

## Moisture Content and CO<sub>2</sub> Exchange of Lichens

### I. Influence of Temperature on Moisture-Dependent Net Photosynthesis and Dark Respiration in *Ramalina maciformis*

Otto L. Lange

Lehrstuhl für Botanik II der Universität Würzburg, Mittlerer Dallenbergweg 64, D-8700 Würzburg, Federal Republic of Germany

**Summary.** Net photosynthesis (10 klx light intensity, 150  $\mu\text{E m}^{-2} \text{s}^{-1}$  PAR) and dark respiration of the lichen *Ramalina maciformis* at different temperatures are measured in relation to thallus water content. Both first increase with increasing hydration. Dark respiration then remains constant with increased water content until thallus saturation. In contrast, a further increase in water content leads to a depression of net photosynthesis, as shown in previous studies, after a maximum of CO<sub>2</sub> uptake has been attained. However, the extent of this depression depends strongly on temperature. In saturated thalli (160% water content in relation to lichen dry weight) the depression amounts to about 15% and 63% of the maximum unsaturated rate at 5° C and 25° C thallus temperature, respectively. The moisture compensation-point of net photosynthesis is also decisively determined by temperature (for 0° C at 20% water content; for 25° C at 15%), and the water content that allows maximum rates of CO<sub>2</sub> uptake (for 0° C at 80%; for 25° C at less than 40% water content). An electrical analogue of CO<sub>2</sub> exchange in a lichen thallus is presented, and it is suggested that the experimental results may be interpreted in terms of temperature-dependent CO<sub>2</sub> diffusion resistances in imbibed lichen thalli.

### Introduction

Due to their poikilohydrous nature, all metabolic activities of lichens, and in particular net photosynthesis and respiration rates, vary greatly with the prevailing moisture content of the thalli. Dry lichens do not show any detectable CO<sub>2</sub> exchange. With low moisture content, in the light, and under steady-state conditions, CO<sub>2</sub> evolution takes place. At higher hydration, a moisture compensation-point is reached, and increasing water content then leads to a more or less proportional increase in net photosynthesis until, at a certain level of moisture content, maximal rates are attained. CO<sub>2</sub> uptake of the thalli as a function of further increase in water content is controversially described in the literature. As early as 1892, Jumelle, and later Stocker (1927), found that lichens have a lower net photosynthesis when fully soaked than at submaximal levels of saturation. This has been confirmed in principle in many subsequent investigations. However, enormous differences in the amount of photosynthesis depression in water saturated lichens are reported for different species and/or by different authors. In some investigations only a slight to negligible decrease in CO<sub>2</sub> assimilation in fully saturated thalli was found (Ellée, 1939; Butin, 1954; Lange and Bertsch, 1965; Lange, 1969). Ried (1960a and b) showed that stronger depressions occur in special

cases. According to the measurements of Kershaw (1972), in water saturated thalli of all twelve lichen species that he investigated, apparent CO<sub>2</sub> assimilation was fully suppressed and an upper moisture compensation-point was reached. There are data indicating that some species even release substantial amounts of CO<sub>2</sub> in light when they are fully soaked (Larson and Kershaw, 1975; Kershaw, 1977a and b). Another point of disagreement in the findings of different authors concerns the moisture content-dependent dark respiration. Usually, under steady-state conditions, CO<sub>2</sub> release follows a saturation-type response curve with an initial rise in respiration leveling off to a constant rate with an additional increase in the water content of the thalli (e.g., Ried, 1960a; Lange, 1969). In some cases, however, dark respiration is reported to increase continually as thallus moisture content is increased, even under conditions of imbibition when net photosynthesis already is highly depressed (Kershaw, 1977a).

Certainly, these discrepancies are due partly to species-specific differences in the investigated material (see Ried, 1960a; Harris, 1976). However, actual environmental factors such as illumination and temperature also decisively affect the moisture-dependent photosynthetic response of lichens. Finally, differences in methods used by the different authors may have influenced the results. Since an understanding of the interaction between water relations and CO<sub>2</sub> exchange is necessary if lichen productivity is to be correctly interpreted, clarification is desirable. Therefore, in a series of investigations, various aspects of the moisture content of lichen thalli in relation to their net photosynthesis and dark respiration will be analyzed. The results may contribute to an ecological explanation of lichen distribution. They should also serve as an improved basis for the modeling of lichen productivity in the field in relation to environmental conditions.

In the present paper, the influence of temperature on moisture-dependent CO<sub>2</sub> exchange under constant light conditions and in the dark is described. The experimental species is *Ramalina maciformis*, a desert lichen of the Negev, the physiological and ecological features of which have been investigated earlier in laboratory as well as in field experiments (Lange, 1969; Lange et al., 1970; Kappen et al., 1979).

### Material and Methods

The habitat and distribution of the fruticose lichen *Ramalina maciformis* (Del.) Bory is described by Lange (1969). As in the previous investigations, the material was collected in the Negev desert (Israel), airmailed to Würzburg, and stored in dry conditions at –18° C until experimentation. It was shown earlier that this proce-

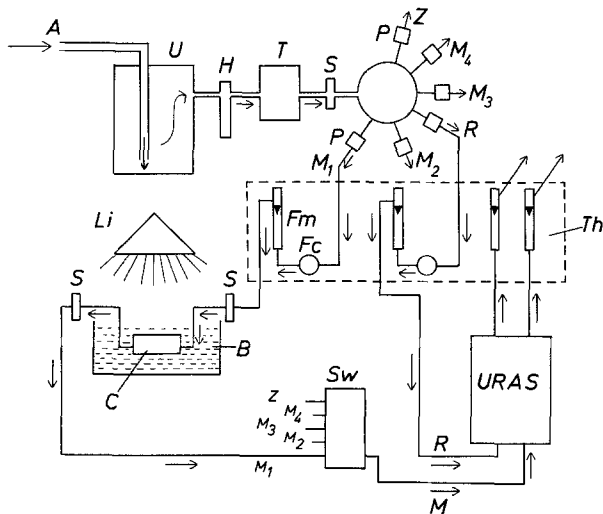


Fig. 1. Schematic diagram of the measuring system showing the pneumatic connections for reference gas stream and for one of four cuvettes. For explanation see text

ture does not influence the photosynthetic capacity of the plant. Prior to the experiments, the thalli were placed in a temperature-controlled growth chamber where they were exposed to 12-h periods of alternating light (10 klx) and darkness at 10° C for at least 3 days. They were moistened daily by spraying.

For net photosynthesis and dark respiration measurement, the lichen thalli were enclosed in Plexiglas chambers (Fig. 1C) submerged in a water bath (B), the temperature of which was kept constant within  $\pm 0.1^\circ\text{C}$ . The temperature of the thalli inside the cuvettes was recorded by means of an attached thin thermocouple; all temperature specifications relate to this thallus temperature. Four cuvettes were run simultaneously parallel to each other in the same water bath.  $\text{CO}_2$  exchange of the enclosed lichens was monitored in an open system following the gas differential procedure. Outside air (A) with an average  $\text{CO}_2$  content of 330 ppm was pumped in (P) and channeled through buffering containers (U). It was then moistened at room temperature in a humidifier (H), and passed a Peltier-controlled water vapor trap (T) in order to set a given dew point which then was recorded by a humidity sensor (S, high precision dew point mirror, Walz Instruments). Subsequently, the air was divided into 6 separate

streams: measuring gas streams ( $M_1$  to  $M_4$ ) passing the cuvettes, zero gas stream (Z) and reference gas stream (R) without cuvettes. Flow rate in each gas stream was set to 30 or 40  $\text{l h}^{-1}$ , measured by flow meters (Fm) and kept constant by means of flow rate controllers (Fc), both installed into thermostats at 50° C air temperature (Th). Humidity could be monitored once again by humidity sensors placed at the air inlet and outlet of one of the submerged cuvettes. The reference air stream was continuously connected with the reference tube of an infrared gas-analyzer (URAS, Hartmann and Braun). A multivalve switch (Sw) connected each of the measuring streams and the zero gas stream to the measuring tube of the URAS at one minute intervals. In the interim periods, when not connected to the instrument, the gases were vented. The flow controllers ensured continually constant flow rates through the cuvettes in spite of changes in flow resistances. Air flow through the URAS was monitored once more at the outlets of the instrument. The infrared gas-analyzer (full scale sensitivity  $+50\cdots 0\cdots -50$  or  $+25\cdots 0\cdots -25$  ppm  $\text{CO}_2$ ) produced two types of signals, the first indicating a  $\text{CO}_2$  concentration difference between measuring and reference air streams and the second, a zero-signal for zero against reference gas stream. The difference between these signals was used to calculate the net  $\text{CO}_2$  exchange of the enclosed lichen thalli.  $\text{CO}_2$  exchange was related to oven dry weight (24 h at 105° C) of the individual lichen samples. The cuvettes were illuminated by mercury high pressure lamps (Li). Light intensity inside the cuvettes was 10 klx; photosynthetically active irradiance was approximately  $150 \mu\text{E m}^{-2} \text{s}^{-1}$  (quantum sensor, Licor).

The lichen thalli (ca. 1.5 g dry weight per cuvette) were loosely fastened with metal thread to a silver wire framework which fit into the cuvettes. Prior to experimentation the plants were fully soaked in deionized water, and excess surface water (droplets only) was removed by slightly shaking and blotting.  $\text{CO}_2$  exchange in light and darkness of this saturated material was measured and the trays with lichens were weighed. Subsequently, the thalli were gradually dried out in the cuvettes by decreasing the air humidity of the passing air stream, and net photosynthesis and dark respiration were continually recorded. About 30 times per experiment, at intervals of several hours, the trays with the lichens were removed, weighed, and replaced again. Each weight was assigned to the  $\text{CO}_2$  exchange of the lichens immediately before the removal. One drying cycle usually lasted about 5 days. In some cases, the dried lichens were remoistened again by treatment with air of high humidity; hysteresis effects were minor and did not

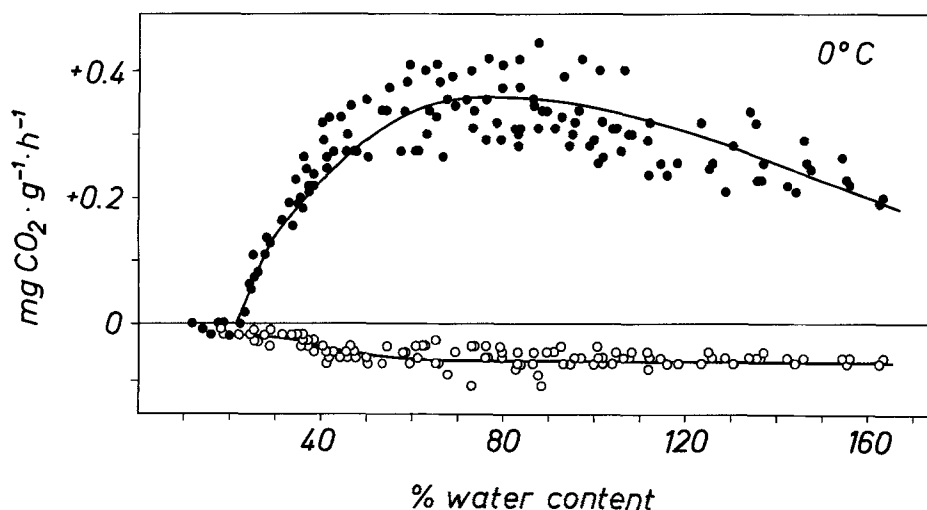


Fig. 2. *Ramalina maciformis*: Net photosynthesis at 10 klx light intensity (points) and dark respiration (circles) as a function of thallus water content; temperature 0° C. Ordinate:  $\text{CO}_2$  uptake (positive) and  $\text{CO}_2$  release (negative)

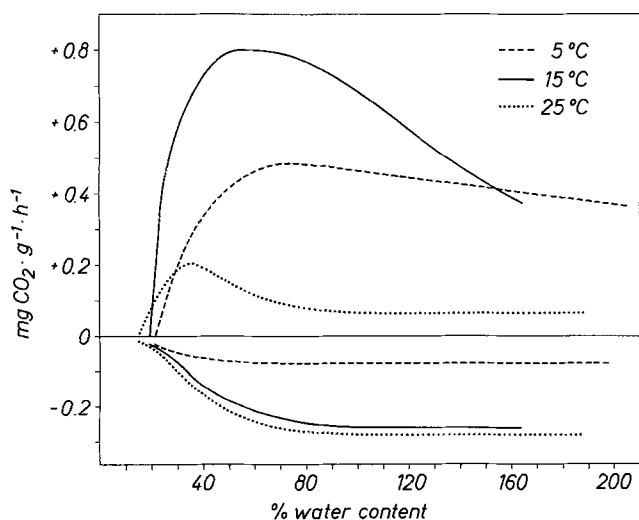
influence the results. Water content of the thalli during the measurements was expressed as a percentage of lichen oven dry weight.

Three to six parallel samples were measured for a given temperature step so that each response curve shown (Figs. 3 and 4) is representative of at least 90 single measuring points. Figure 2 is an example of the scattered data points for one curve.

## Results

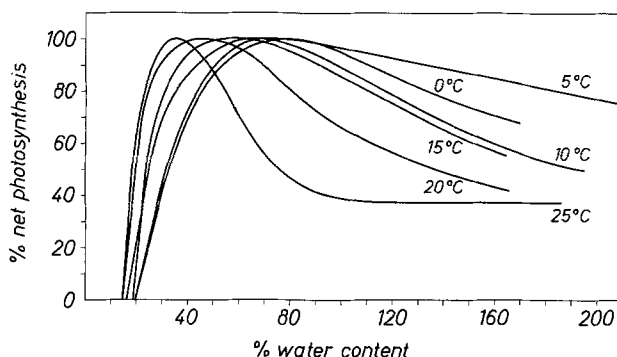
The temperature optimum of net photosynthesis for the hydrated thalli of *R. maciformis* is around 15° C when plants receive light intensities of 10 klx (Lange et al., 1977). This is shown in Fig. 3, where maximal rates of CO<sub>2</sub> uptake at 15° C are higher than at 5° and 25° C respectively. However, temperature not only influences this maximum capacity of photosynthesis but also the moisture-dependent pattern of CO<sub>2</sub> uptake. At 5° C, there is only a very slight depression of net photosynthesis even when thalli have reached full water saturation. This is reached between 160 and 200% water content (maximal possible water content varies within this range from sample to sample). With increasing thallus temperature the depression increases. This is obvious from Fig. 4, where water content-dependent net photosynthesis rates are expressed as a percentage of maximum photosynthesis. At thallus saturation (160% water content taken for all samples) relative net photosynthesis rates clearly depend on temperature (Fig. 5). Between 5° and 25° C the depression increases from only 15% to 63%, respectively, of the maximal rates reached at optimal water content. At 0° C lichen temperature, the moisture dependent depression is higher than at 5° C, possibly due to some ice formation within the thallus.

Other features of the net photosynthesis response curves also change systematically with temperature. The higher the thallus temperature, the lower the water content at which maximum rates of CO<sub>2</sub> uptake are reached (Fig. 6, also Fig. 4). The respective differences are remarkable. Optimal net photosynthesis at 0° C is achieved at about 80% water content, whereas at 25° C maximum rates occur at less than half of this moisture content. Also at low degrees of hydration the interaction between temperature

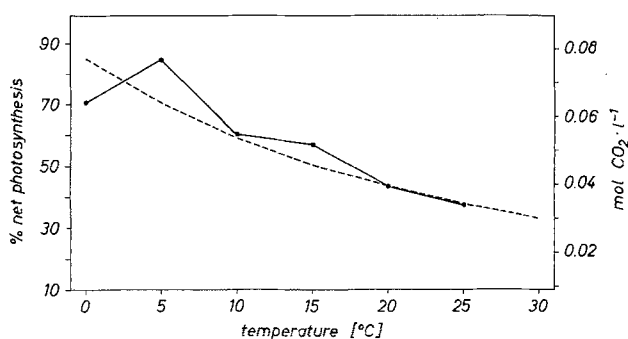


**Fig. 3.** *Ramalina maciformis*: Net photosynthesis at 10 klx light intensity (above) and dark respiration (below) as a function of thallus water content at different, indicated temperatures

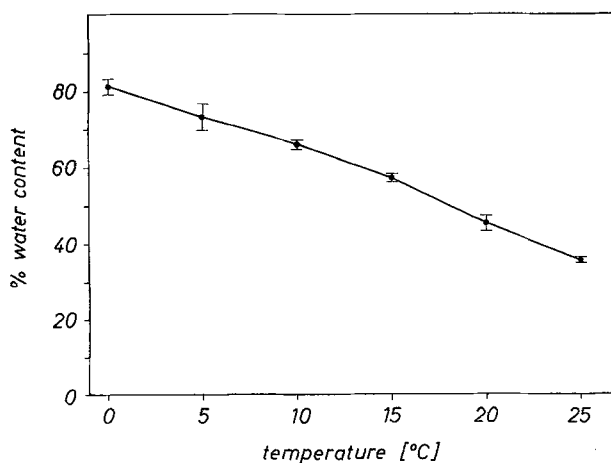
and hydration in influencing CO<sub>2</sub> exchange becomes obvious. The moisture compensation-point, that is, the water content where photosynthetic CO<sub>2</sub> uptake is just compensated by respiration, shifts to lower values of water content with increasing temperature (Table 1). The initial slope of water content-dependent CO<sub>2</sub> uptake, which might be taken to indicate an 'efficiency of hydration' in terms of photosynthesis, also changes in a characteristic manner



**Fig. 4.** *Ramalina maciformis*: Relative net photosynthesis (in percentage of maximum rates) as a function of thallus water content at different, indicated temperatures; 10 klx light intensity



**Fig. 5.** Solid line (left ordinate): Relative net photosynthesis of *Ramalina maciformis* (in percentage of maximum rates) at thallus saturation (160% water content) as a function of temperature; 10 klx light intensity. Dashed line (right ordinate): Solubility of CO<sub>2</sub> in pure water: data from Buch (1960)



**Fig. 6.** *Ramalina maciformis*: Thallus water content at maximum rates of net photosynthesis as a function of temperature; 10 klx light intensity. Deviations of single experiments indicated

**Table 1.** *Ramalina maciformis*: moisture compensation point and initial slope of water content-dependent net photosynthesis at different thallus temperatures; 10 klx light intensity

	0° C	5° C	10° C	15° C	20° C	25° C
compensation point (% water content)	19.75	20.0	16.5	18.75	14.5	15.0
initial slope	2.3	3.4	4.9	12.7	3.5	2.3

in response to temperature. It is lowest at very low and very high temperatures, and it is maximal in the temperature range from 10° to 20° C.

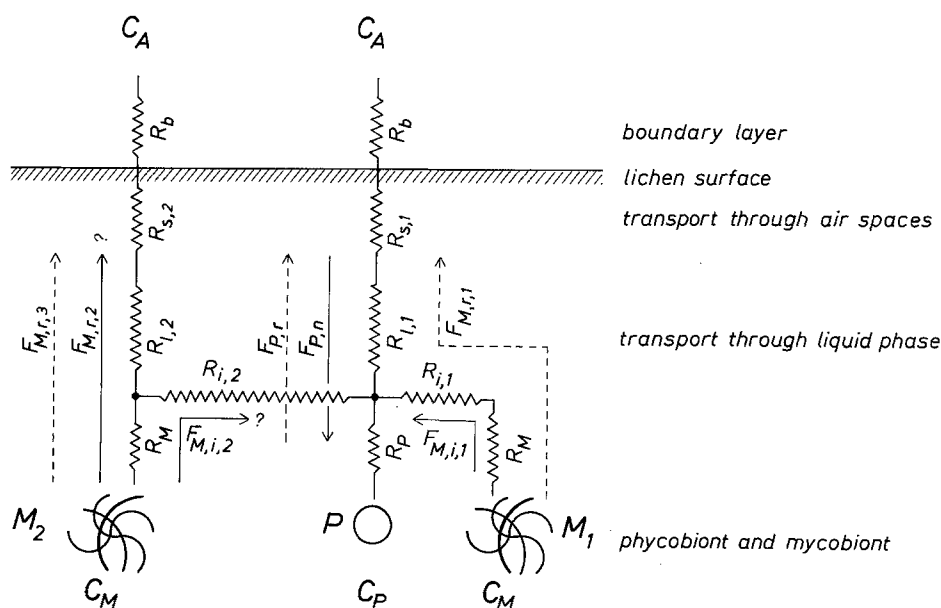
Dark respiration responses are similar at all temperatures (Figs. 2 and 3). CO<sub>2</sub> release first increases sigmoidally with increasing hydration and then reaches a maximal value which remains constant at all investigated temperatures until thallus saturation. Absolute rates of dark respiration naturally depend strongly on temperature. It should be pointed out that at low thallus temperatures maximal rates of dark respiration and of net photosynthesis are reached almost at the same water content of the thalli, whereas at higher temperatures net photosynthesis decreases at water content points which still lead to a further increase in dark respiration.

## Discussion

Figure 7 presents a simple electrical analogue of CO<sub>2</sub> exchange in a lichen (see Nobel, 1974; Tenhunen et al., 1977). CO<sub>2</sub> fluxes ( $F$ ) are determined by gradients in CO<sub>2</sub> concentration ( $C$ ) and by diffusion resistances ( $R$ ). Two samples of the mycobiont are indicated: one ( $M_1$ ) in close association with a phycobiont ( $P$ ), where diffusion resistance ( $R_{i,1}$ ) between both is small, and the other ( $M_2$ ) at some distance from the next phycobiont (for instance in the lower medulla of the lichen), where  $R_{i,2}$  is high. Ambient CO<sub>2</sub> concentration ( $C_A$ ) is assumed to be constant. When light allows sufficient photosynthetic CO<sub>2</sub> fixation, CO<sub>2</sub> concentration around the phycobiont ( $C_P$ ) becomes low. In this case the CO<sub>2</sub> flux of net photo-

synthesis ( $F_{P,n}$ ) transports CO<sub>2</sub> from the ambient air to the sites of carboxylation. This flux encounters first the resistance of the aerodynamic boundary layer ( $R_b$ ), then resistances during transport within the thallus, partly in air spaces ( $R_{s,1}$ ) and partly in the liquid phase ( $R_{l,1}$ ), and finally the resistance in the cytoplasm of the phycobiont ( $R_P$ ). In addition to this, another internal CO<sub>2</sub> flux ( $F_{M,i,1}$ ) must exist which transports respiratorily evolved CO<sub>2</sub> from the mitochondria of the nearby mycobiont (high  $C_M$ ) to the algae, the rate of which is determined by the resistance ( $R_{i,1}$ ) between both symbionts. If, for those parts of the mycobiont ( $M_2$ ) which are spatially distant from the phycobiont,  $R_{i,2}$  becomes greater in relation to the sum of resistances in the pathway from the fungus to the ambient air ( $R_{i,2} + R_{s,2}$ ), it seems possible that some CO<sub>2</sub> may be lost ( $F_{M,r,2}$ ) even in light and is not recycled within the thallus. During darkness, the CO<sub>2</sub> concentration  $C_M$  remains high, and the phycobiont also produces CO<sub>2</sub> (high  $C_P$ ). Thus the gradient in CO<sub>2</sub> concentration is reversed and respiratory CO<sub>2</sub> loss takes place (dashed lines, Fig. 7). Unfortunately, at present, information is not available about absolute numbers of internal CO<sub>2</sub> concentrations of lichens and/or diffusion resistances in a thallus. Therefore, only a discussion about qualitative relationships is possible.

When moisture is added to lichens having low water potential, metabolic activity is stimulated and increases as moisture is increased until cells are fully turgid at a plant water potential near 0, and saturation of the biochemical reactions in terms of hydration is reached. This is clear from the water content-dependent dark respiration of the lichen (Figs. 2 and 3), which follows a characteristic saturation-type curve. At each water content the internal CO<sub>2</sub> concentration of the lichen will continuously increase due to the respiratory processes until the gradient to the ambient air is steep enough that, under steady-state conditions, the outflow of CO<sub>2</sub> equals internal CO<sub>2</sub> production. Consequently, respiratory CO<sub>2</sub> release from the thallus is, to a large extent, independent of diffusion resistances (which agrees with the observation that dark respiration in leaves is usually independent of stomatal resistance). This may explain why dark respiration in the lichens remains constant even at high thallus water content when the internal diffusion resistances are certainly altered. In view of these considerations and on the basis of the present findings with *R. maciformis*,



**Fig. 7.** Electrical analogue of CO<sub>2</sub> exchange in a lichen.  $C$ 's are CO<sub>2</sub> concentrations,  $F$ 's are CO<sub>2</sub> fluxes,  $R$ 's are diffusion resistances. Meaning of letters and subscripts:  $A$  for ambient,  $M$  for mycobiont,  $P$  for phycobiont;  $b$  for boundary layer,  $i$  for internal CO<sub>2</sub> cycling,  $l$  for liquid phase,  $n$  for net photosynthesis,  $r$  for respiration,  $s$  for air spaces. Arrows indicate direction of CO<sub>2</sub> fluxes (during positive net photosynthesis in light: solid lines; during darkness: dashed lines). For explanation see text

we cannot offer an explanation for the results reported by Kershaw (1977a and b) for *Peltigera* species. According to his measurements, these lichens, at least at higher temperatures, exhibit a continuous and substantial increase in dark respiration with increasing thallus water content up to full saturation.

In the light, too, some level of hydration must be reached at which the photosynthetic apparatus is saturated and lack of water no longer inhibits biochemical activity. This probably takes place at water contents of the same order of magnitude as those causing saturation of respiration or, in *R. maciformis*, at a thallus water content of about 60 to 80%. However, the  $\text{CO}_2$  gradient from ambient air to the phycobiont ( $C_A - C_P$ ) always remains relatively small, even at high photosynthetic rates, since it is limited by the external  $\text{CO}_2$  concentration. Because the actual gradient is small, resistance changes result in effectively large changes in  $\text{CO}_2$  transport, and the rates of net photosynthesis are always very sensitive to changes in diffusion resistance. As already pointed out by Ried (1960b),  $\text{CO}_2$  diffusion in the lichen thallus becomes hampered with the increasing content of water. At the first stages of imbibition,  $\text{CO}_2$  flux probably occurs predominantly within the air spaces of the thallus, which offer only small resistance. With increasing water content, however, the role played by  $R_{s,1}$  in total transport resistance decreases, because the free capillary system is constricted by swelling of the hyphae and by engorgement with water; more transport has to take place in the liquid phase with high resistances ( $R_{l,1}$ ). Thus the rate of net photosynthesis ( $F_{P,n}$ ) diminishes with the increasing water content of the lichen (Fig. 3). In lichens other than *R. maciformis* this might lead to the point where  $R_{l,1}$  becomes so high that net inward flux of  $\text{CO}_2$  ( $F_{P,n}$ ) is no longer possible and only internal cycling ( $F_{M,i,1}$ ) takes place. Then the thallus would reach an upper moisture compensation point as described, for instance by Ried (1960a and b) and Kershaw (1977a). On the basis of these considerations, even a net efflux of  $\text{CO}_2$  might become conceivable in extreme cases, such as reported by the above authors for some lichens at very high water contents in spite of strong illumination. That is,  $R_{l,1}$  and  $R_{i,2}$  might become extremely high, causing loss of respiratory  $\text{CO}_2$  from those parts of the mycobiont ( $F_{M,r,2}$ ) which are coupled with lower resistances ( $R_{l,2} + R_{s,2}$ ) to the ambient air.

These experiments have shown that depression of relative net photosynthesis at a high water content becomes greater with increasing temperature in the range between 5° and 25° C (Fig. 4). It is unlikely that biochemical features are responsible for this response rather than temperature-dependent changes in the  $\text{CO}_2$  diffusion resistances of the thalli. Temperature, for example, might promote swelling of the hyphae system and hence affect the resistances. Most probably, however, the solubility of  $\text{CO}_2$  in water plays a decisive role in influencing resistances. As shown in Fig. 5 solubility decreases with increasing temperature almost in proportion to net photosynthesis depression in saturated thalli. This correlation might indicate causal relationships. It leads to many speculations, e.g., as to the influence of the pH of thallus water, which determines the concentration of the different species of ' $\text{CO}_2$ ' present in the aqueous phase, on temperature-dependent transport resistances. However, future experimental results remain to be seen.

Interaction between changes in resistance with temperature on the one hand, and with mass of water present in the thallus on the other, might also be responsible for the shift of the moisture-dependent net photosynthesis optima to lower water contents with higher temperatures (Fig. 6). Thus, at 25° C resistance might already be high enough at 35% water content so that the photosyn-

thetic capacity, which still increases with improvement of hydration, can no longer be balanced due to limited supply of  $\text{CO}_2$ . At lower temperatures, the same might be the case only at much higher water contents. However, conditions are certainly more complicated. This is revealed by the fact that at 25° C lichen temperature – in contrast to lower temperatures – net photosynthesis remains constant over a wide range of water contents after the initial peak. Such a pattern is also typical for *R. maciformis* at higher light intensities and was also found for other lichen species (e.g., Rundel et al., 1979). Possibly other temperature- and moisture-dependent processes, such as changes in tortuosity of the diffusion pathway for  $\text{CO}_2$  or changes in the mobility of  $\text{CO}_2$  within the liquid phase, interfere with  $\text{CO}_2$  solubility in affecting total diffusion resistances in the lichen thallus. Further investigations involving quantitative determination of diffusion resistances may elucidate at least some of these factors.

In earlier studies (Lange and Bertsch, 1965; Lange, 1969) the net photosynthesis of *R. maciformis* in relation to thallus water content at 10° C temperature was established. A negligible or zero depression at thallus water saturation was assumed. (In these studies the main emphasis was given to the ecologically most important lower range of thallus hydration. The response of the lichen at higher water contents was investigated only by occasional spot checks.) Based on these data, photosynthetic  $\text{CO}_2$  exchange in the desert lichen was modeled and simulated for dew-soaked plants under field conditions (Lange et al., 1977). The present findings indicating a strong temperature-dependent influence at high thallus water contents necessitate a revision and at the same time an elaboration of the model. However, this should not essentially affect the earlier results, since dew-moistening of lichens in the field never reaches levels higher than 90% water content (Kappen et al., 1979), and temperatures during active photosynthesis after dew-fall in the morning hours are usually relatively low.

In comparison with other lichen species that have been investigated (see Bewley, 1979) net photosynthesis in *R. maciformis* is relatively slightly depressed at high thallus water contents, and in the course of the described experiments it never reached an upper moisture compensation-point. This might be due to the special structure of the thallus (see Ried, 1960a) of *R. maciformis*. Investigations are being conducted which may help to establish a relationship between the degree of moisture-dependent depression in net photosynthesis, anatomical structure, and habitat ecology of different types of lichens.

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