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Eight days in the life of a desert lichen: water relations and photosynthesis of *Teloschistes capensis* in the coastal fog zone of the Namib Desert

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ABSTRACT

Water content and CO_2 exchange of the fruticose lichen *Teloschistes capensis* were followed for a measuring period of eight days in the coastal fog zone of the Namib Desert north of Swakopmund, Namibia. Fog, dew, or high vapor pressure of the air alone can provide atmospheric water sources for photosynthetic activity. Through a combination of dew condensation and fog, hydration of the thalli during the night resulted in predawn dry weight-related water contents of the thalli greater than 100%. This hydration activated two to three hours of photosynthesis with high peaks of CO_2 fixation in the early morning. Nightly dew condensation without fog resulted in lower but effective hydration for net photosynthesis. One dry day occurred without any activation of positive net photosynthesis. Because solar radiation supplies photons for photosynthesis and promotes water loss of the thalli, it delicately balances the daily carbon gain of the lichens. Immediately after sunrise, the photosynthetic rate of the moist lichens was light limited. Subsequently, metabolic activity was limited by hydration of the thalli and photosynthesis ceased when the moisture compensation point of the lichen was reached at ca. 15% water content. At the hottest and driest time of the day, the lichen's water contents were less than 10%. During the late afternoon, increasing air humidity induced water vapor uptake of the thalli, which on one day caused a small afternoon peak of net photosynthesis. A first rough estimate of the yearly carbon gain of *Teloschistes capensis* is given. Futher studies will have to extend over the different seasons of the year in order to obtain realistic numbers for lichen productivity in this unusual habitat.

INTRODUCTION

Because water is one of the most important requirements for active plant life, the shortage of water limits plant existence in the desert belts of the world. Two different types of structural and functional organization determine plant water relations. The first type consists of homoiohydric, vascular plants, which tend to maintain a high degree of hydration of their organs to metabolize even under dry atmospheric conditions. These plants need a root system for water uptake, conducting tissue for water transport, and an epidermis with a cuticle and stomata for limited and controlled transpiration. Homoiohydric desert cormophytes are characterized by special morphological and functional adaptations which allow them to exist in areas with low rainfall. However, cormophytes depend on a certain minimum soil water supply.

In contrast, poikilohydric plants, the second type of plant organization, includes thallophytes such as lichens. Lichens cannot maintain an imbalance in water potential between their tissue and the surrounding atmosphere for long periods of time. Under dry air conditions, the moist thalli of lichens loose water and after dehydration they enter the state of latent life. Hydration of these organisms takes place through water uptake of the total thallus surface; there is no separation between organs for water uptake and water loss. As a result, the times when hydration allows photosynthetic metabolism are usually short for lichens in semi-arid and arid habitats. Thus, the primary production of lichens is low compared to that of homoiohydric higher plants.

Lichens are able to use not only rain as a source of water but also fog, dew, or atmospheric water vapor for positive net photosynthesis. This ability to reactivate enables lichens to grow in areas with low or no rain but with high amounts of atmospheric moisture, most of which is unavailable to vascular plants. Such arid regions are the coastal fog deserts of the world, where a large biomass of lichens occurs with little or no vascular plant cover, e.g. the Peruvian and Chilean Atacama Deserts, the Sonoran Desert in Baja California, and the Namib Desert in Namibia. Each of these areas is characterized by the same movements of subtropical high pressure centres which cause the transport and upwelling of cold currents adjacent to their coast. Seasonal as well as diurnal temperature differences are moderated by the region's proximity to the sea, which may produce high atmospheric humidity and frequent maritime fog that are in turn extremely favourable for lichen growth.

Ecological and floristic relationship of lichens in the coastal fog deserts of the world have recently been reviewed by Rundel (1978) and Kappen (1988). Extensive studies have described the distribution, vegetation patterns, and morphological and ecophysiological adaptations of typical lichen species in the fog desert of the New World. For example, the species composition of lichen communities in the fog zone of the Atacama Desert has been described by Follmann (1967; see Follmann & Redon 1972). The habitat conditions and distributional patterns of epiphytic lichens in a Chilean fog oasis have been described by Redon and Lange (1983). The CO_2 exchange and water relations of typical fog lichens in this area have also been characterized by Lange and Redon (1983). Fruticose ground lichens, which successfully compete with vascular plants in the coastal region of Baja California, have been studied by Rundel *et al.* (1972) and by Nash *et al.* (1979). Adaptations of one of the most fascinating species growing along the western coast of the United States, namely *Ramalina menziesii*, have been analyzed in the context of its anatomical features (Rundel 1974), water relations (Matthes-Sears *et al.* 1986a), and primary production (Matthes-Sears *et al.* 1986b).

In contrast, the ecology and habitat conditions of the rich fog lichen flora and vegetation of the Namib Desert (Namibia) are still rather unknown. Although the first species list of African lichens (including those of the fog zone of Namibia) was published as early as 1926 by Zahlbruckner, and several new species have been described in recent years (e.g. Wirth & Vezda 1975; Hale & Vobis 1978), many of the lichens in the fog Namib are still taxonomically unknown (M.E. Hale personal comm.). The impressive lichen stands of the coastal zone of the Namib Desert are often mentioned in the literature (see Walter 1937; Giess 1981; Walter 1986), and Mattick (1970) gives a short description of the lichen fields north of Swakopmund. However, there does not yet exist a detailed analysis of the Namib's lichen vegetation (see also Kappen 1988) nor any ecophysiological analysis which can explain existing conditions and functions of these apparently well-adapted organisms. Wessels and van Vuuren (1986) have defined two different major lichen communities and have used satellite (Landsat) imagery to map their distribution. These pictures indicate that lichens cover hundreds of square kilometers along the coast of Namibia. The large expanse and importance of the lichen vegetation of this region are obvious.

Because terricolous lichens form the predominant component of the perennial plant biomass in the coastal Namib, they play a major role in the ecology of this desert habitat. Lichens are very important in stabilizing soil and protecting it from wind erosion. However, some of the terricolous lichen communities may be endangered from off-road vehicles which destroy the delicate lichen cover and promote soil movement (Wessels & van Vuuren 1986). Special conservation measures have become necessary to preserve such lichen communities. In order to learn more about the ecological balance in the lichen-dominated endangered area, the ecological function of the fog lichens has to be determined.

This urgent task has apparently begun to stimulate recent experimental studies. Hale, Wessels, and Wirth (personal comm.) are currently studying the standing biomass and species composition of the different lichen communities of the Namib Desert. Microclimate, especially fog frequency and fog intensity, and its influence on lichen abundance is also being studied by Loris and Schieferstein (personal comm.; see Schieferstein 1989). However, habitat conditions and lichen growth and productivity for the more important members of the lichen communities remained unstudied.

In order to initiate such an effort, we tried to analyze the water relations and photosynthetic CO_2 exchange of fog lichens in the Namib Desert. The ultimate aim of this research is to describe and quantify the photosynthetic performance of different types of lichens in the field and to interpret their primary production and growth from their physiological characteristics. Our research first started in April 1988 with field measurements which we conducted in one of the lichen fields north of Swakopmund. During a sequence of eight measuring days, which characteristically differed from day to day with respect to fog and dew fall, we recorded the water content, photosynthetic and respiratory CO_2 exchange, and microclimatic conditions for the lichen growth forms typical of the region. Here, we report the performance of the fruticose species *Teloschistes capensis*, which is the most conspicuous lichen in this area as it has the highest proportion of biomass in the lichen community.

FIELD SITE AND LICHEN EXPERIMENTAL MATERIAL

The field site was located on the coastal plain between Wlotzkasbaken and Cape Cross about 40 km north of Swakopmund and ca. 800 m east of the coast road. This area belongs to the part of the Namib fog zone which seems ideal for lichen growth as a rich assemblage of saxicolous and terricolous species is present there. Rainfall is extremely irregular (see Walter & Breckle 1984) and records at Swakopmund indicate an annual mean precipitation of 13 mm (Logan 1960; see Wessels & van Vuuren 1986), which occurs one to five days per year. In contrast, fog is a frequent event along the coast and overcast and foggy days or days with dew-fall amount to 202-295 days per year (Walter 1937).

Around the field site, the flat or slightly undulated plain is dissected by sandy washes and interrupted by rock outcrops. Phanerogams are scarce and scattered. A few individuals of *Arthraerua leubnitziae* and *Zygophyllum stapfii* in depressions are the only perennial vascular plants present. A mainly fruticose-foliose lichen communitiy, which is dominated by *Teloschistes capensis* and *Xanthoparmelia walteri* covers as much as 80% of the ground surface. Other fruticose lichens such as *Santessonia hereroensis, Ramalina* or *Alectoria* sp. and the thalli of the vagrant lichen *Xanthomaculina convoluta* are interspaced between the dominant species. Stands of *Xanthomaculina hottentotta* are found on rocks, and small stone pebbles are covered with such species as *Caloplaca elegantissima* and *Neofuscelia namaensis (= Parmelia namaensis.).*

Teloschistes capensis (L.f.) Vain. is a highly branched fruticose lichen, which exposes large areas of branch surface perpendicular to the direct moisture-laden wind. The branches are covered with thin, small ciliae which enlarge the thallus surface and develop an intricately woven network in the lichen thallus. This structure can be seen in Figure 1 where a few single branches are separated. As Rundel (1974) has shown for the American *Ramalina menziesii,* such a thallus structure might facilitate water uptake and speed hydration through atmospheric moisture. The plants of *T. capensis* form cushion-like tufts up to 3-10 cm in height and are loosely connected to the ground. In the region of our field site, almost 50% of the soil surface was covered by this species (Figure 2). To measure water content and photosynthesis, small samples of the thalli were collected and carefully cleaned. The upper, living part of the plants were then cut and fixed in their natural position and density in wire-mesh trays, each of which was ca. 4.0 cm in diameter. One sample consisted of about 0.3-0.5 g dry weight of lichen material. The trays with the lichens were again exposed to natural conditions with microclimatic changes, including moistening and drying (see Figure 4). To determine water content and CO_2 exchange, the trays with the lichens were weighed and exposed in the porometer cuvette. Water content as well as gas exchange were related to thallus dry weight (48 h at 104 °C). In addition, the carbon content of the samples was determined by elementary analysis (ANA 1500, Carlo Erba, Milano, Italy) and consisted of about 33-36% of the dry weight.

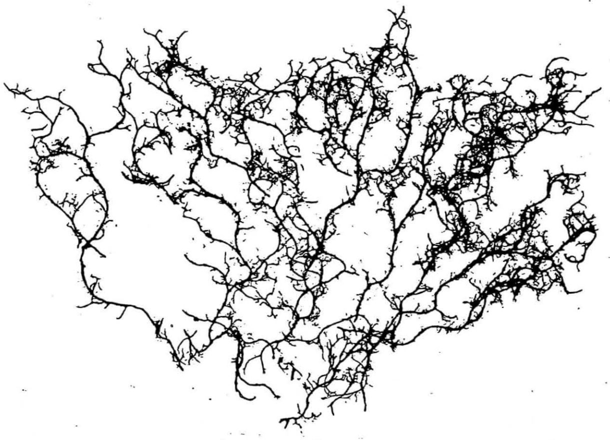


FIGURE 1: *Teloschistes capensis:* the height of the spread thallus sample ca. 7cm.

METHODS

For the CO_2 exchange measurements, H_2O/CO_2 porometers (Walz-Company, Effeltrich, FRG) were used (for a detailed description, see Lange & Tenhunen 1985 and Lange *et al.* 1984). The porometer head consisted of a small cuvette (with a volume of ca. 100 ml) which was closed by a lid covered with a thin polyethylene foil (Figure 3). The cuvette was surrounded by a cylindric radiation shield through which air was blown so that the inside temperature was kept near ambient air temperature. The lid of the cuvette could be opened to insert a tray with a lichen sample (Figure 5). Outside air from a buffer vessel was pulled through the cuvette and the CO_2 exchange of the sample was recorded according to the gas differential procedure by means of an infrared gas analyzer (BINOS, Leybold-Heraeus, Hanau, FRG). In addition, the absolute CO_2 content of the air stream was monitored. Before entering the gas exchange analyzer, measuring and reference air streams were led through Peltier-controlled water-vapor traps to avoid errors in the CO_2 measurements from differences in water vapor partial pressure. The CO_2 signals were continuously recorded by a strip chart recorder to check for transient and steady-state conditions, and the data were read off a digitalized display. At the same time, the air temperature inside the vented cuvette and the photosynthetic active radiation (PAR) incident to the lichens were recorded. The system was powered by an electric generator. Figure 6 shows the arrangement of the instruments, which consisted of two separate porometer units working independently of and in parallel to one another.

The porometer heads were fixed near the ground. For one gas exchange measurement, a lichen sample had to be enclosed for 1-2 min in the cuvette until steady-state conditions were reached and the readings were taken. Immediately after the sample was removed from the cuvette, it was weighed by an electronic balance (Mettler PM 460 Delta Range, Mettler, Giessen, FRG) and the tray with the sample was again positioned in its natural environment until the next gas exchange determination (Figure 4). Due to the great stability and reproducibility of the calibration and the zero-signal of the analyzer, the accuracy of the CO_2 measurements in the field was better than ± 0.1 ppm.

Depending on the time of day, the same lichen sample was enclosed in the porometer cuvette for short periods of gas exchange measurements every 20 to 30 min. During the interim, it remained exposed to its natural environment conditions. This means that the responses of water content and CO_2 exchange which were recorded are a good approximation of the natural performance of the lichen in the field.

In addition to the gas exchange measurements, a microclimate station was set up at the field site. The temperature of several lichen thalli and the air temperature were recorded with copper-constantan thermocouples, the photosynthetic active radiation for the lichens was measured with quantum sensors (Licor, Lincoln, Nebraska, USA) and air humidity was determined by thermocouple-psychrometers (Cernusca, Innsbruck, Austria). The data were recorded by a battery-driven datalogger (21X-Micrologger, Campbell Scientific Inc., Logan, Utah, USA) and stored on tape. The microclimate station held another set of lichens fixed on trays and exposed to their natural environment. The weights of these samples were determined at regular intervals. These results served as a control to the water content of those samples which were used for the gas exchange measurement. Both

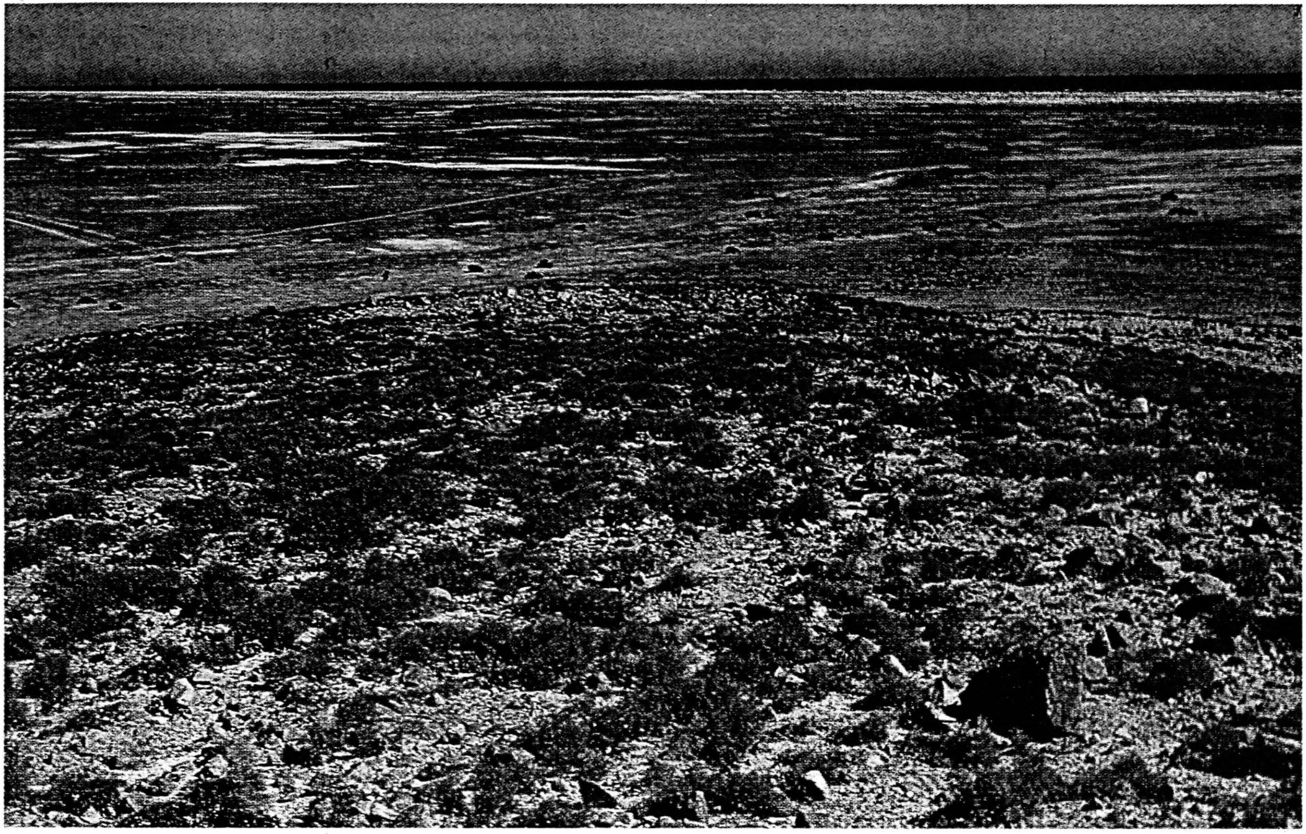


FIGURE 2: Terricolous lichen community at the measuring site with dominating *Teloschistes capensis.*

FIGURE 3: Porometer head with enclosed lichen sample.

FIGURE 4: Experimental lichen samples exposed between the gas exchange measurements.

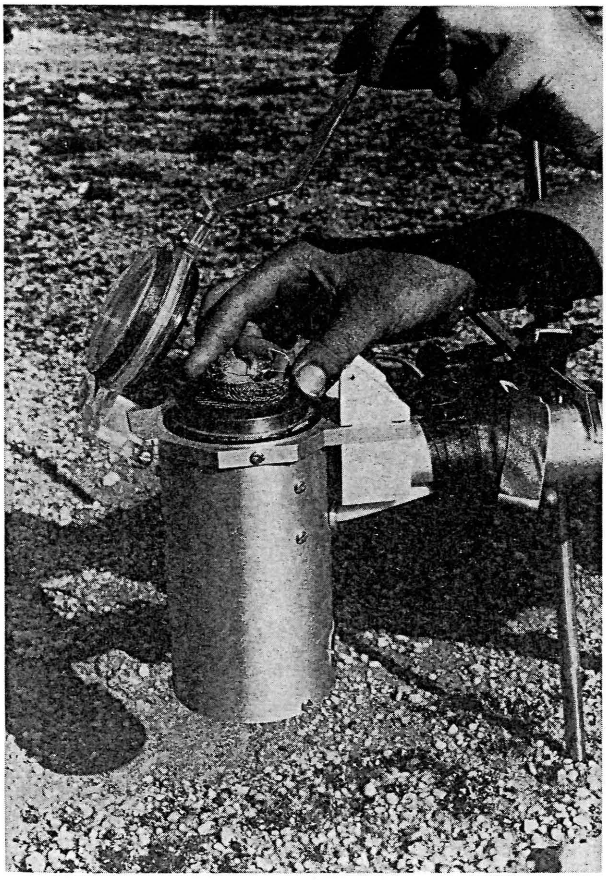


FIGURE 5: Enclosing a lichen sample in the porometer cuvette, the lid of which is opened.

sets of data are depicted in Figure 7. Neither shows any systematic deviation from the other so that the handling of the samples during the determination of their photosynthesis could not have altered their water content.

RESULTS

Figure 7 shows the time courses for temperature, photosynthetic active radiation, thallus water content, and CO_2 exchange of *T. capensis* during the eight days of measurement from April 17 through April 24, 1988. After a series of hot, dry and clear days, the first day of measurement (April 17) was mainly overcast and moderately warm. On the evening before, dew condensation began around 18h00, and during the night a light fog layer drifted from the sea and covered the field site until about 10h00. During the night, the lichens became moistened through condensed dew and precipitated fog. When the measurements began at 06h30, the thalli had a water content of around 100% of their dry weight. Still in darkness, they respired. With increasing light intensity, photosynthesis became activated, and the light compensation point of the well-hydrated samples was passed around 07h30. With greater light intensity, net photosynthesis steeply increased. However, at the same time, the thalli lost water due to the increasing air temperature and the decreasing air humidity. At 09h08, maximum CO_2 assimilation was reached at an intensity of photosynthetic active radiation for 201 $\mu E\ m^{-2}s^{-1}$ and a water

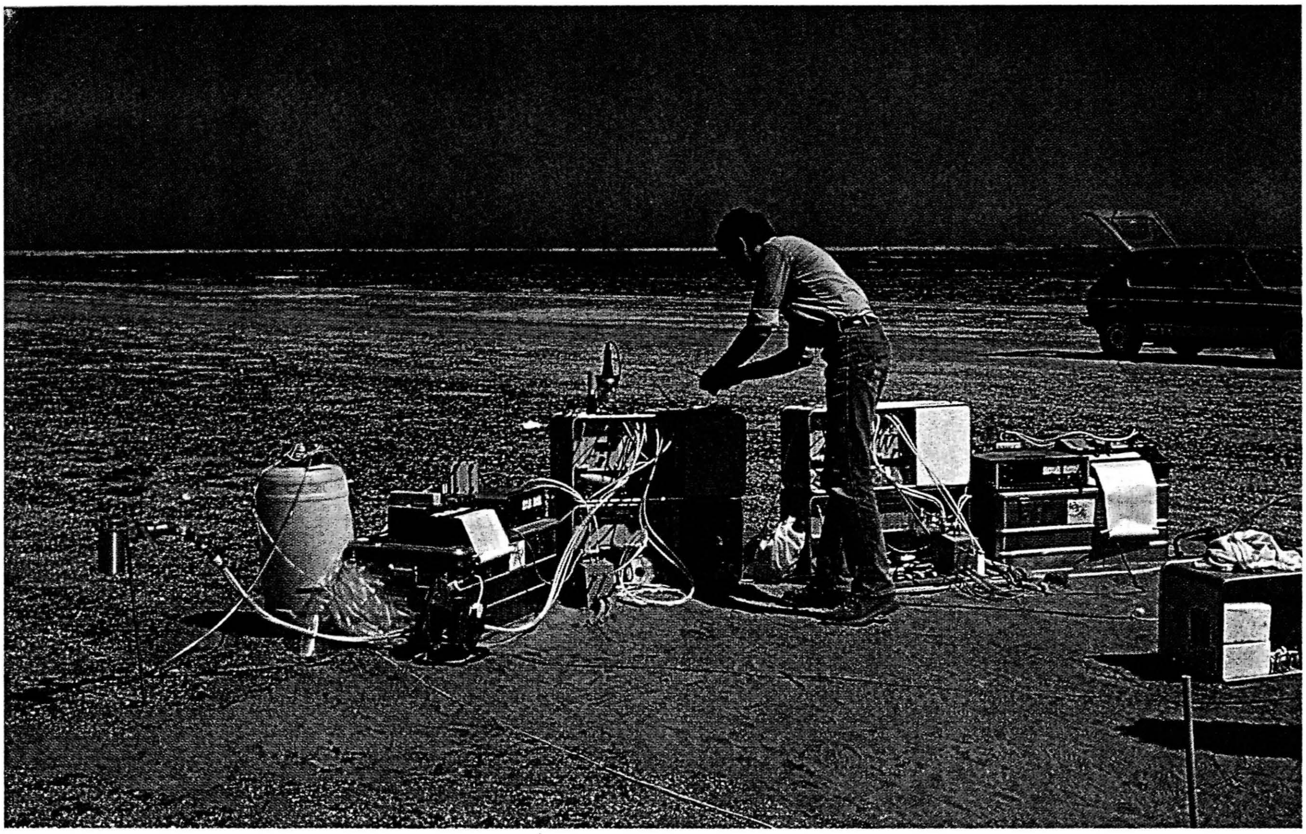


FIGURE 6: Instrumental arrangement at the field site. Above: clear weather conditions; below: fog during the early morning hours.

content of 77%. From then on, the reduction of hydration limited lichen photosynthetic metabolism, and CO_2 uptake abruptly decreased concomitantly with the steep drop in water content. At 11h00, the moisture compensation point for net photosynthesis was reached at a thallus water content of 14.3% and significant gas exchange could no longer be detected for the rest of the day. The dry lichen had entered the state of latent life. Its lowest water content reached 11% at 14h30.

Because dew fall and fog together hydrated the thalli in a combined fashion, three similar events elicited similar responses from the lichens on April 21, 22, and 23. However, the maximum intensity of net photosynthesis and the duration of photosynthetic activity differed. Heavy dew fall took place during the cool and clear night on April 20/21 so that the water content of the lichens had reached 60% by midnight. A low but significant dark respiration was stimulated. The fog, which came up later that night, continuously increased the hydration of the lichens. This relatively high water content in combination with the high light intensity produced the highest measured morning rate of photosynthesis with 15.6 nmol CO_2 $g^{-1}s^{-1}$ of a horizontally exposed lichen sample. On the following day, only a slightly smaller rate was obtained.

Even under these conditions of high CO_2 assimilation, light was still limiting photosynthesis. This became obvious through the following experiment. During the routine measurements, the samples were placed horizontally in their natural position so that the deep sun in the early morning hours illuminated the lichen cushions from the side and shaded the exposed western part of the tufts. When the porometer was turned to the east so that the still overcast sun was directed perpendicular to the top of the lichen sample, the light penetration was facilitated and this led to a pronounced increase in net photosynthesis. Figure 8 indicates that under such conditions, the rates of CO_2 assimilation could almost double compared to those when exposure was horizontal. However, this effect could only be detected as long as the hydration of the thalli was favourable.

Not only dew in combination with fog but also dew condensation alone during the night and early morning activated lichen photosynthesis. Such events could be observed on April 19, 20 and 24. Maximal morning water content reached only 29.4, 38.4, and 63.1% respectively. Nevertheless, these levels still allowed small but significant peaks of photosynthesis until desiccation stopped metabolic activity.

On some days (e.g. April 19 and 20), after the decrease following the maximum of photosynthesis, CO_2 exchange did not merely cease, but a short phase of respiratory CO_2 release was observed, before the gas exchange totally became zero. The same response was more or less apparent on other days, but the rates of the respiration were often too small or the time period of CO_2 loss was too short to be depicted in Figure 7. It is known from studies under controlled conditions with *Ramalina maciformis* in the Negev Desert (Lange 1969) that a certain range of low thallus water potential exists in which the photosynthetic apparatus becomes inactivated, but respiratory CO_2 release still occurs in the the light. This same kind of performance is apparently exhibited by *T. capensis*.

The diurnal course of CO_2 exchange of the experimental lichen on April 20 exhibited another interesting phenomenon. The lowest water content of the lichen was reached between 10h00 and 14h00 with values near 10% in bright sunshine and low relative humidity of minimal 40%. During the afternoon, the air humidity increased and concomitantly, the lichen samples gained weight. In absence of any dew or fog, the lichen obviously took up water vapor from the atmosphere. The degree of hydration became so high that the moisture compensation point of net photosynthesis was again reached and by the late afternoon, another small peak of CO_2 uptake had occurred. This peak had ceased by sunset. Indications of this kind of response were also detected on other measuring days (e.g. on April 17, 19, and 22). However, the rates of photosynthesis due to low light intensity were insignificant.

On only one day in the sequence of field days, i.e. April 18, only negligible, if any, rates of CO_2 exchange of the lichens were observed. The night before had been slightly overcast and warm. Only a small amount of dew had condensed so that the water content of the lichen thalli was less then 25% in the early morning hours. At sunrise, water loss took place very quickly so that the CO_2 uptake became negligible.

In Table 1, the daily CO_2 gains of all of the field days are listed, i.e. the sum of CO_2 fixed without taking into account respiratory CO_2 loss during the night. The variation of the amount of CO_2 gain from day to day is rather high. The maximum gain was reached on the days with fog and dew; on the majority of the days when dew hydration alone occurred, primary production was lower. However, it is remarkable that dew condensation alone made a considerable contribution to the carbon balance of the lichen. The total sum of CO_2 uptake of *T. capensis* during the eight days of measurements amounted to 11.214 mg CO_2 per g dry weight, which means a total carbon gain of 3.058 mg C per g dry weight and a daily mean of 0.382 mg C $g^{-1}d^{-1}$.

DISCUSSION

Three sources of atmospheric moisture, namely fog, dew condensation or high air water vapor pressure alone, can be used by *T. capensis* to reactivate its photosynthetic metabolism. Usually, the lichen exhibited large diurnal changes in its water content with minimum values lower than 10% during the early afternoon, the driest time of day, and maximum values

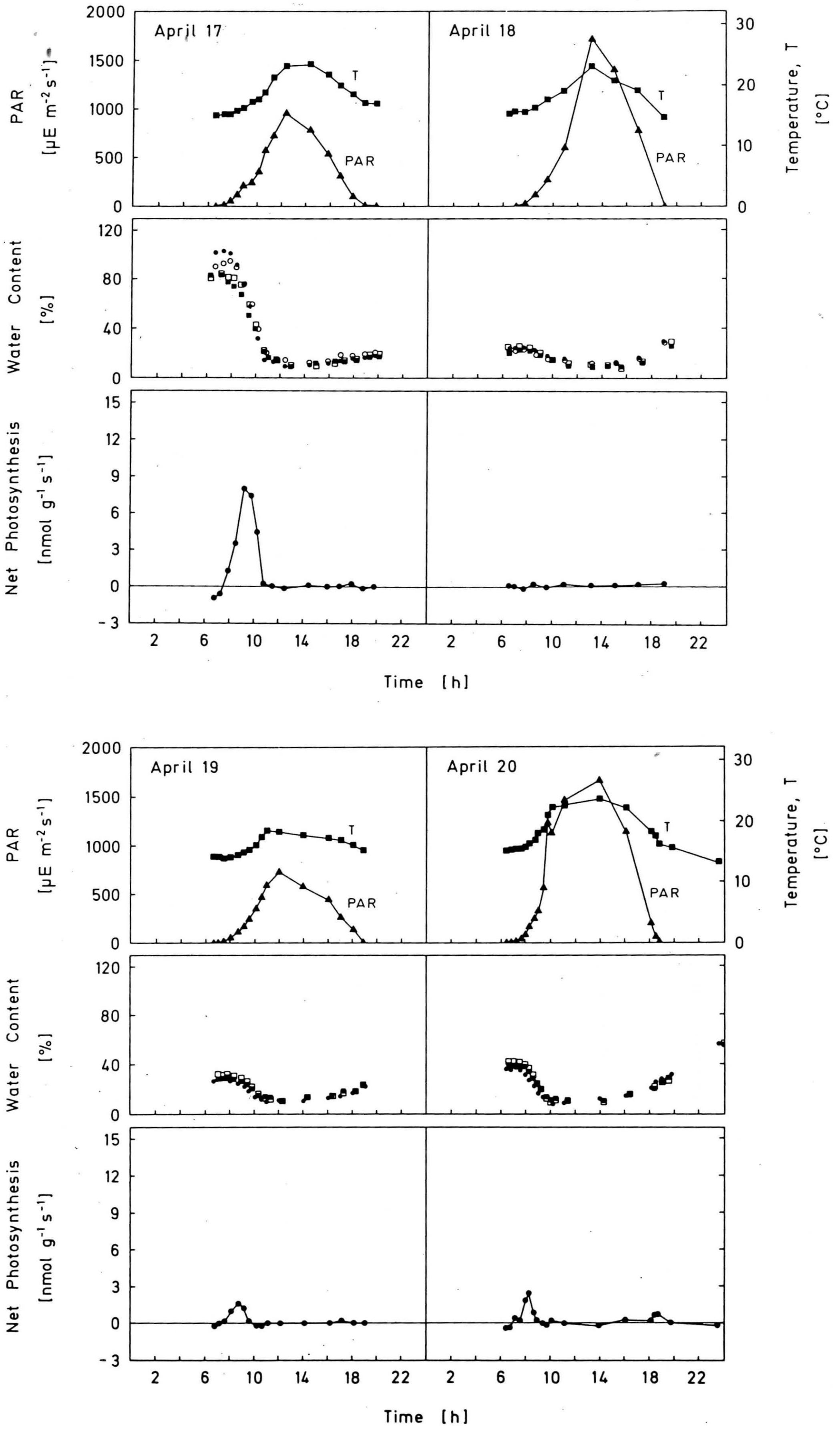
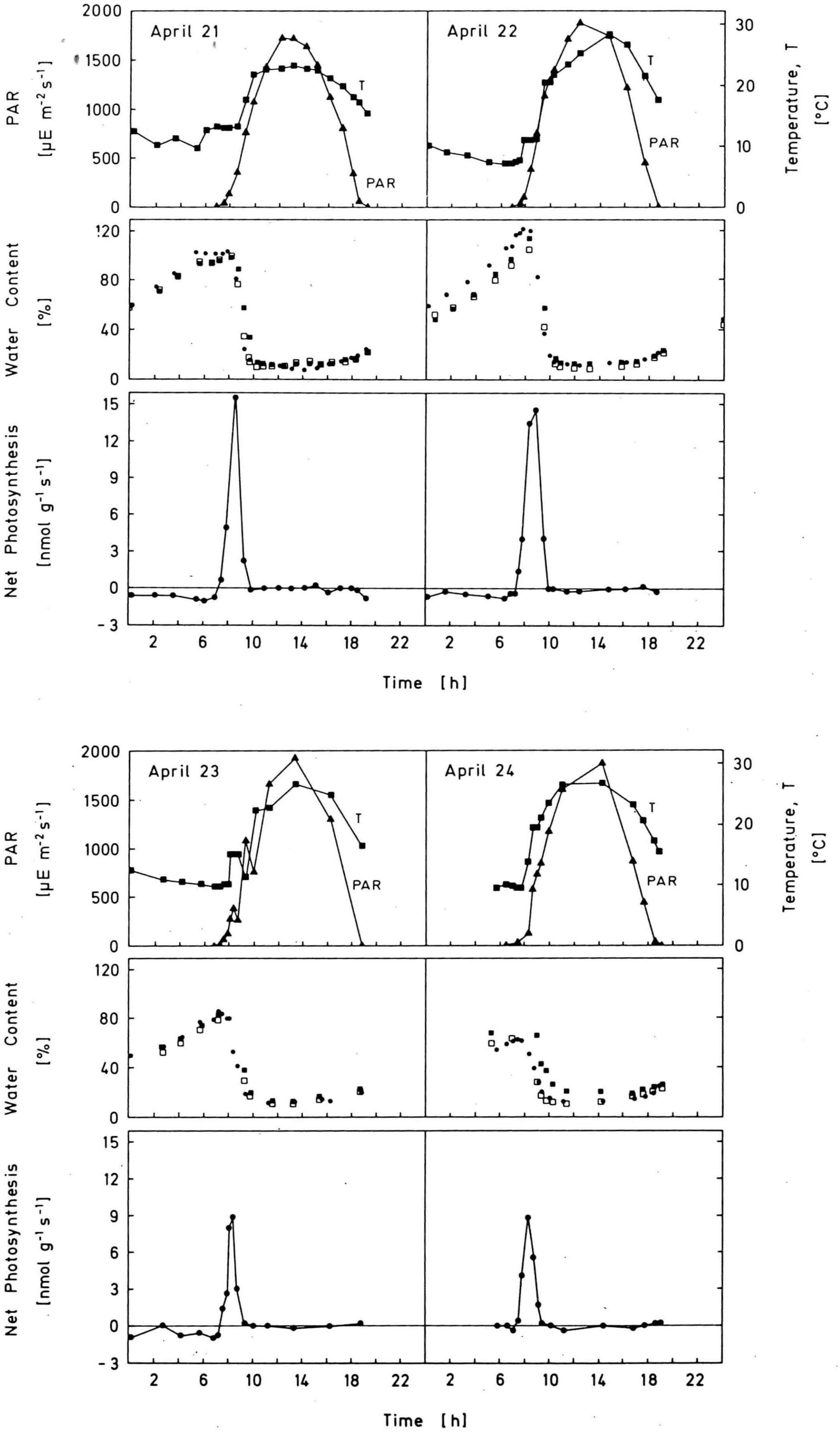


FIGURE 7: Daily time courses of microclimatic parameters and lichen responses from April 17 through April 24. Upper panel: air temperature (T) and photosynthetic active radiation (PAR) horizontally incident to the lichen sample in the porometer cuvette. Center panel: Relative water content of the lichen in relation to thallus dry weight; samples in the porometer cuvette (open symbols) and at the microclimate site



(closed symbols). Lower panel: CO_2 exchange of the lichen samples in relation to thallus dry weight (CO_2 uptake positive). April 17 and 18 average values of two samples, the remaining days one sample.

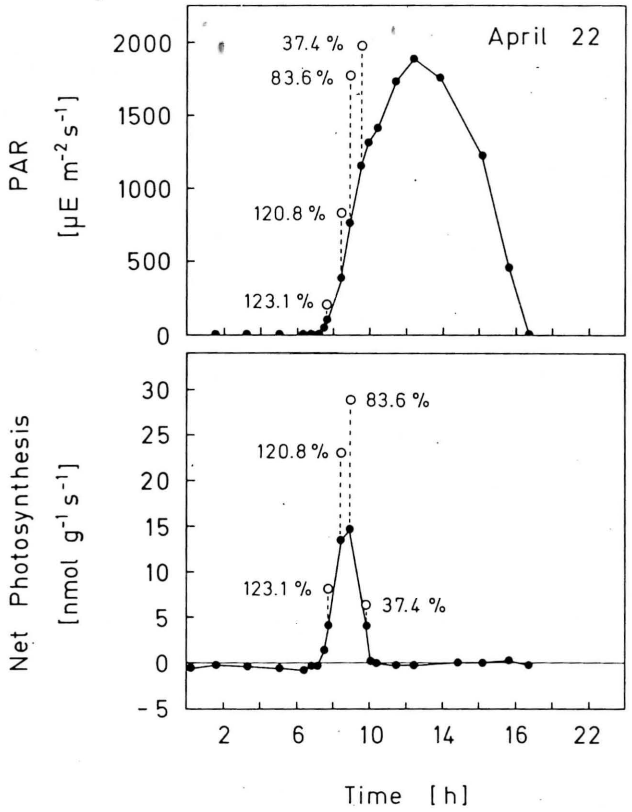


FIGURE 8: Daily time courses of net photosynthesis (below) and of photosynthetic active radiation (above) of the horozontally exposed lichen sampel (closed symbols) and of the same exposed perpendicular to the direction of the sun (open symbols); April 22. The numbers indicate the water content of the sample.

were often higher than 100% under predawn conditions. The absolute maximum of 136.9% was recorded after heavy fog on April 25. From what we can conclude from eight days of measurement, fog produced greater water content in the lichen thalli than dew condensation alone. Nevertheless, dew without fog seemed to be an important parameter in lichen water relations. Initial predawn water content, light intensity, and rate of water loss determined the course of photosynthetic CO_2 uptake of the lichen in the early morning hours. Each of the eight measuring days showed peculiarities with respect to those conditions which resulted in different sums of carbon gain.

The general, and typical, pattern of the morning peak of net photosynthesis after the lichen has become hydrated during the night can be described as follows. Before dawn, the moist lichen respires. The onset of positive net photosynthesis is determined by the light compensation point of CO_2 exchange which can only be roughly estimated from the field measurements. Under the field conditions given here, the compensation point for *T. capensis* may be around 15 μE m^{-2} s^{-2} PAR. The compensating light intensity is quickly surpassed and photosynthesis steeply rises with increasing light intensity. During the initial phase of net photosynthesis, photosynthetic active radiation remains the limiting and decisive factor. However, increasing radiation not only means an increasing photon supply for photosynthesis but at the same time rising thallus and air temperature and consequently increasing water loss for the lichen. This delicate balance between photon and hydration requirements for photosynthesis determines the rate and duration of photosynthetic activity. Conducting gas exchange measurements in the field was a fascinating experience because one could watch how each layer of fog dimmed the rising sun and extended the time period of photosynthesis of the lichen and how CO_2 assimilation immediately came to an end when the direct sunbeam hit the lichen and caused desiccation.

Both prevailing photosynthetic active radiation and water content at the peak of net photosynthesis (Table 1) depended on the predawn water content of the lichen. The higher the initial amount of available water for the lichen, the more time was available during the light-limiting phase so that the greater light intensity could actually be reached under favourable degrees of hydration. On the other hand, it is known that net photosynthesis at high light intensity is more sensitive to the limiting effects of hydration than it is at low light intensities (see Lange & Redon 1983). Consequently, the point of maximal photosynthesis of the thalli under high light conditions was reached with higher water contents of the thalli than it was under conditions of low light intensity.

Following the drop in photosynthesis due to the drying of the thalli, the moisture compensation point of CO_2 exchange was reached on all measuring days at similar water contents and apparently almost independently of the prevailing light intensity. As given in Table 1, the compensation point ranged from 11.3% to 19.1% water content with an average of 15.4%. In comparison to data from the literature for lichens of similar habitats, the compensation point of *T. capensis* appears to be extremely low. Lange and Redon (1983) reported values from between 23% and 33% water content for the start of positive net photosynthesis of their experimental species in a Chilean fog oasis. However, water-potential, which is independent of the specific dry weight of the thalli, might be a better basis of comparison than the water content for metabolic performance. Water-potential dependencies of CO_2 exchange still have to be established for *T. capensis.*

The general pattern of the morning peak of photosynthesis which was exhibited by *T. capensis* under Namib Desert conditions is similar to those patterns reported for lichens from other arid and semi-arid climatic regions, e.g. the Negev Desert (Lange *et al.* 1970 a, b; Kappen *et al.* 1979, 1980), the fog zone of the Atacama Desert (Lange & Redon 1983), the coastal region of Portugal (Lange *et al.* 1985), or even after nightly dew condensation in a local xerothermic grassland formation in Franconia, Germany (Hahn *et al.* 1989). However, a time span of daily positive net photosynthesis for *T. capensis* of not more than two to three hours (see Table 1) seems to be exceptional compared to the

TABLE 1: Characteristic data about the morning peak of net photosynthesis of *Teloschistes capensis* during the time period from April 17 through April 24, 1988.

Date (main source of water)	1 [%]	2 [%]	3 [nmol CO_2 $(gDW)^{-1}s^{-1}$]	4 [%]	5 [$\mu E\ m^{-2}s^{-1}$]	6 [%]	7 [hours]	8 [mg CO_2 $(gDW)^{-1}d^{-1}$]	9 [mg C $(gC)^{-1}d^{-1}$]
April 17 (dew and fog)	99.0 (7:23)	11.4 (14:30)	7.949 (9:08)	76.7	201	14.3	3.9	2.265	1.822
April 18 (dry)	23.9 (7:45)	11.3 (13:28)	0.147 (8:36)	21.0	123	–	0.0	0.120	0.096
April 19 (dew)	29.4 (7:34)	10.2 (11:06)	1.650 (8:45)	25.2	107	11.3	2.7	0.389	0.365
April 20 (dew)	38.4 (7:11)	9.8 (10:08–11:08)	2.473 (8:18)	28.4	162	14.7	2.5	0.568	0.469
April 21 (dew and fog)	104.5 (7:55)	8.6 (13:08–15:08)	15.622 (8:35)	81.4	348	18.0	2.6	2.292	1.894
April 22 (dew and fog)	123.1 (7:49)	11.4 (12:25)	14.592 (8:57)	83.6	765	19.1	2.75	3.014	2.491
April 23 (dew and fog)	86.2 (7:17)	11.8 (11:17)	8.888 (8:24)	53.5	375	15.7	2.75	1.177	0.973
April 24 (dew)	63.1 (7:28)	12.2 (14:22)	8.796 (8:20)	51.3	343	15.0	2.8	1.389	1.148

1. Maximum morning water content (time of occurrence)
2. Minimum water content (time of occurrence)
3. Maximum rate of net photosynthesis (time of occurrence)
4. Water content at the time of maximal net photosynthesis
5. Photosynthetic active radiation at the time of maximal net photosynthesis
6. Moisture compensation point (i.e. water content when net photosynthesis became zero after the morning peak)
7. Time span of positive net photosynthesis
8. Daily sum of CO_2 assimilation (related to thallus dry weight)
9. Daily sum of carbon gain (related to thallus carbon content)

performance of the lichens of other regions. The multibranched structure of the thallus of this lichen enables a quick uptake of a great amount of atmospheric moisture but may result in a rapid water loss which would shorten the duration of photosynthesis activity. Comparing the behaviors of the different lichen species in the same habitat in the Namib Desert would elucidate the importance of this life form for water gain, water retention, and carbon assimilation.

It is already well documented that dry lichens with green phycobionts are able to reactivate their photosynthetic metabolism without liquid water by vapor uptake from the atmosphere alone (Butin 1954; Lange & Bertsch, 1965; Lange *et al.* 1986). There is one lichen community in the Chilean fog oases which seems to depend almost exclusively on water vapor as its only source of hydration (Redon & Lange 1983). *T. capensis* has the same capability to make use of water vapor uptake. Usually, this capability did not determine its gas exchange performance during the eight days of measurement because fog and dew were the dominant water sources during the night. However, during each day, the weight of the lichen samples increased fairly dramatically during the afternoon hours when air humidity became higher and water vapor uptake of the thalli took place. On one day (April 20), the moisture compensation point through water vapor uptake was reached in the afternoon while there was still light, a time which was favorable for photosynthesis, so that a small but significant afternoon peak of CO_2 assimilation occurred. On the other measuring days, such an effect was not so clearly recognizable. It might well be that this water vapor-induced afternoon peak of photosynthesis becomes an important and more frequent contribution to the primary production of the lichen under changing weather conditions during the other seasons of the year.

Table 2 compares recorded maximal rates of CO_2 assimilation of *T. capensis* with data from the literature. The Namib lichen reached similar momentary rates of dry weight-related net photosynthesis as reported from other regions with similar climatic conditions. According to unpublished data of Hale and Wessels, the total lichen biomass in the lichen fields of the coastal Namib desert which are characterized by *T. capensis* ranges from 2.27 to 4.29 tons (dry weight) per hectare. *T. capensis* itself contributes to this from 35.94 (small clumps) to 194.1 (large clumps) g m^{-2}. If we consider 50% of the standing biomass of this lichen to be photosynthetically active, this results in an estimate of about 18 to 97 g active biomass of the lichen per square meter. This range agrees well with our own measurements of 40 g m^{-2} of photosynthetically active dry matter of *T. capensis* for a typical stand near our experimental site. The maximal rate of recorded CO_2 uptake of *T. capensis* under natural conditions amounted to 2.47 mg g^{-1}h^{-1} (Table 2). Related to ground area of the lichen fields this would mean an assimilation by *T. capensis* from 44 to 240 mg CO_2 per square meter and hour. In order to understand the order of magnitude of such numbers it might be useful to compare them with the photosynthetic performance of vascular plants in nature under temperate conditions, e.g the leaves of a beech tree *Fagus sylvatica* in central Europe the gas exchange of which was described by Schulze (1970). During the growing season, the maximal rates of net photosynthesis of beech leaves amounted to 517 (sun crown) and 315 (shade crown) mg CO_2 m^{-2} h^{-1} (leaf area-related) with average rates for the daylight hours of 188 and 78 mg CO_2 m^{-2} h^{-1}, respectively. It is instructive to imagine that every morning after nightly fog and dew for a short period of time *Teloschistes capensis* in the lichen fields of the Namib desert is photosynthesizing with rates similar to those of a closed layer of beech leaves in a forest in Germany.

The daily gain of CO_2 seems relatively small in comparison to species from the Atacama and the Negev Desert because of the short period of metabolic activity during the morning hours. Of course, extrapolation from eight days of measurement to the total year can only be done with great reservations. Nevertheless, if we consider the average daily carbon gain during the eight days as typical and relate this average to the course of the year, we attain a first rough estimate of yearly gross production of 410 mg carbon assimilated per g carbon content of the thallus. If we assume a respiratory loss which amounts to half of the carbon gain (see Kappen *et al.* 1979), this number could be interpreted as a net gain for a yearly growth rate of about 20% of the active biomass of the lichen. However, this number cannot presently indicate more than

TABLE 2: Dry-weight related maximum rates of photosynthesis and maximum diurnal CO_2 gain of fruticose desert lichens under field conditions at different kinds of moistening (see Kappen 1988); 1)Lange and Redon 1983, simulation, 2)Lange et al. 1970 b and Kappen et al. 1979, 3)Lange et al. 1970 a.

	Everniopsis trulla 1) (Atacama) fog	Ramalina maciformis2) (Negev) dew	Teloschistes lacunosus3) (Negev) dew	Teloschistes capensis (Namib) fog + dew	Teloschistes capensis (Namib) dew
Maximum rate of net photosynthesis [mg CO_2 (g DW)$^{-1}$h^{-1}]	1.41	2.6 1.79	0.42	2.47	1.40
Maximum daily CO_2 gain [mg CO_2 (g DW)$^{-1}$d^{-1}]	5.47	5.1	–	3.01	1.39

a very rough estimate. We do not yet have sound information of the respiratory carbon loss of the lichen and of the possible leaching of photosynthates out of the thallus. In addition, we do not yet know the peculiarities of the photosynthetic performance of the lichen during the other seasons of the year.

We plan to extend our data base with field measurements of CO_2 exchange in order to obtain representative information for the yearly performance of the lichens in the Namib Desert. Moreover, we hope to analyze their responses to the most important environmental factors such as light, temperature, and thallus water content in the laboratory for parametrization of a photosynthesis model. This will lead to a realistic estimate of the annual primary production of the lichens in their unusual habitat in the Namib Desert and will also help to explain their physiological function.

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