Epilithic Lichens in the Namib Fog Desert: Field Measurements of Water Relations and Carbon Dioxide Exchange

Epilithische Flechten in der Namib-Nebelwüste: Freilandmessungen von Wassergehalt und Kohlendioxid-Austausch

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Summary: Although there is only negligible rainfall, frequent nocturnal fog and dew support a luxurious lichen vegetation in the coastal zone of the central Namib Desert (Namibia). In earlier publications we have studied ecophysiological performance of several important lichens with the main focus on ground and epiphytic species in the lichen fields north of Swakopmund. Here, based upon measurements in spring and autumn in the field, we have extended this work to four epilithic species of the coastal gravel plain belonging to three different growth forms: one fruticose *(Santessonia hereroensis)*, one foliose *(Xanthoparmelia walteri)*, and two crustose or subcrustose species *(Caloplaca elegantissima* and *Xanthoparmelia incomposita)*.

The daily response patterns for net photosynthesis for the experimental epilithic species were very similar to other lichens at the same site. In both seasons nocturnal hydration, by fog and/or dew, activated dark respiration of the lichens followed, after sun rise, by a short period of positive net photosynthesis (NP) that continued until metabolic inactivation occurred from desiccation. Averaged daily period of photosynthetic activity was

longest for fruticose *S. hereroensis* (3 h 21 min) and shortest for the dark-coloured crustose species *X. incomposita* (2 h 39 min). With *S. hereroensis*, in particular, another period of activation could take place when humidity increased later in the afternoon. The very loose, lacunose cortex of this species enlarges the surface contact between the photobionts and the atmosphere and apparently ensures a quick hydration by water vapour uptake. However, NP rates attained were rather low so that the ecological significance of this feature remains questionable.

Higher fog and dew intensity in spring increased maximal nocturnal water contents, maximal attained NP and integrated daily carbon income (ΣNP) compared to the autumn measurements. When averaged over all species, the carbon income of a day with photosynthetic activity in autumn amounted to less than 40 % of that of a typical day in spring. On its most productive day, *S. hereroensis* had a carbon income of 3.65 mg$_C$ g$_C^{-1}$ day^{-1} meaning that the lichen assimilated on this day as much as 3.65 ‰ of its own thallus carbon content. The average daily carbon income on days with nocturnal dew and/or fog moistening the thalli in spring ranged from 1.24 (*X. walteri*) to 2.21 mg$_C$ g$_C^{-1}$ day^{-1} (*S. hereroensis*).

Zusammenfassung: Obwohl der Regenniederschlag in der Küstenzone der zentralen Namibwüste (Namibia) vernachlässigbar gering ist, ermöglichen häufiger Nebel und Taufall eine reiche Flechtenvegetation. In vorhergehenden Untersuchungen haben wir uns auf die wichtigsten Bodenflechten und auf Epiphyten der Flechtenfelder nördlich von Swakopmund konzentriert. Ausgehend von Messungen in Frühjahr und Herbst berichten wir in der vorliegenden Arbeit über das Verhalten epilithischer Arten verschiedener Lebensformen: eine Strauchflechte (*Santessonia hereroensis*), eine Blattflechte (*Xanthoparmelia walteri*) und zwei nahezu krustige Flechten (*Caloplaca elegantissima* und *Xanthoparmelia incomposita*).

Die Gesteinsflechten verhielten sich sehr ähnlich wie die anderen Arten des Standortes. In beiden Jahreszeiten wird durch nächtlichen Nebel und/oder Tau zunächst die Atmung aktiviert. Dann folgt nach Sonnenaufgang eine kurze Phase positiver Nettophotosynthese (NP), die durch Austrocknen beendet wird. Die mittlere Dauer dieser Aktivitätsperiode währte am längsten bei der strauchigen *S. hereroensis* (3 Std. 21 Min.) und am kürzesten für die dunkel gefärbte krustige *X. incomposita* (2 Std. 39 Min.). Insbesondere bei *S. hereroensis* konnte eine zweite Aktivierungsperiode auftreten, wenn die Luftfeuchtigkeit am späten Nachmittag anstieg. Die sehr lockere und lakunose Rinde dieser Art fördert den Kontakt zwischen den Photobionten und der Atmosphäre, was offensichtlich zu einer schnellen und effektiven Hydratation durch Wasserdampf-Aufnahme führt. Allerdings waren die dabei erreichten Photosyntheseraten nur gering, so dass die ökologische Bedeutung dieses Vorgangs fraglich bleiben muss.

Im Frühjahr führen stärkere Intensität von Nebel und Tau zu höheren maximalen Photosynthese-Raten und zu höherer täglicher Kohlenstoff-Fixierung als im Herbst. Im Mittel über alle Arten betrug die tägliche C-Fixierung im Herbst nur weniger als 40 % derjenigen des Frühjahrs. An ihrem produktivsten Tag hatte *S. hereroensis* eine Kohlenstoff-Fixierung von 3,65 mg$_C$ g$_C^{-1}$ Tag^{-1}, was einer Assimilation von 3,65 ‰ ihres Thallus-Kohlenstoffgehaltes entspricht. Die mittlere tägliche Kohlenstoff-Fixierung

nach nächtlicher Tau- und/oder Nebel-Befeuchtung betrug von 1,24 (*X. walteri*) bis 2,21 mg$_C$ g$_C$$^{-1}$ Tag^{-1} (*S. hereroensis*).

Introduction

The central Namib Desert is famous for its lichen vegetation that covers extended areas of the coastal fog zone. SCHULTZE (1914), almost one hundred years ago, described his impressions and excitement on seeing for the first time the brightly coloured lichen communities of the Namib fog desert: "Bald leuchtend rostrote, bald grüngelbe Büschel von *Physcia*- und *Combea*-Arten überziehen wie üppiger Blumenschmuck die Luvseite abgestorbener Nachtschattengewächse; *Parmelia*- und *Teloschistes*-Arten bilden dünne, tellergroße Pflaster an den Felswänden; *Lecidea, Amphiloma* und eine orangerote *Gasparrinia* umklammern häufig die Namibkiesel im Umkreis von Lüderitzbucht. Auf der Fläche zwischen Nonidas und Haigamkab, noch in 15 km Küstenentfernung, ist der Wüstenboden über und über mit Flechten grünlich-gelb gefärbt; hinter Cap Croß bilden rostrote Büschel stellenweise dichte Rasen. Alle diese Flechten sind typische Glieder einer Nebelvegetation" These communities occur where rain precipitation is negligible and lichens are almost the only autotrophs. Their luxuriant existence is possible because of frequent fog, dew and high humidity. Since then, there have been several descriptions of this impressive lichen vegetation (e.g., MATTICK 1970, GIES 1981, WALTER 1986, SCHIEFERSTEIN 1989, SCHIEFERSTEIN & LORIS 1992, LALLEY & VILES 2005). However, phytosociological analysis of lichen distribution and communities has, until recently, suffered from the lack of a reliable taxonomic study of the lichen species of the area. Many samples could not be correctly determined or were unknown. This situation has changed recently mainly through work by Volkmar WIRTH and his co-workers. He has described several new species from the central Namib area (WIRTH & VĚZDA 1975, HERTEL & WIRTH 2006, WIRTH et al. 2005, WIRTH & ELIX 2005, WIRTH 2006, BUNGARTZ & WIRTH 2007) and, in 2006, WIRTH & HEKLAU analysed and classified the zonation of the epilithic lichen vegetation on the coastal hills of the Central Namib. They produced the first extensive and reliable list of taxa containing 56 to 60 lichen species, an enormous diversity for a desert habitat. Recently, WIRTH et al. (2007) described lichen distribution and community structure along a coast-inland transect. These publications are milestones for lichen ecology in Namibia, for which we are grateful. We feel, therefore, that our present article on ecophysiological aspects of Namibian fog desert lichens, based on a study conducted in the same area, is well suited to be dedicated to Professor Volkmar WIRTH on occasion of his 65th birthday and retirement: in appreciation of his scientific oeuvre, in remembrance of our joint work in Würzburg more than 35 years ago, and with our sincere wishes that he will enjoy a very pleasant

retirement, remains in robust health and can maintain his interests and joie de vivre.

In earlier papers we reported about water relations and CO_2 exchange of lichens of the Namib fog desert with the main focus on ground and epiphytic species (LANGE et al. 1990, 1991, 1994, 2006, 2007). Here, based upon measurements during two seasons in the field, we describe the water relations, net photosynthesis, and carbon income of epilithic species belonging to three different growth forms: one fruticose, one foliose, and two crustose or subcrustose, in the lichen fields on the coastal gravel plain north of Swakopmund.

Site of Field Measurements and Experimental Species

The field measurements took place near Wlotzkasbaken, 40 km north of Swakopmund (Namibia) and about 1500 m east (inland) from the coast on a slightly undulating gravel plain dissected by sandy washes and interrupted by rock outcrops. The site is located near the stations S5 and S6 as described by WIRTH et al. (2007, see their Fig. 1) and has the highest lichen cover on their transect. Rainfall is extremely irregular with an average annual precipitation of ca. 13 mm (LOGAN 1960, NIEMAN et al. 1978). In contrast, nocturnal fog and dew fall are frequent along the coast (LORIS et al., 2004). For a detailed description of the site and its climate, see LANGE et al. (2006). The lichen vegetation of this area is extensively analysed by WIRTH et al. (2007).

Caloplaca elegantissima (NYL.) ZAHLBR. is a crustose (or more precisely subcrustose) species with a radial structure forming small, adnate, brightly orange, conspicuous thallus rosettes. It is frequent on pebbles and colonizes siliceous rock. According to WIRTH & HEKLAU (2006) it is a member of the most xeric group of lichens of the area.

Fruticose *Santessonia hereroensis* (VAIN.) FOLLM. colonizes rock outcrops and stones as loose cushions with its greyish 2 – 4 cm high, irregular tortuose, ramified branches. It is not very frequent in the gravel fields and seems to depend on high and regular fog and dew supply (zone 4 according to WIRTH & HEKLAU 2006).

Xanthoparmelia incomposita (ESSL.) O.BLANCO, A.CRESPO, ELIX, D.HAWKSW. et LUMBSCH (syn. *Neofuscelia incomposita* (ESSL.) ESSL., see BLANCO et al. 2004) is a small, nonlobulate, appressed and very tightly adnate subcrustose (here called crustose), dark brown, saxicolous species on pebbles (and rocks). Together with other closely related and difficult to distinguish *Xanthoparmelia* species, it occurs frequently throughout the gravel plain. In our earlier publication (LANGE et al. 1991) we named our experimental material *Neofuscelia namaensis* (STNR. & ZAHLBR.) ESSL. However, a revision of the brown *Parmelia* species by ESSLINGER (1977) described several new species and, later, more new South African species were established in the *Neofuscelia namaensis* (or *Neofuscelia dregeana*) group by

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ELIX (1999) and by ESSLINGER (2000). Although the original samples have been used for dry weight and chlorophyll determination others are available, collected at the same site and time. Prof. ELIX (Canberra) kindly determined this material. Out of 33 pebbles 88 % were colonized by *X. incomposita*, 9 % by *X. tentaculina* (ESSL.) O.BLANCO et al., and 3 % by *X. arreta* (ESSL.) O.BLANCO et al. Thus, it is very probable that samples measured were dominated by *X. incomposita* mixed with some pebbles with very closely related other species of the lichen group characteristic for the area, and possibly also including *X. namibiensis* (ELIX & T.H. NASH) BLANCO et al. (see WIRTH & HEKLAU 2006; WIRTH et al. 2007).

Xanthoparmelia walteri KNOX is one of the few foliose, lobate lichens of the area. It covers large areas of rock outcrops and is very frequent all over the gravel plain. This lichen establishes initially on pebbles from where the thalli expand onto adjacent sand and soil. In the transect of WIRTH et al. (2007) from ocean to inland *X. walteri* was present in nearly all quadrats.

The field measurements took place from September 10 to 25, 1990 in the south-hemisphere spring season. They are compared to studies conducted in autumn from April 17 to 24, 1988. The latter results have been partly published by LANGE et al. (1990, 1991) however, additional data from 1988 have been used in the present communication.

Measurement of Microclimate, Water Content, and CO_2 Exchange

The techniques applied for measuring of CO_2 exchange of the lichens and data handling are discussed in detail by LANGE et al. (1984, 1991, 2006, 2007). Diel courses of net photosynthesis (NP) and dark respiration (DR) together with climatic parameters were measured under natural conditions by means of "CO_2 porometers" (Walz Company, Effeltrich, Germany). Lichen samples were positioned in small wire-mesh baskets near their growth sites with moistening and illumination being as similar as possible to their original, natural habitat. *Santessonia hereroensis* and *X. walteri* could easily be removed from their substrate, the thalii of *C. elegantissima* and *X. incomposita* were exposed together with their substrate, small quartz pebbles (the thalli were removed after experimentation for dry weight determination). Each sample consisted of several individual thalli, or parts of different thalli, thus representing an average performance of the population. Therefore, albeit with the necessary reservations, we consider the results to be typical for performance of the respective species of the site.

For in situ CO_2 exchange measurements, samples were enclosed at chosen intervals in the porometer cuvette. Steady-state CO_2 exchange was reached within 1 to, at most, 2 min. The sample weight was recorded immediately after each CO_2 exchange measurement so that thallus water content could be determined (WC, % dry weight). Water contents were inevitably overestimated for the two crustose species because dew condensation also occurred on the stone

surface between the thalli. This error was greatest at high WC and rapidly disappeared during desiccation as the dew evaporated from the stones. The products of these measurements were time courses of thallus hydration, CO_2 exchange, and microclimate conditions (air temperature and incident photosynthetically active photon flux density, PPFD) for the lichens. On some days samples were sprayed experimentally with water (adhering droplets being removed by shaking of the samples) at midnight and once again a few hours later, simulating the heaviest possible nocturnal moistening.

In addition, continuous CO_2 exchange measurements were made in the field with a "click-cuvette system", which maintained a constant temperature. The enclosed lichen samples, which were exposed to natural illumination, were first hydrated to maximal water-holding capacity and CO_2 exchange then recorded as the samples dried.

Rates of CO_2 exchange were related to thallus dry weight (4 days drying at 75 °C), thallus total chlorophyll content (RONEN & GALUN 1984), and thallus carbon concentration (elemental analyser; CHNO-Rapid, Foss Heraeus, Hanau, Germany).

Results

Diel Courses of Water Content and Net Photosynthesis

All four experimental species showed very similar responses as compared with other species studied at the same time under the same environmental conditions (the terrestrial lichens *Teloschistes capensis*, *Ramalina* spec. and the epiphytic lichens *Heterodermia namaquana*, *Ramalina lacera*, *Xanthoria turbinata*: LANGE et al. 2006, 2007). Figure 1 depicts the diel performance of *X. walteri* on 15 consecutive days in spring. Each day the thalli dried out to a WC of about 6 to 9% (lowest single data point 5.1 %) and then increased their WC during the nights. On four of the nights, without dew or fog, WC only increased to 21 - 29% by water vapour uptake and this water had evaporated before sun rise. Therefore, no photosynthetic activity took place under such conditions. On September 13 a slight dew fall produced a WC of 51 %, stimulated some respiration, and allowed a low peak of NP at sunrise. Heavier nocturnal dew fall alone, or especially when in combination with fog, resulted in maximal nocturnal water contents, up to 93 %, which, after sunrise, produced higher maximal NP (NP_{max}) and longer periods of NP which ended when increasing temperatures and radiation caused desiccation. The average duration of positive NP lasted 3 h 11 min. On September 25 (a day with natural fog and dew) the lichen sample was additionally sprayed so that it reached a WC of ca. 200 %. In spite of this doubling of the water content, NP_{max} and the length of the photosynthetic period were only slightly increased compared to the day before with almost identical weather conditions.
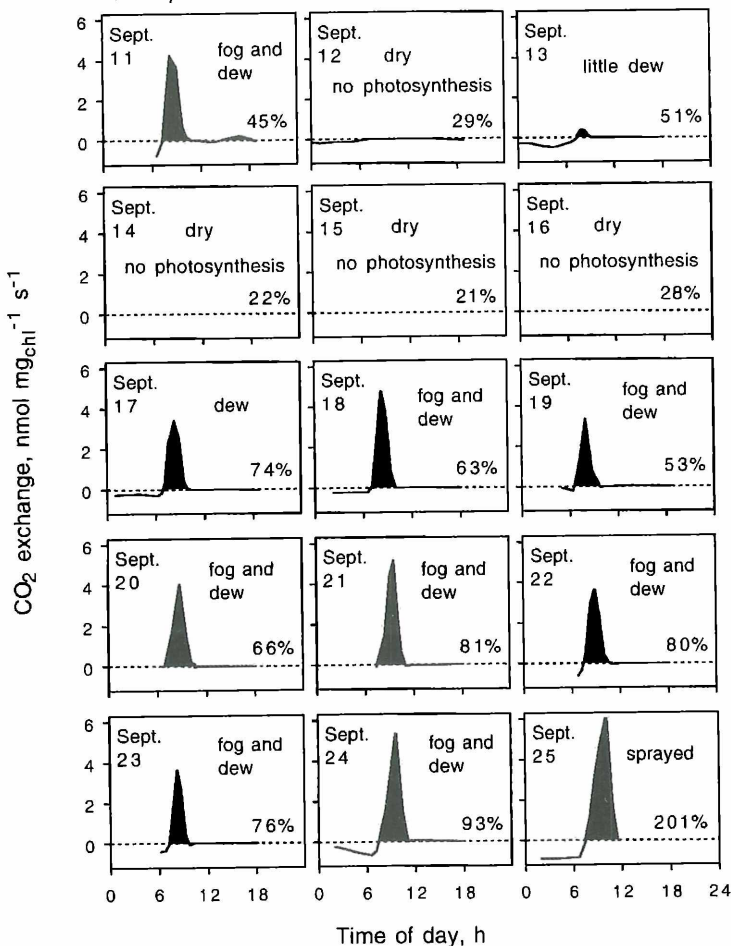
Xanthoparmelia walteri

Fig. 1: *Xanthoparmelia walteri*: diel time-courses of chlorophyll-related CO_2 exchange (CO_2 uptake positive) in spring. September 11 to 24: natural nocturnal moistening; September 25: additionally sprayed with water. For each day the maximal water content reached is indicated (% dry weight).

The two crustose experimental species, *C. elegantissima* and *X. incomposita*, showed similar diel performance. To produce Fig. 2 all data sets from the spring measurements with natural nocturnal wetting are pooled, a total of 12 diel courses for each of the species. The absolute rates of NP of the two species are almost identical, whether related to thallus dry weight or to thallus chlorophyll content.
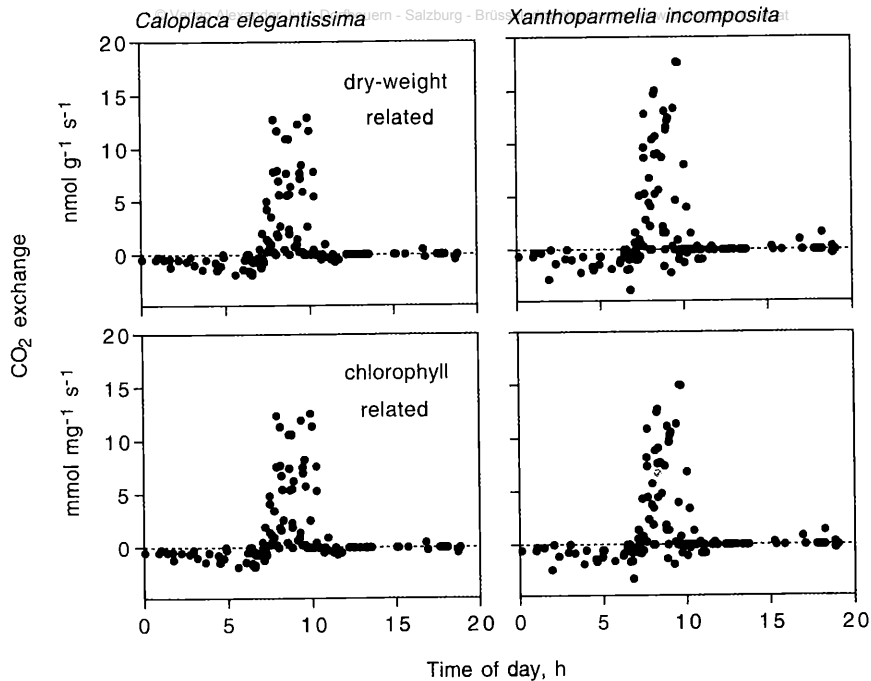
Fig. 2: *Caloplaca elegantissima* (left)· and *Xanthoparmelia incomposita* (right): Natural diel times courses of dry-weight related (upper row) and chlorophyll related CO_2 exchange (lower row). The data have been pooled from days with nocturnal fog and/or dew hydration during the spring measuring period (12 courses for each species).

Fog occurrence, both frequency and amount of related precipitation, shows a clear seasonal pattern for the Swakopmund region (LOGAN 1960; LANCASTER et al. 1984). Our measuring period in spring (September) was within the cooler summer half year with high fog frequency and dew precipitation in contrast to autumn (April, the warmer winter half year) when both factors are lower. This difference was clearly reflected by the lichen thallus water contents reached during the two seasons. For example, Fig. 3 shows pooled data sets for *S. hereroensis* from spring (11 diel courses) and autumn (9 diel courses) when both light conditions (C) and air temperatures (D) were very similar. There was a large difference in lichen water content (B) and maximal hydration at sun rise was almost twice as high in spring than in autumn. This resulted in substantial differences in NP_{max} (A) and, in addition, the period of metabolic activity was also longer in spring than in autumn so that, overall, the lichen was much more productive in September than in April (see below).
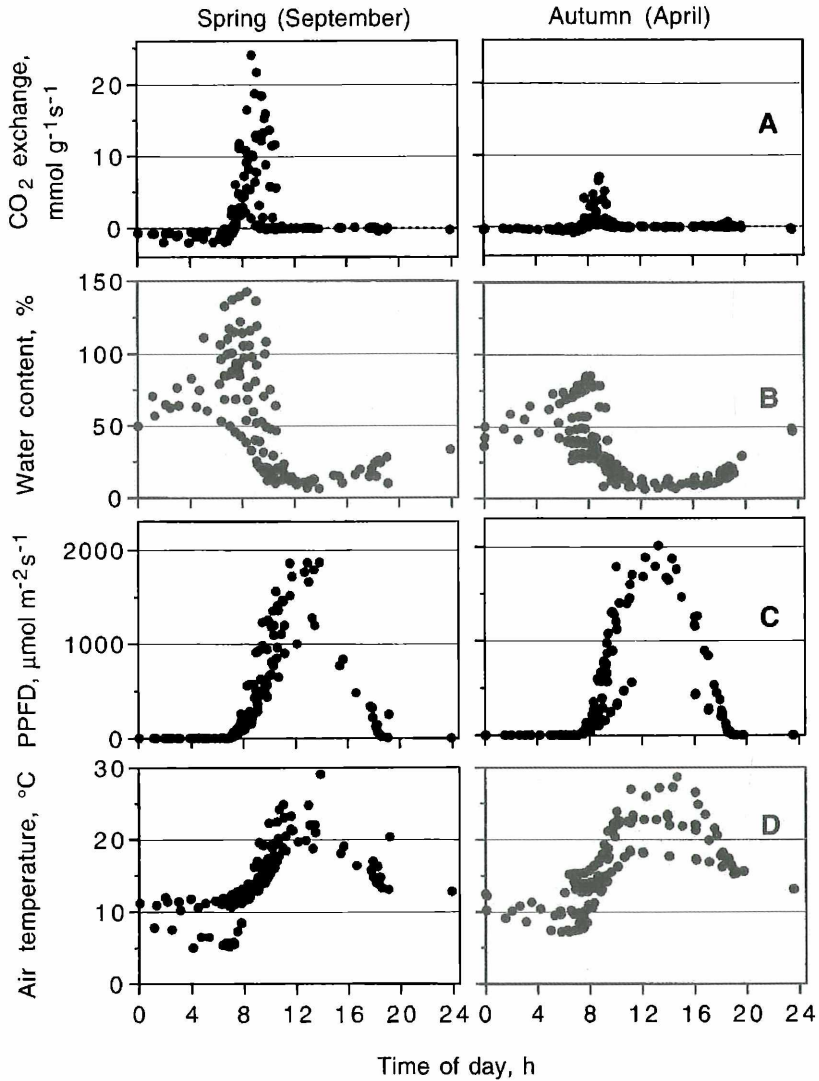
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Santessonia hereroensis

Fig. 3: *Santessonia hereroensis*: Natural diel time courses of **A**, dry-weight related CO_2 exchange; **B**, thallus water content; **C**, incident photosynthetically active photon flux density (PPFD); **D**, air temperature. The data have been pooled from days with nocturnal fog and/or dew hydration during the spring (left panel, 11 courses) and autumn measuring period (right panel, 9 courses).

Air Humidity Activation of *Santessonia hereroensis*

Without doubt, fog and dew were the main sources for moistening the experimental lichens. However, even on hot and dry days, air humidity usually increased in the afternoon as temperatures decreased and a moist breeze from the ocean reached inland. Under these conditions, hydration by vapour uptake alone without liquid water also contributed to photosynthetic carbon gain and several species had a brief period of CO_2 uptake at low NP in the late afternoon (e.g., Fig. 1, Sept. 11). *Santessonia hereroensis* showed this phenomenon most clearly, and one example is shown in Fig. 4. During the night there was a small
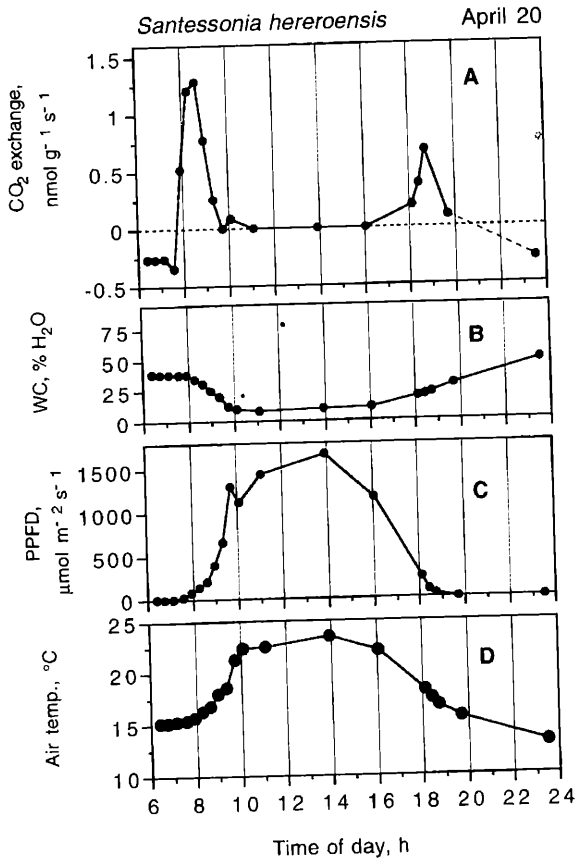

Fig. 4: *Santessonia hereroensis*: Natural diel time courses of **A**, dry-weight related CO_2 exchange; **B**, thallus water content; **C**, incident photosynthetically active photon flux density (PPFD); **D**, air temperature. A day with air humidity activation on the late afternoon.

amout of (visible) dew condensation and WC reached 39 %. This hydration pro-
duced a short period of net photosynthesis in the morning with its maximum at
8:30 h. Subsequently, water content decreased to 8 % at noon but then increased
again with decreasing temperatures and increasing humidity. At 18:00 h WC
was 19 % and, at a light intensity of 238 µmol m^{-2} s^{-1} PPFD and air temperature
of 18.2 °C, low rates of NP (maximal rate of 0.67 nmol g^{-1} s^{-1} at 40 µmol m^{-2} s^{-1}
PPFD) occurred until sunset ended CO_2 fixation. Even though the rates were
rather low, the result was a clear two-peaked diurnal photosynthesis curve with
a long midday period of desiccation between morning dew and late afternoon
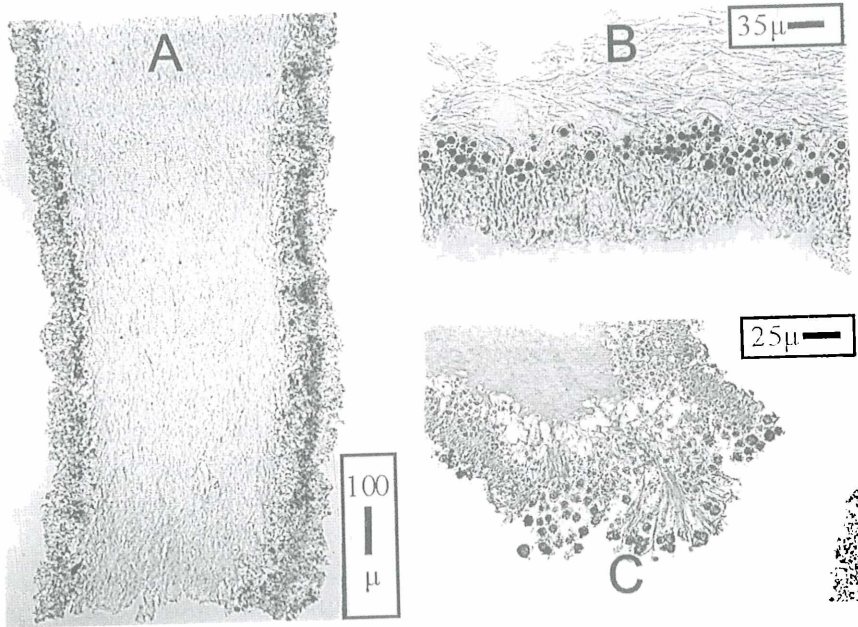humidity hydration.

Fig. 5: *Santessonia hereroensis*: **A**, longitudinal section of a main branch (compact
central axis, photobiont layer, cortex); **B**, cross section of the outer layers
of a main branch (loose, lacunose cortex); **C**, cross section of a soralium
(openly exposed soredias). Scales indicate magnification. From STARCK
(1992).

The anatomical thallus structure of *S. hereroensis*, especially its unusual
cortex, probably explains its performance. (The subsequent anatomical descrip-
tion follows SERUSIAUX & WESSELS 1984 and the synopsis of the genus by FOLL-
MANN 2006, it is based on the study by STARCK 1992). The primary branches of
the lichen are consistently radiate in structure with a diameter between 0.5 and
1 mm. The central medulla is a strong and compact cord consisting of lon-

gitudinal pachydermatous, conglutinate hyphae (Fig. 5, A). In contrast, the cortex of the thallus is strikingly loose: scarcely aggregated hyphae form an irregular net which enclose dead cells (mainly of the mycobiont) and result in a lacunose layer with a thickness up to 45 - 50 μm (B). Due to this lack of a compact cortex, the surface of the thallus appears rough and irregular. Most of the voids in the cortex remain filled with air even when the thallus is saturated with water. The photobiont layer is arranged inside this cortex. The algae (*Trebouxia* spec.) are often positioned in glomerules of several individual cells, loosely surrounded by reticulate hyphae interspersed with rather large hollows similar to the lacunose plectenchyma of the cortex. The upper parts, in particular, of the thallus branches are covered with soralia (C) which are initially more or less rounded, later becoming deformed and are often so abundant that they become confluent. The photobionts of *S. hereroensis* are in immediate contact with the external atmosphere through the loose cortex and the layer of soredia. This ensures not only fast hydration by fog and dew but also appears to promote rapid adjustment of the algal water potential to the external air humidity when the photobionts' water content, and activity, can increase before the bulk water content of the branches with their compact medulla becomes hydrated.
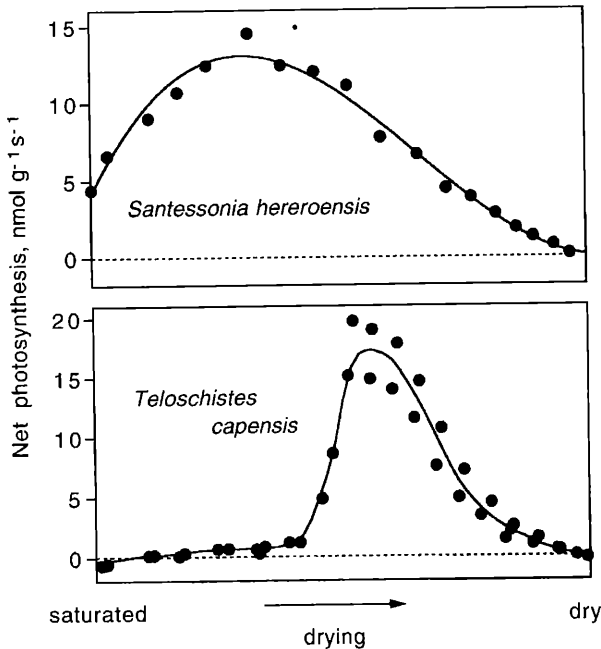

Fig. 6: *Santessonia hereroensis, Teloschistes capensis*: Time courses of dry-weight related net photosynthesis during drying under controlled conditions in the field (20°C, saturating light). The experiment began at maximal thallus water content following artificial wetting.

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The peculiarity of the loose cortex of *S. hereroensis* is confirmed by another response that differentiates it from most of the other studied Namibian lichens. It has been shown, for instance for *Teloschistes capensis*, that high water content can result in a strong suprasaturation depression of net photosynthesis (LANGE et al. 2006). In a drying-down experiment, initial NP of the fully saturated thallus was almost zero, and maximal NP was reached only after considerable water loss (Fig. 6, lower panel). *Santessonia hereroensis* behaved very differently. The fully water saturated thallus had substantial rates of CO_2 uptake (upper panel). Suprasaturation depression was less than 60 % and disappeared much more rapidly than that of *T. capensis* so that *S. hereroensis* reached maximal NP at a WC where NP of *T. capensis* was scarcely positive. The latter species has a continuous and thick thallus cortex compared to the loose cortex of *S. hereroensis*.

Maximal Rates of NP and Carbon Income

The 16 day period in spring contained 4 days that were completely dry with no metabolic activity by the lichens, 2 days that had only dew and 10 days that had fog together with dew. The 9 days in autumn were composed of 1 dry day, 3 days with only dew and 5 days with fog together with dew. Interpolation between consecutive data points of the daily courses of photosynthetic activity was used to calculate carbon income as an integral of diurnal photosynthetic CO_2 uptake (ΣNP, related to thallus carbon content, mg_C g_C^{-1} day^{-1}, i.e. ‰ of diurnal carbon increase of the lichen thallus). Typically, nocturnal moistening by fog in combination with dew condensation resulted in the highest hydration and the highest rates of NP and ΣNP. Dew moistening alone resulted in lower maximal nocturnal WC but substantial rates of NP still occurred (see Fig. 1). In Table 1 the three highest values of daily maximal NP_{max} and ΣNP are listed for the four experimental species with the results for NP_{max} all coming from the spring period. *Santessonia hereroensis* had the highest NP_{max} on a dry weight and thallus carbon content basis, whilst *C. elegantissima* had the highest NP_{max} on chlorophyll content basis (data for dry weight and chlorophyll basis not shown). *Xanthoparmelia walteri* had lowest NP_{max} of the four species although this species is one of the most frequent in parts of the gravel fields. The same sequence of species occurred for maxima of daily carbon income. On its most productive day, *S. hereroensis* had a ΣNP of 3.65 mg_C g_C^{-1} day^{-1} (3.65 ‰ of its thallus carbon content). The carbon income of the two crustose species (2.82 and 2.15 ‰) were also substantial. The productivity values are much lower when daily carbon income is averaged over all days with photosynthetic activity. The difference between the seasons is very obvious; when averaged over all species, ΣNP of a photosynthetically active day in autumn was less than 40 % of one in spring (Table 1). Although the four experimental species showed differences in their performance the range in dry-weight or carbon related maxima were small and

averages of the photosynthetic parameters differed by not more than a factor of ca. 2.

	The three highest values of daily net photo-synthesis, horizontally exposed nmol CO_2 g_{DW}^{-1} s^{-1}	The three highest values of daily carbon income, (ΣNP) mgc g_C^{-1} day^{-1}, [‰]	Average of daily carbon income, (ΣNP) ± standard deviation n = number of diel courses mgc g_C^{-1} day^{-1}, [‰]	
			Spring	Autumn
Santessonia hereroensis	24.08 18.75 16.48	3.65 3.32 2.44	2.21 ± 0.98 (n = 11)	0.40 ± 0.24 (n = 10)
Xanthoparmelia incomposita	17.67 17.61 15.00	2.82 2.81 2.46	1.94 ± 0.57 (n = 10)	0.83 ± 0.12 (n = 3)
Caloplaca elegantissima	16.21 12.95 12.31	2.15 2.01 1.78	1.54 ± 0.38 (n = 10)	0.96 ± 0.45 (n = 5)
Xanthoparmelia walteri	11.90 9.67 9.30	1.64 1.39 1.33	1.24 ± 0.44 (n = 10)	0.43 ± 0.23 (n = 9)

Table 1: The three highest values of daily, dry-weight related net photosynthesis and of daily carbon income (ΣNP, related to thallus carbon content); and the average ΣNP for all diel courses under natural conditions with noc-turnal moistening in spring and autumn for the four experimental species.

On several days, nocturnal moistening was experimentally maximized by additional spraying. When these days were compared with the most productive days of natural moistening only in one case (*X. walteri*) was there a higher NP_{max}, and ΣNP increase of about 30 % (Fig. 1, September 25). For all the other species (data not given in detail), maximal artificial moistening resulted in no change in NP_{max} and productivity, in fact there were signs of a slight decrease (possibly due to suprasaturation depression of NP).

Discussion

The four epilithic species in this study, as did the other lichen types present in the same area (LANGE et al. 2006, 2007), responded similarly to the special conditions of their unusual habitat in the coastal fog zone of the Namib Desert. Typically, they absorb moisture during the night, and this hydration allows a short period of photosynthetic activity after sunrise until they become desiccated. The length of the active period, ΣNP and NP_{max} depended on the maximal amount of nocturnal moistening. This response pattern is characteristic for many other arid and semiarid habitats (KAPPEN 1988). As was also the case with other species at the site (LANGE et al. 2007), adding extra water during the night to produce maximal possible WC in most cases did not result in substantial higher NP_{max} or ΣNP. It appears that the lichens show optimal performance under their natural hydration regime at the measurement site, the area of highest species diversity and lichen cover of the gravel plains (WIRTH et al. 2007).

In addition to the morning peak of photosynthetic activity, several of the Namib lichens occasionally showed a short and low second phase of photosynthetic activity in the late afternoon because of WC equilibration with increasing humidity. This feature was especially common with *S. hereroensis*. SERUSIAUX & WESSELS (1984) drew attention to the special and unusual cortex structure of this genus that "enlarges considerably the surface contact between the lichen and the atmosphere and ensuring a rapid and lasting hydration during the periods of fog" It appears that the cortex structure is one of the characteristics that makes this genus especially suited for these habitats. According to FOLLMANN (2006) the six species of this genus are disjunct endemics of the Atlantic-Namibian and Pacific-Andean fog deserts. The emphasis must be on 'fog', because, although some lichens rely almost exclusively on hydration through water vapour uptake alone (e.g., PINTADO & SANCHO 2002), this type of hydration seems to be of minor importance for the carbon economy of the Namib lichens. This seems to be true even for *S. hereroensis* because NP attained following afternoon humidity activation were rather low. However, there may be habitats or weather situations, when the special capability of this species would be of higher ecological relevance.

In addition to anatomical structure, lichen growth form and morphology also influence water balance and thus photosynthetic productivity. In Table 2 average periods of photosynthetic activity after nocturnal hydration (time span between light compensation point after sun rise and moisture compensation point during desiccation) are listed for the ten diel courses in spring, when all four experimental species were monitored under the same weather conditions. When all lichens were compared there were significant differences in the length of active period between the four species. The crustose *X. incomposita* had the shortest active period which was significantly less than the lobate *X. walteri*, and especially (41 min less) than the fruticose *S. hereroensis*. The advantage of the

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fruticose growth form for hydration by fog and dew seems to be of general importance for lichen productivity; the three species with highest carbon-related average daily ΣNP of all of our measurements (see LANGE et al. 2006, 2007) are the fruticose *Ramalina* spec. and *Teloschistes capensis* (2.72 or 2.41 mg_C g_C^{-1} day^{-1}, respectively) and the caespitose-subfruticose *Heterodermia namaquana* (2.41 mg_C g_C^{-1} day^{-1}) with little difference from *S. hereroensis* (2.21 mg_C g_C^{-1} day^{-1}). *Santessonia hereroensis* also has NP_{max} that are around twice as high as *X. walteri*.

	Santessonia hereroensis	Xanthoparmelia walteri	Caloplaca elegantissima	Xanthoparmelia incomposita
Daily period of photosynthetic activity	3 h 21 min ± 37 min	3 h 11 min ± 37 min	2 h 59 min ± 36 min	2 h 39 min ± 41 min
(Statistical difference)	(a)	(a b)	(b c)	(c)

Table 2: Average daily duration of positive net photosynthesis after natural nocturnal moistening in spring (ten diel courses). Species that do not share the same letter have periods that are significantly different at $P < 0.05$.

According to the analysis of WIRTH & HEKLAU (2006) and WIRTH et al. (2007) our four experimental species are different types in terms of both distribution along the ocean-inland transect and drought resistance. Unfortunately, our results for photosynthetic performance were measured at one single site on the transect, apparently the most favourable one, and cannot contribute to a functional explanation of the differences in distribution found by WIRTH & HEKLAU (2006) and WIRTH et al. (2007). Carbon acquisition is a fundamental requirement for the existence and growth of any lichens, but their distribution and competitive ability is a very complex issue and depends on their interaction with the specific habitat conditions. As a next step in the ecophysiological analysis of the lichen distribution in the Namib fog desert, their water relations and photosynthetic performance need to be studied at different positions on the transect in order to discover the limiting factors for the different species.

Acknowledgements

with Dres. U. HEBER, I. ULLMANN, and D.C.J. WESSELS during different phases of the field work. TGAG held a Ramon y Cajal award during the preparation of this paper.

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