Moisture Content and CO₂ Exchange of Lichens

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

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Summary. Net photosynthesis (10 klx light intensity, 150 µE m⁻² 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 CO₂ 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 CO₂ uptake (for 0°C at 80%; for 25°C at less than 40% water content). An electrical analogue of CO₂ exchange in a lichen thallus is presented, and it is suggested that the experimental results may be interpreted in terms of temperature-dependent CO₂ diffusion resistances in imbied 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 thallii. Dry lichens do not show any detectable CO₂ exchange. With low moisture content, in the light, and under steady-state conditions, CO₂ 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. CO₂ 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 CO₂ 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 CO₂ assimilation was fully suppressed and an upper moisture compensation-point was reached. There are data indicating that some species even release substantial amounts of CO₂ 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, CO₂ 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 CO₂ 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 CO₂ 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 Würtzburg, 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.

dure 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 ±0.1°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. CO2 exchange of the enclosed lichens was monitored in an open system following the gas differential procedure. Outside air (A) with an average CO2 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 (M1 to M4) 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 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...0... -50 or +25...0... -25 ppm CO2) produced two types of signals, the first indicating a CO2 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 CO2 exchange of the enclosed lichen thalli. CO2 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 μE m⁻² 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. CO2 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 CO2 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: CO2 uptake (positive) and CO2 release (negative)