioid orange-yellow lichen, with differentiated marginal lobes. *Squamarina lentigera* (Web.) Poelt has squamulose, somewhat overlapping thallus lobes, and forms more or less regular rosettes up to 6 cm diameter often growing over mosses. All of these species are chlorolichens, i.e. they have green algal photobionts (Lange and Wagenitz 2003). *Collema* (*Co.*) *cristatum* (*L.*) Weber ex Wigg. is a gelatinous cyanolichen with *Nostoc* as its photobiont and has rounded lobes that swell when wet. It grows on calcareous rock particles and also on soil as a member of the soil-crust community. These soil-crust species were transplanted to the measuring site in the Botanical Garden (Würzburg, Bavaria, Germany, 49°46′ N, 9°56′ E) where most of them have now been successfully cultivated for many years under conditions which were essentially identical to those of their natural site. It is documented that at least *S. lentigera* is native in Würzburg where it was reported as

early as 1824 by Hepp from a site not more than 2 km distant from the present Botanical Garden. In addition, the green algal *L. muralis* (Schreber) Rabenh. was also studied. It is a placodioid epilithic lichen which forms circular patches or rosettes closely attached to its substrate at the centre, the thallus becoming lobate at its outer margin. The experimental material of *L. muralis* grew on sandstone slices which were collected from the Spessart region (48 km northwest of Würzburg). They were exposed in the Botanical Garden, Würzburg for about 6 months before the experiments in order to become adapted to the local conditions.

For the measurements under laboratory conditions, samples of *L. muralis* were used which had been kept in a growth chamber so that they do not represent performance of the lichen at a specific season.

CO_2 exchange measurements under controlled laboratory conditions

The instrumentation for respiration measurements in the laboratory is described by Lange (2002). A "minicuvette system" was used (Walz, Effeltrich, Germany) operating under fully controlled conditions of temperature and humidity. For determination of the dependence of DR (CO_2 release, negative numbers) on thallus water content (WC) lichen samples were maximally hydrated and enclosed in the cuvette. CO_2 exchange was then recorded as the sample slowly dried. Lichen thallus WC was determined by briefly removing the sample and weighing it on a digital balance. Drying-down curves were repeated at different temperatures, and temperature response-curves were generated from maximal respiration of the lichen at optimal WC. It has been reported that lichens show enhanced respiration immediately after temperature is increased (Sundberg et al. 1999). We avoided this effect in these experiments by allowing the measuring system to equilibrate at each new temperature and measurements were not commenced until steady-state conditions had been reached both for the system and also for the lichen after it had been replaced in the cuvette after each change of temperature.

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, Effeltrich, Germany). The technical details of this "klapp cuvette" and a discussion of possible errors can be found in Lange et al. (1997) and Lange (2002). The lichen sample was positioned on a basal part of the cuvette where it was fully exposed when the cuvette was open, and experienced the microclimatic environment and moistening by dew, fog, or rain as if it was growing naturally. Each sample was checked to ensure that the substrate of the lichens (e.g. the sandstone slice on which *L. muralis* was growing) did not affect the CO_2 exchange. At regular intervals an upper lid automatically enclosed the lichen in a Plexiglass cuvette. Outside air was pumped through the cuvette and the CO_2 exchange of the sample was measured by using a differential infrared gas analyser. In addition, photosystem II chlorophyll fluorescence was measured during part of the measuring periods. Microclimate data were recorded during each closing event. In addition to thermocouples which were used for special experiments, three different sensors recorded air or lichen temperature. Air temperature outside the cuvette was measured by a ventilated Pt-100 resistance thermometer; another small Pt-100 temperature sensor was mounted near the lichen recording air temperature when the sample was exposed and when it was enclosed in the cuvette; thallus temperature was recorded by a non-contact infrared thermometer. All data reported here are from the second sensor, the Pt-100 measurements of (stirred) air temperature taken when the cuvette was closed. This standardization was necessary because infrared temperature measurements were not possible with the foliose *C. convoluta*. In fact, air and thallus temperatures of all of the species proved to be similar at least during the dark period. 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 proved to be a reasonable compromise between the opposing needs to generate sufficient data points to reveal activity patterns and to minimize disturbance to the lichen sample from too frequent closure of the cuvette.

Two klapp cuvettes were operated simultaneously. For measurements with the epilithic *L. muralis*, one instrument was built into a low, 40-cm-high brick wall, covered by sandstone slabs. The wall was located at an open site in the Botanical Garden and was surrounded by other stonewalls, rocks and pavement, all covered for decades with several epilithic lichens including *L. muralis*. The second instrument was installed nearby on the ground where the experimental epigaeic lichens in the cuvette were exposed at the level of the surrounding soil surface. This instrument was also surrounded by soil, stones and rocks, with attached lichens in a quasi-natural arrangement similar to the open, local steppe formation where the experimental material had been collected. Thus, measurements took place under close to natural environmental conditions for these lichens.

Würzburg represents a relatively dry form of the temperate, central European climate with high sunshine duration (1,600 h $year^{-1}$), annual mean temperature of 9°C, and an annual rainfall of ca. 600 mm.

Data basis and data evaluation

The study lasted from March 1995 until August 1997, inclusive. The extent and period of the data bases differ for each lichen. For *L. muralis* it contains around 22,000 data sets over a continuous period of 15 months. Each day contains 48 data sets and 106 days were available for evaluation for *C. convoluta*, 113 for *Co. cristatum*, 174 for *D. muscorum*, 160 for *F. fulgens*, and 123 for *S. lentigera*.

In the latter cases the data bases were composed of groups of weeks spread more or less evenly through the year and are considered to be representative of the annual performance of the lichen. Diel courses of CO_2 exchange and productivity of the experimental lichens are reported in Lange (2000, 2003a, b), Lange and Green (2003, 2004).

For the present analysis we first selected all days with any metabolic activity at any time as indicated by the lichens' gas exchange and chlorophyll fluorescence. Subsequently we extracted DR, the respiration rate in darkness, defined as the carbon dioxide exchange rate when incident light was zero. These measurements were then used to prepare a response matrix of respiration rate to temperature. For three typical life forms of the experimental lichens characteristic seasonal periods are presented in detail in Figs. 3, 4 and 5. For each period, the average temperature for all measurements are indicated. An envelope line was generated by first sorting the data into classes of one degree, and then fitting a polynomial to the highest rate of respiration in each class. The line delineates the maximal respiration rate for the lichen at any particular temperature. For a further interpretation of these envelope lines see Results.

Results

Dependence of lichen respiration on thallus water content and temperature under controlled condition

Lichens are poikilohydric organisms so that their WC and, therefore, metabolic activity depends on the water status of the environment. Their respiration rate is highly influenced by thallus hydration, especially at the lower WCs. Respiration does not occur in the desiccated lichen and 30–60% of maximal thallus water holding capacity is necessary to achieve maximal rates of DR. As an example, Fig. 1 shows performance of *L. muralis*. Respiratory activity first becomes measurable at a relative thallus WC of about 0.13 mm (precipitation equivalent, litre water per m^2). Maximal rates of DR were reached at about 0.6 mm and remained relatively constant at higher thallus WC until thallus water saturation at 1.6 mm. The other experimental species had the same kind of response pattern, with the exception of *Co. cristatum* which showed decreased DR (ca. 70%) at high WC. On average, under natural conditions, the lichen thalli were dry and metabolically inactive for 35–65% of the year, depending on their individual thallus structure. Thallus temperature is the second external factor determining lichen respiration. As with other organisms, DR increased exponentially with rising temperature for all of our experimental species under steady-state conditions (Fig. 2).

Temperature dependence of lichen respiration under natural conditions

Figures 3, 4 and 5 show the data matrix of temperature dependence of DR for three of the six experimental lichen species under natural conditions. In each case the data have been subdivided at least into defined winter and summer periods. All three lichens showed a clear seasonal shift in the temperature response of DR, i.e. acclimation. The extent of the acclimation is easily seen by comparing the respiration rates at the same temperature, for instance at 8 or 5°C, in the different seasons. The respiration rates for all three species were several times higher in the winter than in the summer.

The database for *C. convoluta* has been subdivided into three seasons, autumn, winter, and summer with mean temperatures for all nocturnal readings in each season of 9.7, 4.2 and 13.6°C, respectively. The DR response was exactly as expected for acclimation with the differences in the (maximal) envelope line rates being very obvious at 5°C, −0.42, −1.11 and −0.09 nmol CO_2 g^{-1} s^{-1}, respectively, giving a tenfold increase in rate of respiration at this temperature between summer and winter. Importantly, the acclimation of DR progressed in opposite directions as temperature first decreased from autumn (1996) to winter (early 1997) and then rose into summer (1997), i.e. the acclimation was reversible. Actual DR (envelope line values) at the nocturnal mean temperatures were −1.11, −0.93 and −1.45 nmol CO_2 g^{-1} s^{-1} for

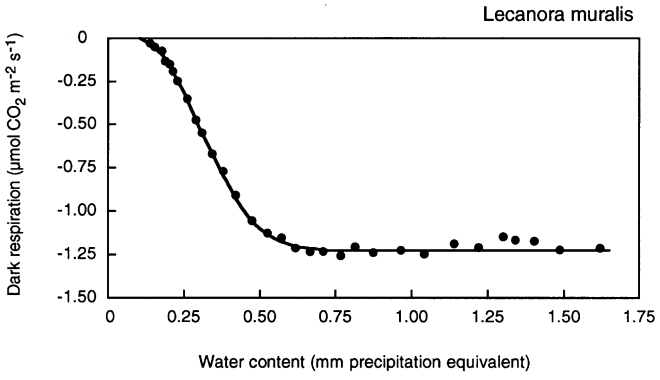

Fig. 1 The dependence of DR (ordinate, CO_2 loss) on thallus relative WC (abscissa, mm "precipitation equivalent") for *L. muralis* (controlled conditions, 17°C)

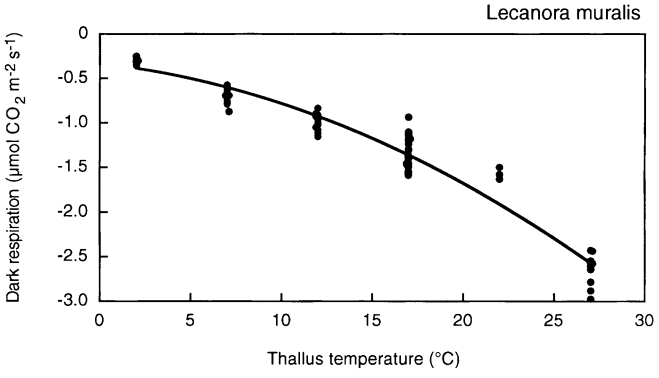

Fig. 2 The dependence of DR (ordinate, CO_2 loss) on thallus temperature (abscissa, °C) for *L. muralis* (controlled conditions, saturating thallus water content; see text for details)

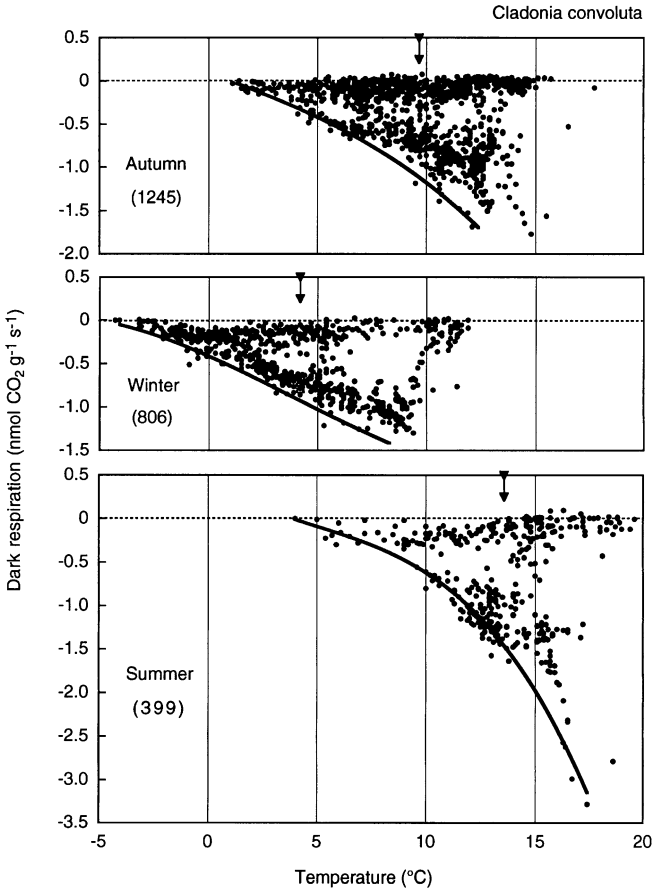

Fig. 3 The dependence of DR on temperature for *C. convoluta* during three different seasons of the year (Botanical Garden, Würzburg). *Vertical axes* CO_2 exchange with negative values indicating respiration (CO_2 loss); *horizontal axes* temperature (^oC). *Upper panel* autumn, 13 September 1996–28 October 1996; *middle panel* winter, 10 February 1997–27 March 1997; *lower panel* summer, 6 June 1997–3 July 1997. The number in each panel is the number of data points and each data point (taken every 30 min) represents a nocturnal measurement on a day on which there was at least some CO_2 exchange. The *line* represents the envelope curve fitted as described in the Methods Section and delineates maximal respiration at any chosen temperature. The *arrow* at the top of each panel indicates the mean temperature for all measurements in the panel

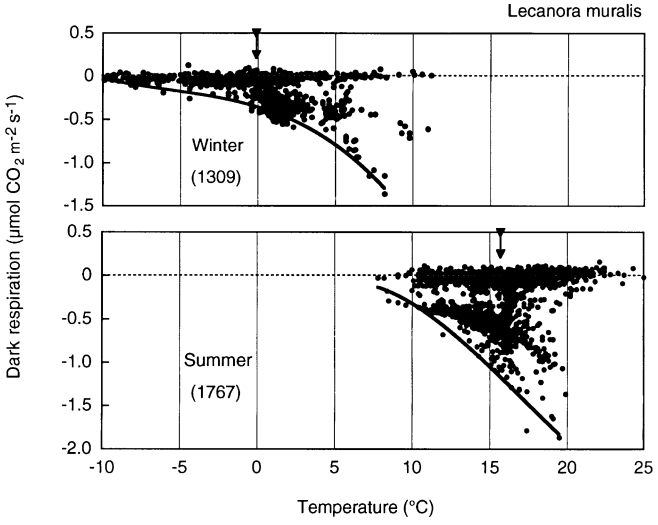

Fig. 4 The dependence of DR on temperature for *L. muralis* during two different seasons of the year. *Upper panel* winter, 1 January 1996–31 March 1996; *lower panel* summer, 1 July 1996–31 August 1996. Other details as for Fig. 3

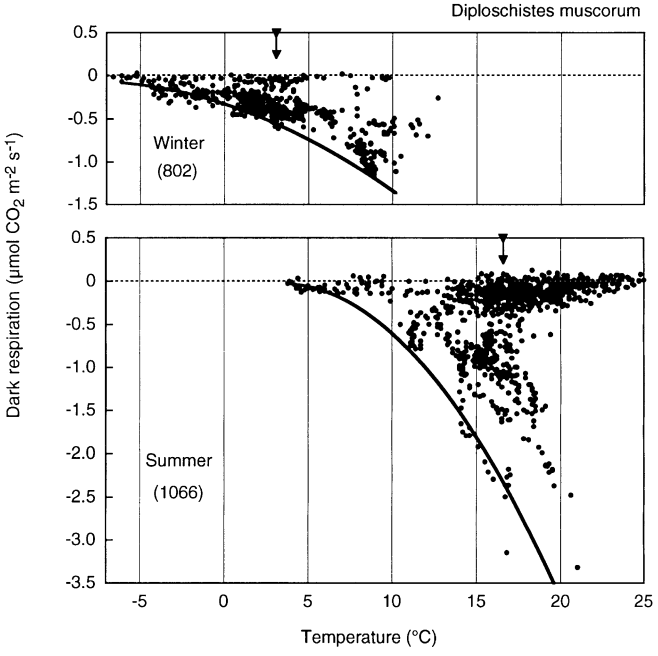

Fig. 5 The dependence of DR on temperature for *D. muscorum* during two different seasons of the year. *Upper panel* winter, 17 December 1996–9 February 1997, and 11 April 1997–30 April 1997; *lower panel* summer, 30 July 1996–8 August 1996, and 2 June 1997–29 August 1997. Other details as for Fig. 3

autumn, winter, and summer, respectively. This is close to "full acclimation" as defined by Larigauderie and Körner (1995) and Körner (2003) as being when identical respiration rates occur for plants grown and measured at two different temperatures. Acclimation was so strong for *L. muralis* (Fig. 4) that there was only a very small range of overlap between the respiration responses in the winter and summer months which is particularly impressive when it is noted that there were over 3,000 data points in the total data set. DR at 8°C was about −1.5 and −0.3 µmol CO_2 m^{-2} s^{-1} for the winter and summer, respectively. Similar responses were found for *D. muscorum* (Fig. 5) and *S. lentigera* (data not shown). In the latter case envelope line DR were almost identical at −0.5 µmol CO_2 m^{-2} s^{-1} at the mean nocturnal temperatures for the lichen thallus in spring and summer (6.2 and 14.8°C, respectively).

Detailed analysis of the data measured in the field is complex. The fitted envelope curves characterize for each season the highest respiration rates at any given lichen temperature under optimal conditions of hydration. The magnitude of the respiration rates and the form of these fitted curves were similar to those obtained from laboratory measurements (see Fig. 2). In the field data sets, however, the vast majority of the measured DR do not

actually fall on, or even near, the envelope curve but lie between it and the zero DR line. Several different factors could contribute to this variability. The first possibility, and one that is certain to have occurred, is that the data not on the line represent suboptimal hydration conditions for DR. Maximal respiration i.e. on the envelope curve, requires optimal WC of the lichen thallus (Fig. 1) and many of the depressed values must represent a dry (DR was zero) or drying thallus. However, in contrast to net photosynthesis which often shows strong suprasaturation depression (see Lange 2002), DR was relatively constant over a wide range of thallus WC in these lichens (Fig. 1), so a large number of depressed values due to drying would not be expected. An inspection of some of the data for individual nights revealed lower values even when the chlorophyll fluorescence signal was indicating a fully hydrated lichen thallus. Suboptimal hydration conditions, therefore, do not seem to be the full explanation. A second possible explanation for deviation from the envelope curves is that the data set of one season is actually composed of many individual response curves and reflects acclimation at different times to several different temperatures including transient situations. Thus, a DR value lower than the envelope curve might represent a fully active lichen but one that is acclimated to a higher temperature. This source of variation must be present to some extent. The general fit between laboratory and field generated measurements and the strong differences between the seasons suggest that acclimation must be rapid. However, it is not possible to distinguish between these two possibilities, suboptimal hydration or acclimation to another temperature, from the results presented here. A third possible contributor to the variability might be due to short-term transient responses of the lichens to rapid changes in external conditions. Previous habitat conditions (light or dark, desiccation) are known to influence the following DR but the effects can take place over several days (Brown et al. 1981; Palmqvist 2000). Sudden moistening of dry thalli can result in a short CO_2 outburst, known as "resaturation respiration" (Nash 1996), and sudden increases in temperature might result in an initial intensification of DR followed by a gradual decrease (Sundberg et al. 1999). Examples of these latter two possibilities were found when diel courses were inspected but they appear to be of irregular occurrence and to be of little ecological significance in the field (Lange 2003a).

The three depicted lichen species all showed clear acclimation. This was also found for two other species, both chlorolichens, *F. fulgens* and *S. lentigera*. In contrast we found no recognizable temperature acclimation with *Co. cristatum* and we have no explanation for this difference which could be a result of insufficient data, or its cyanobacterial nature (with a low proportion of mycobiont mass in its thallus). It does show, however, that acclimation may be species specific.

Discussion

"Full acclimation" has been defined as being when identical respiration rates occur for plants grown and measured at two different temperatures (Körner 2003; Larigauderie and Körner 1995). In this sense, at least *C. convoluta* and also *S. lentigera* substantially met this definition with respect to night-time temperature showing acclimation that was so strong that there was, effectively, homeostasis of respiration over a mean temperature range of about 9 K. As a result of the full acclimation there was also a tendency for homeostasis of net carbon exchange and maximal net photosynthetic rates were very similar in all seasons (Lange 2003b; Lange and Green 2003, 2004). All the other species reported here, except *Co. cristatum*, also showed strong, but not full, acclimation to changing seasonal temperatures.

We compared the response of lichen respiration to the mean temperatures that they experienced during the dark periods of the different seasons. In the calculations we included data from all days during which the lichens were hydrated, however briefly (see Methods Section). This meant that, on many days, the thalli were dry with zero respiration for a substantial proportion of the measuring points (see Figs. 3, 4, 5). It is probably reasonable to assume that any process that leads to temperature acclimation depends on metabolic activity i.e. hydration. Therefore, temperature means calculated for periods that include data when the lichens were desiccated might not correctly reflect the thermal conditions that induce acclimation. To test this possible source of errors, we eliminated all data points from the analyses that were obtained when the lichens were desiccated, i.e. did not show any CO_2 release. In fact, the nocturnal temperature means did not change substantially. For example, mean temperature of *C. convoluta* was 9.67°C for all nocturnal data points during the autumn period and 9.74°C for the metabolically active lichen; the equivalent means were 4.19 versus 4.24°C, and 13.58 versus 13.14°C for winter and summer, respectively (see Fig. 3). However, it is also possible that not only did the thermal conditions during the dark periods contribute to acclimation of DR but also the temperatures during the daylight hours. Diel (24 h) temperature means for the metabolically active thalli of *C. convoluta* were 11.8°C during the autumn measuring period, 6.3°C in winter, and 16.2°C in summer. DR rates (envelope curves, Fig. 3) at these mean temperatures were about −1.53, −1.19, and −2.60 nmol CO_2 g^{-1} s^{-1}, respectively for the three seasons. Effective acclimation for *C. convoluta* is obvious even when these daily temperature means are used and this was also the case for the other species.

Our findings concern the entire lichen organism, i.e. the symbiotic community consisting of mycobiont and photobiont and we are unable to judge the individual contributions of the symbionts. It is most probable that respiratory CO_2 release mainly reflects the metabolic activity of the fungal partner of a lichen (Quispel 1960). This assumption is supported by the much larger propor-

tion of mycobiont biomass than that of the photobionts in a heteromerous lichen thallus. There are estimates that the photobiont partner may constitute as little as 10% of the lichen biomass (Sundberg et al. 1999) or 5–10% of "the plant body" (Hale 1973). There could also be differences in the specific respiratory activity of the symbionts that might modify the differences due to biomass. There are, however, only few data available in the literature which quantify any differences in the relative contribution of the two partners to lichen respiration (Kershaw 1985). Kappen and Lange (1972) compared DR of intact thalli of *C. rangiferina* with that of the cultivated mycobiont and they also measured CO_2 release of mechanically separated photobiont layer (plus upper cortex) and medulla of *Lobaria pulmonaria*. They came to the conclusion that dry-weight related DR of the two partners of these lichens was almost identical. In their experiments with dissected discs of *Peltigera polydactyla*, Harley and Smith (1956) and Smith (1960) found that dry-weight related DR of the algal zone was ca. 1.8 times larger than that of the medullary zone. However, the higher respiratory activity is not enough to compensate for the much lower proportion of algal biomass in heteromerous lichens. Although we do not have detailed information about our experimental species, we have to assume that the respiratory CO_2 release that we have measured was mainly the product of the lichen mycobiont.

Our results have several implications. First, if lichens and thus lichenized fungi can substantially acclimate their respiration to temperature changes then it is reasonable to expect this to also be possible by other fungi, in both symbiotic and free-living states. Such fungi are an important component in the soils of most ecosystems dominated by phanerogams such as trees and grasses and make a substantial contribution to soil carbon dioxide release with implications for global climate change models (Chapin and Ruess 2001). There is growing acceptance that climate change will lead to an increase in global temperature in the next century with estimates of between 1.4 and 5.8 K in the latest report by the Intergovernmental Panel on Climate Change (IPCC) (Houghton et al. 2001). However, the higher predicted values are the result of a positive feedback mechanism in which the higher temperatures cause increased CO_2 release by respiration substantially from soils. Valentini et al. (2000) found soil respiration to be the component determining carbon balance in European forests with roots and microorganisms being the main contributors to soil carbon losses. These higher predicted values have recently been brought into question by Luo et al. (2001) who found that the expected increase in carbon dioxide release at experimentally increased higher temperatures did not occur in a tall grass prairie ecosystem. The soil respiration acclimated so that the sensitivity to temperature increase decreased. Similar acclimation was found for Alaskan arctic ecosystems where carbon dioxide release has not increased in response to recent rises in temperature (Oechel et al. 2000) and also for soil respiration in the Bornhöved Lake district, north Germany (Kutsch and Kappen 1997). It was uncertain for these ecosystems whether the acclimation was through physiological adjustment by the soil organisms or by change in the composition of the microbial community. Grace and Raymont (1999) suggest that soil respiration parameters are crucial in models of global change.

If these fungi, especially symbiotic soil fungi, have the same potential as lichens, especially soil-crust lichens, then stability of fungal soil respiration is explicable by physiological acclimation. This provides a possible explanation for the lack of response to temperature change of the tall grass prairie soil ecosystem (Luo et al. 2001), of ecosystem carbon dioxide exchange in Alaska (Oechel et al. 2000), and of arable soils in north Germany (Kutsch and Kappen 1997). Decreased sensitivity of respiration to temperature change is possible by physiological change without considering alteration of microbial populations, at least as far as the fungal component is concerned. We suspect this effect would be particularly important in experiments where warming is not high and occurs over a relatively short period, a potential problem that has already been identified (Grace and Raymont 1999).

Second, it is perhaps surprising that, although the lichenized fungi measured were poikilohydric, a life-style thought to avoid the impacts of environmental extremes (Kappen and Valladares 1999) they showed as much acclimation of their DR as found for homoiohydric plants. Lichens are also known as usually being slow-growing organisms but it is clear that their metabolic processes are as equally responsive as other organisms. Acclimation must be fast because the lichens were often only active for a few hours per day and it may be possible that we have greatly underestimated the ability of lichens to adapt to changing habitat conditions, an ability first reported in the classic paper of Stålfelt (1938). In one of the few reports on acclimation to low temperatures by fungi it was found that a 2 h treatment was sufficient to produce a change in low temperature tolerance for *Fusarium oxysporum* f.sp. *lycopersici* (Robinson and Morris 1984).

Third, the result has obvious implications for the annual carbon budget of lichens. This is a group that dominates many marginal environments, especially polar and alpine regions that are predicted to show more rapid climate change. Acclimation has obvious importance for, and should be taken into account in, any modelling simulations for these communities. It is clearly possible that measurements of respiration rates at one time of the year may not be validly extended to other seasons. Some of the considerable variability found in large scale comparisons of respiration rates in lichens (Lange et al. 2000; Palmqvist et al. 2002) might also be explicable by acclimation of the specimens to temperatures other than those at which they were surveyed.

The results presented here provide strong justification for long term studies of the ecophysiology of lichens and probably other plants. The acclimation found was not the initial focus of the present study but emerged without any special experimental manipulation of the lichens from the information gathered over several seasons. This extraction

of the data from a larger data base without prior specification could be thought to be a strength of the interpretations presented here.

Acknowledgements This research was funded by the Deutsche Forschungsgemeinschaft and by the Alexander-von-Humboldt-Stiftung, Bonn. Assistance and help of Wilma Samfaß, Gerhard Radermacher, and Hans Reichenberger with generating, handling, and evaluating the data are gratefully acknowledged. Prof. B. Büdel kindly provided lichen material.

References

Addy HD, Boswell EP, Koide RT (1998) Low temperature acclimation and freezing resistance of extraradical VA mycorrhizal hyphae. Mycol Res 102:582–586

Ahmadjian V (1993) The lichen symbiosis. Wiley, New York

Ahmadjian V (1995) Lichens are more important than you think. BioScience 45:124

Arnone JA, Körner C (1997) Temperature adaptation and acclimation potential of leaf dark respiration in two species of *Ranunculus* from warm and cold habitats. Arct Alp Res 29:122–125

Belnap J, Büdel B, Lange OL (2003) Biological soil crusts: characteristics and distribution. In: Belnap J, Lange OL (eds) Biological soil crusts: structure, function and management (Ecological studies 150). Springer, Berlin Heidelberg New York, pp 3–30

Brown DH, Snelgar WP, Green TGA (1981) Effects of storage conditions on lichen respiration and desiccation sensitivity. Ann Bot 48:923–926

Chapin FS III, Ruess RW (2001) The roots of the matter. Nature 411:749–752

Cox PM, Betts RA, Jones CD, Spall SA, Toterdell IJ (2000) Acceleration of global warming due to carbon-cycle feedbacks in a coupled climate model. Nature 408:184–187

Grace J, Raymont M (1999) Respiration in the balance. Nature 404:819–820

Green TGA, Lange OL (1994) Photosynthesis in poikilohydric plants: a comparison of lichens and bryophytes. In: Schulze E-D, Caldwell MM (eds) Ecophysiology of photosynthesis (Ecological studies 100). Springer, Berlin Heidelberg New York, pp 319–342

Hale ME (1973) Growth. In: Ahmadjian V, Hale ME (eds) The lichens. Academic Press, New York, pp 473–492

Harley JL, Smith DC (1956) Sugar absorption and surface carbohydrate activity of *Peltigera polydactyla* (Neck.) Hoffm. Ann Bot 20:513–543

Hepp P (1824) Lichenen-Flora von Würzburg, oder Aufzählung und Beschreibung der um Würzburg wachsenden Flechten. Florian Kupferberg, Mainz

Houghton JT, Ding Y, Griggs DJ, Noguer M, van der Linden PJ, Xiaosu D (eds) (2001) Climate change 2001: the scientific basis. Cambridge University Press, Cambridge

Kappen L, Lange OL (1972) Die Kälteresistenz einiger Makrolichenen. Flora 161:1–29

Kappen L, Valladares F (1999) Opportunistic growth and desiccation tolerance: the ecological success of poikilohydrous autotrophs. In: Pugnaire FI, Valladares F (eds) Handbook of functional plant ecology. Marcel Dekker, New York, pp 9–80

Kershaw KA (1985) Physiological ecology of lichens. Cambridge University Press, Cambridge

Kirk PM, Cannon PF, David JC, Stalpers JA (2001) Ainsworth and Bisby's dictionary of the fungi, 9th edn. CAB International, Wallingford

Klement O (1955) Prodromus der mitteleuropäischen Flechtengesellschaften. Feddes Reper 135:5–194

Körner C (2003) Alpine plant life, 2nd edn. Springer, Berlin Heidelberg New York

Kutsch WL, Kappen L (1997) Aspects of carbon and nitrogen cycling in soils of the Bornhöved Lake district. II. Modelling the influence of temperature increase on soil respiration and organic carbon content in arable soils under different managements. Biogeochemistry 39:207–224

Lange OL (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 OL (2002) 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. Flora 197:233–249

Lange OL (2003a) Photosynthetic productivity of the epilithic lichen *Lecanora muralis:* long-term field monitoring of CO_2 exchange and its physiological interpretation. II. Diel and seasonal patterns of net photosynthesis and respiration. Flora 198:233–249

Lange OL (2003b) Photosynthetic productivity of the epilithic lichen *Lecanora muralis:* long-term field monitoring of CO_2 exchange and its physiological interpretation. III. Diel, seasonal, and annual carbon budgets. Flora 198:277–292

Lange OL, Green TGA (2003) Photosynthetic performance of a foliose lichen of biological soil-crust communities: long-term monitoring of the CO_2 exchange of *Cladonia convoluta* under temperate habitat conditions. Bibl Lichenol 86:257–280

Lange OL, Green TGA (2004) Photosynthetic performance of the squamulose soil-crust lichen *Squamarina lentigera*: laboratory measurements and long-term monitoring of CO_2 exchange in the field. Bibl Lichenol 88:363–390

Lange OL, Wagenitz G (2003) What is a 'phycolichen'? Differences and changes in the meaning of an old lichenological term. Lichenologist 35:341–345

Lange OL, Reichenberger H, Walz H (1997) Continuous monitoring of CO_2 exchange of lichens in the field: short-term enclosure with an automatically operating cuvette. Lichenologist 29:259–274

Lange OL, 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

Larcher W (2003) Physiological plant ecology, 4th edn. Springer, Berlin Heidelberg New York

Larigauderie A, Körner C (1995) Acclimation of leaf dark respiration to temperature in alpine and lowland plant species. Ann Bot 76:245–252

Larson DW (1980) Seasonal change in the pattern of net CO_2 exchange in *Umbilicaria* lichens. New Phytol 84:349–369

Larson DW, Kershaw KA (1975) Acclimation in arctic lichens. Nature 254:421–423

Luo Y, Wen S, Hui D, Wallace LL (2001) Acclimation of soil respiration to warming in a tall grass prairie. Nature 413:622-625

Nash TH III (ed) (1996) Lichen biology. Cambridge University Press, Cambridge

Oechel WC, Vourlltis GL, Hastings SJ, Zulueta RC, Hinzman L, Kane D (2000) Acclimation of ecosystem CO_2 exchange in the Alaskan Arctic in response to decadal climate warming. Nature 406:978–981

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

Palmqvist K, Dahlman L, Valladares F, Tehler A, Sancho LG, Mattsson J-E (2002) CO_2 exchange and thallus nitrogen across 75 contrasting lichen associations from different climate zones. Oecologia 133:295–306

Quispel A (1960) Respiration of lichens. In: Wolf J (ed) Pflanzenatmung einschliesslich Gärung und Säurestoffwechsel (Handbuch der Pflanzenphysiologie, vol XII/2). Springer, Berlin Heidelberg New York, pp 455–460

Robinson CH (2001) Cold adaptation in Arctic and Antarctic fungi. New Phytol 151:341–353
Robinson PM, Morris GM (1984) Tolerance of hyphae of *Fusarium oxyspermun* f.sp. *lycopersici* to low temperature. Trans Br Mycol Soc 46:609–613
Smith DC (1960) Studies in the physiology of lichens. 3. Experiments with dissected discs of *Peltigera polydactyla*. Ann Bot 24:186–199
Stålfelt MG (1938) Der Gasaustausch der Flechten. Planta 29:11–31
Sundberg B, Ekblad A, Näsholm T, Palmqvist K (1999) Lichen respiration in relation to active time, temperature, nitrogen and ergosterol concentrations. Funct Ecol 13:119–125
Valentini R et al. (2000) Respiration as the main determinant of carbon balance in European forests. Nature 404:861–865
Zotz G (1999) Altitudinal changes in diversity and abundance of non-vascular epiphytes in the tropics—an ecophysiological explanation. Selbyana 20:256–260
Zotz G, Winter K (1994) Photosynthesis and carbon gain of the lichen, *Leptogium azurem*, in a lowland tropical forest. Flora 189:179–186