

# Water relations and photosynthetic performance of fruticose lichens from the semiarid Southeast of Spain

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## Summary

The lichen species *Teloschistes lacunosus* (RUPR.) SAV. and *Ramalina bourgeana* NYL. are characteristic of the semiarid southeast Iberian Peninsula. These species showing different distribution patterns and ecological requirements, were collected at the coast (*R. bourgeana*) and in the inland (*T. lacunosus*). Laboratory experiments revealed that net photosynthesis (NP) and dark respiration (DR) responses to temperature differed between both species. Optimal temperatures of NP were higher in *T. lacunosus* than in *R. bourgeana* at optimal thallus water content at the various photosynthetic photon flux density (PPFD) levels. In the upper temperature range studied (20–25°C), *R. bourgeana* proved to be less efficient than *T. lacunosus*. In both species, lower and upper temperature compensation points were below 0°C and above 30°C, for moderate and high PPFD levels, respectively. At high temperatures and high thallus water content, *T. lacunosus* showed lower DR rates than *R. bourgeana*. NP response to PPFD also showed differences between both species. The light compensation points were high in both species for temperatures above 20°C (at 20°C around 50  $\mu\text{mol m}^{-2}\text{s}^{-1}$  in *T. lacunosus*, and around 60  $\mu\text{mol m}^{-2}\text{s}^{-1}$  in *R. bourgeana*). Light saturation of NP was higher in *T. lacunosus* at all temperatures in the experiments. In *T. lacunosus*, the value was below 1200  $\mu\text{mol m}^{-2}\text{s}^{-1}$  at 0–15°C, but at temperatures above 15°C, it was above 1200  $\mu\text{mol m}^{-2}\text{s}^{-1}$ . In *R. bourgeana* the values were always below 1200  $\mu\text{mol m}^{-2}\text{s}^{-1}$ . In both species, NP was strongly depressed at supraoptimal water content. The physiological differences observed between *R. bourgeana* and *T. lacunosus*, and their relation to the distribution patterns of these lichens are discussed.

Key words: Lichen, photosynthesis, water content, temperature, light, semiarid.

## 1. Introduction

The southeast of the Iberian Peninsula, and particularly the province of Almería, is the most arid region of Europe. This area is characterized by its high temperature (annual mean 17–21°C), and less than 250 mm rainfall (FONT TULLOT 1983). However, in this arid region there are two different zones: a coastal band (Cabo de Gata), and a continental area (Tabernas Desert). In both zones the high temperature and the scarce rainfall make the growth of vascular plants difficult. However, poikilohydric organisms such as lichens are abundant in these arid ecosystems; not only many crustose lichens are found, but also macrolichens of the genera *Teloschistes*, *Ramalina*, *Parmelia*, and *Cladonia* among others (EGEA & LLIMONA 1981). It is probable that these lichens can effectively use hydration sources other than rainfall, such as atmospheric humidity, fog and dew, as has been observed in other desert lichens

(LANGE et al. 1970, NASH et al. 1977, 1979, KAPPEN et al. 1980, KAPPEN 1988).

This work shows an ecophysiological study on two fruticose lichens: *Teloschistes lacunosus* (RUPR.) SAV. and *Ramalina bourgeana* NYL. Both are characteristic and plentiful in the semiarid southeast of the Iberian Peninsula, but present different autoecology. *T. lacunosus* is a terricolous vagrant (sometimes epiphytic) lichen. It is characteristic of the gypsicolous communities of Tabernas Desert in Almería province (GUTIÉRREZ & CASARES 1994). Instead, *R. bourgeana* is a frequent saxicolous lichen from the coast of the Cabo de Gata (EGEA & LLIMONA 1983).

In this work the temperature, light and hydration optima for NP were determined, with the aim of understanding the adaptative strategies of these species to the continental semiarid climate and to the coastal semiarid climate in which they grow.

In the last few decades ecophysiological investiga-

tions have been carried out with desert lichens, including *R. maciformis* in the Negev Desert (LANGE 1969, LANGE et al. 1970, KAPPEN et al. 1979, 1980, PALMER & FRIEDMANN 1990), and *T. capensis* (LANGE et al. 1990, SCHEIDEGGER et al. 1995) from Namib Desert, which are similar to the species studied in this work. Some studies concerning *T. lacunosus* from the Negev Desert have been reported by LANGE et al. (1970), PALMER & FRIEDMANN (1990), SCHEIDEGGER et al. (1995), but none concerning Mediterranean semiarid zones, where diversity and biomass of lichens are remarkable. For this work we have selected the Cabo de Gata area, which at present benefits from a partial protection as a Natural Park, which has contributed to preserving well developed communities of saxicolous and terricolous lichens.

## 2. Materials and methods

### 2.1. The species: Morphological description and distribution

– *Ramalina bourgeana* NYL. is a green-yellow fruticose lichen, ascending, with a rosette appearance. In some cases, the thalli have a well-defined holdfast, but other specimens have a tendency to form turfs. In these specimens the holdfast is badly defined and the identification of individual thalli is difficult. This lichen has flat, solid and reticulate laciniae, of variable length and width (0.5–2.5 cm and 0.2–1.5 cm respectively). Lecanorine apothecia, (up to 1 cm in diameter) usually numerous, are frequently distributed over the whole surface of the laciniae (EGEA 1980, KROG & OTHAGEN 1980, GARCÍA ROWE 1985, ARROYO 1991).

It inhabits the South-East of the Iberian Peninsula (EGEA & LLIMONA 1983), Corsica (POELT 1969, NIMIS 1993), and the Canary Islands (KROG & OTHAGEN 1980). This lichen was collected at the Cerro de Enmedio (San José, Cabo de Gata, 30 m a.s.l.), on siliceous volcanic rocks in ornitocoprophilous communities in the birdpearch of the rock. *R. bourgeana* may also grow on steep rocky slopes facing north.

– *Teloschistes lacunosus* (RUPR.) SAV., is also fruticose, with a cushion shape of 4–10 cm broad and 3–5 cm long. It has flat laciniae with coiled edges. The upper side of the laciniae is brown-grey and is covered by a fine hair, and the underside is white. The laciniae branch forming acute angles and are connected by anastomoses. At the end of the laciniae the branches are thin and appear as tiny fingers. The width of the laciniae is variable (3–5 mm to 1–1.5 mm in the last branches). Lecanorine apothecia are absent in some thalli, but numerous, well-developed and distributed over the whole surface of the laciniae in others.

This species is known to be xerophytic and heliophytic (LLIMONA 1973), and its distribution seems to be connected with the presence of high salt concentrations in the soil. It is abundant on gypsum soils in Almería and on the edges of small ponds of the inner part of the Iberian Peninsula (CRESPO et al. 1980). This lichen also inhabits the Negev Desert (GALUN

1970, PALMER & FRIEDMANN 1990). This lichen was collected in Venta de los Yesos (Tabernas Desert, 520 m a.s.l.), on north-exposed slopes with slight inclination.

### 2.2. Gas exchange measurements

Both species were collected in June 1996 at two different localities in the Spanish province of Almería. Once collected, the dry samples were frozen and stored at a temperature of  $-20^{\circ}\text{C}$ , until the experiments were carried out. During the three days prior to the start of the measurements, the samples were reactivated under natural light ( $0-400\ \mu\text{mol m}^{-2}\text{s}^{-1}$  PPFD) and temperature conditions of  $10-15^{\circ}\text{C}$  by spraying the thalli with deionized water. Substrate remnants were then removed from the reactivated thalli in order to prevent them from interfering with the measurements.

Laboratory  $\text{CO}_2$  gas exchange measurements, which were carried out under controlled light and temperature conditions, and by reactivating the lichens with liquid water, were performed using a Minicuvette CMS400 system (Walz, Germany), already described by SCHROETER et al. (1994) and PINTADO (1996). The PPFD involved was obtained by means of a cold light source (FL-400, Walz, Germany). Two different  $\text{CO}_2$  gas exchange studies were carried out:

#### 2.2.1. Study of the relation between NP and water content (WC) of the thallus

Thalli were hydrated up to saturation by spraying them with deionized water. Then they were gently shaken in order to remove the water excess from the thallus surface, and finally weighed to determine their initial WC. Thereafter they were introduced in the above mentioned cuvette at  $15^{\circ}\text{C}$ ,  $400\ \mu\text{mol m}^{-2}\text{s}^{-1}$  PPFD, and with a permanent air flow of  $0.655\ \text{l min}^{-1}$ . During the entire dehydration cycle which the thalli experienced in the cuvette, the NP was automatically recorded every two minutes, while the WC of the thalli was gravimetrically measured every 30 minutes, by taking the sample out of the cuvette and weighing it on a MK-50 precision balance. The experiment proceeded until the NP readings reached zero. As the air flow in the cuvette was kept constant during the whole experiment, the thallus NP dependence with the hydration degree could be calculated. Moreover, the hydration point yielding the optimum NP performance was established for the temperature of  $15^{\circ}\text{C}$ . This study involved eight samples of *T. lacunosus* and six samples of *R. bourgeana*.

#### 2.2.2. Measurement of the dependence of NP with temperature and PPFD

Measurements were carried out at temperatures of 0, 5, 10, 15, 20, 25 and  $30^{\circ}\text{C}$ . The NP response was measured at each of these temperatures by using eight different PPFD (0, 25, 50, 100, 200, 400, 800 and  $1200\ \mu\text{mol m}^{-2}\text{s}^{-1}$  PPFD). Prior to the measurements performed for any of these pairs light/tempera-

ture, lichens were hydrated by spraying with deionized water, then they were gently shaken in order to remove the excess of surface water. The highest NP value of the record was kept for any of the light/temperature combinations, for further calculations. Thallus hydration was also measured in order to determine the hydration point yielding the optimum NP performance at various light/temperature conditions. For any value of temperature, measurements at the different PPFD steps were carried out starting at the lowest light intensity value, and increasing it up to the highest limit. These experiments involved three samples of any of the species.

## 2.3. Data evaluation

The NP and DR rates were related to oven-dry weight and chlorophyll content of the thalli, and were expressed as  $\mu\text{mol CO}_2 \text{ kg dw}^{-1} \text{ s}^{-1}$  and  $\text{mg CO}_2 \text{ mg chl}^{-1} \text{ h}^{-1}$  respectively. WC was related to oven-dry weight. This was determined after a 24-hour exposure to 100–105 °C. The chlorophyll content was analyzed with DMSO following the method described by BARNES et al. (1992). Chlorophyll a and b concentrations were calculated from the extinction coefficients at 648.2 nm and 664.9 nm by means of a UVIKON 930 Spectrophotometer (Kontron Instruments, Japan). The turbidity of the extracts was measured at 750 nm. For the evaluation of the pigment condition the coefficient  $\text{PQa} = \text{OD } 435 / \text{OD } 415$  (RONEN & GALUN 1984, MANRIQUE et al. 1989, BALAGUER & MANRIQUE 1991) was used. Graphical displays and regression fits within this study were carried out using the software SIGMAPLOT 2.0.

Temperature response curves for NP and DR at different PPFD levels were obtained by fitting the data to a second degree polynomial function. The temperature compensation point ( $T_c$ ) and the NP temperature optimum ( $T_{opt}$ ) were calculated from the curves so fitted.  $T_c$  is the point in which the curve cuts the zero axis, while  $T_{opt}$  is the point in which the first derivative of the curve equals zero.

The NP and DR responses to different PPFD levels at different temperatures were fitted using the exponential function

$$\text{NP}_{(I)} = \text{NPmax}_{(I)} - (\text{NPmax}_{(I)} - \text{DR}) \exp(-a I)$$

Where:

$\text{NP}_{(I)}$  stands for the net photosynthesis at PPFD

$\text{NPmax}_{(I)}$  stands for the net photosynthesis at maximum PPFD

$\text{DR}$  is the dark respiration

$a$  is an empirical temperature-dependent factor, and

$I$  is the irradiance expressed in  $\mu\text{mol m}^{-2} \text{ s}^{-1}$ .

The light saturation point ( $I_s$ ) was calculated from the curve fitted for each temperature. It was assumed that  $I_s$  is achieved at the point where the curve reaches 99.5% of the maximum light value measured during the experiment. The NP measured at the light saturation point was considered to be the maximal NP.

The light compensation point ( $I_c$ ), light intensity value in which NP reaches zero, was determined by fitting the four NP values closest to zero to a second degree polynomial (two values above zero and two values below).  $I_c$  was considered to be the point at which the curve goes to zero.

The Quantum use efficiency ( $\alpha$ ), was calculated by fitting the dry-weight related NP between  $I_c$  value and  $90 \mu\text{mol m}^{-2} \text{ s}^{-1}$  to a linear regression (LARCHER 1995).  $\alpha$  was calculated for low and moderate temperatures (0–15/20 °C), because at high temperatures  $I_c$  was nearly  $90 \mu\text{mol m}^{-2} \text{ s}^{-1}$  or higher.

## 3. Results

### 3.1. Net Photosynthesis (NP) response versus thallus water content

Figure 1 shows the NP response versus thallus water content (WC) for the two species under study. In *T. lacunosus*, NP showed a deep depression when WC was

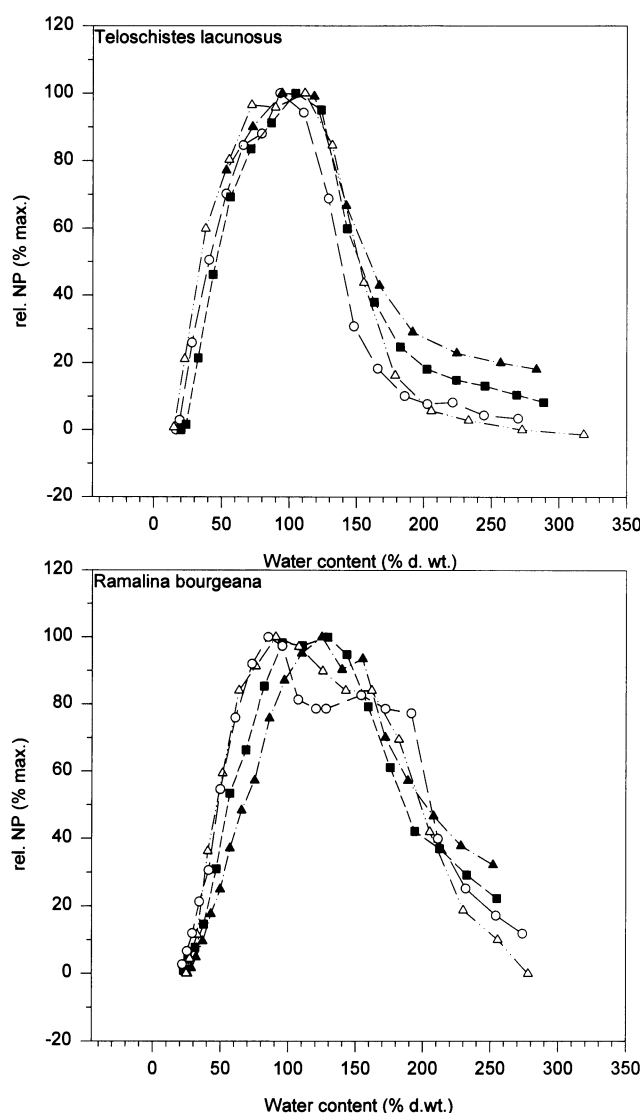


Fig. 1. Relationship between net photosynthesis (NP) and thallus water content in *T. lacunosus* and *R. bourgeana*. Measurements were carried out at 15 °C and  $400 \mu\text{mol m}^{-2} \text{ s}^{-1}$  PPFD. Each graph represents one lichen thallus.

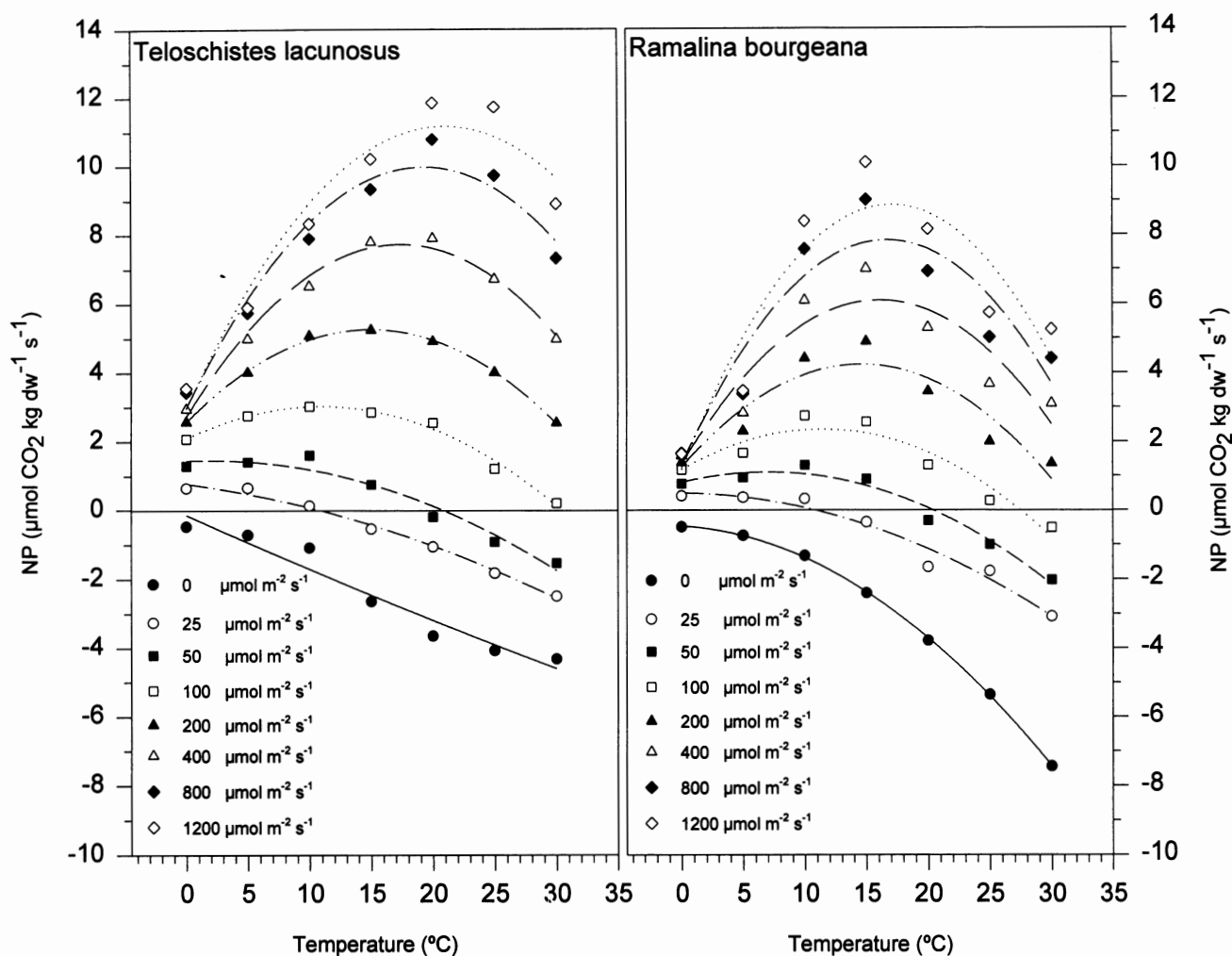


Fig. 2. Effect of temperature on net photosynthesis (NP) at different PPFD levels and on dark respiration related to dry weight in *T. lacunosus* and *R. bourgeana*. All measurements were carried out at optimal thallus water content. Different symbols represent different PPFD levels. Each data point represents the mean of 3 replicates. Standard errors ranged between  $\pm 0.019$  at  $5^{\circ}\text{C}/0 \mu\text{mol m}^{-2}\text{s}^{-1}$  PPFD and  $\pm 0.4$  at  $10^{\circ}\text{C}/100 \mu\text{mol m}^{-2}\text{s}^{-1}$  PPFD for *T. lacunosus*; and between  $\pm 0.019$  at  $15^{\circ}\text{C}/0 \mu\text{mol m}^{-2}\text{s}^{-1}$  PPFD and  $\pm 0.08$  at  $0^{\circ}\text{C}/50 \mu\text{mol m}^{-2}\text{s}^{-1}$  PPFD for *R. bourgeana*. Curves were fitted using a second-order polynomial regression.

above 185%–220% dry weight (dw). At this high hydration, the thallus NP never exceeded 20% of the maximum NP. From this point on, NP increased steadily up to its maximum value. The WC for maximal NP varied between different thallus samples ranging from 95 to 130% dw. The hydration interval in which the optimum WC value stabilised was very narrow. Moreover, with decreasing WC from optimal, NP decreased rapidly. When the WC of the thallus reached 15–20% dw, the NP equalled zero. *R. bourgeana* also showed an initial photosynthetic depression, caused by a very high water content. But, in contrast to the sharp decrease of NP around 150% dw in *T. lacunosus*, the depression in *R. bourgeana* was less rapid with increasing WC and half of the maximum rate was maintained still at 200% dw (see Fig. 1). The NP increased in *R. bourgeana*

as the thallus dehydrated, reaching a photosynthetic maximum for WC between 85 and 150% dw, depending on the thallus. Therefore, the optimum hydration point showed a greater variability for *R. bourgeana* compared with *T. lacunosus*. As can be seen from figure 1, both species reached their photosynthetic maxima (the point at which the maximum NP is reached) during narrow hydration ranges. However, if the thallus WC interval in which NP is equal to or higher than 80% of the NP maximum is considered, such interval is wider in *R. bourgeana*. Thallus WC ranged between 130–70% dw for *T. lacunosus* and between 160–80% dw for *R. bourgeana*. NP of *R. bourgeana* reached a zero value for WC of 20–25% dw. From the analysis of the low hydration tail of the curves, it can be said that *T. lacunosus* yields higher NP rates than *R. bourgeana* for low WC of the

Table 1. Temperature compensation point ( $T_c$ ), maximum rate of net photosynthesis (NPmax), and optimum temperature of net photosynthesis ( $T_{opt}$ ) obtained at different PPFD levels in *T. lacunosus* and *R. bourgeana*. The first value of each pair corresponds to *T. lacunosus* and the second to *R. bourgeana*.

	PPFD ( $\mu\text{mol m}^{-2}\text{s}^{-1}$ )						
	25	50	100	200	400	800	1200
<b><math>T_c</math> (<math>^{\circ}\text{C}</math>)</b>	10.8/10.7	20.7/20.3	> 30/27.4	> 30	> 30	> 30	> 30
<b>NPmax</b>							
( $\mu\text{mol CO}_2 \text{ kg dw}^{-1}\text{s}^{-1}$ )	0.65/–	1.60/1.31	3.03/2.74	5.25/4.90	7.91/7.00	10.79/9.01	11.86/10.11
( $\text{mg CO}_2 \text{ mg chl}^{-1}\text{h}^{-1}$ )	0.09/–	0.22/0.17	0.42/0.16	0.78/0.65	1.12/0.93	1.46/1.19	1.61/1.34
<b><math>T_{opt}</math> (<math>^{\circ}\text{C}</math>)</b>	5/–	10/7	10.9/11.4	14.9/14.6	17.4/16.1	19.3/16.7	21/17

– out of the temperature range of measurements which were conducted between  $0^{\circ}\text{C}$  and  $30^{\circ}\text{C}$

tallus. When the WC was only 25–30% dw, *T. lacunosus* still yielded 25–30% of its NP maximum, while *R. bourgeana* hardly yielded 10% of its NP maximum, for the same WC. *R. bourgeana* reached 20–25% of its maximum NP when the WC was 35–40% dw.

### 3.2. DR and NP response versus temperature

Figure 2 shows the NP response versus temperature ( $T$ ) of *T. lacunosus* and *R. bourgeana*, at different PPFD levels, at optimum water content. Each point represents the average value of three samples. The parameters obtained from the curves of Fig. 2 are summarised in the table 1. For both species, regardless of the calculation basis (dry weight or chlorophyll content, not shown here), the optimal temperature for NP increases with increasing irradiance level. The shift ranged from sub-zero to  $18^{\circ}\text{C}$  in *R. bourgeana* and from  $5^{\circ}\text{C}$  to  $22^{\circ}\text{C}$  in *T. lacunosus*.

Based on chlorophyll content, NP rates of both species were very similar particularly at low PPFD levels. At about  $400 \mu\text{mol m}^{-2}\text{s}^{-1}$  the rates of *T. lacunosus* were by 5–20% higher than those of *R. bourgeana* over the whole temperature range (Fig. 3). This tendency was also visible if thallus dry weight-related NP rates were compared (Fig. 2).

At the higher temperatures ( $20$ – $25^{\circ}\text{C}$ ), *R. bourgeana* proved to be less efficient than *T. lacunosus*. Moreover, for moderate and high PPFD levels, when performing measurements at a fixed PPFD and moving from mode-

rate ( $10$ – $15^{\circ}\text{C}$ ) to high temperatures ( $20$ – $25^{\circ}\text{C}$ ), NP of *T. lacunosus* changes slightly, being highest at  $25^{\circ}\text{C}$  and highest PPFD. By contrast, *R. bourgeana* NP values at  $20$ – $25^{\circ}\text{C}$  are remarkably lower than values obtained at  $10$ – $15^{\circ}\text{C}$ , at the same PPFD (Table 2).

Lower temperature compensation points were out of range, i.e. below  $0^{\circ}\text{C}$ , for both species. Higher temperature compensation points have been obtained only at

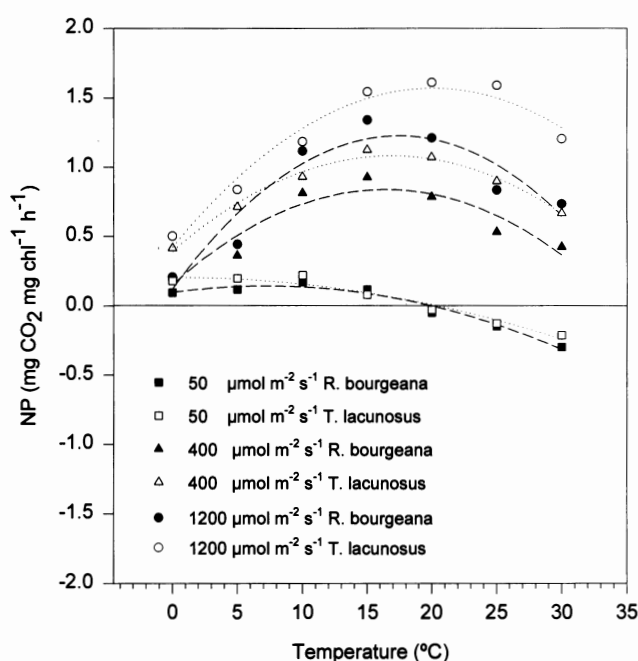


Fig. 3. Effect of temperature on net photosynthesis (NP) at different PPFD levels and on dark respiration related to chlorophyll content in *T. lacunosus* and *R. bourgeana*. All measurements were carried out at optimal thallus water content. Different symbols represent different PPFD levels. Each data point represents the mean of 3 replicates. Standard errors ranged between  $\pm 0.006$  at  $20^{\circ}\text{C}/400 \mu\text{mol m}^{-2}\text{s}^{-1}$  PPFD and  $\pm 0.07$  at  $0^{\circ}\text{C}/1200 \mu\text{mol m}^{-2}\text{s}^{-1}$  PPFD for *T. lacunosus*; and between  $\pm 0.018$  at  $0^{\circ}\text{C}/50 \mu\text{mol m}^{-2}\text{s}^{-1}$  PPFD and  $\pm 0.14$  at  $10^{\circ}\text{C}/1200 \mu\text{mol m}^{-2}\text{s}^{-1}$  PPFD for *R. bourgeana*. Curves were fitted using a second-order polynomial regression.

Table 2. % of NP decay or increase between  $15^{\circ}\text{C}$  and  $25^{\circ}\text{C}$  at different PPFD levels observed for each species.

PPFD ( $\mu\text{mol m}^{-2}\text{s}^{-1}$ )	% NP decay (–)/increase (+) between $15^{\circ}\text{C}$ and $25^{\circ}\text{C}$ <i>T. lacunosus</i> / <i>R. bourgeana</i>
200	– 23.7/– 60.6
400	– 13.9/– 47.5
800	+ 4.1/– 44.3
1200	+ 12.93/– 43.3

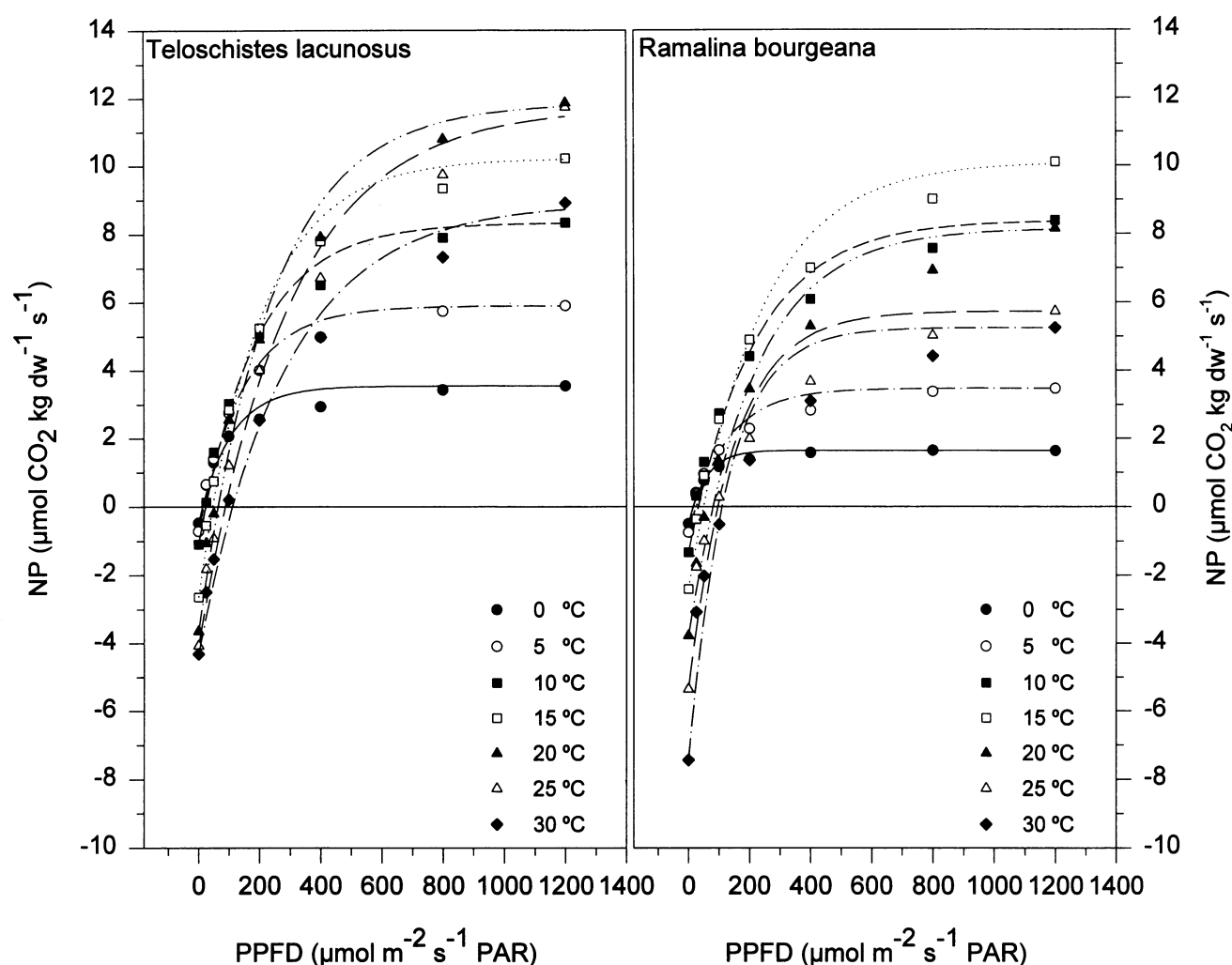


Fig. 4. Effect of PPFD at different temperatures on net photosynthesis (NP) related to dry weight in *T. lacunosus* and *R. bourgeana*. All measurements were carried out at optimal water content. Different symbols represent different temperature levels. Each data point represents the mean of 3 replicates. Standard errors were the same as in figure 2. Curves were fitted using the exponential function described in data evaluation section.

low PPFD (see Table 1). For the remaining PPFD used within the experiments, higher temperature compensation points were also out of range, i.e. above 30 °C. It is remarkable that, when both the temperature and the water content is high, the respiration rates of *T. lacunosus* are considerably lower than those for *R. bourgeana*, and also lower than the usual rates that lichens show at such temperatures (Fig. 2).

### 3.3. NP response versus PPFD

Figure 4 shows the NP response versus PPFD of *T. lacunosus* and *R. bourgeana*, at different temperatures. Each point represents the average value of three samples. The parameters obtained from the curves of Fig. 4 are

summarised in the Table 3. The maximum NP (NPmax) rates were higher in *T. lacunosus* than in *R. bourgeana* at all studied temperatures except at 10–15 °C. At these temperatures, NPmax rates were similar for both species. Light saturation points ( $I_s$ ) were higher in *T. lacunosus* at all temperatures used within the experiments. In *T. lacunosus*, at low to moderate temperatures (0–15 °C), this point ranged between 600 and 1200  $\mu\text{mol m}^{-2}\text{s}^{-1}$ . But at higher temperatures,  $I_s$  was out of the range of this experiment, i.e. above 1200  $\mu\text{mol m}^{-2}\text{s}^{-1}$ . However,  $I_s$  in *R. bourgeana* was below 1200  $\mu\text{mol m}^{-2}\text{s}^{-1}$  at all studied temperatures. For both species, the higher the temperature, the higher the light compensation point ( $I_c$ ). Beyond 20 °C, *R. bourgeana*  $I_c$  were higher than those of *T. lacunosus*, although from this temperature both species showed high values

Table 3. Quantum use efficiency ( $\alpha$ ), maximum rate of net photosynthesis (NPmax), and light compensation point (Ic) obtained at different temperatures (T) in *T. lacunosus* and *R. bourgeana*. The first value of each pair corresponds to *T. lacunosus* and the second to *R. bourgeana*.

	T (°C)						
	0	5	10	15	20	25	30
$\alpha$ ( $\mu\text{mol CO}_2 \text{ kg dw}^{-1}$ $\mu\text{mol PPFD}^{-1} \text{ m}^2$ )	0.024/0.017	0.032/0.022	0.037/0.034	0.046/0.041	0.048/		
<b>NPmax</b> ( $\mu\text{mol CO}_2 \text{ kg dw}^{-1} \text{ s}^{-1}$ )	3.55/1.65	5.90/3.47	8.33/8.39	10.23/10.11	> 11.86/8.15	> 11.74/5.74	> 8.91/5.25
(mg CO <sub>2</sub> mg chl <sup>-1</sup> h <sup>-1</sup> )	0.50/0.21	0.84/0.44	1.18/1.12	> 1.54/1.34	> 1.61/1.21	> 1.59/0.84	> 1.21/0.74
<b>Ic</b> ( $\mu\text{mol m}^{-2} \text{ s}^{-1}$ )	9.4/11.9	11.7/15.4	22.6/19.3	35.15/32.3	47.56/61.1	69.4/87.9	94/126.6

of Ic (around 50  $\mu\text{mol m}^{-2} \text{ s}^{-1}$  and 60  $\mu\text{mol m}^{-2} \text{ s}^{-1}$  in *T. lacunosus* and *R. bourgeana* respectively). Concerning the quantum use efficiency ( $\alpha$ ), *T. lacunosus* showed higher values than *R. bourgeana* (Table 3).

## 4. Discussion

A decrease in NP has been observed for the two species at high thallus WC. This behaviour, which many lichens, though not all, happen to show, has been documented by different authors (KERSHAW 1972, LANGE 1980, LANGE & TENHUNEN 1981, 1982). Accordingly they were classified into four categories, depending on the extent of NP depression for high thallus WC (LANGE et al. 1993, LANGE et al. 1995). In this classification, *T. lacunosus* should be included within the *Cladonia pocillum* type (this type shows a very strong depression but its response curve has an inflection, so that NP is low but almost constant at higher WC), while *R. bourgeana* would belong to *Toninia sedifolia* type (lichens belonging to this type also show a large depression at higher WC, but the response curve has no inflection – instead, the photosynthetic depression starts soon after optimal WC is reached). The differences found between the two species concerning the extent of the NP drop caused by oversaturation might be related to their anatomical differences. In this way, PALMER & FRIEDMANN (1990) studied the relation between structure and water economy for *T. lacunosus* and *R. maciformis*, both from the Negev Desert, concluding that, for *T. lacunosus*, the absence of a lower compact cortical layer together with the absence of hydrophobic hyphae enable the ready absorption of liquid water, making unavoidable the NP drop in oversaturation conditions. However, they remarked that *R. maciformis* absorbed water only in the cortical layer, but not in the medullar layer. From an anatomical point of view, *R. bourgeana* and *R. maciformis* belong to the same type (KROG & OTHAGEN 1980), thus their behaviour is likely to be very similar in all that

concerns water absorption and its location within the thallus. *R. bourgeana* and *T. lacunosus* show similar values of maximum hydration of the thallus (around 270–285% dw). For a high WC, in *R. bourgeana*, the medullar layer is free of water, while in *T. lacunosus* the lack of a compact lower cortical layer and of hydrophobic hyphae may facilitate an accumulation of water in the interior of the thallus. This could be the reason for the different behaviour, which is shown by the depression at oversaturation in these lichens.

The study of NP and DR versus temperature has revealed differences between the two lichens. Laboratory data showed that for high PPFD levels (600–1200  $\mu\text{mol m}^{-2} \text{ s}^{-1}$  PPFD), the temperature optimum for NP was higher for *T. lacunosus* than for *R. bourgeana*. When comparing the optimum temperature of the species covered by this work with the optimum for other lichen species found in different habitats, it can be observed that the NP maximum for *T. lacunosus* falls within the range reported for tropical and hot desert lichens (LANGE 1953, 1969, MATTHES-SEARS et al. 1987, LARCHER 1995). On the other hand, the temperature optimum for *R. bourgeana* NP resembles the values for mountain and cold area lichens (BLISS & HADLEY 1964, KAPPEN & REDON 1987, SANCHO & KAPPEN 1989, LARCHER 1995).

The dependence of DR on temperature shows an increase with increasing temperature in *R. bourgeana* to a higher degree than that of *T. lacunosus*. Compared with other lichen species, DR rates of *T. lacunosus* are very similar to those observed in the desert lichen *R. maciformis*, at 25 and 30 °C (LANGE 1969), while *R. bourgeana* rates resemble those measured at 25–30 °C for several species typically found in colder areas, such as alpine or mountain *Umbilicaria* and *Lasallia* lichens studied by SANCHO & KAPPEN (1989), and by SANCHO et al. (1997). Nevertheless, the analysis of the NP/DR ratio at 15 °C, a parameter which provides an indication of the habitat conditions (SANCHO & KAPPEN 1989), reveals that values shown by both *R. bour-*

Table 4. Chlorophyll a and chlorophyll b content, total chlorophyll content and a/b chlorophyll ratio of *T. lacunosus* and *R. bourgeana*. Each value represents the average of nine samples in *T. lacunosus* and the average of eight samples in *R. bourgeana*.

	Chlorophyll Content (mg g dw <sup>-1</sup> )			
	Chl a	Chl b	Chl a + b	Chl a/b
<i>T. lacunosus</i>	0.890 ± 0.07	0.171 ± 0.014	1.070 ± 0.09	5.24 ± 0.18
<i>R. bourgeana</i>	0.998 ± 0.06	0.183 ± 0.010	1.180 ± 0.06	5.47 ± 0.14

*geana* and *T. lacunosus* are more similar to desert species ( $\geq 3$ ) than to species from colder areas ( $< 3$ ) (SANCHO & KAPPEN 1989). These differences, found in the high temperature range of the DR rate explain the NP optimum temperature shift of *R. bourgeana* towards lower temperatures, with respect to *T. lacunosus*, as well as the higher efficiency of *T. lacunosus* at high temperatures.

The anatomic investigations carried out so far, show structural differences between the two species: *T. lacunosus* almost totally lacks a medullar layer, while *R. bourgeana* presents a thick one (KROG & OSTHAGEN 1980). The differences found in the behaviour concerning DR rate versus temperature seem to point out a low activity of *T. lacunosus* mycobiont, which might be related to the anatomical differences mentioned above. As both species have a similar chlorophyll content (Table 4) and, possibly, a similar population of algae, it is not very likely that the differences in DR rates are caused by a different temperature dependence of the photobiont response.

The temperature compensation points for these lichens were similar to those found for other arid lichens, such as *Ramalina maciformis* from the Negev Desert (LANGE 1969), and higher than values measured for alpine and polar lichen species, which did not reach their compensation points above 30°C when exposed to PPFD over 600  $\mu\text{mol m}^{-2}\text{s}^{-1}$  (KAPPEN 1993, SANCHO & KAPPEN 1989, SANCHO et al. 1997). For both species, the light saturation points are high, at the optimum temperature, and they are aligned with the values found for other species well adapted to tolerate high irradiance levels (LANGE 1969, LARCHER 1995, SCHLENSOG et al. 1997). These data match the light regimen of the natural habitats of both species. The light compensation points (Ic) observed for both species were high. The comparison with other lichens adapted to high irradiance levels shows that the Ic values measured at different temperatures are similar or smaller than those found for the desert lichens *R. maciformis* (LANGE 1969) and *Teloschistes capensis* (LANGE et al. 1990). Both species had a low chlorophyll b content (which yields a high a/b chlorophyll ratio) (Table 4) (BJÖRKMAN 1981, DALE & CAUSTON 1992). Since chlorophyll b is responsible for photosynthesis processes at low light intensities, the low

content in chlorophyll b might be related with the high compensation points measured for the two species studied.

The larger net photosynthesis rates observed for *T. lacunosus*, even when data were expressed as chlorophyll content, suggest a higher chlorophyll efficiency in *T. lacunosus* than in *R. bourgeana*. The maximal NP rate measured for *T. lacunosus* is fairly similar to rates found for *R. maciformis* from Negev (LANGE 1969, 1980), *R. cactacearum* from Chile (LANGE & REDON 1983) and *T. capensis* (LANGE et al. 1990), as well as to rates found for the most productive species of the *Ramalina polymorpha* group in the Central range of Spain (PINTADO 1996). The rates of *R. bourgeana* are slightly smaller when compared with the lichens mentioned above, and its values are similar to rates found for the most productive species of the genera *Umbilicaria* and *Lasallia*, studied in the Central range of Spain (SANCHO & KAPPEN 1989, SANCHO et al. 1997). Both *R. bourgeana* and *T. lacunosus* NP rates are greater than the rates measured for alpine and polar lichens (KAPPEN & REDON 1987, SANCHO & KAPPEN 1989, FALK 1990, PINTADO 1996, SCHLENSOG et al. 1997). GROULX & LECHOWICZ (1987) suggested that high NP maximum rates might be an alternative path to maximise the carbon gain in fast drying conditions.

Although the lichens studied in this work had been collected in the same semiarid region, they have showed physiological differences, in accordance with coastal or inland distribution. *T. lacunosus*, a more continental species, is better adapted to higher temperatures than *R. bourgeana*, which is growing at the coast. *R. bourgeana* uses moderate radiation more efficiently (even though both species can be classified as photophytic according to their light behaviour). This may be related to the different distribution patterns of both species. *R. bourgeana* grows in rocks in coastal locations, frequently on rocky slopes with steep inclination and northern orientation, while *T. lacunosus* inhabits soils in inland and desert locations. Also, the low DR rates typical of *T. lacunosus*, even from an overhydrated thallus and at high temperatures, allow positive NP in a wide range of environmental conditions, as well as during episodes of flooding which may sporadically happen on the soil surface where it grows. On the other hand,



the high DR rates that *R. bourgeana* presents at high temperatures with very hydrated thalli, correlated well with the distribution of this species in cooler and better-drained habitats.

The development of the species in different locations is also related to the ability to exploit the hydration sources available. LANGE et al. (1969, 1970) and SCHEIDEGGER et al. (1995) demonstrated that *Ramalina maciformis*, a very close species to *R. bourgeana* in many ways, exploits night relative humidity (RH) more efficiently than *T. lacunosus*. *R. maciformis* obtained positive NP rates at early morning for night values of RH of 80%, while *T. lacunosus* required night RH rates of 90% to reach its compensation point in the early hours of the morning. This is in agreement with the data reported by LLIMONA (1973) for *T. lacunosus* from Los Monegros (Central Spain). Instead, the anatomical differences between both species seem to indicate that *T. lacunosus* is well adapted to taking up dew, which has been already correlated by PALMER & FRIEDMANN (1990) with the microclimatic and ecological differences between the locations where *T. lacunosus* and *R. maciformis* grow. The better efficiency in dew utilisation which *T. lacunosus* features, seems to be supported by a tomentum at the surface of its laciniae. LLIMONA (1973) suggested that such structures play a role in the retention and transferring of dew drops toward the photobiont layer. Additionally, ROS & WERNER (1997) linked, for desert mosses, the presence of hyaline hairs with the increase in dew drop absorption, as the hair puncturing the drop reduces its surface tension.

Growing in the same semiarid region, *T. lacunosus* and *R. bourgeana*, showed different photosynthetic performance with respect to both the temperature and the hydration. The relation of these results with the microclimatic conditions in the localities of each species is still an open question for further investigations.

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