PHOTOSYNTHETIC PERFORMANCE OF TWO CLOSELY RELATED *UMBILICARIA* SPECIES IN CENTRAL SPAIN: TEMPERATURE AS A KEY FACTOR

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Abstract: Net photosynthesis (NP) and dark respiration (DR) of thalli of the lichen species *Umbilicaria grisea* and *U. freyi* growing together in the same habitat in the Sierra de Guadarrama, central Spain, were measured under controlled conditions in the laboratory and under natural conditions in the field over a range of photosynthetic photon flux densities (PPFD), thallus temperatures and thallus water contents. Laboratory experiments revealed that the photosynthetic response to PPFD at optimum thallus water content is very similar in both species. The light compensation points of NP increased from PPFD of *c.* 20 μmol m^{-2} s^{-1} at 0°C up to *c.* 100 μmol m^{-2} s^{-1} PPFD at 25°C. In both species light saturation was not reached up to 700 μmol m^{-2} s^{-1} PPFD except at 0°C. By contrast, the temperature dependence of CO$_2$ gas exchange differed substantially between *U. grisea* and *U. freyi*. Both species gave significant rates at 0°C. Optimal temperatures of NP were always higher in *U. grisea* at various PPFD levels if the samples were kept at optimal thallus water content. NP showed maximal rates at 95% dw in *U. grisea* and 110% dw in *U. freyi* respectively. In *U. grisea* a much stronger depression of NP was observed with only 5% of maximal NP reached at 180% dw. At all PPFD and temperature combinations *U. freyi* showed higher rates of NP and more negative rates of DR if calculated on a dry weight basis. This was also true under natural conditions at the same site, when *U. freyi* was always more productive than *U. grisea*. The differences in the photosynthetic response to temperature between both species correlated well with the different distribution patterns of both species. The possibility of genetic control of the physiological performance of these species and its influence on their distribution patterns and autecology is discussed.

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Introduction

For many Arctic-Alpine and Antarctic lichen species significant physiological adaptations to microhabitat and seasonal variations have been described (see Kershaw 1985; Kappen 1988). It is known that in several species the intraspecific variability of the light and temperature optimum of photosynthesis in a population through different microhabitats and seasons seems to be greater than the interspecific variability within the same community (Kappen 1985; Schipperges 1994). In this case the question arises whether taxonomically closely related species that grow at the same locality differ in their ecophysiological behaviour or if an adaptive convergence in the ecophysiological response caused by the influence of the microhabitat occurs. Furthermore, in the case of species with a widespread altitudinal and

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latitudinal distribution, the question is whether its distribution pattern reflects more an ecological adaptation capability or their tolerance to the environmental conditions.

In the lichen genus *Umbilicaria* several species have been recognized as 'Artenpaare' (species pairs, Poelt 1972; see DuRietz 1925; Frey 1936*a*; Poelt 1977) or have been understood as anamorph-teleomorph pairs of taxa postulating a relationship with evolutionary trends (Hestmark 1991*a*, *b*). In these species pairs both taxa show the same morphology and chemistry but differ in reproductive strategies. For some species that do not constitute a 'species pair', such as *U. aprina-U. africana*, close phylogenetic connections based on morphological and distributional patterns have also been proposed (Hestmark 1991*a*). However, no ecophysiological data are available that might confirm the proposed evolutionary trends and adaptative strategies.

Umbilicaria grisea Hoffm. and *U. freyi* Codogno, Poelt & Puntillo constitute a very good example of closely related *Umbilicaria* species, although they cannot be recognized as a species pair in the strict sense. Within the genus *Umbilicaria*, *U. freyi* and *U. grisea* together with *U. hirsuta* (Sw. ex Westr.) Hoffm. constitute a well-defined taxonomic group. They share many morphological, anatomical, chemical and ecological characteristics (Codogno *et al.* 1989; Sancho *et al.* 1991; Valladares 1993). *Umbilicaria grisea* is widely distributed from North Africa to the Scandinavian Peninsula with a wide altitudinal range (0–1600 m a.s.l.: Frey 1936*b*; Hakulinen 1962; Wirth 1980), while *U. freyi* is known only from the western Mediterranean region, where it is abundant in the mountains of the Italian and Iberian Peninsulas (1100–1600 m a.s.l.: Codogno *et al.* 1989; Sancho *et al.* 1991). In some of these localities it grows sympatrically with *U. grisea*.

As a first step towards a better understanding of the ecological strategies of these two closely related species ecophysiological investigations of samples of *U. grisea* and *U. freyi* growing together in the same microhabitat under similar microclimatic conditions were carried out by means of CO_2 exchange measurements in the laboratory under controlled conditions and at the natural site.

Materials and Methods

Site description and plant material

In the Sierra de Guadarrama, north-western Mediterranean region, *Umbilicaria grisea* Hoffm. and *U. freyi* Codogno, Poelt & Puntillo often grow together on sheltered surfaces, sometimes in small water-seepage channels in a narrow altitudinal belt between 1100 m and 1600 m. They grow mainly on strongly inclined or vertical rock surfaces, more or less protected from rainfall.

The material for the laboratory experiments was collected in July 1993 near La Morcuera pass (1550 m, Sierra de Guadarrama, Madrid) from a vertical granitic rock with a NE exposure. The lichens were transported in the air-dry state to the laboratory at Kiel, Germany. The experiments started within three days after collection in order to avoid acclimation effects. Before the beginning of the experiments the lichen samples were activated by spraying with deionized water regularly in a growth chamber (Rubarth, Germany) at 10°C, 70% relative humidity (RH) and a 12/12 h dark/light regime (photosynthetic photon flux density, PPFD=100 µmol m^{-2} s^{-1}). All laboratory experiments were done with specimens from the same locality and microhabitat. To investigate the photosynthetic performance of both species in their natural habitat, field experiments were carried out in the vicinity of this locality at the same altitude and exposure. Field

experiments started in October when the first rainfall initiated the end of the dry season and enabled *in-situ* metabolic activity of the poikilohydrous lichen thalli. Because the lichens were metabolically inactive for the dry season it is assumed that the lichens are in the same seasonal stage as in July when the samples for the laboratory experiments were collected.

Laboratory measurements

CO_2 exchange was measured in the laboratory as the difference between the air passed through a cuvette containing lichens and the ambient air using an infrared gas analyser (IRGA; Binos, Leybold-Haereus, Germany) in an open-flow system (Walz, Germany), as described in Sancho & Kappen (1989). Two incandescent lamps (HQIL 1000 W, Osram, Germany) served as light sources with plexiglass neutral grey filters to reduce PPFD as necessary. PPFD was monitored inside the cuvettes (LI 190 SB, LiCor, USA). The water vapour concentration in the cuvettes was kept near dewpoint by bubbling the air through water flasks kept at the same temperature as the cuvettes.

Each cuvette contained four to eight mature thalli (0·6–1·1 g dry weight). The samples were hydrated by spraying with deionized water and blotted with filter paper to remove adhering surface water. The samples were hydrated individually at the beginning of the measurement of each PPFD/temperature combination. A slow dehydration of the thalli at each combination was allowed and CO_2 gas exchange was monitored continuously until the maximal photosynthetic rate was clearly reached. Therefore, only CO_2 gas exchange rates at optimal water content, i.e. when CO_2 gas exchange was maximal, were considered for data evaluation. Four sets of each species were used, two replicates in parallel cuvettes at 10, 5 and 0°C and another two sets at 10, 15, 20 and 25°C. This procedure avoided adaptive effects or stress from extensive exposure in the cuvettes (Sancho & Kappen 1989). For each temperature five levels of PPFD and darkness were measured. The net photosynthetic response was calculated on an oven dry weight (dw) basis (105°C, 24 h).

Net photosynthesis response to thallus hydration was studied using a minicuvette gas exchange system (CMS400, Walz, Germany). This system allowed accurate measurements of CO_2 and H_2O exchange using a differential IRGA (Binos 100, Fisher-Rosemount, Germany) together with control of temperature and RH in the cuvette (300 ml volume, for further details see Schroeter *et al.* 1994). For this experiment the cuvette was set to 10°C, 70% RH, with an air stream of 800 ml min^{-1} and a PPFD of 400 µmol m^{-2} s^{-1} provided by a lighting unit (FL-400, Walz, Germany). The value of NP was recorded and the water content of the thalli was measured gravimetrically every 20 min until the CO_2 exchange readings gave zero. Prior to the first weighing, thalli were fully saturated and shaken to remove adherent surface water. For each species three independent experiments using different thalli of similar size, were carried out. Water content was calculated on an oven dry weight basis individually for each sample (105°C, 24 h).

Field measurements

A field laboratory was installed in an igloo tent close to a big granitic rock, about 0·5 km from the Estación de Biogeologia del Ventorrillo (CSIC), Sierra de Guadarrama, Madrid, at 1550 m altitude. The rock was more or less cubical, 4–6 m high and 4–5 m wide. It was almost totally covered by mosses and lichens. On this rock *Umbilicaria freyi* and *U. grisea* occur only on vertical surfaces with a north-east exposure. The northerly and westerly exposed side walls showed a rich cryptogamic vegetation with many others species of the family Umbilicariaceae (*U. polyphylla*, *U. crustulosa*, *U. polyrrhiza*, *U. spodochroa*, *Lasallia hispanica*, *Lasallia pustulata*) together with other macrolichens such as *Parmelia omphalodes*, *P. saxatilis*, *Platismatia glauca* and *Pseudevernia furfuracea*. The eastern and southern vertical walls were also densely covered by lichens but not as much by mosses.

The CO_2 exchange in the field was measured using a CO_2/H_2O porometer (CQP 130, Walz, Germany), as described by Lange *et al.* (1984). For a detailed description see Kappen *et al.* (1990). The CO_2 exchange was monitored by a differential IRGA (Binos 100, Fisher-Rosemount, Germany) connected with a cooling trap (MGE 130, Walz, Germany). Diurnal courses of CO_2 gas exchange of two thalli of *Umbilicaria freyi* and *U. grisea*, respectively, were measured at 20-min intervals. A series of four to five measurements was registered for every sample at every interval

to ensure steady-state conditions. Between the measurements samples were exposed to ambient conditions at their natural site. Temperature probes at the lichen site together with Peltier temperature control ensured that the cuvette temperature was the same as at the lichen habitat. The measuring cuvette was exposed at the same angle to the sun as the rock surface. Five days (15–19 October 1993) of field measurements were carried out with lichens naturally hydrated by rain. On 16 October several hours of heavy rainfall interrupted the daily course of CO_2 measurements. From 19 October on, dry weather conditions prevented further diurnal measurements of CO_2 gas exchange in the lichens under natural hydration conditions.

Pigment analysis

Chlorophyll content was determined at the end of the experiments within two weeks according to the method of Barnes et al. (1992). The samples were washed with 100% $CaCO_3$-saturated acetone and the chlorophyll was extracted in $CaCO_3$-saturated dimethyl sulphoxide. Extinction coefficients of chlorophyll a+b were determined by means of an Uvikon 930 spectrophotometer (Kontron Instruments, Japan).

Data evaluation

CO_2 exchange data were related to total chlorophyll content and oven dry weight (24 h, 105°C) using a calculation and plot programme PHOTOPLOT (B. Schroeter and W. Heitland; unpublished). Graphs and curve fittings were produced using SIGMAPLOT 5·0 (Jandel, USA). The curves of net photosynthesis related to thallus temperature were fitted using polynomial regressions (2nd degree). The temperature optimum of photosynthesis was calculated as the point at which the derivate to the polynomial regression becomes zero. Upper and lower temperature compensation points were calculated from the polynomial regressions if not reached within the measured temperature range. The curves of net photosynthesis related to PPFD were fitted on the data using the Levenberg-Marquardt-algorithm (Seber & Wild 1989) in the equation:

$$NP(PPFD) = NP_{maxPPFD} - (NP_{maxPPFD} - DR)^* exp^{(k^* PPFD)}$$

with $NP_{maxPPFD}$=net photosynthesis at maximum PPFD, DR=dark respiration and k= coefficient (see Schroeter 1991; Schroeter et al. 1995).

Light saturation and the light compensation point were calculated from the curve fittings for each temperature measured.

Results

Laboratory measurements

Light-dependent CO_2 exchange is shown for *Umbilicaria grisea* and *U. freyi* in Fig. 1. The light response of net photosynthesis was similar in both species. With increasing temperature the light compensation point of CO_2 exchange increased from 20 µmol m^{-2} s^{-1} PPFD at 0°C to about 93 µmol m^{-2} s^{-1} PPFD at 25°C in *U. grisea* and from 22 µmol m^{-2} s^{-1} PPFD at 0°C to about 104 µmol m^{-2} s^{-1} PPFD at 25°C in *U. freyi* (Fig. 1). Light saturation of net photosynthesis was reached in *U. grisea* at about 650–700 µmol m^{-2} s^{-1} PPFD and in *U. freyi* at about 700 µmol m^{-2} s^{-1} PPFD at 0°C, but no light saturation was reached within the measured range of PPFD (up to 700 µmol m^{-2} s^{-1}) at temperatures above 5°C in both species.

Figure 2 depicts the temperature dependency of CO_2 exchange, related to dry weight, at various levels of PPFD for *U. grisea* and *U. freyi*. Regardless of the calculation basis (dry weight or chlorophyll content, not shown here) the temperature optimum of net photosynthesis increased with increasing PPFD level in *U. grisea* as well as in *U. freyi*. Whereas the temperature optimum in *U. grisea* was at *c.* 5°C at low PPFD (50–100 µmol m^{-2} s^{-1}), no pronounced
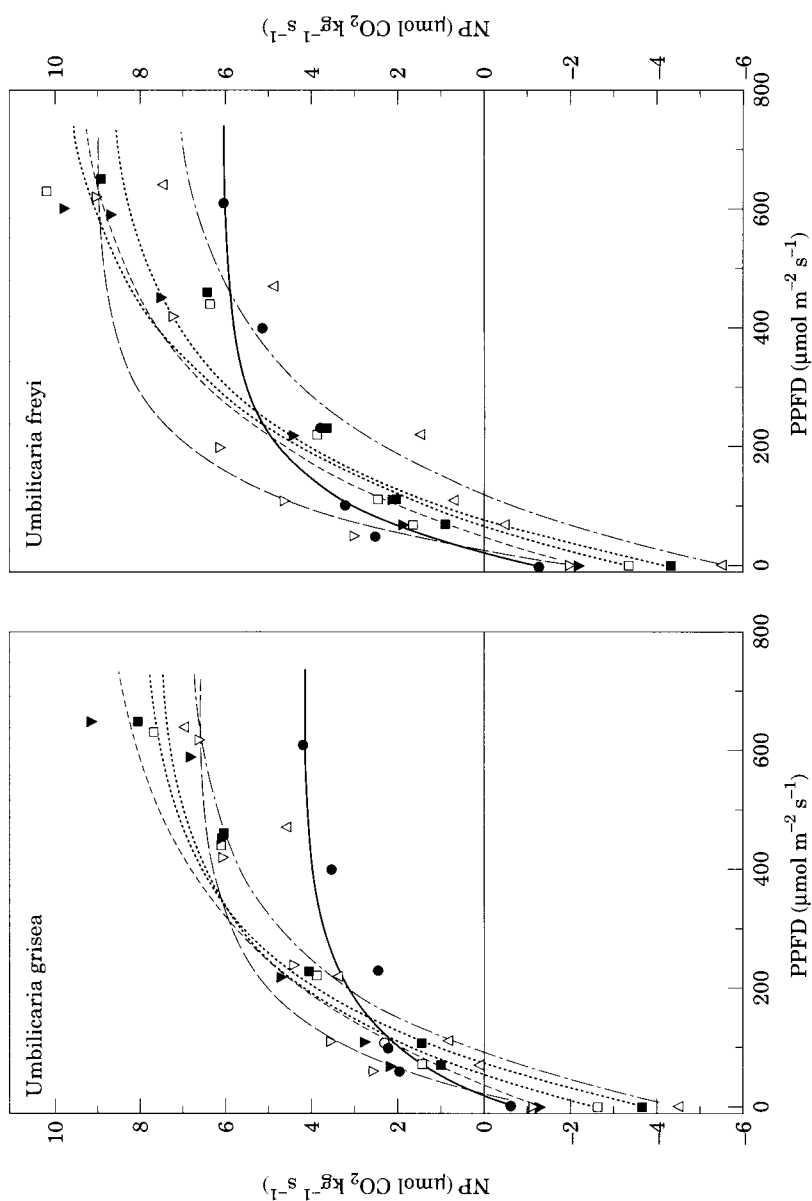
FIG. 1. Effect of PPFD at different temperatures on net photosynthesis (NP) related to oven dry weight in *Umbilicaria grisea* and *U. freyi*. All measurements were carried out at optimal water content. Each data point represents the mean of 2–4 replicates. Different symbols represent different temperature levels: 0°C (●), 5°C (▽), 10°C (▼), 15°C (□), 20°C (■), 25°C (△). Curves were fitted using the Levenberg-Marquardt-algorithm as described in the method section. *U. grisea*: $r^2 = 0.8659$ (0°C), 0.9533 (5°C), 0.9289 (10°C), 0.9741 (15°C), 0.9707 (20°C), 0.9585 (25°C). *U. freyi*: $r^2 = 0.8927$ (0°C), 0.9437 (5°C), 0.9776 (10°C), 0.9285 (15°C), 0.9529 (20°C), 0.9360 (25°C).
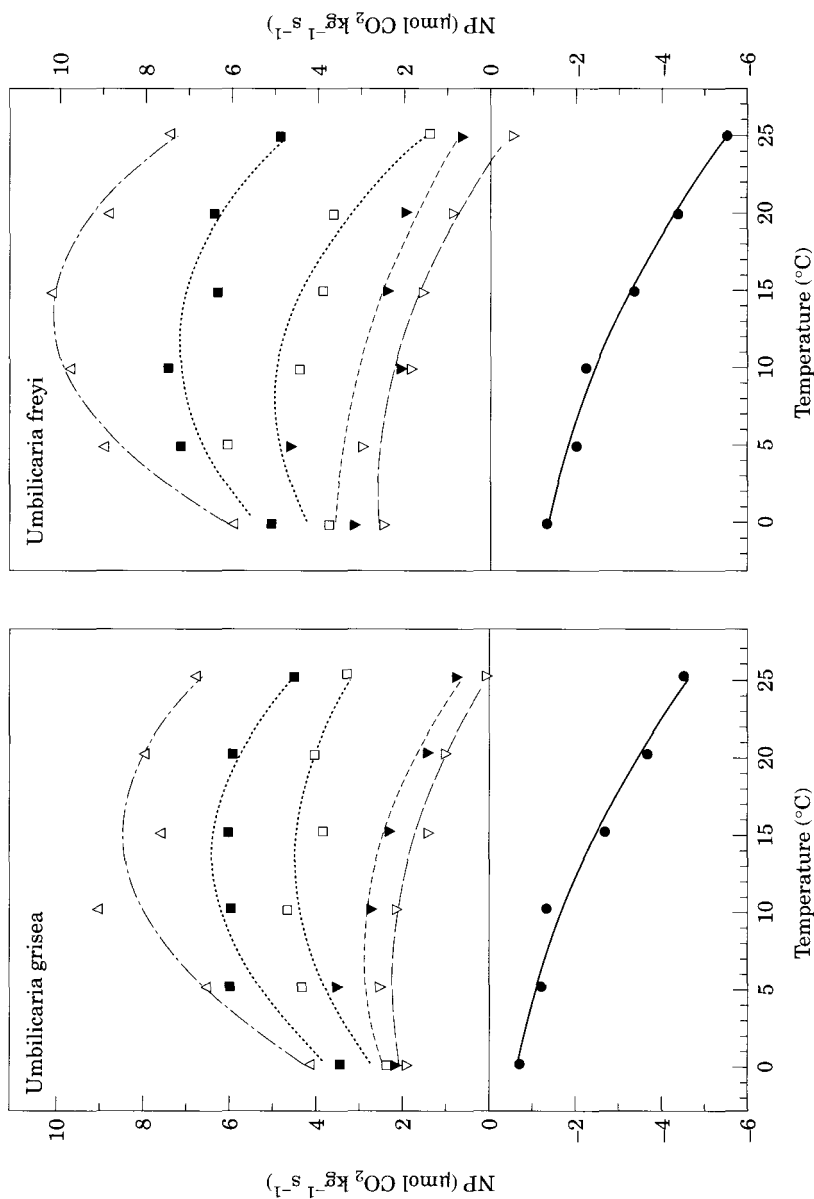
FIG. 2. Effect of temperature on net photosynthesis (NP) at different PPFD levels and on dark respiration related to dry weight in *U. grisea* and in *U. freyi*. All measurements were carried out at optimal water content. Each data point represents the mean of 2–4 replicates. Different symbols represent different PPFD levels: darkness (●), 60–70 μmol m^{-2} s^{-1} (▽), 110 μmol m^{-2} s^{-1} (▼), 220–240 μmol m^{-2} s^{-1} (□), 400–470 μmol m^{-2} s^{-1} (■), 610–650 μmol m^{-2} s^{-1} (△). Curves were fitted using a second-order polynomial regression. *U. grisea*: $r^2 = 0.9899$ (0), 0.9757 (60), 0.9204 (110), 0.8512 (220), 0.937 (400), 0.9261 (650). *U. freyi*: $r^2 = 0.9957$ (0), 0.976 (60), 0.8375 (110), 0.8861 (220), 0.9042 (400), 0.9840 (650).

TABLE 1. *Main ecophysiological parameters in* Umbilicaria grisea *and* U. freyi

Parameter*	U. grisea	U. freyi
Chl. a+b (mg g dw^{-1}) (mean of 6 replicates)	$1 \cdot 09 \pm 0 \cdot 115$	$1 \cdot 66 \pm 0 \cdot 179$
WCopt (% dw)	91–101	108–115
WCmax (% dw)	174–183	200–206
LCP5 (μmol m^{-2} s^{-1})	22	25
LCP20 (μmol m^{-2} s^{-1})	74	80
Topt220 (°C)	13·4	7·8
Topt650 (°C)	14·9	13·5
NPmax5 (μmol CO$_2$ kg^{-1} s^{-1}/mg CO$_2$ mg Chl h^{-1})	4·3/0·57	6·2/0·59
NPmax20 (μmol CO$_2$ kg^{-1} s^{-1}/mg CO$_2$ mg Chl h^{-1})	4·1/0·55	3·6/0·35

*Total chlorophyll content (Chl. a+b); optimal water content (WCopt); maximum water content (WCmax); light compensation point at 5°C (LCP5) and at 20°C (LCP20); optimum temperature at 220 μmol m^{-2} s^{-1} (Topt220) and at 650 μmol m^{-2} s^{-1} (Topt650); maximum rate of net photosynthesis at 220 μmol m^{-2} s^{-1}, at 5°C (NPmax5) and 20°C (NPmax20) related to dry weight and total chlorophyll content.

temperature optimum was found at these PPFD levels down to 0°C in *U. freyi*, although both species showed substantial rates of CO$_2$ gas exchange at 0°C. At higher PPFD levels (200–700 μmol m^{-2} s^{-1}) the temperature optimum increased in *U. grisea* from 13·4 to 15°C (Fig. 2). In contrast, the temperature optimum of net photosynthesis in *U. freyi* increased from 7·8°C at 220 μmol m^{-2} s^{-1} up to 13·5°C at 650 μmol m^{-2} s^{-1} (Table 1). This difference is also reflected in the maximal net photosynthetic rate at 220 μmol m^{-2} s^{-1}, when *U. grisea* maintained its level of net photosynthesis between 5°C and 20°C, while in *U. freyi* the maximal net photosynthetic rate decreased at 20°C to more than 40% of its rate at 5°C (Fig. 2). The differences in the temperature response of net photosynthesis between both species, shown by the optimal temperature (Fig. 3), were 3·3°C at 60 μmol m^{-2} s^{-1}, 7·0°C at 110 μmol m^{-2} s^{-1} and 5·6°C at 220 μmol m^{-2} s^{-1} PPFD, with *U. freyi* always showing lower temperature optima for net photosynthesis (Table 1). This difference was also obvious at higher PPFD, although the differences between the temperature optima for net photosynthesis in both species decreased with increasing PPFD (Fig. 3). The lower temperature compensation point was always below 0°C, while the upper temperature compensation point of net photosynthesis at low PPFD conditions was reached at 23·3°C in *U. freyi* and 25·0°C in *U. grisea*, respectively.

Despite an observed variability in the CO$_2$ exchange rate of individual samples of each species, both PPFD and temperature curves, fitted to the average values, exhibited an excellent correlation, as shown by r^2> =0·9 (see Figs 1 & 2).

Both species show a strong depression of net photosynthesis at high thallus water contents (Fig. 4). In *U. grisea* NP was depressed most severely at high water contents with only 5% of maximal NP reached at 180% dw. The optimal water content for NP differed between the two species: the maximal NP for *U. freyi* was 108–115% dw but in *U. grisea* it was 91–101% dw. No CO$_2$ exchange was detected below a thallus water content of 30% dw.
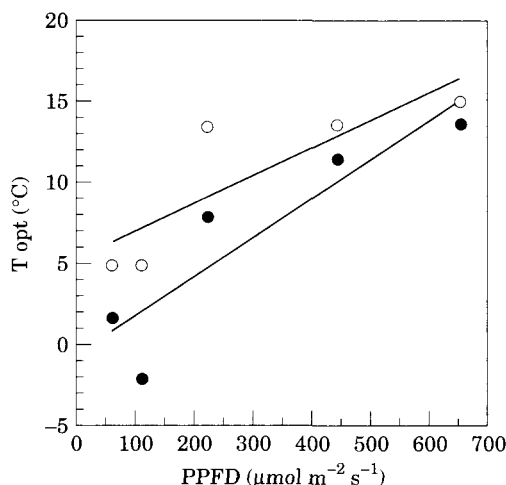
FIG. 3. Effect of PPFD on temperature optima of net photosynthesis (NP) in *U. grisea* (○) and *U. freyi* (●). The data is derived from the fitted curve shown in Fig. 2. Linear regression analysis gave $r^2=0\cdot811$ in *U. freyi* and $r^2=0\cdot710$ in *U. grisea*.

Field measurements

CO_2 exchange, thallus water content, thallus temperature, and PPFD are shown in Figs 5 and 6 for *Umbilicaria grisea* and *U. freyi*, respectively, under natural conditions at the field site in Sierra de Guadarrama for four days in October 1993. The climatic conditions during this period were quite variable, as is typical during autumn in the Mediterranean region. On the 15 October rain fell intermittently in the morning; during the day the sky was overcast but without rainfall, with temperatures around 6°C. On 16 October several hours of heavy rainfall and storm interrupted the measurements. It was considerably colder on 17 October, with temperatures between 0 and 3°C, the sky was overcast and rain fell during most of the day. On 18 October the sky was overcast again but the weather was quite dry with only occasional rain showers. The temperatures were warmer than on the previous day. October 19 was a cloudless, dry day with cold temperatures in the morning around 0°C, and mild at noon. From 19 October, two weeks of dry weather kept the lichens metabolically inactive and prevented further measurements under natural water conditions. Because both species grow closely together at the same rock, facing in the same compass direction, both species experienced very similar PPFD and temperature conditions.

During the period 15–19 October *U. grisea* and *U. freyi* were moist and photosynthetically active at their natural site. During these days net photosynthetic activity was mainly controlled by the changing PPFD and temperature conditions and, except for 16 and 17 October, by a slow decrease in thallus water content during the day. On 16 October heavy rainfall interrupted the measurements and in the morning of 17 October the samples were highly hydrated. During this day continuous rainfall kept thallus hydration at levels above 200% dw in *U. grisea* and *U. freyi*. Superoptimal thallus water content
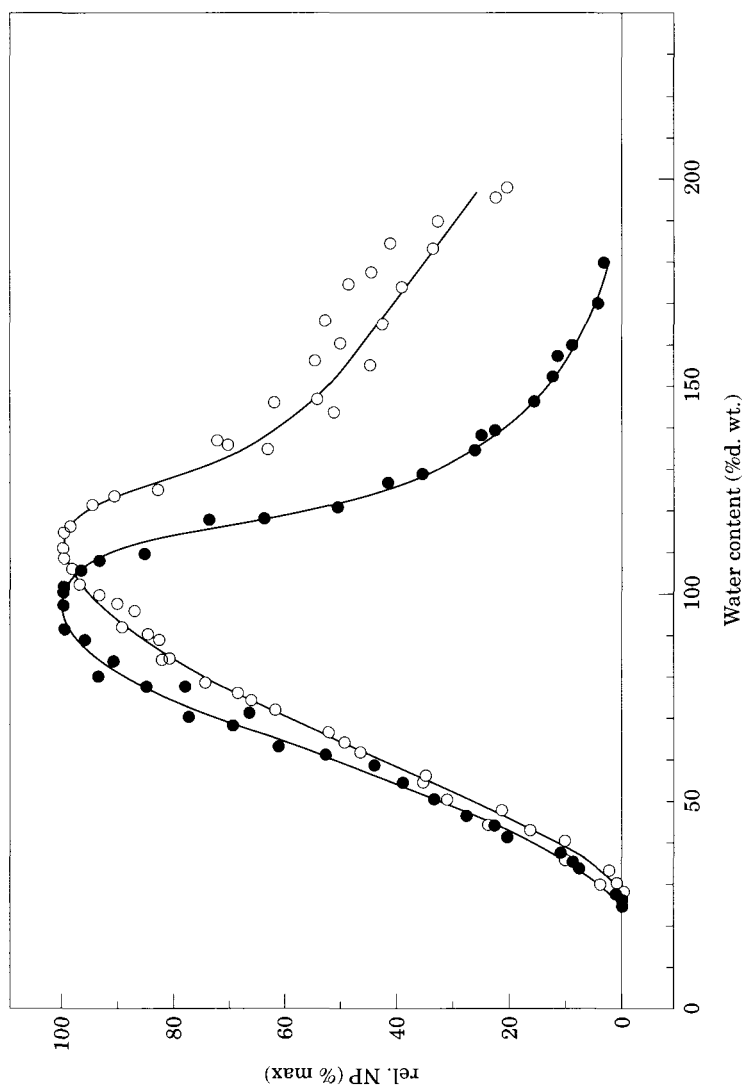
FIG. 4. Relationship between net photosynthesis (NP) and thallus water content in *U. freyi* (○) and *U. grisea* (●). Measurements were carried out at 10°C and 400 μmol m^{-2} s^{-1} PPFD. For each species three different thalli were measured individually.
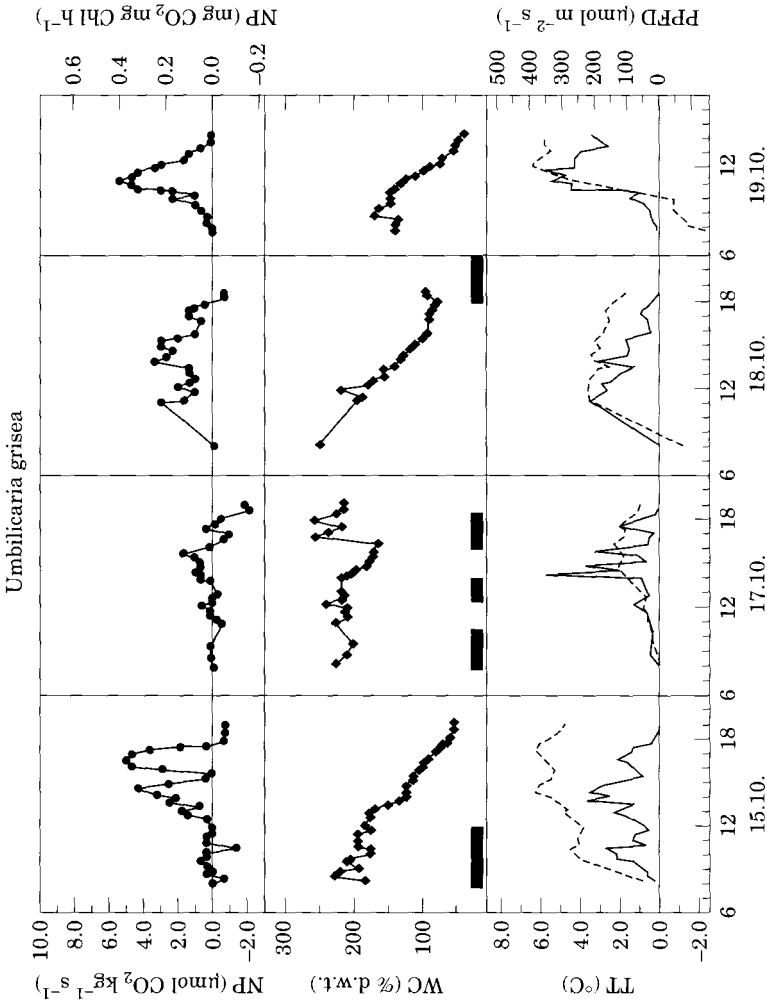
FIG. 5. Diurnal course (15–17, 18–19 October 1993) of thallus temperature (TT, broken line), PPFD (solid line), thallus water content (WC, squares) and CO$_2$ exchange (NP, circles) related to dry weight and to total chlorophyll content in *U. grisea* in the field at Sierra de Guadarrama. Black bars indicate periods of rainfall.
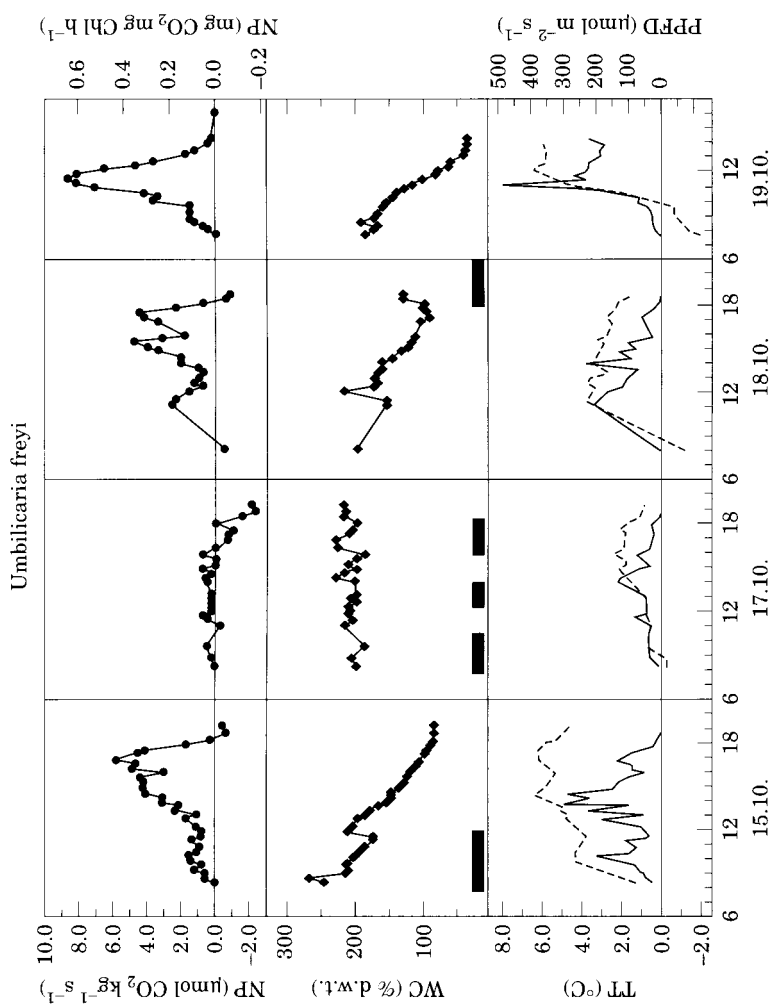
FIG. 6. Diurnal course (15–17, 18–19 October 1993) of thallus temperature (TT, broken line), PPFD (solid line), thallus water content (WC, squares) and CO_2 exchange (NP, circles) related to dry weight and to total chlorophyll content in *U. freyi* in the field at Sierra de Guadarrama. Black bars indicate periods of rainfall.

(>200% dw) together with low light conditions severely limited the net photosynthetic rates of both species during this day. On 15 and 18 October for both species thalli dehydrated slowly during the day except for occasional rehydration by sporadic rainfall. On 15 October the highest photosynthetic rate was reached in *U. grisea* in the afternoon when the thallus water content was below 150% dw and PPFD reached about 200 μmol m^{-2} s^{-1}. The photosynthetic response of *U. freyi* was very similar during this day even though the thallus water content was slightly higher in *U. freyi*. This close correlation between PPFD and the net photosynthetic rates was also observed on 18 October. At water contents lower than 150% dw, both species reacted very sensitively to minor variations of the PPFD levels.

In the morning of 19 October net photosynthesis increased with increasing PPFD until continuous dehydration of the thalli decreased net photosynthetic rates. Maximal net photosynthesis was achieved at a water content of about 130% dw. in *U. grisea* and about 100% dw in *U. freyi*. CO_2 exchange ceased around 14·30 h when thallus water content was less than 50% dw in *U. grisea* and less than 40% dw in *U. freyi*, respectively.

Both species seemed to be incapable of achieving significant rates of net photosynthesis at highly saturated thallus water contents (>200% dw), during the humid, cold 17 October. At this water-saturated stage the compensation point was hardly reached by the thalli, although the irradiance level was sometimes higher than 300 μmol m^{-2} s^{-1} and the temperature was near 0°C.

Discussion

The photosynthetic productivity of *Umbilicaria grisea* and *U. freyi* is similar or even higher if compared with other Mediterranean (Sancho & Kappen 1989) and North American (Larson 1980) *Umbilicaria* species. The differences in the maximal photosynthetic rates between both species investigated here are related to their different total chlorophyll content (Table 1): *U. freyi* shows a higher maximal net photosynthesis related to dry weight, but, because of its substantially higher chlorophyll content, no difference in the net photosynthetic maximum was found if calculated on a total chlorophyll content basis. Similar differences in chlorophyll content are also reported by Valladares (1993), who found that *U. freyi* showed a higher chlorophyll content than *U. grisea* regardless of sampling season. However, other aspects of photosynthetic behaviour of the two species differ substantially.

The temperature optimum of net photosynthesis of *U. freyi* was always lower than that of *U. grisea*, regardless of the PPFD level. At low PPFD conditions, these differences were more pronounced (Fig. 3). *Umbilicaria grisea* shows a broad temperature optimum from 5°C to 20°C at low PPFD conditions (<200 μmol m^{-2} s^{-1}), and appears to be adapted to warmer temperatures. The photosynthetic response of *U. freyi* reflects an adaptation to colder climates with its comparatively lower optimal temperature for net photosynthesis and a narrow temperature optimum at low PPFD conditions between 0 and 7°C (Fig. 2). Because both species show a similar dark respiratory response to temperature, the observed differences in photosynthetic behaviour must rely on a different temperature response of the

photobionts. *Umbilicaria grisea* shows a stable maximal net photosynthetic rate from 5 to 20°C at 200 μmol m^{-2} s^{-1} (Table 1). By contrast, in *U. freyi* the net maximal net photosynthetic rate decreases dramatically (42%) from 5 to 20°C. The photosynthetic behaviour of *U. freyi* resembles that of the Arctic-Alpine species *U. havaasii* (Sancho & Kappen 1989), which shows a small optimal temperature range. The photosynthetic behaviour *Umbilicaria grisea* resembles that of *U. spodochroa*, which has a broad temperature optimum and an oceanic distribution (Sancho & Kappen 1989; Kappen *et al.* 1996).

In contrast to the temperature-related differences in net photosynthesis in *U. freyi* and *U. grisea*, both species show similar responses to different PPFD levels regarding the light compensation points and light saturation levels of net photosynthesis (Table 1). The overall adaptation to low PPFD levels in *U. freyi* and *U. grisea* correlates well with their preference for habitats under overhanging rock and at other shaded sites.

Under natural conditions, thalli of both species reached thallus water contents of more than 250% dw. However, part of this water corresponds to adherent surface water, since the thalli were not shaken during field experiments, in order to maintain natural conditions as far as possible. At these high water contents the CO_2 exchange was significantly depressed, as occurs in several lichen species (Schroeter *et al.* 1991; Lange *et al.* 1995) due to increased diffusion resistances (Cowan *et al.* 1992). The optimal water content for net photosynthesis was at about 100% dw in both species, depending on field light and temperature conditions. These values agree well with our laboratory measurements (Fig. 4) and with previous studies of several *Umbilicaria* species from different climatic regions (Ried 1960; Larson 1980, 1983; Kappen & Breuer 1991). The difference in the optimal water content for net photosynthesis of *U. freyi* (108–115% dw) and *U. grisea* (91–101% dw) observed in the laboratory experiment (Fig. 4) could be caused by the presence of dispersed rhizinomorphs in the lower surface of *U. freyi*. Rhizinomorphs can increase water storage and retention capacities at the whole thallus level without affecting the gas exchange in the algal layer.

During the field measurements *U. freyi* and *U. grisea* showed a similar photosynthetic response to the hydration, but *U. freyi* was clearly more productive, independent of the PPFD level, as can be seen during 18 and 19 October (Figs 5 & 6). The higher production of *U. freyi* at relatively low temperature conditions observed in the field experiment was consistent with the temperature optimum for net photosynthesis in the laboratory.

Several lichen studies have compared different species of the same genus for their ecophysiological performance under natural or artificial conditions (Lechowicz & Adams 1974; Moser *et al.* 1983; Kappen 1985; Kappen & Breuer 1991; Mázsa 1994). However, most of these studies compare species growing in different habitats. In these studies, it is not possible to differentiate between the genetic basis of the ecophysiological performances and the adaptive response to the microhabitat conditions. In two species of the family Umbilicariaceae, *U. propagulifera* and *Lasallia papulosa*, growing in the same habitat, differences in water relations related to the morphology of the thallus have been interpreted as a mechanism of niche segregation (Larson 1984). In contrast, the species investigated here are taxonomically closely related and

show a similar morphology (Codogno *et al.* 1989), anatomy (Valladares 1993), and water relations (Valladares 1993, 1994). Therefore, differences in the photosynthetic response under the same environmental conditions may reflect a genetic control of physiological performance.

Our results reveal substantial differences in the photosynthetic performance between the two species. Whereas *U. freyi* seems to be adapted to low temperatures and low or moderate PPFD levels, *U. grisea* shows a wider optimal temperature range. The success of both species in the colonization of the same habitat may be a result of the exploitation of different microclimatic situations throughout the year. In this way, *U. freyi* appears to be better adapted to colder climatic situations, as in autumn and winter. This is also reflected in its geographic distribution in the Iberian Peninsula being restricted to a narrow altitudinal range between 1100 and 1600 m a.s.l. In contrast, the physiological performance of *U. grisea* as a more eurythermous species is reflected in a wide altitudinal and latitudinal range of distribution. It occurs from North Africa to southern Fennoscandia and is the only *Umbilicaria* species found in the lowland, mesomediterranean belt of the Iberian Peninsula (Frey 1936*a*; Hakulinen 1962; Codogno & Sancho 1991; Sancho *et al.* 1991).

Interpretation of the data presented here leads to the conclusion that the wide and narrow distributions of *U. grisea* and *U. freyi*, respectively, are genetically determined. However, further measurements are needed to verify this hypothesis, for instance with samples of both species from contrasting habitats. Moreover, measurements with other species pairs *sensu* Poelt (1972) during various environmental situations throughout the year would lead to a more complete understanding of the ecological strategies in *Umbilicaria* species.

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