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2.8 Photosynthetic Production of the Lichen *Ramalina terebrata* Hook. f. et Tayl., in the Maritime Antarctic

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Summary: *Ramalina terebrata* is an ornithocoprophilic macrolichen frequently occurring on coastal rocks of Kind George Island, Lesser Antarctica. Simple models, based on laboratory and field measurements of the CO_2 exchange, were developed to describe the dependence of net photosynthesis and respiration on temperature, quantum flux, and thallus water content. Temperature and quantum flux were first used to produce a response surface plot for an optimally wet lichen by means of regression analysis. The fit of the model was tested by comparing the laboratory data with actual values from field measurements on King George Island. The variation of the CO_2 exchange with the water content of the lichen was then modelled using laboratory data. Continuous measurements of light, temperature and thallus water content at the natural habitat during December 1984 were used to calculate the daily courses of CO_2 exchange of *R. terebrata* by means of the models. As a result, the mean carbon production in this Antarctic summer month was found to be remarkably high. A relatively high growth rate seems to be indicated also by ^{14}C-age analyses in fruticose lichens of the maritime Antarctic botanical zone.

Zusammenfassung: Die ornithocoprophile Flechte *Ramalina terebrata* ist auf Küstenfelsen der King George Insel, Westantarktis, häufig. Basierend auf CO_2-Gaswechselmeßergebnissen im Labor und im Freiland werden einfache Modelle entwickelt, die die Abhängigkeit der Nettophotosynthese und der Atmung von der Temperatur, der Quantenfluxdichte und dem Thallus-Wassergehalt beschreiben. Zunächst wurde mittels Regressionsanalyse ein Modell für die Reaktion optimal feuchter Flechtenthalli auf Licht und Temperatur formuliert. Im Test und Abgleich des Modells wurden die aus Laborwerten voraussagbaren CO_2-Gaswechselwerte mit solchen an natürlichen Standorten in der Antarktis gemessenen Werten verglichen. Die Abhängigkeit der Gaswechselraten vom Wassergehalt der Thalli wurde im Labor bestimmt und als Term in das oben genannte Modell eingearbeitet. Thalluswassergehalte, Licht und Temperaturverlauf wurden am natürlichen Standort einen Monat lang (Dezember 1984) kontinuierlich registriert. Folglich konnte für diesen Monat mit Hilfe des Modells eine CO_2-Bilanz errechnet werden. Die Produktionsrate ist für antarktische Flechten verhältnismäßig hoch. Hierauf deuten auch Ergebnisse einer ^{14}C-Altersdatierung von Strauchgeflechten aus diesem Gebiet der Antarktis hin.

1. INTRODUCTION

Many lichens are adapted to the extreme environmental conditions in the Antarctic because they are highly resistant to temperature- and water-stress and are only active at a low metabolic level. Consequently they grow very slowly. It is recorded that fruticose Antarctic lichens may reach an age of several centuries (LINDSAY 1978, HOOKER 1980).

One approach to investigate the growth of lichens and mosses is to measure their photosynthetic production and its main controlling parameters during relatively long periods of time (OECHEL & SVEINBJÖRNSSON 1978, KAPPEN et al. 1979). If, however, as well as long term recordings of habitat parameters, laboratory data for net photosynthesis and respiration are available a carbon balance can be calculated by use of a photosynthesis model, such as was developed by LANGE et al. (1977), COLLINS & CALLAGHAN (1980), DAVIS (1983), SILVOLA (1985) and, with respect to water content in lichens, by MATTHES-SEARS & NASH III (1986).

In the following paper an attempt is made to calculate the photosynthetic production of a maritime Antarctic lichen during an Antarctic summer month, based on comparisons of field and laboratory measurements of CO_2 exchange together with continuous recording of light, temperature and thallus water content.

2. MATERIAL AND METHODS

Ramalina terebrata Hook. f. et Tayl. is a ribbon-shaped macrolichen with a fenestrated or perforated thallus. It reaches a length of about 7 cm. It is a frequent and obvious lichen in the maritime Antarctic botanical zone, comprising the South Orkney and South Shetland Islands as well as the Antarctic Peninsula, and also in the cold temperate parts of South America. It colonizes mostly coastal rocks under the influence of salt spray and places influenced by bird perching. It is therefore considered a character species of the ornithocoprophilous lichen

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association Ramalinetum terebratae with other species, such as *Caloplaca regalis*, *Rhizocarpon griseolum*, *Pertusaria solitaria*, *Xanthoria candelaria* (FOLLMANN 1965).

Net photosynthesis and respiration were measured in the laboratory with optimally moistened thalli at various temperatures and light conditions (KAPPEN & REDON 1987). These results were then described by a photosynthesis and respiration model.

Field measurements were carried out 500 m east of Arctowski station, King George Island, South Shetland Islands, at a basaltic rock with rich lichen colonization. During the period from December 1—31, 1984, air- and thallus

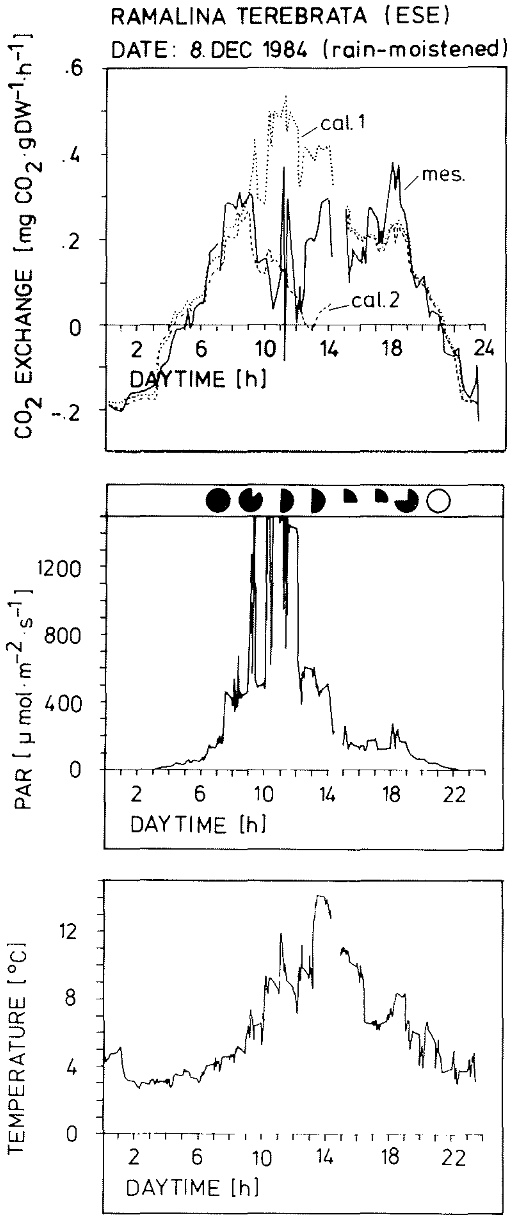


Fig. 1: CO_2-exchange of *R. terebrata* measured (solid line) in the field (at a coastal rock near Arctowski station, Admiralty Bay, King George Island) during the course of the 8th of December 1984. Light (PAR), cloudness (overcast: black, clear: white circle) and thallus temperature are indicated in the lower two boxes. CO_2-exchange predicted by model 1 and 2 is shown by the dotted line, and predicted by model 3—4 is shown by the dashed line. DW = dry weight.

temperatures (thermocouples), quantum flux densities (Licor sensors Li 190 SB) and thallus water contents (Hiltner dew balance, KAPPEN et al. 1979) were recorded continuously.

Measurements of CO_2 exchange were carried out with equipment installed close to the habitat of the sampled lichens. The CO_2-analyzer (Binos) and the recording system were installed in a shelter and thus protected against extreme climatic conditions (KAPPEN et al. 1986). CO_2 exchange was determined by a differential system with flow rate kept constant by pumps. A Peltier-system allowed the temperatures in the fan-ventilated plexiglass plant chamber to be controlled electronically, either at a constant value or tracking environmental temperatures by a feed-back control. Thus, we were able to carry out CO_2-measurements under natural temperature and light conditions. Two parallel plant chambers were exposed in two compass directions on the basaltic rock.

3. RESULTS

Figure 1 shows a diurnal course of the CO_2 exchange of sprayed thalli at the ESE facing site of a basaltic rock. Such field data have the advantage that they show the response to natural light quality and also to higher quantum flux densities than could be generated in the laboratory. However, when these CO_2 exchange rates were plotted versus PAR quantum flux density a great variation of values became obvious at flux densities above 400 µmol m^{-2} s^{-1} and no light saturation was apparent. This indicated interference from another factor in this range. In the lower — much more relevant quantum flux range — the environmental relationships of the field data were clearer and in broad agreement with the laboratory data.

A non-linear multiple regression model was developed for the relationship between photosynthesis, light and temperature, using the laboratory data obtained with optimally moist thalli (Fig. 2):

Net photosynthesis:

(1) $NP = a_0 + a_1 T + a_2 T^2 + a_3 \ln (L + 1) + a_4 (\ln [L + 1])^2 + a_5 \ln (L + 1) T$

and respiration

(2) $R = b_0 + b_1 T + b_2 T^2$

where T = thallus temperature (°C), L = PAR (µmol m^{-2} s^{-1}), a_0 to a_5 and b_0 to b_2 are constants for net photosynthesis and respiration, respectively.

The equations significantly ($r_{(1)}^2 = 0.97$; $r_{(2)}^2 = 0.99$) described the measured values (Fig. 2). These equations are a modified version of those suggested by DAVIS (1983) to calculate net photosynthesis of Antarctic bryophytes. The data-base available was too small for a non-linear regression model according to LINDSEY et al. (1970).

By application of the above model to data from a whole month's continuous measurements of thallus-temperatures and quantum flux-densities in a fruticose lichen on a basaltic rock at this site, an average hourly photosynthetic rate of *R. terebrata* during December 1984 was 0.3 mg CO_2 g d. wt.$^{-1}$ h^{-1}, and the respiratory rate in the dark hours (below 30 µmol m^{-2} h^{-1}) was 0.15 mg CO_2 g d. wt.$^{-1}$ h^{-1}. As a result the monthly production would have amounted to 120 mg CO_2 g d. wt.$^{-1}$. However, this figure was based on the assumption that the thalli were always optimally moist.

Deviations from an optimally moist thallus response are apparent in Figure 1. Photosynthesis was decreased at higher quantum flux densities because radiation causes overheating, even on cloudy days, and consequent reduction of moisture content in the thalli. It is also possible that oversaturation of the thalli causes a decrease of net photosynthesis. Thus, the model greatly overestimated the photosynthetic gain of the lichens (Fig. 1, dotted line).

In the laboratory photosynthesis and respiration were also analyzed as a function of water content (Fig. 3). As formerly shown by LANGE (1980), with *Ramalina maciformis*, the net photosynthetic rates of *R. terebrata* increased with increasing thallus water contents until an optimum was reached, and then decreased due to

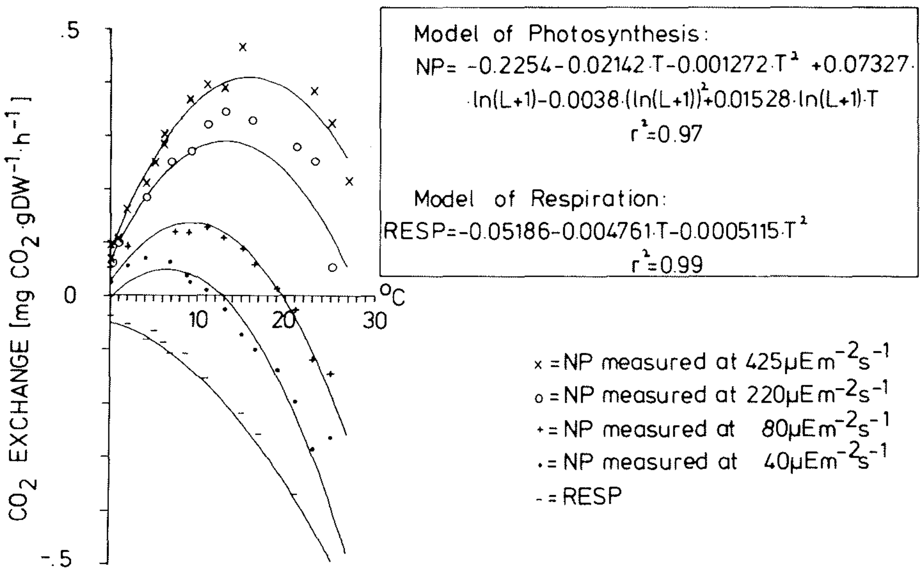


Fig. 2: Model of the temperature and light related CO_2 exchange (lines) based on laboratory measurements (single symbols) with *R. terebrata*. DW = dry weight.

increased CO_2-diffusion resistances. This was apparent at several light intensities with temperatures above +1.5° C, but not below this temperature and also not with dark respiration. Apparently at the lower temperature level the CO_2 solubility was high enough and the optimum but low photosynthetic rate could be maintained in the highly imbibed thallus.

These differences had to be taken into account in a model of water content-dependent net photosynthesis. According to Figure 3, data of photosynthetic rates at various water contents, at 4 thallus temperatures, and within a range of 250—515 µmol m^{-2} s^{-1} were available. A mean relative degree of depression from optimum (= 100%) was calculated for all light intensities with 3 coefficients:

(3) $NP\% = c_0 + c_1\,WC + c_2\,WC^2$

The following functions were obtained for net photosynthesis versus light and temperature and their percentage variation by water content within two different temperature ranges.

Equation (3a) is relevant to T > 1.5° C (Fig. 4):

(3a) $NP = (a_0 + a_1\,T + a_2\,T^2 + a_3 \ln(L+1) + a_4 (\ln[L+1])^2 + a_5 \ln(L+1)\cdot T)\cdot(c_0 + c_1\,WC + c_2\,WC^2)$

$c_0 = -61.5171;\ c_1 = 2.9234;\ c_2 = 0.01336$

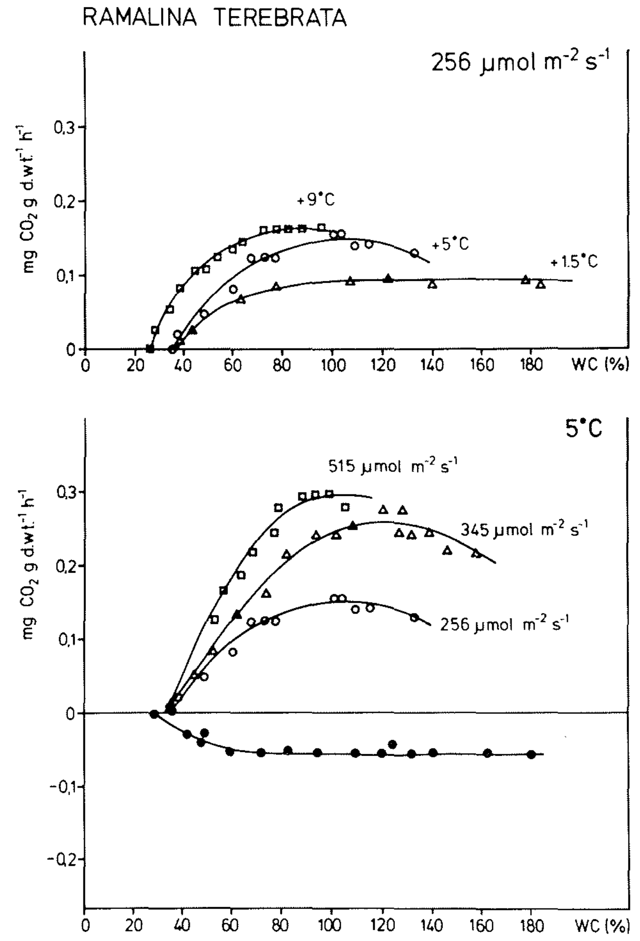
For T < 1.5° C (Fig. 5):

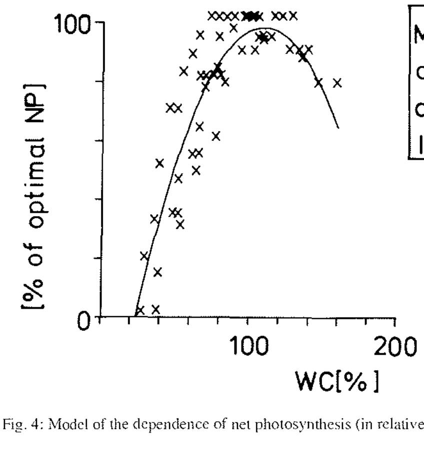
(3b) $NP = (a_0 + a_1\,T + a_2\,T^2 + a_3 \ln(L+1) + a_4 (\ln[L+1])^2 + a_5 \ln(L+1)\cdot T)\cdot(c_0 + c_1\,WC + c_2\,WC^2)\cdot S$

$c_0 = -51.6218;\ c_1 = 2.3367;\ c_2 = 0.008619$

The term S functions as a switch which prevents the values of the function being decreased at water contents above optimum. It was "1" if thallus water contents were lower than 107% d. wt. At higher water contents the function was always equal to 100%.

Fig. 3: Photosynthetic response to light and temperature, and dark resparation versus thallus water content (wc) of *R. terebrata*. Laboratory measurements from KAPPEN & REDON (1987).





Model of Dependence of CO_2 Exchange on Water Content

a) Photosynthesis (if T>1.5 °C)

$IN[\%]=-61.5171+2.9234\cdot WC-0.01336\cdot WC^2$

Fig. 4: Model of the dependence of net photosynthesis (in relative values) on thallus water content (wc) at temperatures above +1.5° C.

(4) Dark respiration was similarly formulated in relative values (Fig. 5):

$$R = (b_0 + b_1\,T + b_2\,T^2) \cdot (c_0 + c_1\,WC + c_2\,WC^2) \cdot S$$

Water contents of lichen thalli were gravimetrically recorded at the ESE facing site of the basaltic rock by exposing *Usnea antarctica* to the open at the balance arm of a Hiltner dew balance. By comparing water contents during parallel drying cycles with *U. antarctica* and *R. terebrata* under the same ambient conditions a calibration curve for *R. terebrata* was gained. This was used to determine the approximate water contents of *R. terebrata* during the period of December 1984 (Fig. 6).

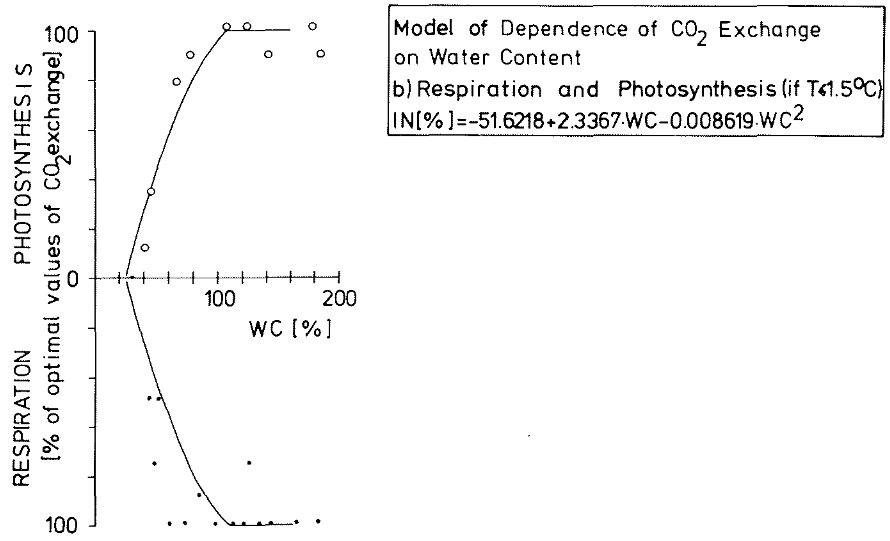


Fig. 5: Model of the dependence of net photosynthesis and dark respiratin (relative values) on thallus water content (wc) at temperatures below +1,5° C.

The predicted values of net photosynthesis, based on our model and its modification due to the recorded water content, coincided with the measured curve (broken and solid line in Fig. 1) during most of the day. The thalli were rain-moistened in the morning and slowly dried out during the morning under the overcast sky. They were then sprayed at 2.15 p. m. and stayed active until the other day. For this period a similar pattern of water loss as during the morning was assumed for the calculation. The upper part of Figure 6 shows the daily courses of water content of *R. terebrata* during December 1984. Rainy and snowy days caused extended periods of water soaking in the thalli, which reached maximum values of more than 200% d. wt. within the first half of the month. A very dry period then allowed the lichen to only reach water contents below 25% d. wt. so that thalli were mostly inactive. Later on, scattered rainfall or morning dew had activated the lichens to some extent. The lower part of Figure 6 shows the corresponding photosynthetic activity. In total, *R. terebrata* was active on 17 of 28 days measured in December. According to our calcualtion *R. terebrata* gained a total of 22.31 mg CO_2 g d. wt.$^{-1}$ and lost, by respiration, a total of 8.43 mg CO_2 g d. wt.$^{-1}$ during this month. The photosynthetic net gain was 13.89 mg CO_2 g d. wt.$^{-1}$. Since 1 g dry weight of *R. terebrata* contained 340 mg Carbon, the Carbon production was 3.79 mg which is 11‰ during this summer month, respectively.

4. DISCUSSION

The presented model here is considered a reasonable approach at simulating the natural photosynthetic rates and the productivity of a lichen during a summer month in the maritime Antarctic botanical zone. As a colonizer of habitats with high nitrogen supply *R. terebrata* certainly belongs to the faster growing Antarctic lichens. Carbon^{14}

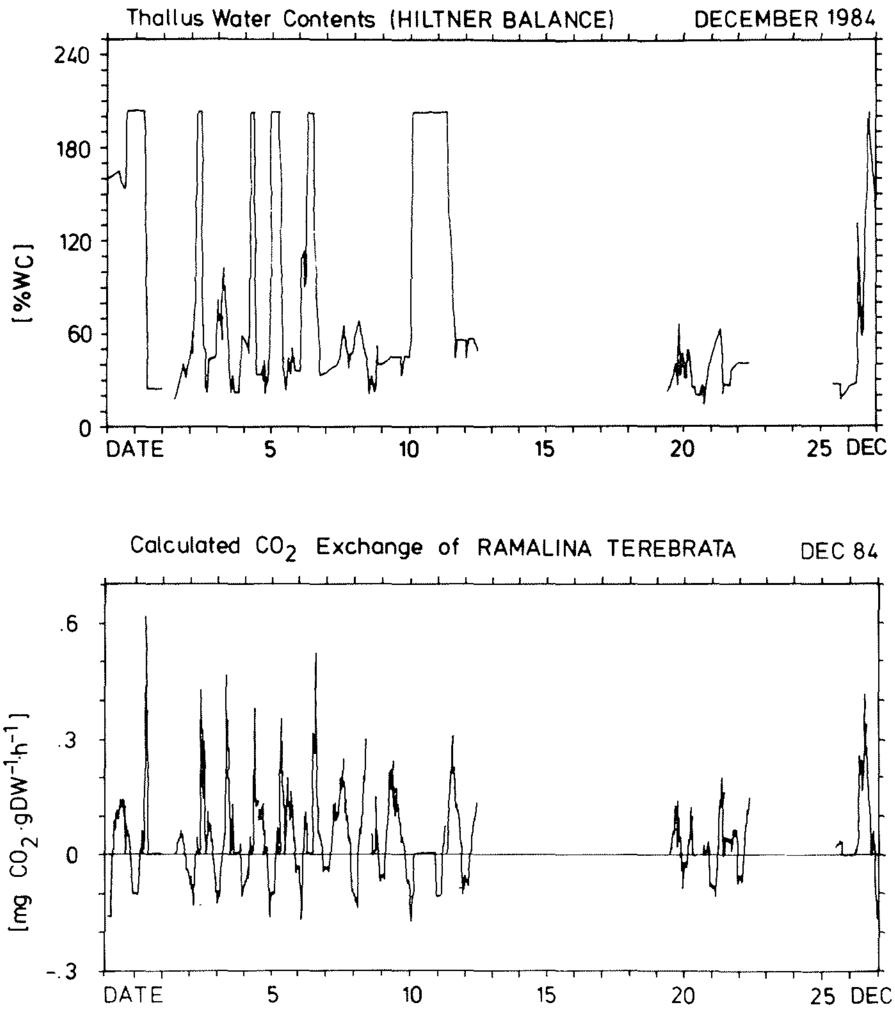


Fig. 6: Thallus water contents recorded in the field by a Hiltner dew balance and corrected for *R. terrabrata*, and calculated CO2 exchange of this lichen during a whole month. The calculation is based on the model 3—4. Recordings from days with maximum thallus water contents below 20% d. wt. were deleted, because CO_2 exchange was insignificant under these conditions. DW = dry weight.

age determinations revealed that the present phytomass of a large thallus of this species was not older than 30—40 years. This is, at least, the turnover rate of the organic-bond carbon and gives the impression that the individual age is in the order of decades instead of centuries.

For comparison, a monthly yield of 14 mg CO_2 g d. wt.$^{-1}$ is in the same order of magnitude as that of the hot desert lichen *R. maciformis* Bory which relies on dew moistening and a few rainfalls. For instance, in March 1971 it was 15 mg CO_2 g d. wt.$^{-1}$ month^{-1}, in the dry hot months May, June, August it was much less, but it was larger in the months September 1971 — February 1972 with high dewfall, fog and some rainfalls (KAPPEN et al. 1979).

The aim of our investigations was to develop a more sophisticated model to allow calculation of the annual production and finally an estimate of the growth rate. The greatest problem is still the lack of a reliable method to record the water relations of the lichen thallus which are the main controlling parameters of its activity.

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