Photosynthetic performance of rock-colonising lichens in the Mountain Zebra National Park, South Africa

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The photosynthetic behaviour of endolithic and epilithic lichens characteristic of sedimentary and volcanic rock was investigated *in situ* in the Mountain Zebra National Park, South Africa. The park forms part of an inland semi-desert known as the Karoo, in the Cape Province. Temperatures within Balfour sandstone were monitored, the results showing that during the early morning, temperatures within the sandstone were nearly 5°C lower than ambient air temperatures. This may enhance the frequency of water condensing on the sandstone, which may be particularly important for the endoliths *Lecidea* aff. *sarcogynoides* and *Sarcogyne* cf. *austroafricana.* Maximum photosynthetic rates of the investigated species were found at temperatures between 20°C and 30°C, far higher than the recorded optimum temperatures for lichens from temperate and desert regions. *Parmelia chlorea* was the most productive species. Compared to the other epiliths, *Peltula capensis* was found to be a moderately productive species. The photosynthetic gain of *Lecidea* aff. *sarcogynoides* and *Sarcogyne* cf. *austroafricana* was low, but the photosynthetic gain of these two species still exceeded that of *Acarospora* sp.

Key words: Lichens, endolithic, photosynthesis, sandstone, micro-climate, Karoo.

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Introduction

Except for studies by Coxson & Kershaw (1983), Lange *et al.* (1970), and Nash *et al.* (1982), few reports on the CO_2 exchange of epilithic and endolithic lichens in the field exist. A possible reason for this paucity may be that lichen colonised rocky substrates are too large to fit a gas exchange cuvette. Alternatively, due to the chemical composition of the rock, such substrates may interfere with the CO_2 signal from the lichen. As demonstrated by Kappen *et al.* (1990), the use of a Walz CQP 130 porometer facilitates measurement of CO_2 exchange on lichens in their natural environment, or corresponding sites close by where electric power is available.

Southern Africa has a rich lichen flora which occurs in habitats ranging from tropical rain forests to snow-covered mountain ranges at high altitudes, and from temperate savannas to arid deserts. The ecophysiology of lichens in southern Africa is poorly known and only a few such studies exist (Büdel & Lange 1991; Kappen 1988; Lange *et al.* 1990; Schieferstein 1989). However, floristic studies of southern African lichens with reference to ecological conditions are known from Almborn (1966, 1988), Büdel (1987, 1990), Henssen *et al.* (1985), Kärnefelt (1988), Mattick (1956), Scott (1967), Vogel (1955), Wessels & Büdel (1989), Wessels & Schoeman (1988), and Wessels & Wessels (1991).

We aim to describe the photosynthetic behaviour of endolithic and epilithic lichens characteristic of three climatologically different sites in South Africa in a series of three papers. We undertook these studies in the Mountain Zebra National Park near Cradock in the eastern Cape, Mutamba south of Messina in the northern Transvaal, and the Golden Gate Highlands National Park near Clarens in the eastern Orange Free State. The first two sites are in arid regions of South

Africa while Golden Gate lies amongst the foothills of the Maluti Mountains in a mesic region of South Africa. Sandstone occurs in all three sites and we could, in addition, select similar growth forms and genera to study in the three areas. The selected species are endoliths in sandstone and epiliths with crustose and foliose growth forms.

In this, the first paper we report on a study undertaken in the Mountain Zebra National Park (MZNP) in the Cape Province. The climate of this park can be characterised as transitional between Mediterranean winter rainfall and East African summer rainfall climatic types. True to the latter climatic type, the larger portion of the park's average annual precipitation of 414 mm falls during the summer. Precipitation usually occurs as heavy thunderstorms, frequently accompanied by hail. Snow is often recorded during winter. Evaporative forces equivalent to 1 100 mm of rainfall per year result in the prevalent arid character of the climate in this area.

We report on the CO_2 exchange of different lichen species in the MZNP investigated during the summer of 1991. Incidences of rainfall during the investigation resulted in natural moistening of the lichen thalli. Being poikilohydrous organisms the lichens are consequently at their most productive during this time (summer) of the year and we aimed to quantify their respective productivities. In addition, our study should give some insight into the competitive capabilities of these lichens under natural conditions in the MZNP. We also aimed at quantifying the microclimatological environment, both within and on the surface of sandstone, during summer conditions.

Study site

Approximately 40% of the surface of the lowland areas of the Republic of South Africa could be classified as inland semi-deserts (Van der Walt 1980). These areas receive an average annual precipitation of less than 425 mm and are known for having distinct floras (Van der Walt 1980). Of these areas, the Karoo is by far the better known and includes the MZNP which lies 24 km southwest of the town of Cradock in the Cape Province. The MZNP lies in a vegetation type known as Eastern Mixed Karooveld (Van der Walt 1980). This 6 536 ha park, with geographical coordinates 32°15'S, 25°41'E, was proclaimed in 1937 for the special protection of a herd of exceptionally rare mountain zebra *Equus zebra zebra* Linn. Several aspects of the park were investigated, of which discussions of the geology by Toerien (1972) and vegetation of the park by Van der Walt (1980) are relevant.

We chose the MZNP in particular as it is climatologically between the other localities in which we undertook similar studies. The MZNP forms part of the northern slope of the Bankberg and Bakenkop, the highest point in the park, lies 1 957 m a.s.l. Conversely the lowest point lies at 1 200 m a.s.l. (Grobler & Hall-Martin 1982). According to Toerien (1972), the landscape of the MZNP evolved on sedimentary rock types belonging to the Beaufort Series.

Lichen specimens for photosynthetic performance studies and micro-climatological data were gathered in the north western corner of the park on an extensive plateau called Rooiplaat, 1 350 m a.s.l. At this site a large sandstone outcrop belonging to the Balfour Formation occurs. Naturally weathered Balfour sandstone varies in colour from brown to ash-coloured. Freshly exposed surfaces vary in colour from dirty-green to dark grey and in texture from medium to fine grained (Toerien 1972). Impurities such as feldspar and darkly coloured cementing material may constitute more than 50% of the composition of the sandstone (Toerien 1972). Sandstone of the Balfour Formation forms part of the Beaufort Series which belongs to the Karoo Sequence. Outcrops of biogenically weathered sandstone are common in the park. In such outcrops colonised patches occur on all sizes of rock and on all exposed sides. As a result of colonisation these rocks differ in microtopography form uncolonised rocks. Colonised patches also differ in colour from uncolonised areas, resulting in colonised sandstone standing out from uncolonised rocks. The sandstone outcrop from which lichen specimens were collected lies amongst scattered dwarf Karoo shrubs and a mixture of grass species.

Material

The following species were investigated:

Endolithic species

Lecidea aff. *sarcogynoides* Körb.

Sarcogyne cf. *austroafricana* (Zahlbr.) H. Magn.

Epilithic species

Acarospora Mass. (*Xanthothallia*) species

Parmelia (*Paraparmelia*) *chlorea* Stizenb. This and the above-mentioned species were collected at Rooiplaat, 5 km west of the measuring site.

Peltula capensis (Brusse) Büdel. Specimens were collected from large rain tracks on an extensive east-facing dolerite boulder, 2 km from the measuring site.

Xanthoparmelia marroninipuncta (Brusse) Hale. Specimens collected at the measuring site where the species grows on dolerite outcrops along the WSW-facing side of the hill.

Specimens of the experimental material are deposited in the lichen collection of the National Botanical Institute (PRE), Pretoria.

Methods

Macro-climatological data

Macro-climatological data, covering the period March 1983 until March 1991, were obtained from the Grootfontein Agricultural College, Grootfontein. These data were collected at a weather station near the residence of the park's game ranger, ca. 1 km from our measuring site in the Weltevrede tourist camp.

Micro-climatological data

A sandstone boulder 667 mm long and 468 mm high, was used for micro-climatological measurements. The north-facing side of the boulder slants at an angle of 38°. Vertical and horizontal slants at the centre of the east-facing side of the rock are 40° and 9° respectively. Along the centre of the west-facing side the vertical and horizontal slants are 44° and 20° respectively. A sandstone boulder, approximately similar in size, lying flat on the soil next to the described one was used to measure internal temperature beneath a flat horizontal surface.

Air temperatures as well as those within and on the surface of the sandstone boulder were measured with mini-thermistors (Grant, Cambridge) for a period of 101 hours. The probes were inserted into tight fitting holes (3 mm in diameter) drilled with an electric drill and lightly blown clear of any particles. "Terostate" (Teroson, Heidelberg, FRG) was used to plug the holes with inserted thermistors. All the probes were inserted to measure within the endolithic thalli of *L.* aff. *sarcogynoides*. The influence of direct solar radiation on rock surface temperatures was measured by an uncovered thermistor stuck to the west-facing surface of the sandstone. Air temperature was measured by a single thermistor suspended at a distance of 200 mm above the ground and one meter away from the rock with sensors. This thermistor was screened from direct solar radiation by a reflective dome. All thermistors were connected to a Squirrel Data Logger (Mod. 1209; Grant, Cambridge). The data records, made at 5 min intervals, started at 14:00 on 5 March 1991 and ended at 17:00 on 9 March 1991.

The position of the probes will be indicated by the following abbreviations:

AIR = Air temperature, shielded probe

WIN = Inside temperature of the southwest-facing side of the sandstone. Temperature measured 3,0 mm below the southwest-facing surface and 4,5 mm inside the sandstone.

WOP= Surface temperature of the southwest-facing side of the rock. Probe uncovered.

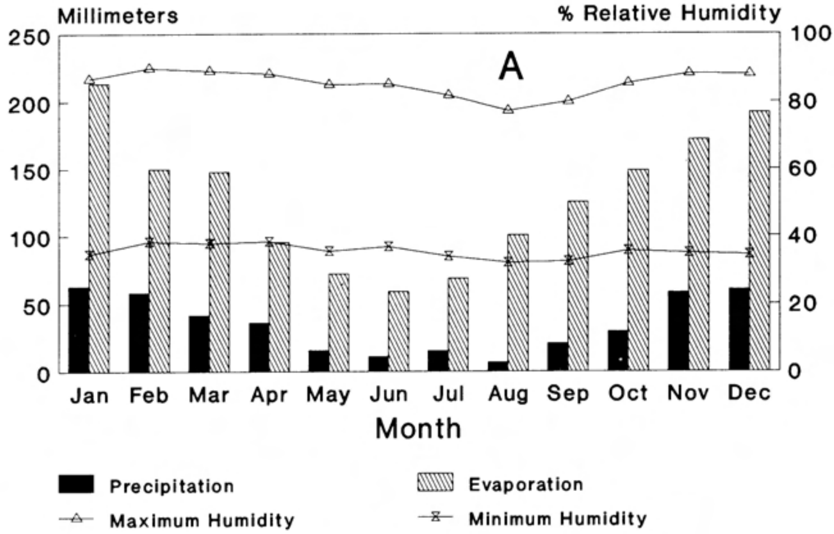
EIN = Inside temperature of the east-facing side of the sandstone. Temperature was measured 4,0 mm below the top surface of the sandstone. The probe was inserted to a depth of 14,0 mm into the sandstone.

TIN = Interior temperature below the upper flat surface of a sandstone boulder adjacent to the one in which the above measurements were made. The probe was inserted 19,0 mm into the side of the sandstone and 2,0 mm below the horizontal surface.

Gas exchange studies

Field measurements of CO_2 (carbon dioxide) exchange were carried out at the Weltevrede rest camp, ca. 5 km from the site where the microclimate was measured. We used a compact computer-controlled CO_2/H_2O porometer CQP 130 (H. Walz, Effeltrich, FRG) measuring in an open system with a differential CO_2 signal analysed by an infrared gas analyser (IRGA) (Binos 100). The use of this instrumentation was described by Kappen *et al.* (1990). Principally the instrument's ease of application and versatility lies in the use of an open plexiglass porometer head which is connected to a plexiglass ring, attached and sealed air tight to the rock sample with lichen growth by means of "Terostate". For every data point a series of five intermittent readings were recorded, three of which were in steady-state conditions of CO_2 exchange (around 5-8 minutes in total).

Prior to measuring colonised sandstone, wet uncolonised samples were tested for the development of CO_2; all measurements were negative. We ensured that the surface of colonised sandstone within the experimental chamber was always totally covered by the lichen thallus. Each lichen sample thus had a surface area of 180 mm^2. The CO_2 rates of epilithic lichens were related to surface area and chlorophyll content, those of endolithic lichens to chlorophyll content only. For the determination of chlorophyll content, epilithic thalli were quantitatively scraped from the rock surface and rinsed three times for 30 seconds with acetone to remove lichen acids from the dry thallus (Brown 1980). The chlorophyll content of endolithic lichens was analysed from the upper 8-10 mm of sandstone crushed in a mortar. Thallus homogenates were then extracted with 80% acetone in the presence of $MgCO_3$ as a buffer. Chlorophyll was determined in the supernatant with a spectrophotom-



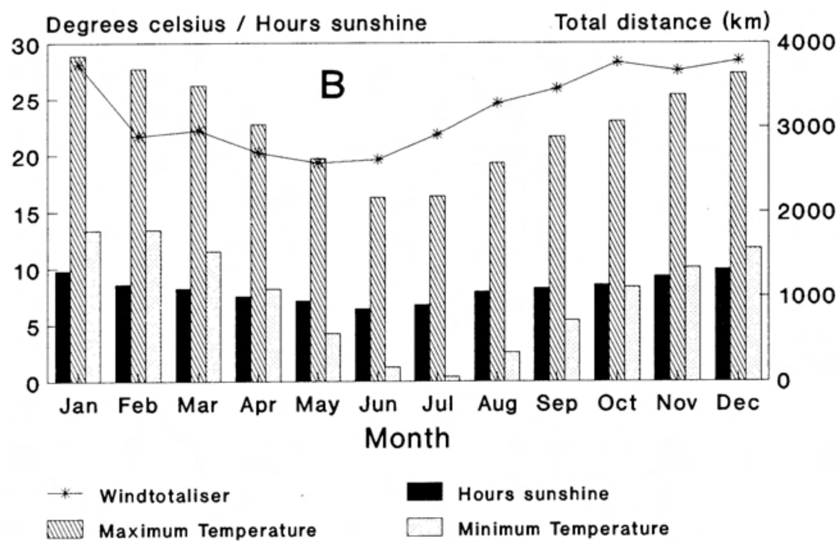


Fig. 1. Averaged macro-climatological data recorded at weather station number 6022 represents the period March 1983 to March 1991. **A**. Average monthly values of precipitation, evaporation and maximum and minimum air humidity; **B**. Average monthly values of wind totaliser, sunshine and maximum and minimum temperatures.

eter at 645 (647) nm and 663 (667) nm, depending on the position of the peak of the absorption curve.

Laboratory measurements were carried out with material of *P. capensis*. Thalli of the lichen, still attached to their substrates, were transported air-dry to Kiel in the cabin luggage of Kappen. Analyses were performed in Kiel one month after collection. During this period the material was kept air-dry until 3 days before the measurements, when they were reactivated by spraying with distilled water. Measurements were made according to a method described by Sancho & Kappen (1989). Thalli of *P. capensis* and their substratum were sprayed with distilled water. The CO_2 exchange measuring device has four 0,5 *l* plexiglass cuvettes, conditioned by being submerged in a water bath and illuminated by means of HQIL incandescent lamps. Surface area was measured by scanning paper copies of lichen contours. Chlorophyll content was measured as in the field measurements.

Results

Macro-climate

Climatological characteristics of the MZNP are presented in Figs. 1A & B. Figure 1A shows that although precipitation occurs throughout the year, more than 70% occurs during the warm summer period of October to March. The average annual precipitation of the MZNP is 414 mm. Hail frequently accompanies thunderstorms while heavy frosts and snow falls regularly occur during the winter months of April to September (Grobler & Hall-Martin 1982). On average 61 precipitation incidences are recorded each year. During such an incident an average amount of 6,2 mm of rain falls.

Figure 1A shows the substantial average monthly evaporation experienced in the area which amounts to a daily average of 4,2 mm. The average annual water deficit exceeds 1 100 mm — indicative of the prevalent dry conditions in the area. Maximum annual humidity values range between 29% and 100% while similar minimum values range between 11% and 92%. On average, maximum relative humidity values exceeding 90% occur on 183 days per year.

Extremes in temperature are characteristic of the area and summer temperatures can reach 38°C, while winter temperatures as low as -6°C may occur. Daily average annual maximum and minimum temperatures are 22,9°C and 7,5°C. Average monthly maximum and minimum temperatures are depicted in Fig. 1B wherein January stands out as the warmest and July as the coldest months. As shown in Fig. 1B the average daily hours of sunshine on a monthly basis remains fairly constant throughout the year. On a yearly basis, the average daily hours of sunlight total 9,7 hours. Figure 1B highlights the regular occurrence of wind in the park, which on a daily basis averages 105 km. The windiest months are January and October (Fig. 1B).

Micro-climate

Figure 2 compares diurnal courses of temperature measured at AIR, TIN, WIN and EIN. The graphs show that temperatures at the latter three localities far exceed air temperatures during the day. Of the latter three positions, the highest temperatures were recorded at TIN. Temperatures within the sandstone closely followed temperature changes in the air and cloudy nights resulted in elevated minimum temperatures. During the night of 8 March 1991, 10,6 mm of rain fell, resulting in an equalisation of air temperatures and those within the sandstone. Cloudy conditions prevailed on 8 March 1991 and 9 March 1991, resulting in lower maximum but also more fluctuating temperatures. A late afternoon thunderstorm, accompanied by heavy winds and hail occurred on 9 March 1991. This resulted in a rapid decline in temperatures, both within the sandstone boulder and of the air (Fig. 2).

Temperature is an important limiting factor for cryptoendolithic lichens. Daytime temperatures within the sandstone, and the resulting thallus temperatures, are considerably higher than air temperatures (Fig. 3). Similar, but less marked temperature differences remain until around midnight, whereafter the differences became smaller as the interior of the rock cools. As sandstone is a poor conductor of heat, the interior of the sandstone is

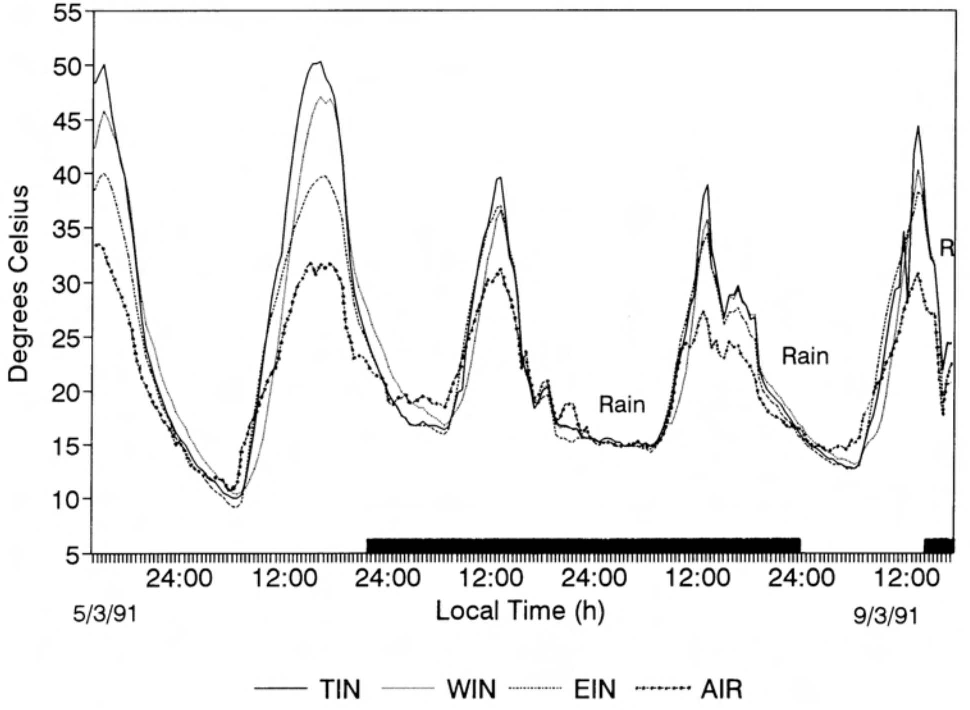


Fig. 2. Microclimatic situation of a sandstone lichen habitat in the Mountain Zebra National Park. Diurnal courses of temperatures measured during a period of 101 hours. Values represent measurements recorded every five minutes. TIN = Top internal; WIN = West facing internal; EIN = East facing internal; AIR = Air temperature; ■ = Cloudy conditions.

cooler than the air temperature around sunrise. This general pattern is influenced by prevailing weather conditions, such as cloudy days (compare Figs. 2 & 3). As the sun continues to strike the surface of the sandstone, the interior temperature of the sandstone rises sharply above that of the air. Differences as to the time, rate and degree to which the interior of the sandstone at localities EIN, TIN and WIN heat up and cool down are indicated by individual temperature curves in Fig. 3.

Prevailing temperatures within sandstone boulders, during our time of measurement in the park, are shown in Fig. 4. The plotted values are averages of all measurements recorded inside the sandstone expressed over a 24 h period. As shown in Fig. 4, the average temperature within the sandstone remains lower than air temperature until about 09:30, whereafter the interior of the sandstone rapidly becomes warmer than the air. If the rock temperature is below the dew point, moisture will condense out of the air onto the rock. This is advantageous to endolithic lichens which grow in the semi-arid environment of the Karoo. Being cooler than the surrounding air, endoliths will dry out less quickly than had the situation been the reverse. Following a wetting incidence, such conditions during the morning will obviously promote and prolong photosynthesis before critical environmental conditions such as temperature, desiccation of the sandstone/thallus, and light intensity within the sandstone become restrictive. It is interesting to note that averaged temperatures at WOP follow the same pattern

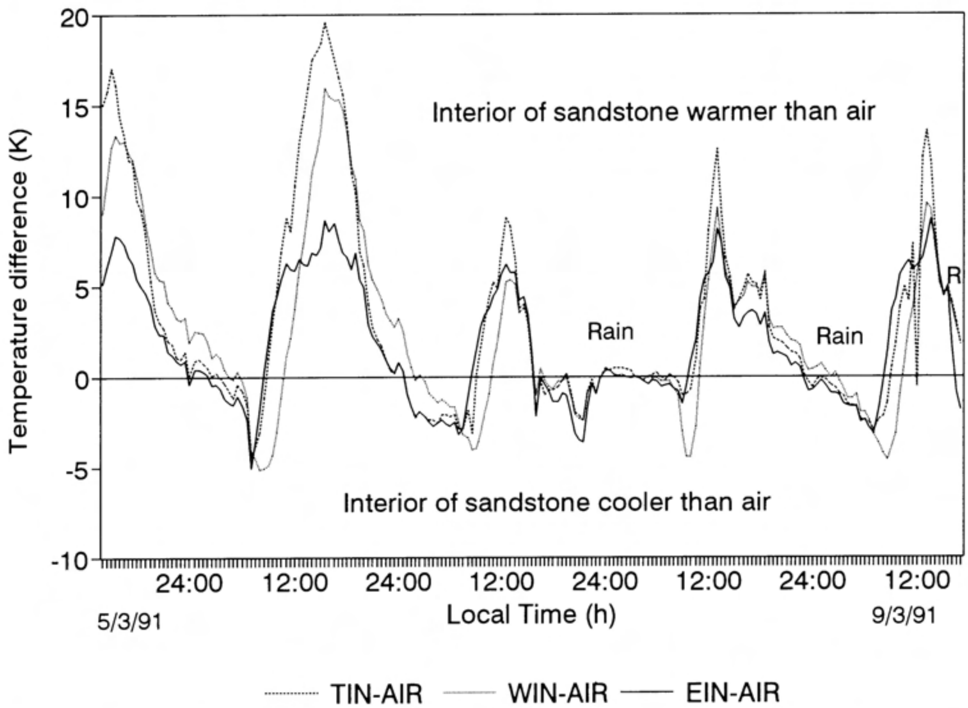


Fig. 3. Microclimatic situation of a sandstone lichen habitat in the Mountain Zebra National Park. Values represent differences between the air temperature (AIR) and internal temperatures of the sandstone at TIN, WIN and EIN.

(Fig. 4), but that temperatures at this locality rapidly rise to higher values as soon as the sun strikes this side of the rock.

Photosynthetic performance of the different species

Epilithic species

Peltula capensis (Brusse) Büdel

Peltula capensis generally grows on rocky slopes facing east or south east. In the MZNP their distribution follows large rainwater run-off tracks where they predominate. In such habitats the small shrublike thalli grow in patches several centimetres in diameter. Several cyanobacterial and algal species occur together with *P. capensis*. Different lichen species exist along the periphery and further away from the rain tracks, reminiscent of granite outcrops described by Scott (1967) from Central Africa. *Peltula capensis* favours the wet central parts of such rainwater runoff tracks. These rainwater runoff tracks flow for short periods of time after some rain has fallen.

We measured the photosynthesis of *P. capensis* patches on dolerite samples collected at the natural site, 2 km from our campsite. Our investigation shows that photosynthesis was most effective during the morning hours after a nighttime thunderstorm. The process was also effective during a morning preceded by heavy rainfall the previous afternoon. It was, however, remarkable that no significant photosynthetic activity could be recorded immediately after an afternoon rainfall incident — data not shown. Evidently this lichen does not photosynthesise immediately when moistened in a relatively warm state and at low quantum flux densities — conditions that prevail during late afternoon thunderstorms.

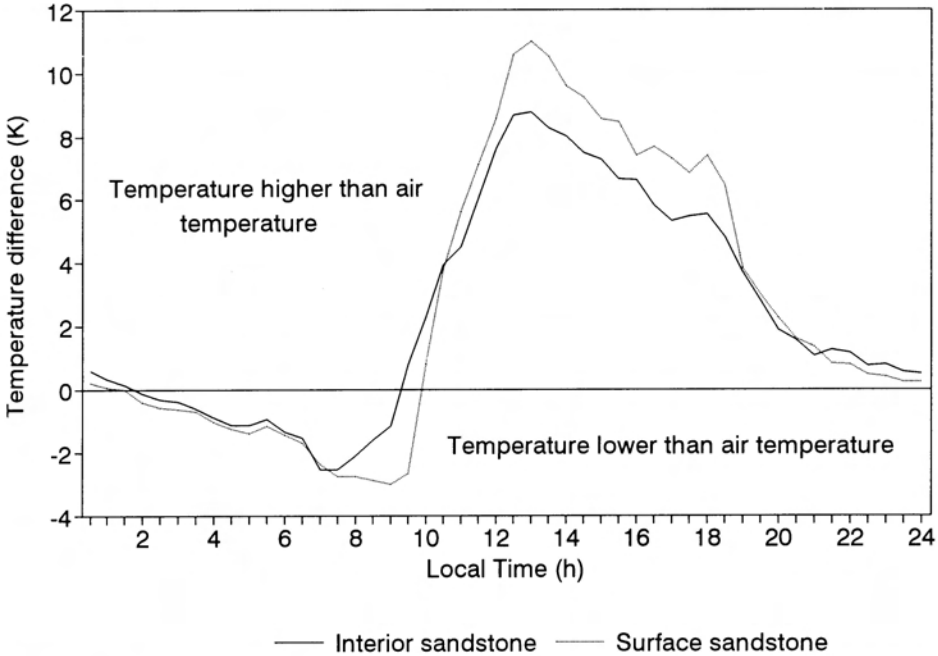


Fig. 4. Differences in temperature between pooled, average internal temperatures (WIN, EIN, TIN) of the sandstone boulder (Interior sandstone) and average air temperature (AIR). In addition, differences between averaged surface temperature along the western facing slant of the sandstone (WOP) and average air temperature (AIR) are also shown.

The photosynthetic performance of thalli during a foggy morning (8 March 1991), subsequent to a heavy rainfall during the night, is shown in Fig. 5. Thalli at a temperature of 17°C very effectively utilise a quantum flux density of ca. 200 µmol $m^{-2}s^{-1}$. The next cloudy morning (9 March 1991), again after a rainy night, thallus temperatures between 13°C and 17°C were apparently limiting. A quantum flux density of about 1 100 µmol $m^{-2}s^{-1}$ resulted in the highest measured net photosynthetic rates at 26°C. At higher temperatures and irradiance, photosynthesis drastically decreased with the concomitant water loss from the thallus. During the course of the next day (9 March 1991), a temperature range of between 25°C and 29°C provided higher net photosynthetic rates at quantum flux densities between 700 and 1 200 µmol $m^{-2}s^{-1}$ (Fig. 5).

Laboratory measurements of net photosynthesis (NP) at elevated irradiances show that the upper temperature compensation point may reach values around 35°C or higher (Fig. 6). The optimum temperature for net photosynthesis is around 23°C. At this temperature light saturation of net photosynthesis still lies beyond 1 000 µmol $m^{-2}s^{-1}$ (Fig. 7). Light saturation was found only at temperatures below 10°C. In addition the graphs indicate that the lichen is able to use irradiances as low as 200 µmol $m^{-2}s^{-1}$, with compensation points between 30 and 110 µmol $m^{-2}s^{-1}$. The maximum measured net photosynthesis rate was 1,5 mg CO_2 mg $Chl^{-1}h^{-1}$ or 3,9 µmol CO_2 $m^{-2}s^{-1}$ in the lab and 0,9 mg CO_2 mg $Chl^{-1}h^{-1}$ or 2,05 µmol CO_2 $m^{-2}s^{-1}$ in the field.

The respiratory rates are comparatively low and do not strongly increase at higher thallus temperatures — data not shown. In general, our results demonstrate that *P. capensis* is photosynthetically very efficient in a wide irradiance range and is adapted to be active under comparatively high temperatures.

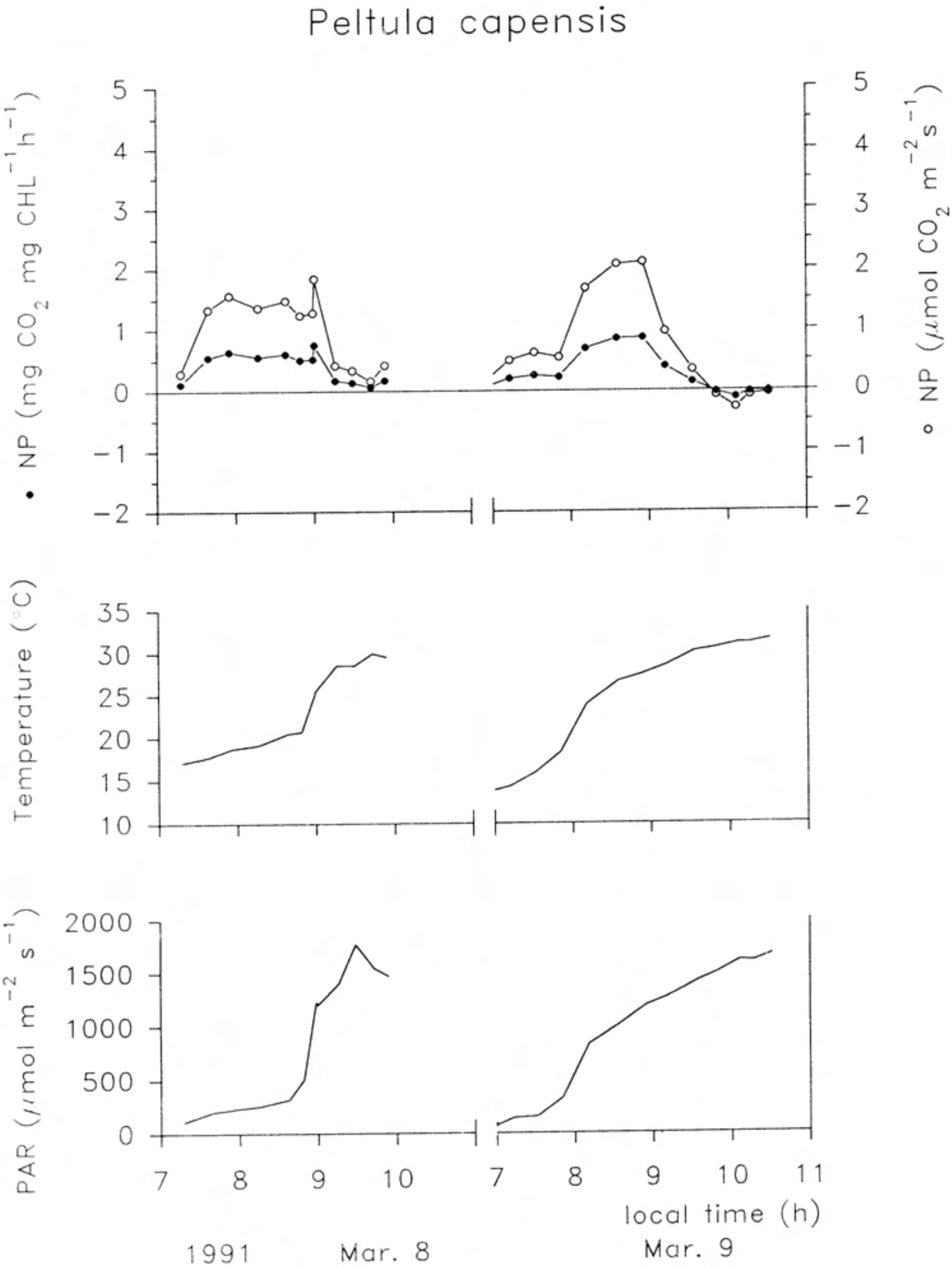


Fig. 5. CO_2 exchange related to chlorophyll content and surface area, of *Peltula capensis* porometrically measured under natural light and temperature conditions. Time courses of two days with rain-wetted thalli growing on dolerite. (PAR = Photosynthetically active radiation).

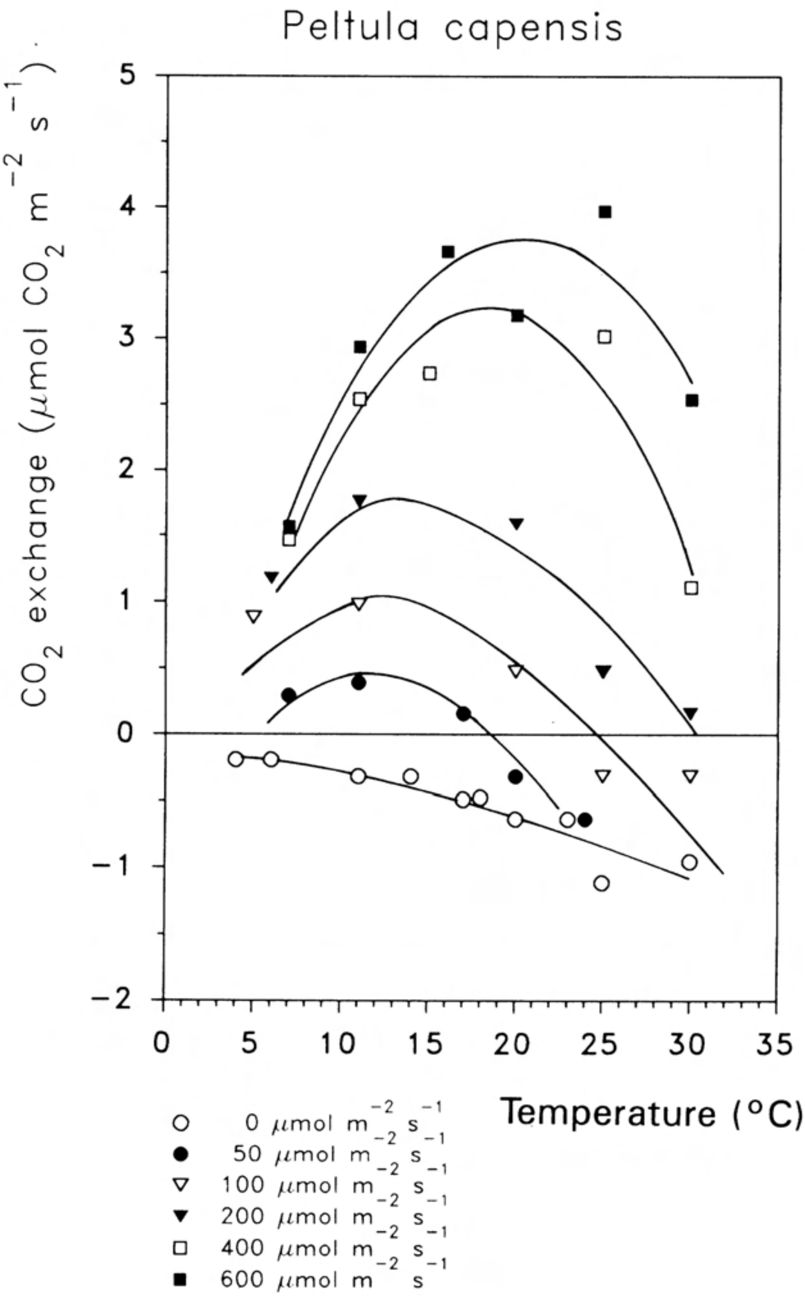


Fig. 6. CO_2 exchange related to chlorophyll content (and to surface area) of *Peltula capensis* according to laboratory measurements. The curves depict net photosynthesis at various irradiance levels (50-600 μmol m^{-2} s^{-1}) and dark respiration as functions of temperature.

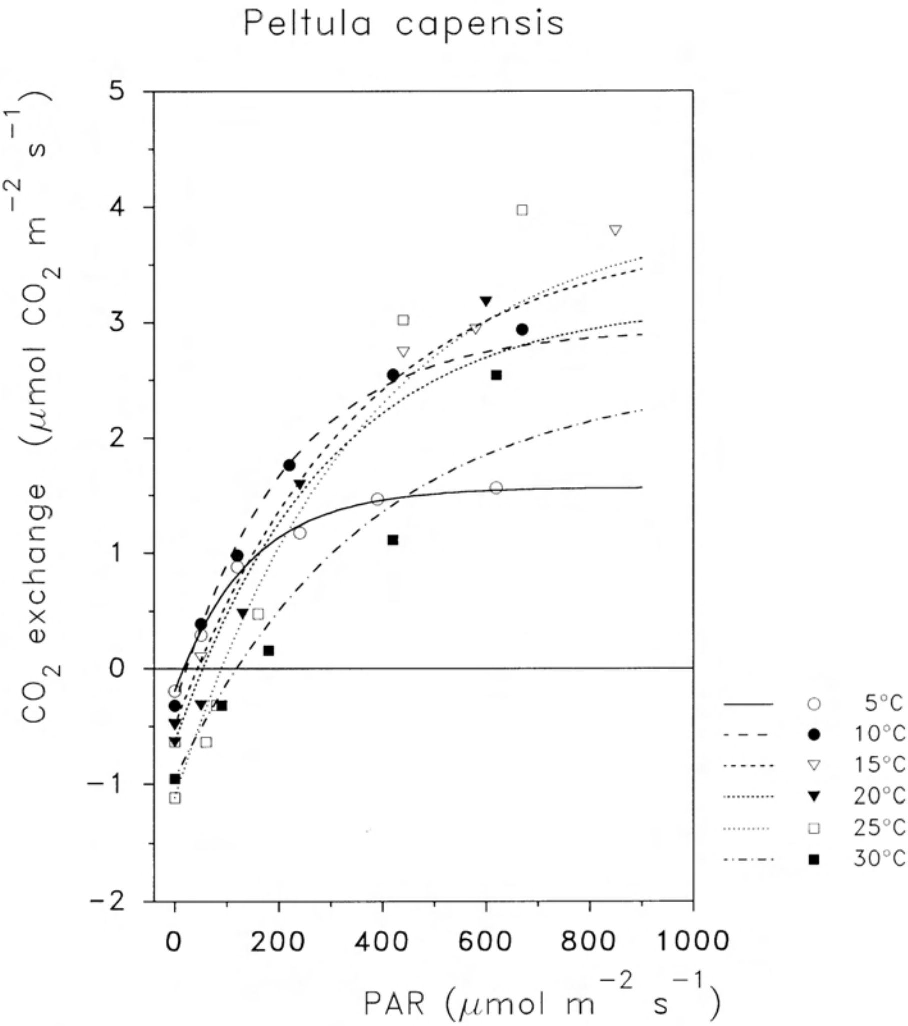


Fig. 7. CO_2 exchange related to chlorophyll content (and to surface area) of *Peltula capensis* according to laboratory measurements. The curves depict net photosynthesis at various levels of temperature (5°C-30°C) (PAR = Photosynthetically active radiation).

Parmelia (*Paraparmelia*) ***chlorea*** Stizenb.

Parmelia chlorea is one of the largest lichens in the park. Thalli of *P. chlorea* are foliose, whitish in colour and grow loosely attached to the substrate. This lichen colonises small dolerite and sandstone roll blocks scattered over the Rooiplaat plateau. Thalli of this species mainly occur on the southeast side of rocks and boulders. It is interesting to note that an infusion of this lichen is used by the Xhosa (a local black tribe), as a remedy against toothache.

Measurements of photosynthesis were made on the same days as with *Peltula capensis*. Our results show that the initial increase in photosynthetic rate during the early morning with increasing irradiation is remarkable (Fig. 8). However, the slightest decrease in

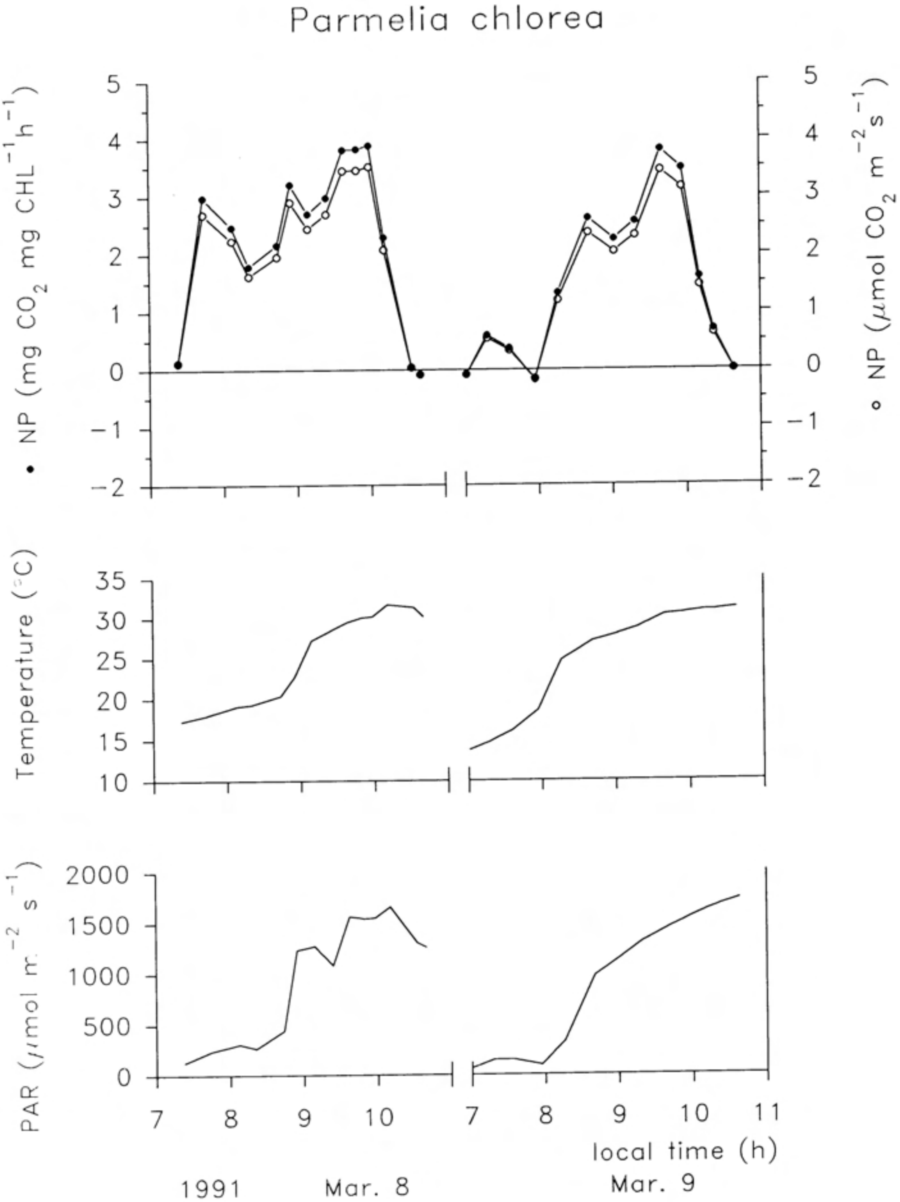


Fig. 8. CO_2 exchange of *Parmelia chlorea* porometrically measured under natural light (PAR) and temperature conditions. Time courses of two days with rain- wetted thalli growing on sandstone. (PAR = Photosynthetically active radiation).

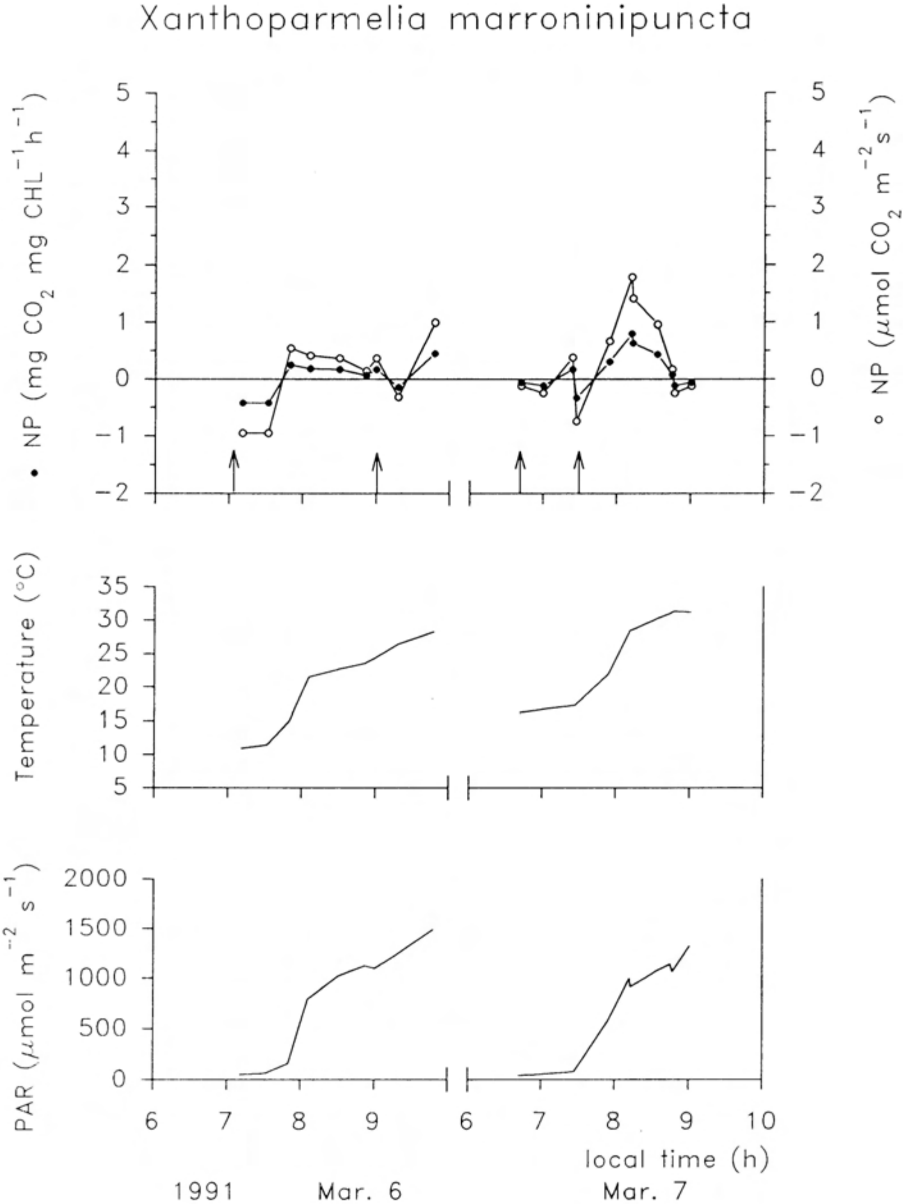


Fig. 9. CO_2 exchange of *Xanthoparmelia marronipunctata*; porometrically measured under natural light (PAR) and temperature conditions. Time courses of two days; thalli growing on dolerite and sprayed with borehole water from the field site (↑). (PAR = Photosynthetically active radiation).

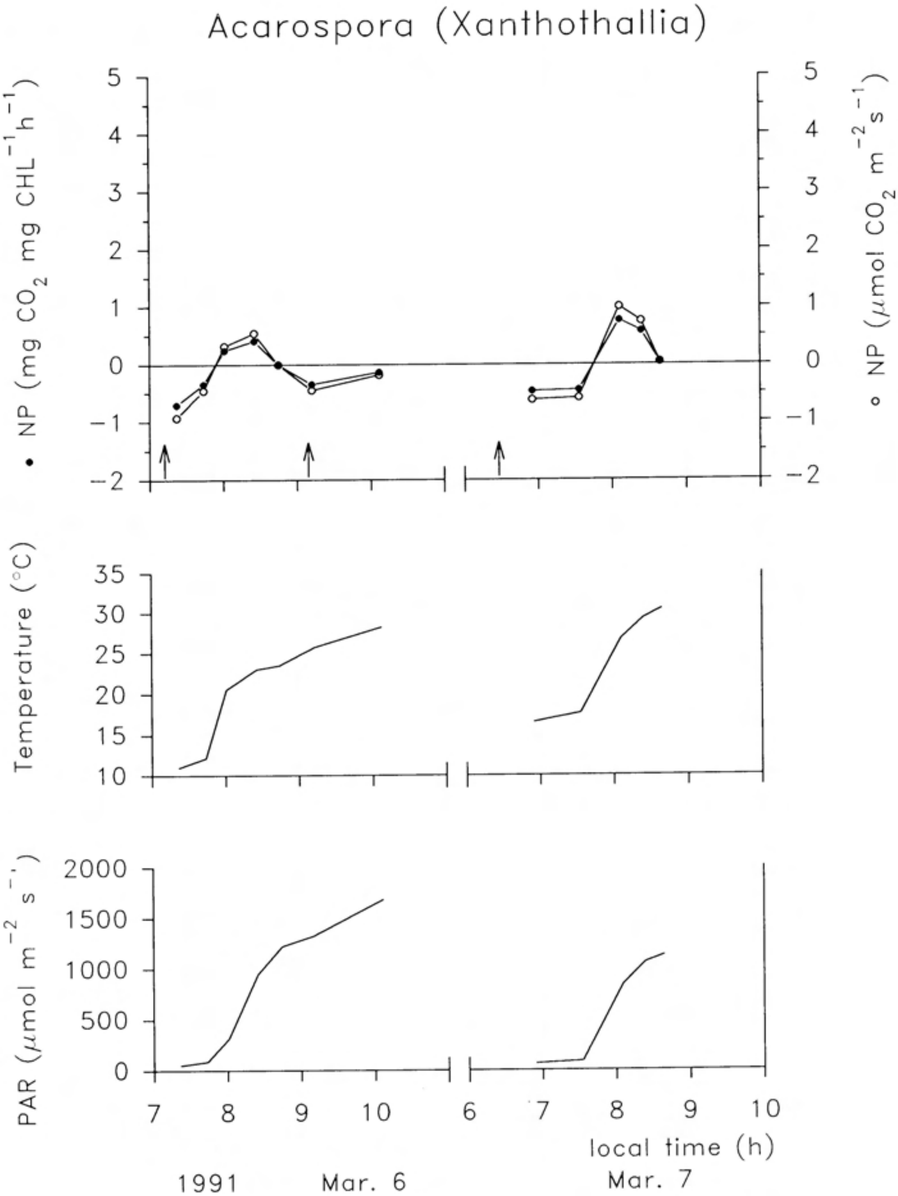


Fig. 10. CO_2 exchange of *Acarospora* (*Xanthothallia*) sp.; porometrically measured under natural light (PAR) and temperature conditions. Time courses of two days; thalli growing on sandstone, sprayed with borehole water from the field site (↑). (PAR = Photosynthetically active radiation).

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quantum flux density resulted in a decrease in net photosynthesis. An air temperature of 19°C and a quantum flux density of 100 µmol $m^{-2}s^{-1}$ was too low for net CO_2 uptake. The highest net photosynthetic rates were recorded at 28–30°C and 1300–1500 µmol $m^{-2}s^{-1}$. The effective retention of water in the thallus of *P. chlorea* resulted in an extension of effective photosynthesis for about one hour (compare Figs. 5 & 8). This is partly due to colour and anatomical-morphological differences between these two growth forms. As thalli of *P. capensis* are black in colour, it is assumed that they increased in temperature more rapidly than white thalli of *Parmelia chlorea*.

Of the lichens we investigated, *Parmelia chlorea* has the highest photosynthetic efficiency with a maximum net rate of photosynthesis of 3,4 µmol CO_2 $m^{-2}s^{-1}$ (3,9 mg CO_2 mg $Chlorophyll^{-1}$ h^{-1}) (Fig. 8). The balance of photosynthetic production during the two days of observation was 8,6 and 5,05 mg CO_2 /mg Chlorophyll.

Xanthoparmelia marroninipuncta (Brusse) Hale

Compared to other epilithic species we examined, *X. marroninipuncta* grows in the least exposed sites. Specimens for study were collected on dolerite boulders partly shaded by small trees and shrubs. These boulders occurred along the west-facing side of the hill along which the rest camp was built. The lobes of this light-green foliose lichen are smaller than those of *Parmelia chlorea* and the thallus is more tightly attached to the substrate than the latter species.

During our investigation thalli were watered by spraying with borehole water from the field site. Negative values of net photosynthesis always occurred after spraying of the thalli (Fig. 9). In the early morning, irradiances below 100 µmol m^{-2} s^{-1} prevented net photosynthesis to pass the lower light compensation point at temperatures between 11 and 14°C. Within an irradiance range of 120–1200 µmol $m^{-2}s^{-1}$ and a temperature range of 12–25°C net photosynthesis was significant but low (Fig. 9). The highest measured rate was 1,8 µmol CO_2 $m^{-2}s^{-1}$ (26°C; 850 µmol $m^{-2}s^{-1}$). From the data available it seems as if this lichen is well adapted to be photosynthetically active during periods of high light intensities and temperatures. These conditions usually occur at this site during cloudless periods immediately after an early afternoon thunderstorm. Our results furthermore show that *Xanthoparmelia marroninipuncta* has a low productivity as it's daily balances reached only a fraction (0,16 and the next day 0,86 mg CO_2/mg Chlorophyll) of that of *Parmelia chlorea*.

Acarospora Mass. (*Xanthothallia*) species

This *Acarospora* (*Xanthothallia*) species commonly occurs on both dolerite and sandstone in the MZNP. At Rooiplaat it grows on rock faces associated with *Caloplaca*, *Lecidea* and *Sarcogyne* species. Together these species form a xerophilous saxicolous lichen community. The greenish yellow crust of *Acarospora* may reach diameters of a hundred millimetres or more. Photosynthesis was measured on an *Acarospora* colonised rock measuring 400 mm x 300 mm.

This rock was heavily sprayed with borehole water from the field site before dawn and thalli of *Acarospora* responded to this treatment by a gradual increase in the release of CO_2. The ensuing period of net photosynthetic CO_2 uptake was short. A maximum rate of only 0,5 µmol CO_2 $m^{-2}s^{-1}$ was reached at a temperature of 22,5°C and a quantum flux density of 900 µmol $m^{-2}s^{-1}$. The response was not essentially different on the next warmer morning when the irradiance was higher than 250 µmol $m^{-2}s^{-1}$ and the air temperature above 20°C (Fig. 10). A maximum rate of only 1 µmol CO_2 $m^{-2}s^{-1}$ was measured at a temperature of 24°C and a quantum flux density of 700 µmol $m^{-2}s^{-1}$.

Negative rates of photosynthesis were due to low quantum flux densities on both days.

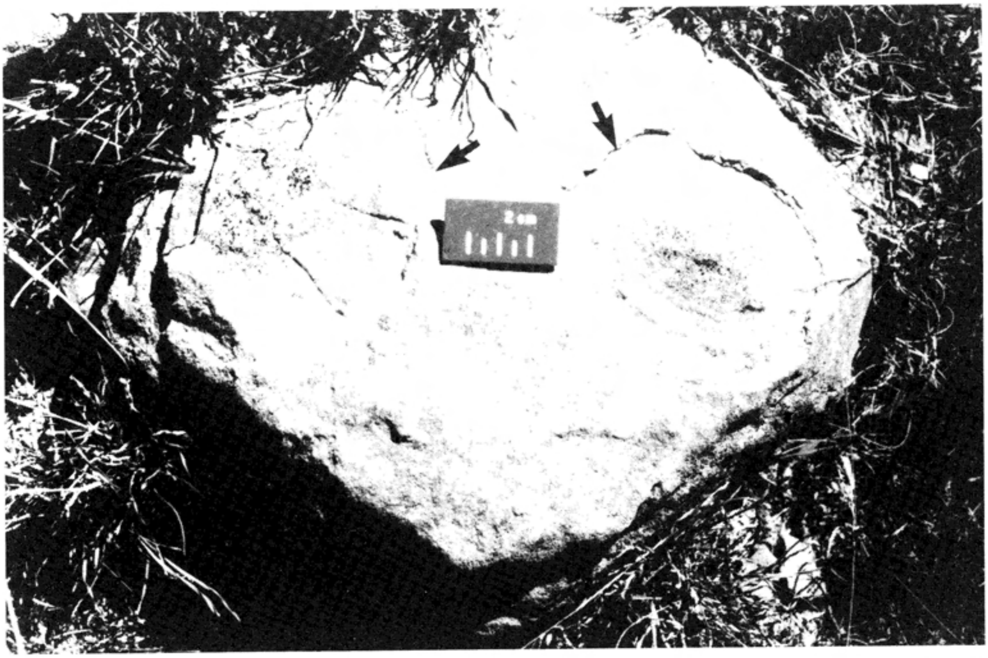

Fig. 11. Thalli of the endolithic lichen *Lecidea* aff. *sarcogynoides* (↑) on Balfour sandstone.

The thalli responded quickly to increased quantum flux densities as depicted by the results of 7 March 1991. Unfortunately the second spraying on 7 March 1991 was insufficient and the lichen dried out before reaching the lower photosynthetic compensation point. Our results suggest that low light intensity was the limiting factor during these two measuring days (Fig. 10). Could it be that this lichen is adapted to short bursts of photosynthesis after thunderstorms when high light intensities and presumably high substratum temperatures prevail? Figure 10 suggests that the productive period of this *Acarospora* species may always be low with a resultingly slow growth rate.

Endolithic lichens

Lecidea **aff.** ***sarcogynoides*** Körb.

Thalli of *Lecidea* aff. *sarcogynoides* (Fig. 11) occur on horizontal or slightly inclined faces of Balfour sandstone boulders and rocks on the Rooiplaat plateau. This species is frequently associated with other crustose lichens, or it may be the sole coloniser of the sandstone. This lichen occurs in a number of climatic regimes and types of sandstone in South Africa.

Net photosynthesis was measured on an intact rock collected at Rooiplaat. The area of sandstone colonised by the lichen needed heavy spraying to ensure a response. Low early morning irradiance limited photosynthetic activity (Fig. 12). Shortly after the photosynthetic incidents shown in Fig. 12, no positive photosynthetic rate was measurable. It is obvious that this was not due to water loss as no positive photosynthetic rate could be detected for 2 hours after the second spraying incident on 9 March 1991. The most likely explanation for these responses are a reaction of the lichen to strong irradiative heating and high quantum flux densities. The compensation point was passed when temperatures on the two successive days were higher than 24°C and 29°C, and quantum flux densities exceeding 1 100 µmol $m^{-2}s^{-1}$, even after slight

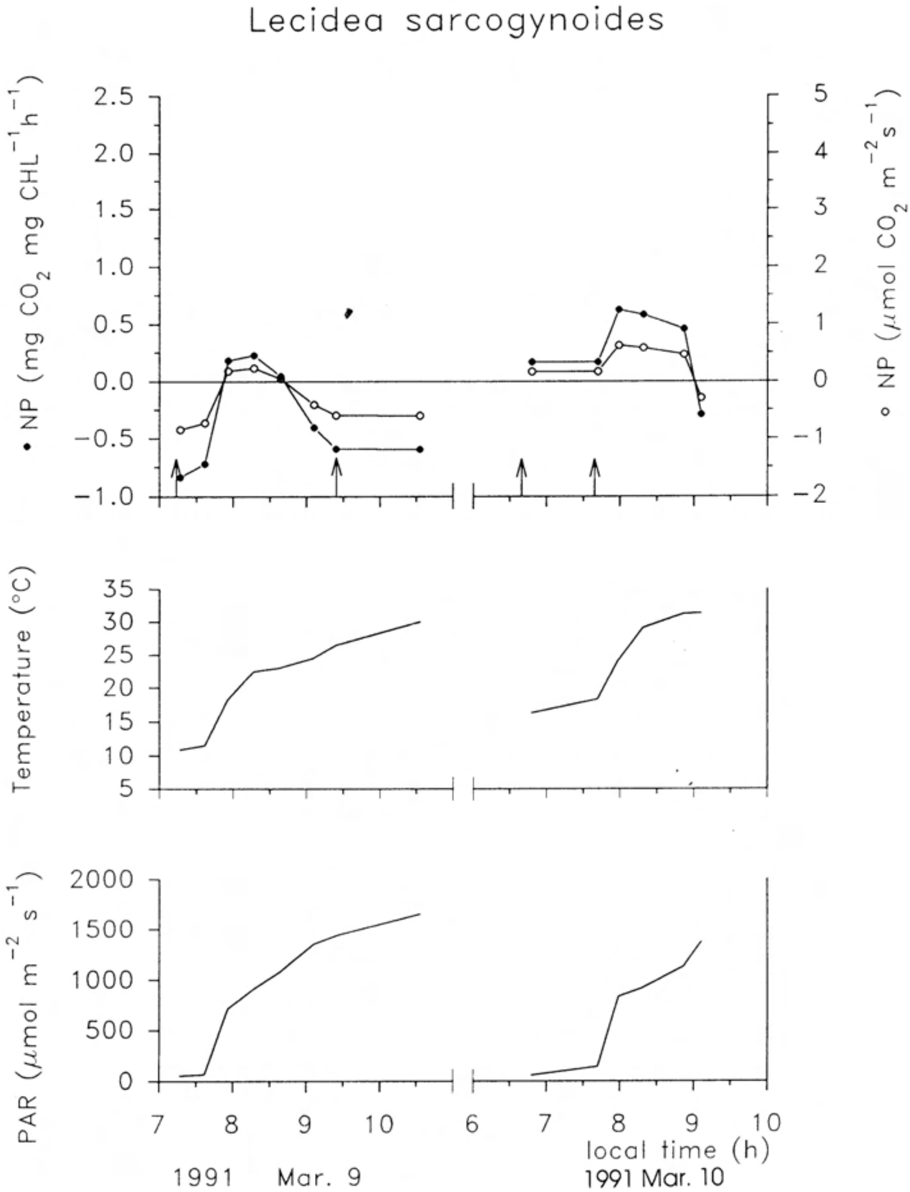

Fig. 12. CO_2 exchange of *Lecidea* aff. *sarcogynoides*; porometrically measured under natural light (PAR) and temperature conditions. Time courses of two days; thalli growing on Balfour sandstone, sprayed with borehole water from the field site (↑). (PAR = Photosynthetically active radiation).

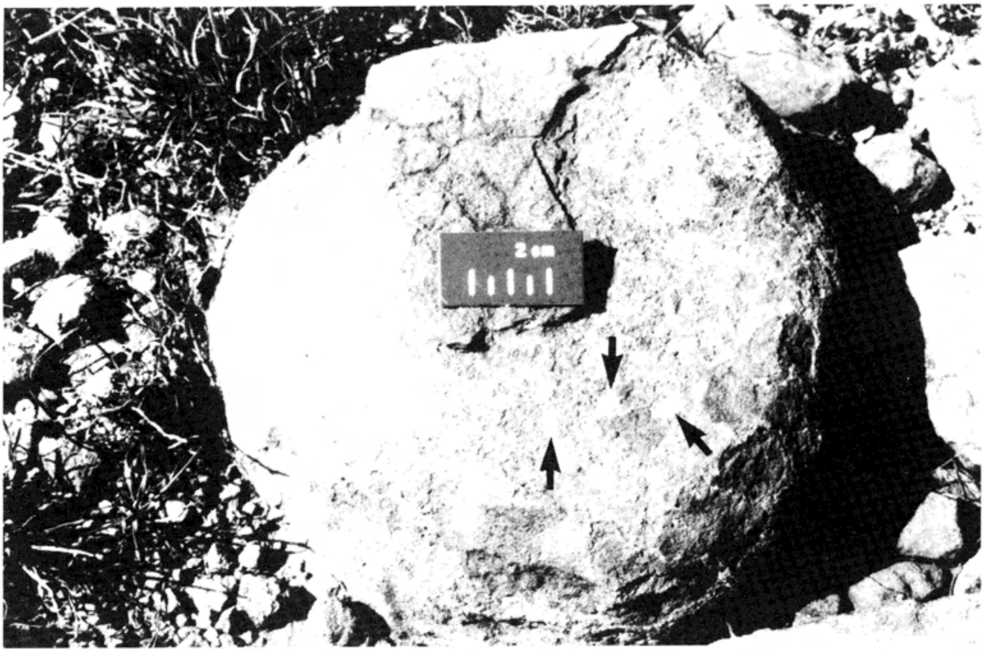

Fig. 13. Thalli of the more cryptoendolithic lichen *Sarcogyne* cf. *austroafricana*. Arrows indicate areas where scales of sandstone have peeled off due to weathering by the lichen.

spraying. The photosynthetic production of *L.* aff. *sarcogynoides* is undoubtedly low and as shown in Fig. 12 there was an overwhelming loss of carbon on the first day of measurement.

Sarcogyne cf. ***austroafricana*** (Zahlbr.) H. Magn.

The photosynthetic activity of *S.* cf. *austroafricana* thalli (Fig. 13) in rain-moistened sandstone is extremely low (Fig. 14). In the early morning hours the negative photosynthetic values were presumably due to the low irradiance levels which were below 150 µmol $m^{-2}s^{-1}$. Positive rates were measured at ranges of irradiance between 650 and 1 500 µmol $m^{-2}s^{-1}$ and temperatures between 20°C and 29°C.

Discussion

There is a scarcity of literature dealing with field measurements on lichens similar to those we have investigated (Lange *et al.* 1970; Nash *et al.* 1982; Kappen *et al.* 1990; Lange *et al.* 1991). In addition to a comparison of species performance it can also be shown to what extent our method for *in situ* measurements gives data that are in the same order of magnitude as measurements obtained through other methods.

The widely different maximum rates we have observed in *Parmelia chlorea* (3,9 mg CO_2 mg $chl^{-1}h^{-1}$; 3,5 µmol $m^{-2}s^{-1}$) and of *Xanthoparmelia marroninipuncta* (0,8; 1,8 respectively) correlates with the size of the two morphologically similar taxa but also reflects different adaptations to environmental conditions. In the Namib desert *Xanthoparmelia walteri* Knox had a maximum rate of 2,1 mg CO_2 mg $chl^{-1}h^{-1}$ (Lange *et al.* 1991) and if the given data is transformed, *Parmelia kurokawae* (*Xanthoparmelia lavicola* (Gyenik) Hale) measured in the Sonoran desert had a maximum gross photosynthetic rate (^{14}C fixation technique, Nash *et al.* 1982) of 6,3 µmol $m^{-2}s^{-1}$. Although both of these desert lichens have higher rates than correspond-

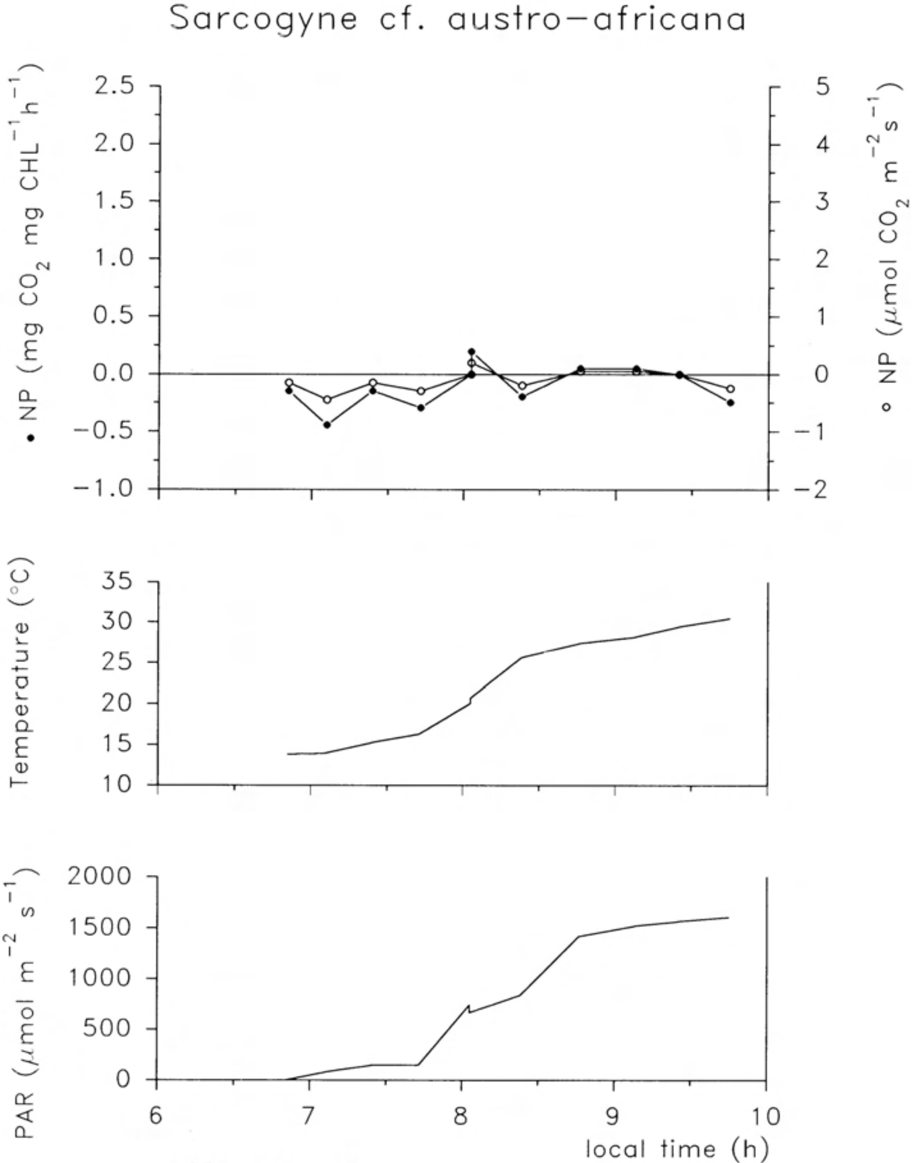

Fig. 14. CO_2 exchange of *Sarcogyne* cf. *austroafricana*; porometrically measured under natural light (PAR) and temperature conditions. Time course of one day; thalli growing on sandstone. Thalli naturally wetted by rain. (PAR = Photosynthetically active radiation).

ing genera in our study, Nash *et al.* (1982) reported a gross photosynthetic rate of 10 µmol $m^{-2}s^{-1}$ for *Acarospora schleicheri* from the Sonoran desert. The value reported by Nash *et al.* exceeds our data for *Acarospora* sp. by ten times. However, they interpreted their results as a methodological artifact. Compared to crustose lichens measured in the maritime Antarctic by the same method we used (Kappen *et al.* 1990), the present data falls well within the same order of magnitude (0,5-1,4 mg CO_2 mg $chl^{-1}h^{-1}$). In addition, the endolithic *Lecidea* aff. *sarcogynoides* also fits into this range.

The frequency of dew events and precipitation presumably results in sufficient moistening and photosynthetically active events to ensure continued, albeit slow, growth of *L.* aff. *sarcogynoides* thalli. Figure 11 highlights the erosive force this lichen exerts on Balfour sandstone. The rate at which the surface of Balfour sandstone is weathered by *L.* aff. *sarcogynoides* has not yet been determined. However, Wessels & Schoeman (1988) found that the largest thalli of *L.* aff. *sarcogynoides* had formed pits 215 mm wide and 5,8 mm deep on Clarens sandstone surfaces exposed for 44 years.

Thalli of *Sarcogyne* cf. *austroafricana* are more endolithic (Golubic *et al.* 1981) than thalli of *Lecidea* aff. *sarcogynoides*. Whereas thalli of *L.* aff. *sarcogynoides* stand out by the erosive traces on sandstone surfaces (Fig. 11), areas colonised by thalli of *S.* cf. *austroafricana* show thin scaly peeling (Fig. 13). Large apothecia occur along these edges or in small depressions which may have been produced by the species. Thalli of *S.* cf. *austroafricana* regularly occur on freshly exposed surfaces of Balfour sandstone. This species is widespread in South Africa and occurs on different types of sandstone and climatic areas. In all these habitats it seems as if this endolithic lichen is a primary coloniser.

Weathering of Balfour sandstone by thalli of *S.* cf. *austroafricana* results in a patchy weathering pattern. This pattern is similar to the weathering pattern on Beacon sandstone caused by cryptoendolithic lichens of the Ross Desert, Dry Valleys, Antarctica (Friedmann 1982; Friedmann & Weed 1987). The photosynthetic rates of *S.* cf. *austroafricana* and morphologically similar cryptoendolithic lichens of the Ross Desert are extremely low, although the temperature ranges differ widely (0–6 °C, Kappen & Friedmann 1983) and perhaps 20–29 °C respectively. The erosion rate of this species has not yet been measured, but for the Antarctic species a rate in the order of magnitude of millennia (Bonani *et al.* 1988) is estimated.

The CO_2 fixation rates of *Peltula capensis* thalli, a cyanophilous lichen with *Chroococcales* as photobiont (Büdel 1987), are the first to be reported for this species. However, these values are relatively high compared with the other epilithic species tested, indicative of a quite productive species. The maximum photosynthetic rates of these African lichen species were found at temperatures between 20°C and 30°C, far beyond recorded optimum temperatures for lichens from temperate and desert regions. It is remarkable that photosynthesis was positive in five of the species at temperatures beyond 31°C. It is therefore likely that all these lichens can profit from rock moistening even when the rock is highly heated.

Results from the short period of microclimatic measurements in and on the sandstone at Rooiplaat indicate that microclimatological conditions during the morning hours are profitable to endolithic lichens. Most of the lichens are able to keep up photosynthetic activity until about 10:00 local time when thallus temperatures may reach 30°C (Figs. 2 & 3). Differences between pooled average internal temperatures and air temperatures (Fig. 4) reveal that during the early morning the sandstone is cooler than the ambient air temperature, which increases the possibility and incidence of dew condensation. Taking into account that on average 183 days of the year have periods with air humidity higher

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