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## CO<sub>2</sub> exchange of the endolithic lichen *Verrucaria baldensis* from karst habitats in northern Italy

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**Abstract** CO<sub>2</sub> exchange of the endolithic lichen *Verrucaria baldensis* was measured in the laboratory under different conditions of water content, temperature, light, and CO<sub>2</sub> concentration. The species had low CO<sub>2</sub> exchange rates (maximum net photosynthesis: *c.* 0.45 μmol CO<sub>2</sub> m<sup>-2</sup> s<sup>-1</sup>; maximum dark respiration: *c.* 0.3 μmol CO<sub>2</sub> m<sup>-2</sup> s<sup>-1</sup>) and a very low light compensation point (7 μmol photons m<sup>-2</sup> s<sup>-1</sup> at 8°C). The net photosynthesis/respiration quotient reached a maximum at 9–15°C. Photosynthetic activity was affected only after very severe desiccation, when high resaturation respiratory rates were measured. Microclimatic data were recorded under different weather conditions in an abyss of the Trieste Karst (northeast Italy), where the species was particularly abundant. Low photosynthetically active radiation (normally below 40 μmol photons m<sup>-2</sup> s<sup>-1</sup>), very high humidities (over 80%), and low, constant temperatures were measured. Thallus water contents sufficient for CO<sub>2</sub> assimilation were often measured in the absence of condensation phenomena.

**Key words** CO<sub>2</sub> gas exchange · Endolithism · Lichen · *Verrucaria baldensis* · Water content

### Introduction

Endolithic lichens are a highly specialized group of organisms that live embedded in calcareous substrata (Degelius 1962). Data on the metabolic performance of such organisms are rare (Lange et al. 1970; Wessels and Kappen 1993, 1994; Tretiach and Pecchiari 1995). This is for several reasons (Tretiach 1995): (1) the ecological importance of endolithic lichens has often been underestimated; (2) large, common genera such as *Thelidium* and *Verrucaria* are burdened with synonyms (Nimis

1993) and therefore the identification of many infrageneric taxa is uncertain; and (3) the substratum, which cannot be removed without damaging the lichen thalli, is a source of several methodological problems.

In temperate Europe, endolithic lichens are particularly abundant in habitats with high air humidity and low light, often being the major autotrophic components of cryptogamic communities of calcareous rocks. One of the commonest species is *Verrucaria baldensis* Massal., a shade-tolerant species that is particularly common in the darkest parts of abysses and gorges. The chlorophyll content of *V. baldensis* is the lowest ever found in endolithic lichens (Tretiach and Pecchiari 1995), and therefore its CO<sub>2</sub> gain is presumably very low. Surprisingly, however, the species has a very high biomass, approximately twice that of other endolithic species (Tretiach 1995). To explain this phenomenon, the CO<sub>2</sub> gas exchange of *V. baldensis* in relation to the environmental conditions of its habitat was investigated. CO<sub>2</sub> response curves were generated in the laboratory under different regimes of thallus water content, temperature, light and CO<sub>2</sub> concentration, and photosynthetic and respiratory optima were thus determined. Microclimate and thallus hydration values were measured in an abyss of the Karst plateau (northeast Italy) where *V. baldensis* forms pure stands over large surfaces, to determine at which environmental conditions the lichen is metabolically active. Furthermore, the desiccation sensitivity was tested, since the species typically occurs in habitats with constantly high humidity.

### Materials and methods

#### Plant material

*V. baldensis* is an endolithic lichen with a trebouxoid alga as photobiont, which occurs on hard calcareous or dolomitic rocks, in more or less shaded and moist situations. Species identification was problematic; the material, however, fits well with the detailed description given by Bricaud and Roux (1991). Voucher specimens are deposited in TSB, and are available upon request.

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## Study area

Sampling of specimens for laboratory measurements, and field-work, were carried out in the outer part of a karstic abyss, locally named Abisso di Gropada (Regional Cave Cadaster VG 46, 45°39'38"59 N, 13°51'07"44 E), located on the Karst Plateau (Trieste, Italy) at 410 m. The abyss is c. 100 m deep, and its mouth opens at the bottom of a small dolina, approximately 50 m in diameter; it is densely covered with deciduous trees, which considerably reduce the light during the growing season.

## The substratum

The substratum is a hard, homogeneous Cretaceous biomicrite with very low water retention (Cucchi and Gerdol 1989). No CO<sub>2</sub> release or absorption was detected when the substratum was watered. This result has been verified by Prof. O.L. Lange (Würzburg) with a Walz apparatus in open circuit, and agrees with dissolution data (Forti et al. 1975).

## Gas exchange measurements

Gas exchange measurements were carried out in the laboratory using fragments of substratum, completely covered on one side by well-developed lichen thalli, cut with a circular saw (mean thickness: c. 3–4 mm). Eight to ten fragments (total area 135–150 cm<sup>2</sup>) formed an experimental sample; previous experiments showed that this method gives reliable mean values (Tretiach 1995). The area of the samples was measured with a graphic tablet (HI-GRAPH II, Apple System, Houston Instruments). After the measurements, the samples were kept in dim, natural light at room temperature in a chamber lined with paper previously wetted by spraying distilled water. The same samples were used for generating the CO<sub>2</sub> response curves; this part of the study lasted approximately 40 days. Neither evident signs of damage, nor variation in CO<sub>2</sub> exchange rates were observed during this time.

The CO<sub>2</sub> exchange rates were measured in a closed system with an infrared gas analyzer (IRGA), model LICOR-6250 (Licor Inc., Lincoln, Neb, USA; estimated precision ±0.2–0.3 ppm CO<sub>2</sub>; cuvette volume 4,000 cm<sup>3</sup>; internal volume 130 cm<sup>3</sup>; flow rate 1,100–1,200 cm<sup>3</sup> min<sup>-1</sup>). The cuvette contained a fan for air stirring and sensors for sample and air temperature, air humidity and photosynthetically active radiation (PAR); these parameters were automatically recorded by a data-logger. Fresh weight was determined immediately after two or three measurements, each of them lasting 40 s. Because c. 40–60 s were necessary to reach a stable gradient of CO<sub>2</sub> depletion within the cuvette, each series of measurements lasted c. 2–3 min. Natural spectrum light was provided by an Osram HQI T250 W/B fluorescent tube; PAR flux in the 400–700 nm waveband was measured using a Licor Quantum meter model LI 185A inserted within the cuvette at the same position as the lichen thalli. To measure the variation of CO<sub>2</sub> exchanges in relation to temperature, the temperature of the whole laboratory was changed, and the lichen thalli kept at room temperature for at least 3 h before experiments. Increase in air temperature within the cuvette caused by the lamp was efficaciously limited by using a water bath.

## Water content, light, temperature and CO<sub>2</sub> response curves

Maximal net photosynthesis and dark respiration at different conditions for temperature, light and CO<sub>2</sub> concentration were calculated as the average of the two highest values of three to six CO<sub>2</sub> gas exchange curves obtained at decreasing thallus water content (Fig. 1). This method had the shortcoming that samples were submitted to frequent, unnatural drying-wetting cycles. To restore normal CO<sub>2</sub> exchanges it was necessary to keep some water for 10 min over the lichen surface at dim light (Tretiach 1995).

## Effects of desiccation on CO<sub>2</sub> exchange rates

Five samples (total area: c. 700 cm<sup>2</sup>) were kept humid overnight, and their gas exchange measured in the darkness (respiration) and at 200 μmol photons m<sup>-2</sup> s<sup>-1</sup> (net photosynthesis), at c. 15°C, normal CO<sub>2</sub> concentration and optimum thallus water content, from three to six times. Subsequently, the samples were put into a chamber containing silica gel for increasing times (2, 16, and 48 h). At the end of each drying cycle, the samples were weighed, and wetted with a water spray. The water film was left for 60 s, and the samples blotted with dry paper (lower surfaces) or humid paper (lichen surface), re-weighed, and introduced into the cuvette at increasing time intervals, always in the same order. Dark respiration was measured first, because in endolithic lichens it has a maximum at higher thallus water contents than net photosynthesis (Tretiach 1995). At the end of the measurements, the samples were re-weighed, copiously wetted, and put into a chamber lined with humid paper. Next day, the CO<sub>2</sub> exchanges were measured following the same procedure to verify whether they had been modified by the drying process. Afterwards, the samples were left to dry out in dim light, c. 16°C and 60% relative humidity (R(RH)), and put again into the chamber with silica gel for the following, longer drying cycle. The CO<sub>2</sub> gas exchange rates were expressed as a percentage of the maximum rate of each sample measured at the beginning of the experiment (c. 0.45 μmol CO<sub>2</sub> m<sup>-2</sup> s<sup>-1</sup>). The substratum was used as reference: when wetted, its CO<sub>2</sub> release was nil.

To verify how long the species could sustain severe desiccation without evident damage, the same samples were left in the chamber with silica gel for increasing times, from 1 week to 2 months. The CO<sub>2</sub> gas exchange measurements followed the usual procedure, with the only exception that increasing rewetting times were applied, from c. 12 to 48 h, in order to allow the completion of resaturation respiration (see Discussion).

## *In situ* measurements of thallus water content

These measurements were carried out with the Protimeter mini III (Protimeter plc., Marlow, UK), a portable instrument currently used to estimate the humidity content of solid, porous materials. The electronic circuit of the protimeter measures the resistance (from 1 kΩ to 20 GΩ, A. Boughtwood, protimeter plc., personal communication) of the substratum to the passage of a low voltage current between two needles driven in at a distance of 1 cm. The values are given as ordinal numbers, from 6 (low humidity) to 24 (high humidity). The substratum resistance depends upon several factors (chemical composition, porosity, conductivity of the solution, temperature), and therefore five thin fragments covered by lichen thalli and five fragments of substratum (area: c. 8–10 cm<sup>2</sup>; weight: c. 5 g) were used for calibration, according to a standard procedure. A thin water film was maintained on their surface for 10 min in dim light, at c. 15°C and 60% RH. The protimeter values were recorded, and the samples immediately weighed, at intervals of 5–10 min, until the thalli dried out and the lowest reading value was reached. The samples were oven-dried at 80°C to constant weight, and their area measured.

Hydration values of 10–12 individuals of *V. baldensis* were measured *in situ* in two vertical faces of the abyss every hour.

## Environment of collection site

Microclimatic measurements were carried out during selected days of October and November 1994 and in March 1995, at the bottom of the upper cavity of the VG 46 abyss at c. 1.8 m from the ground surface. They were: (1) air temperature (°C); (2) air relative humidity (%RH); (3) air saturation deficit (SD, mb); (4) photosynthetically active radiation [PAR, μmol photons (μE) m<sup>-2</sup> s<sup>-1</sup>]. The same parameters were simultaneously monitored in two sites at 10 cm from the rock surface of the vertical faces, together with the thallus temperature of several individuals of *V. baldensis*.

The following instruments were used: (1) Assmann aspirated psychrometer, to measure air temperature, % RH, SD; (2) Quantum Radiometer LI-COR, to measure the PAR flux; (3) digital thermometer with a touching thermocouple, to measure thallus temperature. Air dew-point temperature was calculated following Unwin (1980).

#### Statistics

Statistics were carried out with the programme Lotus (Microsoft). Polynomial curves of Figs. 3, 6 and 8 were obtained with the programme Curvefit (IMTEC, Bowie, Md., USA), while those of Figs. 1, 2, 4 and 5 were fitted to the data points by eye. In the captions to the figures, the mean values ( $\pm$ SD) of temperature, light, and CO<sub>2</sub> concentration during each series of measurements are given.

## Results

### Carbon dioxide exchanges

#### CO<sub>2</sub> exchange rates versus thallus water content

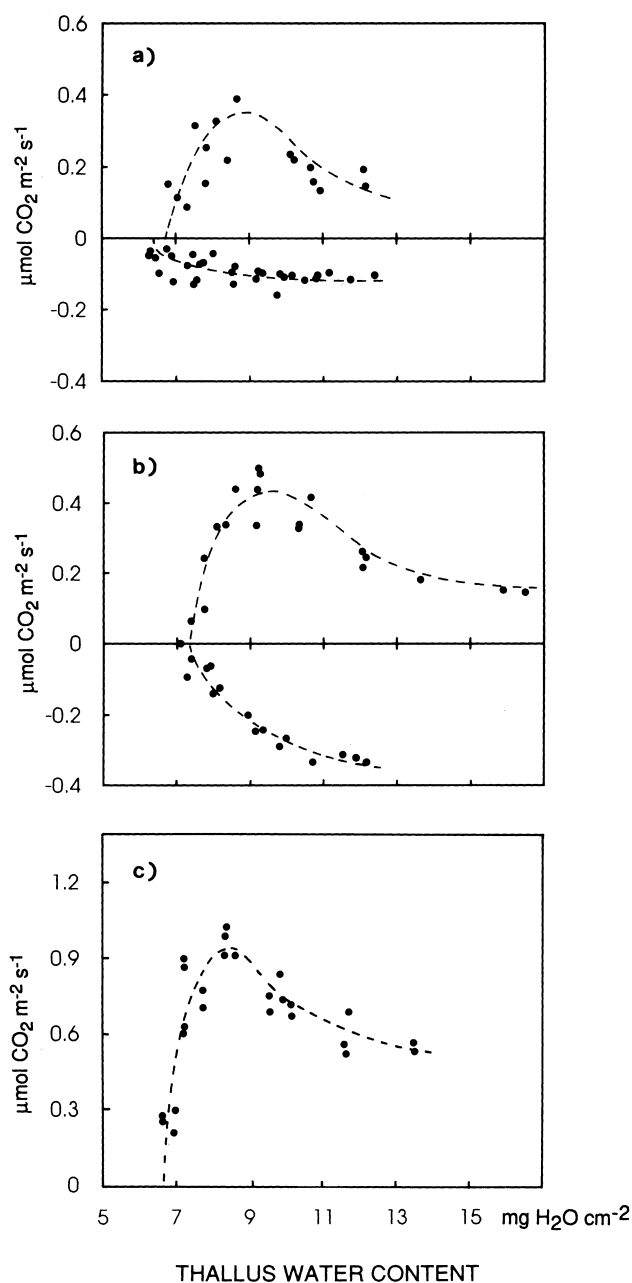
At 8 and 20°C and normal CO<sub>2</sub> partial pressure, gas exchange rates became detectable when thallus water content was *c.* 7 mg cm<sup>-2</sup>. The species reached the maximum net photosynthetic rate (0.45 μmol CO<sub>2</sub> m<sup>-2</sup> s<sup>-1</sup>) at *c.* 9 mg cm<sup>-2</sup> (Fig. 1b). At higher water contents photosynthesis was progressively inhibited: at 13 mg cm<sup>-2</sup>, when liquid water was present on the lichen surface, it was only 40–50% of the maximum value, although other epi- and endolithic lichens, such as *Aspicilia radiosa*, *Petractis clausa* and *Rinodina immersa*, showed more marked inhibition (Tretiach and Pecchiari 1995).

Dark respiration maxima ranged between -0.15 at 8°C and -0.35 μmol CO<sub>2</sub> m<sup>-2</sup> s<sup>-1</sup> at 20°C; it was not depressed by high thallus water contents, the rates being slightly higher at 12 than at 9 mg cm<sup>-2</sup>.

Water content response curves of net photosynthesis were also obtained at 1,300 ppm CO<sub>2</sub> (Fig. 1c): in such conditions maximum net photosynthetic rate was considerably higher (*c.* 1.1 μmol CO<sub>2</sub> m<sup>-2</sup> s<sup>-1</sup>) and the inhibition at high thallus water contents less conspicuous than at 360 ppm.

#### Temperature

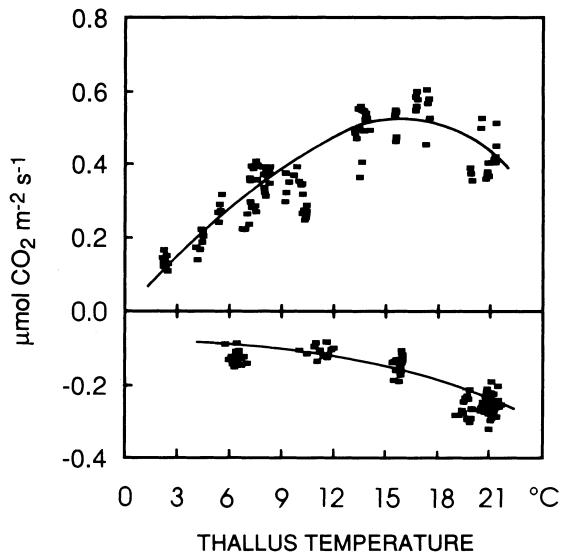
CO<sub>2</sub> gas exchange rates were measured over the temperature range 3–21°C, at normal CO<sub>2</sub> concentration. Light saturated net photosynthesis reached the maximum value (0.50 μmol CO<sub>2</sub> m<sup>-2</sup> s<sup>-1</sup>) at *c.* 16°C (Fig. 2). At 3°C net photosynthesis was only 0.15 μmol CO<sub>2</sub> m<sup>-2</sup> s<sup>-1</sup>, and increased almost linearly to the maximum. Respiration showed an exponential increase with temperature, from *c.* -0.15 μmol CO<sub>2</sub> m<sup>-2</sup> s<sup>-1</sup> at 6°C up to -0.3 μmol CO<sub>2</sub> m<sup>-2</sup> s<sup>-1</sup> at 21°C. The net photosynthesis/respiration quotient was particularly high in the temperature range 9–15°C.



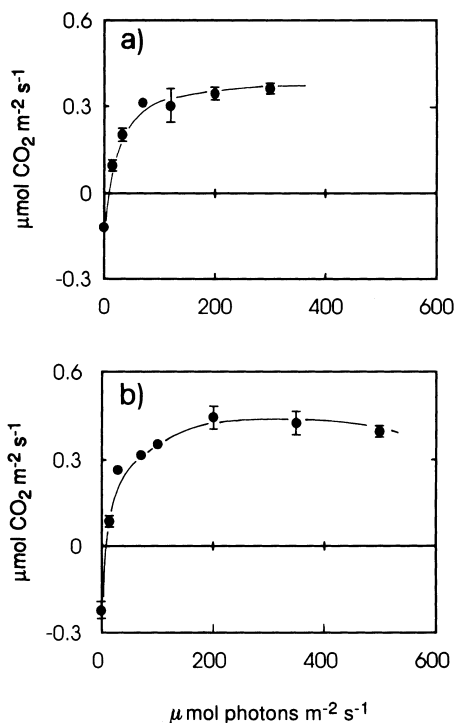
**Fig. 1** Dark respiration (negative values) and net photosynthesis (positive values) of *Verrucaria baldensis* at different thallus water contents (mg H<sub>2</sub>O cm<sup>-2</sup>) at **a** 200 μmol photons m<sup>-2</sup> s<sup>-1</sup>, 357 ± 6 ppm CO<sub>2</sub>, 7.5 ± 1.6°C, **b** 20.2 ± 0.7°C, and **c** 1,297 ± 18 ppm CO<sub>2</sub> and 20.2 ± 0.6°C

#### PAR

Saturation was reached at *c.* 200 μmol photons m<sup>-2</sup> s<sup>-1</sup> at both 8 and 20°C (Fig. 3). Light compensation values ranged between 7 and 11 μmol photons m<sup>-2</sup> s<sup>-1</sup> at 8 and 20°C, respectively. No decrease in net photosynthesis was detected at PARs as high as 200 μmol photons m<sup>-2</sup> s<sup>-1</sup> during the whole series of experiments.



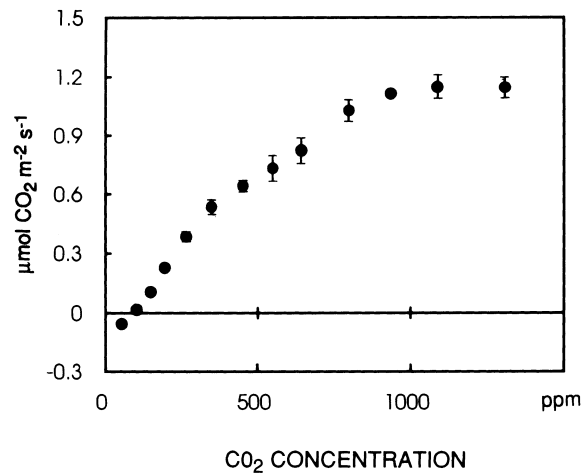
**Fig. 2** Relationship between temperature and CO<sub>2</sub> exchange rates in *V. baldensis*: net photosynthesis (positive values) and dark respiration (negative values) at optimal thallus water content, 200 μmol photons m<sup>-2</sup> s<sup>-1</sup>, and 357 ± 7 ppm CO<sub>2</sub>



**Fig. 3** Relationship between light and net photosynthesis in *V. baldensis* at **a** 8.2 ± 0.9 and **b** 19.9 ± 0.8°C, optimal thallus water content; μmol 356 ± 7 ppm CO<sub>2</sub>. Means are given ±SD unless exceeded by the symbol

#### Carbon dioxide concentration

Light-saturated net photosynthesis increased almost linearly with increase in external CO<sub>2</sub> concentration (Fig. 4). Saturation was apparently reached at the



**Fig. 4** Relationship between net photosynthesis (μmol CO<sub>2</sub> m<sup>-2</sup> s<sup>-1</sup>) and CO<sub>2</sub> concentration in *V. baldensis* at optimal water content, 20 ± 1°C, and 200 μmol photons m<sup>-2</sup> s<sup>-1</sup>. Means are given ±SD unless exceeded by the symbol

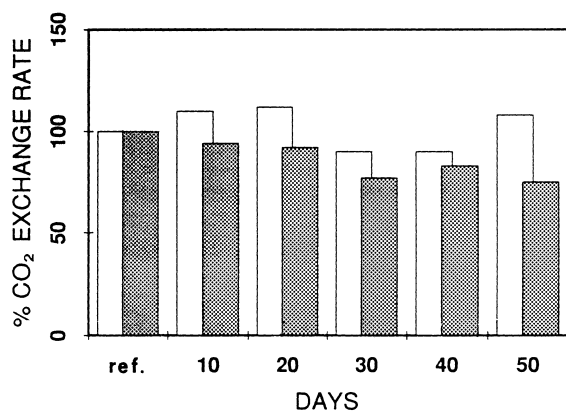
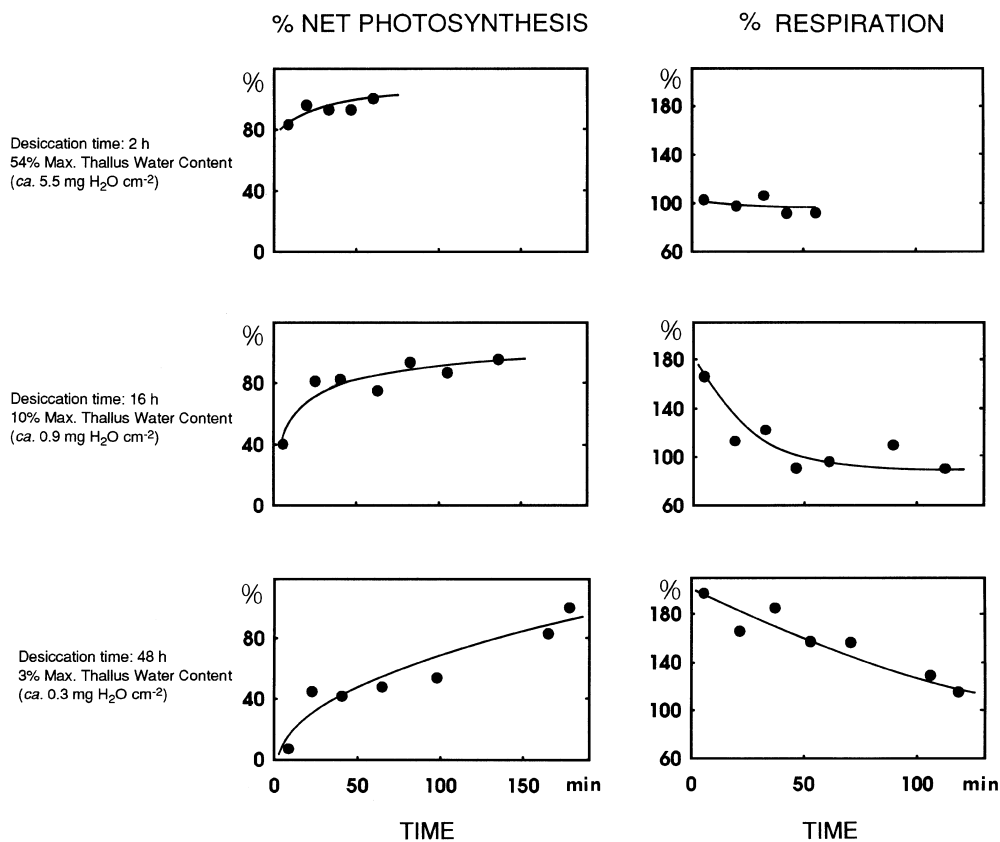
maximum value compatible to the IRGA used in the experiments (*c.* 1,300 ppm). Net photosynthesis at 360 ppm was lower than 50% of the rate measured at the upper CO<sub>2</sub> concentration limit; this value is comparable with previous results obtained for other endolithic lichens using the same technique (see Tretiach and Pecchiari 1995).

#### Effects of desiccation on CO<sub>2</sub> gas exchange rates

CO<sub>2</sub> exchanges of samples abruptly rewetted after prolonged desiccation are shown in Fig. 5. After 2 h over silica gel, the thallus water content was *c.* 54% of the maximum, corresponding to *c.* 5.5 mg H<sub>2</sub>O cm<sup>-2</sup>. When the lichens were wetted, dark respiration was soon re-established, being *c.* 100% of the normal value, whereas net photosynthesis was lower (*c.* 80% of the normal value) in the first few minutes; however, it soon recovered, and after *c.* 20 min the normal value was reached. When the lichens experienced more pronounced dehydration, dark respiration strongly increased ("resaturation respiration" *sensu* Smith and Molesworth 1973), and the time necessary to achieve normal gas exchange activity was evidently longer. Thus, after 16 h over silica gel, when thallus water content was reduced to only 10%, dark respiration was 180% higher than usual, and *c.* 1 h was necessary to re-establish the routine activity. After 48 h of desiccation, when the thallus water content was reduced to only 3%, dark respiration was still slightly higher (*c.* 190%), and standard values were measured only after 2 h.

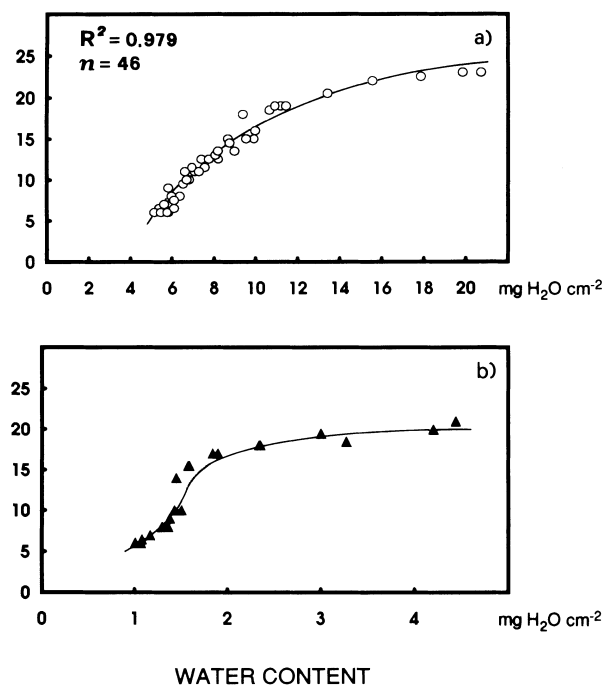
Long-term consequences of the drying treatment were assessed by repeated gas exchange measurements on experimental thalli held for increasingly longer periods in sealed chambers containing silica gel. Such samples were rewetted and kept humid for progressively

**Fig. 5** Percentage variation of  $\text{CO}_2$  gas exchange rates measured at optimal conditions in five samples of *V. baldensis* at increasing time intervals after thallus rehydration. 100% =  $0.45 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$



**Fig. 6** Percentage variation of  $\text{CO}_2$  gas exchange rates measured at optimal conditions in five samples of *V. baldensis* kept dry for increasing time intervals (days): □ dark respiration; ▨ net photosynthesis; ref.: reference. 100% =  $0.45 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$

longer times in order to allow the completion of resaturation respiration. The results are reported in Fig. 6. Dark respiration did not change considerably even after 50 days, when thallus water content was only  $0.1 \text{ mg H}_2\text{O cm}^{-2}$ . In contrast, net photosynthesis progressively declined, being reduced to 75%.



**Fig. 7** Calibration curves of the Protimeter Mini III obtained with samples of **a** *Verrucaria baldensis* and **b** rock, at  $15^\circ\text{C}$ , 10 min after wetting the upper surface of the samples with distilled water

Calibration curves for the estimation of thallus water content *in situ*

The correlation between thallus water contents and values obtained with the protimeter are shown in Fig. 7. No significant differences were detected among the samples of *V. baldensis* (Fig. 7a) or among those of pure limestone (Fig. 7b). The data spread was very low and consequently the polynomial fitting curve relative to *V. baldensis* was highly significant ( $r^2 = 0.947$ ,  $n = 46$ ), and different from that relative to the substratum (Fig. 7b). At 5°C the values did not change significantly. Curves similar to that of Fig. 7 were obtained also in five other epi- and endolithic lichens (see e.g. Tretiach 1995), suggesting that the protimeter can be appropriately used to quantify the water content of endolithic lichens *in situ*.

#### Lichen environment

Field measurements showed that the habitat of *V. baldensis* is characterized by dim light, high air humidity and stable, low temperatures. PAR levels were always very low, with maximum values of *c.* 40  $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ , and below 10  $\mu\text{mol photons m}^{-2} \text{s}^{-1}$  for most of the day. Air humidity was always very high, with minimum values rarely lower than 80%. Temperatures ranged between 6°C and 10°C, probably representing normal values for most of the year.

The microclimatic conditions within the abyss during heavy, persistent rain (*c.* 40 mm/day) are shown in Fig. 8 (bottom). Low air temperatures and PAR values, and water vapour saturation (100% RH) were constantly recorded from sunrise to sunset. Thallus hydration increased regularly during the whole day, reaching a maximum value at the end of the day, because the low temperature of the substratum determined a consistent dew fall (Fig. 8, top). In contrast, water percolation affected only areas mainly covered by bryophytes such as *Homalothecium sericeum*, *Plagiochila asplenoides* and *Thamnium alopecurum*.

The constant increase in thallus hydration during the central hours of the day was verified under different weather conditions. Figure 9 shows microclimatic conditions (bottom) and thallus hydration (top) recorded after a rainy night that followed several days with persistent, dry winds ("bora"). The thalli evidently began to absorb air water vapour during the night, and the phenomenon continued during the whole day because air humidity remained around 93–97% due to percolation of water down the vertical faces of the abyss, whereas radiation was too low to warm up the thalli. During sunny days, when air humidity was lower (between 80 and 92%), *V. baldensis* also showed a consistent variation in thallus hydration (Fig. 10), that was evidently related to water vapour absorption and to brief dew-fall events (Fig. 10, arrow). The other endolithic lichens investigated so far (*Acrocordia conoidea*, *Petractis clausa*, *Rinodina immersa*, *Verrucaria marmorea*) are not

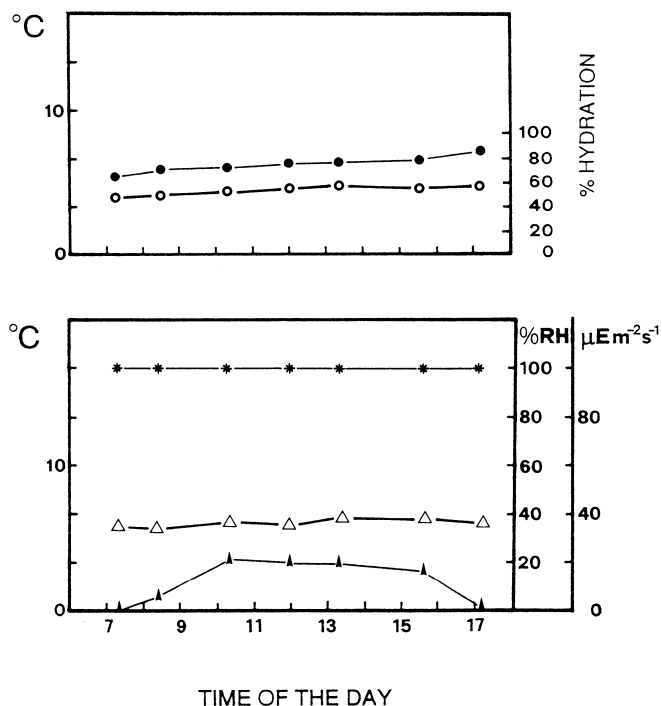


Fig. 8 Lichen hydration (●) and thallus temperature (○, top), and microclimatic data (bottom) measured in the study area on 3 March 1995 during heavy, persistent rain: (\*, %RH) air humidity; (▲,  $\mu\text{E m}^{-2} \text{s}^{-1}$ ) light, and (Δ, °C) air

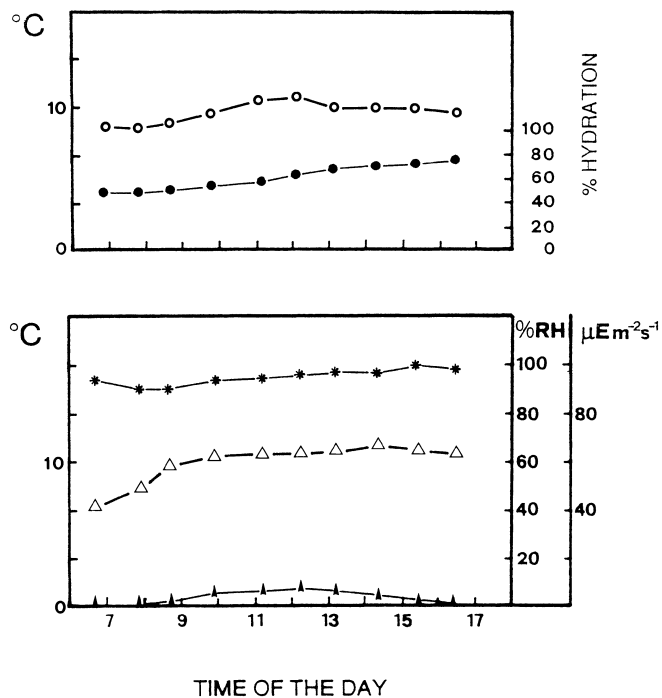


Fig. 9 Lichen hydration (●) and thallus temperature (○, top), and microclimatic data (bottom) measured in the study area on 27 October 1994 after a rainy night: (\*, %RH) air humidity, (▲,  $\mu\text{E m}^{-2} \text{s}^{-1}$ ) light, and (Δ, °C) air

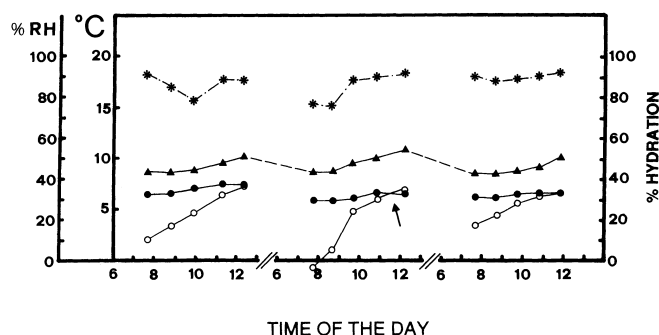


Fig. 10 Lichen hydration ( $\blacktriangle$ , %), thallus temperature ( $\bullet$ ,  $^{\circ}\text{C}$ ), air dew-point ( $\circ$ ,  $^{\circ}\text{C}$ ), and air humidity ( $*$ , %RH) measured in the study area on three sunny days in November 1994

as efficient as *V. baldensis* in water vapour absorption (data not shown).

## Discussion

*V. baldensis* was shown to have several features typical of a shade-adapted autotrophic organism; for instance, the species performed efficiently at low light intensities: net photosynthesis was light-saturated at values lower than  $200 \mu\text{mol photons m}^{-2} \text{s}^{-1}$  and compensation ranged between 7 and  $11 \mu\text{mol photons m}^{-2} \text{s}^{-1}$  (Fig. 3). Both these values are low in comparison to other endolithic lichens (see Tretiach 1995; Tretiach and Pecchiari 1995), and are more similar to those of the foliose lichen *Pseudocyphellaria dissimilis*, a highly shade-adapted lichen that occurs on the floor of lowland, evergreen forests of Australasian regions (Galloway 1988). In that species, light compensation is only  $1 \mu\text{mol photons m}^{-2} \text{s}^{-1}$ , and net photosynthesis is saturated at only  $20 \mu\text{mol photons m}^{-2} \text{s}^{-1}$  (Green et al. 1991). However, in *P. dissimilis* the photobiont cells are covered by a plectenchymatic layer of thin-walled cells (Galloway 1988), whereas those of *V. baldensis* are covered not only by hyphae, but also by calcite crystals. Therefore, the fraction of incident light reaching the photobiont cells is probably considerably lower due to reflection and absorption, as discussed by Nienow et al. (1988). In many shade-demanding lichens, net photosynthesis is highly inhibited by high photon flux densities (Demmig-Adams et al. 1990), and photoinhibition could be considered as a further character that distinguishes shade- and sun-loving plants. *Acrocordia conoidea*, the only other shade-demanding endolithic lichen studied so far, proved to be rather sensitive to high radiation levels (Tretiach and Pecchiari 1995); however, the wide data spread suggests caution in interpretation.

Other typical features of a shade-loving phototrophic organism (see Boardman 1977) are the low net photosynthetic and respiratory rates (approx. 0.45 and  $0.3 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ , respectively: see Fig. 1) when expressed on an area basis. Other endolithic lichens from the Trieste Karst have higher rates, ranging between

$0.75$  (*V. marmorea*, see Tretiach 1995) and  $1.3 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$  (*Rinodina immersa*, see Tretiach and Pecchiari 1995). However, the maximum photosynthetic rate of *V. baldensis* is similar to those of other endolithic species when it is expressed on a chlorophyll basis (c.  $6.2 \text{ nmol CO}_2 \text{ mg Chl}_a^{-1} \text{ s}^{-1}$ ), because *V. baldensis* has a very low chlorophyll content (data from Tretiach and Pecchiari 1995, Table 1).

Shade plants usually have a low weight per unit area (Boardman 1977, Green et al. 1991). However, this is not the case of *V. baldensis*, which has the highest biomass among endolithic lichens (c.  $11.7 \text{ mg cm}^{-2}$ : Tretiach 1995). A substantial part of it is contributed by fatty acids, stored in the so-called oil hyphae (Zukal 1886). Such structures are common to many endolithic lichens (Kushnir et al. 1978); however, their abundance in *V. baldensis* should certainly be regarded as exceptional. Because the species is incapable of high  $\text{CO}_2$  gain, the high biomass is probably related to the microclimatic conditions within the karstic cavity. For instance, after rain thalli remain humid longer in the abyss than in external habitats, because of lower evaporation. Furthermore, in the abyss dew-fall typically occurs during the central hours of the day and not before sunrise, as in exposed habitats. This is due to the peculiar temperature regime within the cavity: immediately after sunrise, rock surfaces are warmer than air. However, during the day rock temperature increases more slowly than air temperature because of the thermal inertia of the substratum, and the dew-point temperature is thus often reached because the air is nearly water-vapour saturated. Therefore, it can be hypothesized that during the night, when only respiration occurs,  $\text{CO}_2$  release is scarce because thallus water content is low, whereas during the day water absorption from the air and dew-falls allow relatively high assimilation rates. It is unlikely that such high humidity values are constant throughout the year. In submediterranean regions, short periods of prolonged dryness are not rare in summer, when sunflecks are more frequent at the bottom of the karstic cavities because the sun is higher above the horizon. In this season *V. baldensis* is likely to experience frequent thallus dehydration without serious consequences, because the species can certainly be regarded as desiccation-resistant (Fig. 6). Furthermore, no organic substrata are lost by resaturation respiration, because this is negligible when the lichen is at equilibrium with 40% air RH, although it becomes important when the thallus has sustained more intense desiccation (Fig. 5).

Of course, the biomass of a crustose lichen is something more than the mere integration of photosynthetic and respiratory rates over time; for instance, the net income is used for the production of spores or vegetative propagules, or to repair damage possibly caused by animals. However, in *V. baldensis* both these factors are probably negligible, because the species typically has abortive spores, and endolithic lichens are only seldom eaten by snails, epilithic lichens being usually preferred (Fröberg et al. 1993). In fact, no damage by snail radulas

was observed in the field on the thalli of *V. baldensis*, although snails are particularly abundant on the humid faces of the abyss. A further important factor influencing the lichen biomass is the mean age of the sampled population. Unfortunately, this cannot be easily determined, although a karstic abyss can be certainly regarded as a conservative habitat, and the thalli of *V. baldensis* as very old ones. At the study site they cover almost all the available surfaces: the absence of free space implies that for a long time the endolithic thalli have grown only in depth, and not at their margins. Therefore, the unusually high biomass of *V. baldensis* could be the result of prolonged, unidimensional growth under constant ecological conditions.

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