

THE ROLE OF MICROCLIMATE FOR THE LICHEN VEGETATION PATTERN ON ROCK SURFACES IN THE SUBARCTIC

Differenzierung ausgewählter subarktischer epilithischer Flechtengemeinschaften nach ihren mikroklimatischen Bedingungen

by

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Schlagwörter: Saxicole Flechten, Mikroklima, Gemeinschaftsanalyse, Wasserversorgung, Schweden, Subarktis.

Summary: The aim of this study was to investigate whether microclimatic conditions influence the distribution pattern of epilithic lichens. For this purpose saxicolous - mainly crustose - lichen communities found on boulders of garnet-mica-schist in the valley Kärkevagge (near Abisko, northern Sweden) were described and their microclimatic conditions during the summer period 1993 analyzed.

From June to August light, temperature and relative humidity of 4 plots were measured on 2 boulders. A reference set of sensors was installed between the boulders. Diurnal courses and the proportions between „wet“ and „dry“ periods were compared for the different plots. The lichen communities of the plots were recorded by percentage cover of the species.

No correlation was found between the microclimatic conditions during the summer and the distribution pattern of the crustose lichen communities on the boulders. This was also supported by observations of the wetting pattern on the rock surfaces during rainfalls. It showed no

relation to any community during the summer, but according to preliminary findings it appears to be correlated well to the investigated communities in autumn, when rainfalls with NW winds prevailed. These observations and the results of the measurements suggest that the summer conditions are not decisive for the community pattern on the rocks.

Zusammenfassung: In dem Tal Kärkevage (in der Nähe von Abisko, Nordschweden) wurde untersucht, ob mikroklimatische Faktoren die Ausprägung epilithischer Flechtengemeinschaften maßgeblich beeinflussen. Hierzu wurde die Zusammensetzung von überwiegend aus Krustenflechten bestehenden Gemeinschaften auf Granatglimmerschieferblöcken untersucht und ihre mikroklimatischen Bedingungen während des Sommers 1993 analysiert.

Durch Aufnahmen, die die Arten und deren prozentuale Deckung erfaßten, wurden auf zwei Blöcken vier Gemeinschaften charakterisiert. Einstrahlung, Temperatur und relative Luftfeuchte der Standorte der untersuchten Gemeinschaften und einer Referenzmeßstelle zwischen den Blöcken wurden kontinuierlich von Juni bis August 1993 aufgezeichnet. Typische Tagesgänge und die Befeuchtungsdauer der Flechten wurden für die vier Standorte verglichen und in Beziehung zu den Gemeinschaften gesetzt.

Es konnte kein Zusammenhang zwischen den untersuchten Kryptogamengemeinschaften und ihrem jeweiligen Mikroklima während des untersuchten Sommers gefunden werden. Dieses Ergebnis wurde durch Feldbeobachtungen der Befeuchtungsverhältnisse bei unterschiedlichen Regenereignissen bestätigt. Im Sommer ergab sich zwischen der Verteilung des Wasser auf den Felsflächen und den darauf wachsenden Gemeinschaften kein Hinweis auf eine ursächliche Beziehung, wohingegen erste Beobachtungen im Herbst bei Regenfällen mit NW Wind auf eine Korrelation zwischen Befeuchtung und Gemeinschaftstyp hinweisen. Die Meßergebnisse und Beobachtungen legen nahe, daß das sommerliche Mikroklima die Ausprägung der untersuchten saxicolen Flechtengemeinschaften nicht entscheidend beeinflußt.

Introduction

Lichens are known to be able to thrive splendidly in - at least seen from an anthropocentric point of view (HAUSMANN & KREMER 1993) - „extreme“ habitats and ecosystems (KAPPEN 1973). Among them epilithic lichens are recognized as inhabiting especially poor and inhospitable environments. Despite high, quickly changing and unpredictable fluctuations of temperature and light conditions (e.g. COXSON & KERSHAW 1983a), long desiccation periods (ROUX 1980) and often low nutrient supplies (WIRTH 1972), lichens are able to colonize and flourish on rock surfaces.

At present the environmental (i.e. abiotic and biotic) factors which are determining the distribution of epilithic lichen species and thus are shaping the colourful community patterns are still poorly understood. Among these the microclimatic conditions belong to the better studied factors. They are either studied in detail for single species, mostly to explain field- and laboratory-measurements of metabolic responses, e.g. photosynthetic activity, chloro-

phyl fluorescence or nitrogenase activity (e.g. KAPPEN et al. 1991; LANGE et al. 1991; SCHROETER et al. 1992; FRITZ-SHERIDAN & COXSON 1988), or they are estimated from exposure and inclination of the substratum and related to distribution and abundance of the lichens (e.g. ORWIN 1972; ARMSTRONG 1974; LARSON 1980; FAHSELT 1988; JOHN & DALE 1990). Within these investigations microclimatic measurements have been performed punctuated at most. More intense recordings of the microclimatic conditions within whole communities on rock surfaces were carried out by ROUX (1980) and KAPPEN (1985a,b).

Ecophysiological investigations of lichens mostly concentrate on foliose and fruticose lichen species and communities dominated by them. Crustose lichens got less attention because of taxonomic problems, their intricate connection to the substratum, their low productivity and their species richness (but compare e.g. COXSON & KERSHAW 1983a,b; KAPPEN et al. 1990).

This paper presents data on the microclimatic conditions of selected local saxicolous lichen communities dominated by crustose species in the Subarctic. The aim of this study was to measure light, temperature and relative humidity within the communities in summer and to examine the influences and importance of these factors on the distribution pattern of the lichen species on the different rock faces.

Site Description and Methods

The study was carried out in the valley Kärkevagge (68° 26' N, 18° 8' E; 600-800 m above sea level), which runs from NNW to SSE and is situated in the Torneträsk area near the Scientific Research Station of Abisko in northern Sweden (Fig. 1). Kärkevagge is a typical U-shaped glacial valley and characterized by the great amount of large boulders and the extended boulder fields on the valley floor. It is enclosed by steep, still active rock cliffs at the S- E- and W-side. For morphology and history of the valley compare RAPP (1960, 1992).

The geology of the Torneträsk area is coined by the Scandes, the Scandinavian part of the Caledonian mountain chain. In Kärkevagge the rock walls are mostly consisting of garnet-mica-schist layers, with bands of marble, quartzite and other schists. Most of the rocks are iron-rich (ERICKSON & PETERSSON 1973).

The macroclimate of the Torneträsk area is marked by a steep climatic gradient from oceanic in the West to continental in the East (SONESSON & LUNDBERG 1974). Kärkevagge is situated some kilometers East of the main mountain divide of the Scandes and therefore experiences a more oceanic climate. Until 1993 the mesoclimate of the valley has been discontinuously recorded, so that figures of temperature and precipitation are available just for single years. In 1993 the annual average of temperature was -1.2° C. Monthly averages of temperature were above 0° C within the period from May to

September and ranged from 10.2° C in July to -10.3° C in December. Temperature changes within a month were most pronounced during winter. In 1993 the temperature amplitude during January (20.3 K) was as large as the annual range of the monthly averages. Thus, daily averages above zero occurred throughout the winter and, as a consequence, freeze-thaw-cycle situations were frequent. In addition RAPP (1960) reports that freeze-thaw cycles can be observed during the whole year, being most frequent in spring and autumn.

In 1980 the annual precipitation was 1140 mm (STRÖMQUIST & REHN 1980). This is higher than the long-term average at the climate station of Riksgränsen at the mountain divide (1931-1960: 939 mm; KARLÉN 1973). According to STRÖMQUIST & REHN (1980) the precipitation has a maximum in September/October. They also describe that in general the snow cover stays from the beginning of October to the beginning of June in Kärkevagge. Its depth varied in 1993 from over 5 meters to snow-free patches, because of the very irregular ground level (personal observation).

The investigated boulders (Fig. 1) are located on the W-slope of a small ridge, which runs along the valley. They consist of garnet-mica-schist and are situated in a lichen-rich heath vegetation.

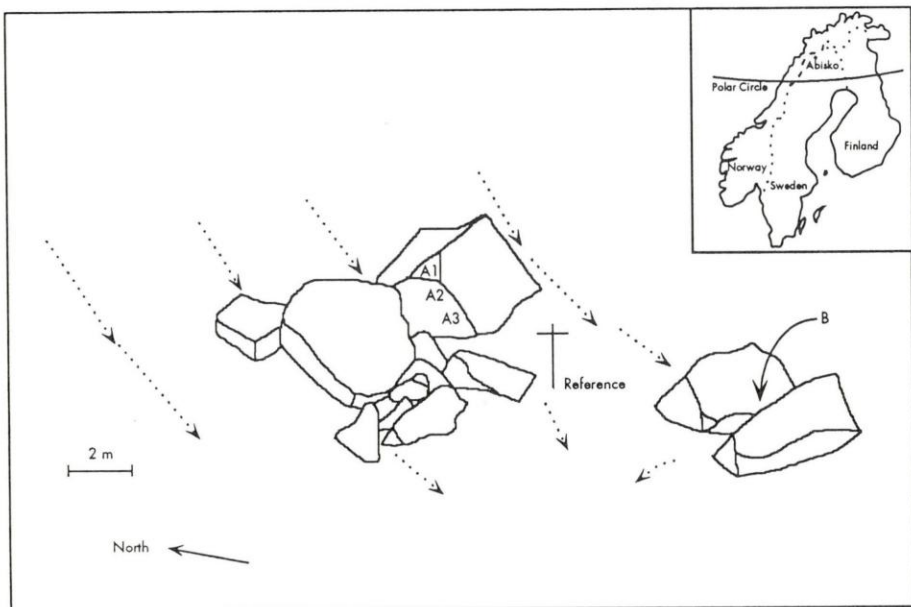


Fig. 1: Location of Abisko near the valley Kärkevagge in northern Sweden (inlay). View of the investigated garnet-mica-schist boulders situated on the West facing slope (dotted arrows) of a small ridge running along the valley. The position of the plots on the boulders is shown.

Measurements were taken at 4 plots on 2 boulders (A and B). The three plots on boulder A (2.5 x 3 x 2.5 m) are facing W 15° N, with one open-exposed plot (A1; 80° inclination), a plot (A2; 130°) on the upper part and one on the lower part (A3; 130°) of an overhang. On a nearby boulder (3 x 1.5 x 2.5 m) another plot (B; 45°) facing N 15° E was examined. For reference a set of sensors was installed on a 2 m high post standing between the boulders.

From June to August the microclimatic conditions were recorded every 5 minutes and stored by dataloggers (Squirrel; Grant, Cambridge UK). Light (photosynthetic photon flux density PPF_D; $\mu\text{mol m}^{-2} \text{s}^{-1}$) was measured by LiCor-sensors (Li190SB; Lincoln, Nebraska USA) and self-made equivalents (gallium-arsenit sensors), temperature (° C) by mini-thermistors (Grant, Cambridge UK) and self-made copper-constantan thermocouples. Relative humidity (%) was recorded by capacity sensors (Vaisala, SF).

At plots A1, A2 and B two temperature sensors were installed at a time. One was placed on top of a *Rhizocarpon inarense*-thallus (yellowish-greenish) and one on top of *Orphniospora moriopsis* (A1, B) respectively *Miriquidica leucophaea* (A2), both dark brown to brownish-gray in colour. Despite the contrasting colour of the thalli the measurements gave no difference and were averaged for the purposes of this paper. In plot A3 the temperature sensor was placed on top of *Pleopsidium chlorophanum*. The sensors could not be inserted into the lichen thalli directly, because of the low thickness of the thalli, so they were pressed to their surface. To avoid radiation effects the temperature sensors were covered by a paste of grinded lichen thalli of the corresponding species which was fixed by covering with a thin and loosely woven fabric tape.

The microclimatic data was analyzed by a comparison of the diurnal courses and the proportions of wet (> 95% rel. humidity) to „dry“ (< 95% rel. humidity) periods of the different plots. The microclimatic results finally were related to the community types on the rocks.

The lichen communities of the plots were described by species composition and percentage cover of the species. The relevée sizes ranged from 0.15 m² (A1 and A3), 0.16 m² (A2) to 0.5 m² (B). Specimens of all species were collected and identified in Kiel. The taxonomic classification followed SANTESSON (1993) with the exception that *Rhizocarpon frigidum* was not discerned from *R. geographicum*.

Results and discussion

Community analysis:

58 species of cryptogams were identified within the four plots (Fig. 2). Lichens were represented by 52 species, mosses by 4 species and 2 species belonged to free-living, unicellular algae. Among the lichens 41 species had a crustose thallus, 4 belonged to the umbilicarioid morphotype, 2 species were foliose and 3 fruticose.

Fig. 2: Species list and percentage cover [%] of the species within the plots. Bold figures represent dominant species; "+" := present, but cover not estimated.

Species	Plot			
	A 1	A2	A3	B
<i>Miriquidica lulensis</i> (HELLB.) HERTEL & RAMBOLD	1	< 1	< 1	5
<i>Rhizocarpon inarense</i> (VAIN.) VAIN.	37	25		12
<i>Orphniospora moriopsis</i> (A. MASSAL.) D. HAWKSW.	20	17		3
<i>Rimularia impavida</i> (TH. FR.) HERTEL & RAMBOLD	1	1		15
<i>Rhizocarpon jemtlandicum</i> (MALME) MALME	6	+		< 1
<i>Allantoparmelia alpicola</i> (TH. FR.) ESSL.	2	1		3
<i>Miriquidica nigroleprosa</i> (VAIN.) HERTEL & RAMBOLD	1	2		+
cf. <i>Porpidia tuberculosa</i> (SM. in SM. & SOWERBY) HERTEL & KNOPH in HERTEL	< 1	< 1		< 1
<i>Ophioparma ventosa</i> (L.) NORMAN var. <i>ventosa</i>	3			
<i>Arctoparmelia incurva</i> (PERS.) HALE	< 1			
<i>Miriquidica griseoatra</i> (FIOT.) HERTEL & RAMBOLD	< 1			
<i>Schaereria endocyanea</i> (STIRT.) HERTEL & GOTTH. SCHNEID. in GOTTH. SCHNEID.	< 1			
<i>Tephromela aglaea</i> (SOMMERF.) HERTEL & RAMBOLD	< 1			
<i>Tephromela armeniaca</i> (DC. in LAMB. & DC.) HERTEL & RAMBOLD	10	1		
<i>Tephromela testaceoatra</i> (VAIN.) HERTEL & RAMBOLD	3	< 1		
<i>Umbilicaria rigida</i> (DU RIETZ) FREY	1	< 1		
<i>Rhizocarpon copelandii</i> (KORB.) TH. FR.	< 1	+		
<i>Rhizocarpon carpaticum</i> RUNEMARK		1		
<i>Caloplaca magni-filii</i> POELT		< 1		
<i>Lecanora polytropa</i> (EHRH. ex HOFFM.) RABENH.		< 1		
<i>Lecidea</i> sp. 1		< 1		
<i>Umbilicaria cylindrica</i> (L.) DELISE ex DUBY		< 1		
<i>Miriquidica leucophaea</i> (FLÖRKE ex RABENH.) HERTEL & RAMBOLD		+		
<i>Sporastatia testudinea</i> (ACH.) A. MASSAL.	< 1	10	< 1	
<i>Umbilicaria torrefacta</i> (LIGHTF.) SCHRAD.	< 1	< 1	< 1	
<i>Acarospora smaragdula</i> (WAHLENB. in ACH.) A. MASSAL.		1	< 1	
<i>Pleopsidium chlorophanum</i> (WAHLENB. in ACH.) ZOPF			3	
cf. <i>Rhizocarpon copelandii</i> (KÖRB.) TH. FR.			< 1	
<i>Rhizoplaca subdiscrepans</i> (NYL.) R. SANT. (1984)			< 1	
<i>Sporastatia polyspora</i> (NYL.) GRUMMANN			< 1	
<i>Rhizocarpon geographicum</i> (L.) DC.	6			9
<i>Lecidea praenubila</i> NYL.	1			3

<i>Lecanora latro</i> POELT	< 1			1
<i>Umbilicaria proboscidea</i> (L.) SCHRAD.	< 1			1
cf. <i>Chroococcus</i>	< 1			+
<i>Lecidea</i> sp. 2		< 1		< 1
<i>Porpidia melinodes</i> (KÖRB.) GOWAN & AHTI				10
<i>Lecidea confluens</i> (WEBER) ACH.				4
<i>Rhizocarpon eupetraeoides</i> (NYL.) BLOMB. & FORSELL				3
<i>Amygdalaria panaeola</i> (ACH.) HERTEL & BRODO in BRODO & HERTEL				2
<i>Ochrolechia androgyna</i> (HOFFM.) ARNOLD				2
<i>Rhizocarpon expallesces</i> TH. FR.				1
<i>Andreaea rupestris</i> L. ex HEDW.				< 1
cf. <i>Cephalociella dentata</i> (RADDI) MIGULA				< 1
<i>Cetraria hepatizon</i> (ACH.) VAIN.				< 1
<i>Cladonia</i> sp.				< 1
<i>Gymnomitrium coralloides</i> NEES				< 1
<i>Lecanora intricata</i> (ACH.) ACH.				< 1
<i>Lecidella subcongrua</i> ("VAIN.")				< 1
<i>Lepraria neglecta</i> (NYL.) LETTAU				< 1
<i>Ochrolechia</i> cf. <i>frigida</i> (SW.) LYNGE				< 1
<i>Protoparmelia badia</i> (HOFFM.) HAFELLNER				< 1
<i>Protoparmelia leproloma</i> (R. SANT. in MOBERG) RAMBOLD & POELT in POELT & LEUCKERT				< 1
<i>Pseudephebe pubescens</i> (L.) M. CHOISY				< 1
<i>Racomitrium lanuginosum</i> (HEDW. ex HEDW.) BRID.				< 1
<i>Stereocaulon vesuvianum</i> PERS.				< 1
<i>Umbilicaria</i> cf. <i>hyperborea</i> (ACH.) HOFFM.				< 1
cf. <i>Scytonema</i>				+
Species Number per Plot	24	22	8	36
Total Cover	96 %	65 %	4 %	75 %

On an average 23 cryptogam species grew in every plot, but the differences in species richness and cover between the plots were great. Plot A3 had a very low species richness with just 8 species and a very sparse lichen cover (4%), while A1 had the highest cover (96%) of all plots and an intermediate species richness (24 species). The highest species number was found in plot B (36 species), which had an intermediate cover of 75%. Plot A2 was intermediate with respect to species richness (22 species) and cover (65%).

No extended phytosociological description of the epilithic lichen communities of northern Sweden exists. For example KLEMENT (1959) excluded the predominantly crustose communities from his study. Also the here investiga-

ted communities do not fit well into the descriptions of WIRTH (1973) and CREVELD (1981). Therefore we will describe the communities of the plots simply according to the variation of their species composition and canopy structure.

The communities of plots A1 and A2 were dominated by the yellowish-greenish *Rhizocarpon inarense* and the darkbrown *Orphniospora moriopsis*. They can be discerned by the high covers of *Tephromela armeniaca* in A1 and *Sporastatia testudinea* in A2. Plot B was characterized by a relatively high cover of foliose and fruticose lichens (e.g. *Ochrolechia* spp., *Umbilicaria* spp., *Cetraria hepaticum*). The highest covers in this plot revealed the crustose lichens *Rimularia impavida* (darkbrown), *Rhizocarpon inarense* and the bright orange coloured *Porpidia melinodes*. *Pleopsidium chlorophanum* was the dominant species in A3, which characterized the plot by its bright yellow colour.

Microclimatic conditions:

The microclimatic conditions of the plots on a sunny summer day are shown in Fig. 3, whereas Fig. 4 illustrates the conditions of a rainy day. Besides the subapical plots (A 1 and B) and the plots on the overhang (A2 and A3) the reference is shown.

During the dry and fine weather conditions of July 13th, 1993 the microclimatic situation was very contrasting between the plots. The westerly facing plot A1 was sunlit during the whole day, incident irradiance and temperature were maximal around noon; accordingly rel. humidity was minimal during this time. Plot B was also open-exposed, but facing towards North. It was sunlit only during the morning- (the sharp rise of the PPFD correlates to the ascend of the sun over the neighbouring mountain tops) and evening-hours; during these periods the temperatures were highest too. The only time period the plots on the overhang were insolated was from 3 p.m. to 10 p.m., with phases of shade in between originating from adjacent boulders. The temperature curves show similar, less expressed maxima, while the relatively short time of insolation on A2 and A3 had no big effect on the relative humidity above the surface. Maximum irradiance of A1 was three times higher than on A2, A3 and B, which also is mirrored by the temperatures. The boulder surfaces were warmer than the surrounding air during the whole day and even during nighttime. In the early morning hours the temperatures could approach ambient temperature, if the energy balance of the preceding day(s) was low.

However, such weather pattern have no relevance for the productivity of the lichens, because of their dry and inactive status. KAPPEN et al. (1980) demonstrated that even during hot and sunlit periods lichens can be activated in shade by dewfall in the morning hours, but such dewfall events could not be observed during this study.

The diurnal course of a rainy and moist day (August 1st, 1993) shown in

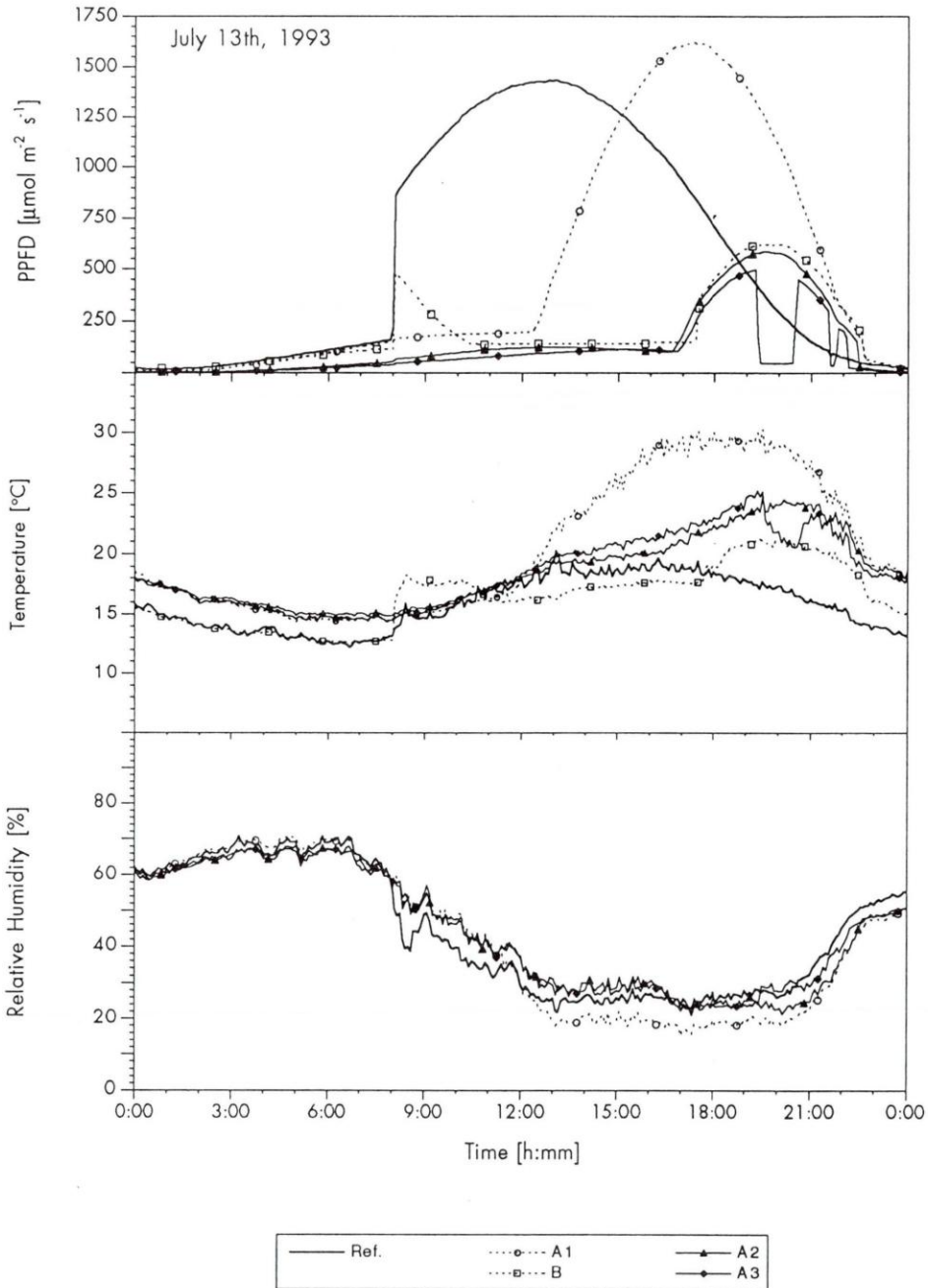


Fig.3: Diurnal courses of the microclimatic conditions during a sunny and dry day (July 13th, 1993). A1 and B: subapical plots; A2 and A3: plots on the overhang.

Fig. 4 is an example out of 20 moist and rainy days. The day was overcast throughout the whole time, with irradiance levels ranging from 100 to 500 $\mu\text{mol m}^{-2} \text{s}^{-1}$, measured at the subapical faces and the reference. The light intensities for A2 and A3 were below 50 $\mu\text{mol m}^{-2} \text{s}^{-1}$ during the whole day. The fluctuations of the irradiance level did not significantly influence temperatures and relative humidities of the plots. The temperatures were only slightly different for all plots, irrespective of whether the communities were moistened by liquid water or not. Thus the different community structures of the plots can not be explained by prevailing specific temperature regimes (cp. KERSHAW 1983, KAPPEN 1985) during these rainy days.

An evaluation of all measured microclimatic diurnal courses shows the proportions between the durations of the „dry“ (< 95 % rel. humidity) and „wet“ (> 95 % rel. humidity) situations of the plots during the summer period (Fig. 5). These are compared with the species composition of the plots.

A1 and A2 were very similar with regard to community structure, both were dominated by *Rhizocarpon inarense* and *Orphniospora moriopsis*, but the duration of their potentially active periods (PAP) varied by 500 %. In contrast, the two plots in the overhang situation (A2 and A3) differed totally with community structure despite their equally short potentially active periods. Similarly, the subapical plots (A1 and B) had different communities, but experienced both long-lasting periods of potential activity.

Likewise there was no relationship if the proportion between „light“ (>10 $\mu\text{mol m}^{-2} \text{s}^{-1}$) and „dark“ (< 10 $\mu\text{mol m}^{-2} \text{s}^{-1}$) phases during the wet periods are compared. The plots in overhang-position had the lowest percentage of light and wet periods (A2 : 42 %; A3 : 38 %), while 50 % respectively 71 % of the wet periods of plots A1 and B supplied enough irradiant energy for the cryptogams.

These results show, that during the investigated summer period no correlation between the measured microclimatic conditions and the distribution pattern of the crustose lichen communities on the boulders could be found. This result is also supported by observations of the wetting pattern during rainfalls. During the summer most of the rain showers were associated with south-easterly winds. The wetting pattern on the rock surfaces due to this kind of rainfalls was not correlated to certain lichen communities. However, a relationship was detected in the middle of August when NW-winds started to prevail. The rain then produced a moisture pattern, which fitted very well to the distribution of the *Rhizocarpon inarense* and *Orphniospora moriopsis*- and the *Pleopsidium chlorophanum*-dominated communities on the rock faces.

As a preliminary example for the evolution of the wetting pattern the situation in the plots on boulder A during such a rainfall event can be described as follows: The rain-exposed plot A1 got wet at every NW-rain event. If the rainfall was long and intense enough the water started running down from A1

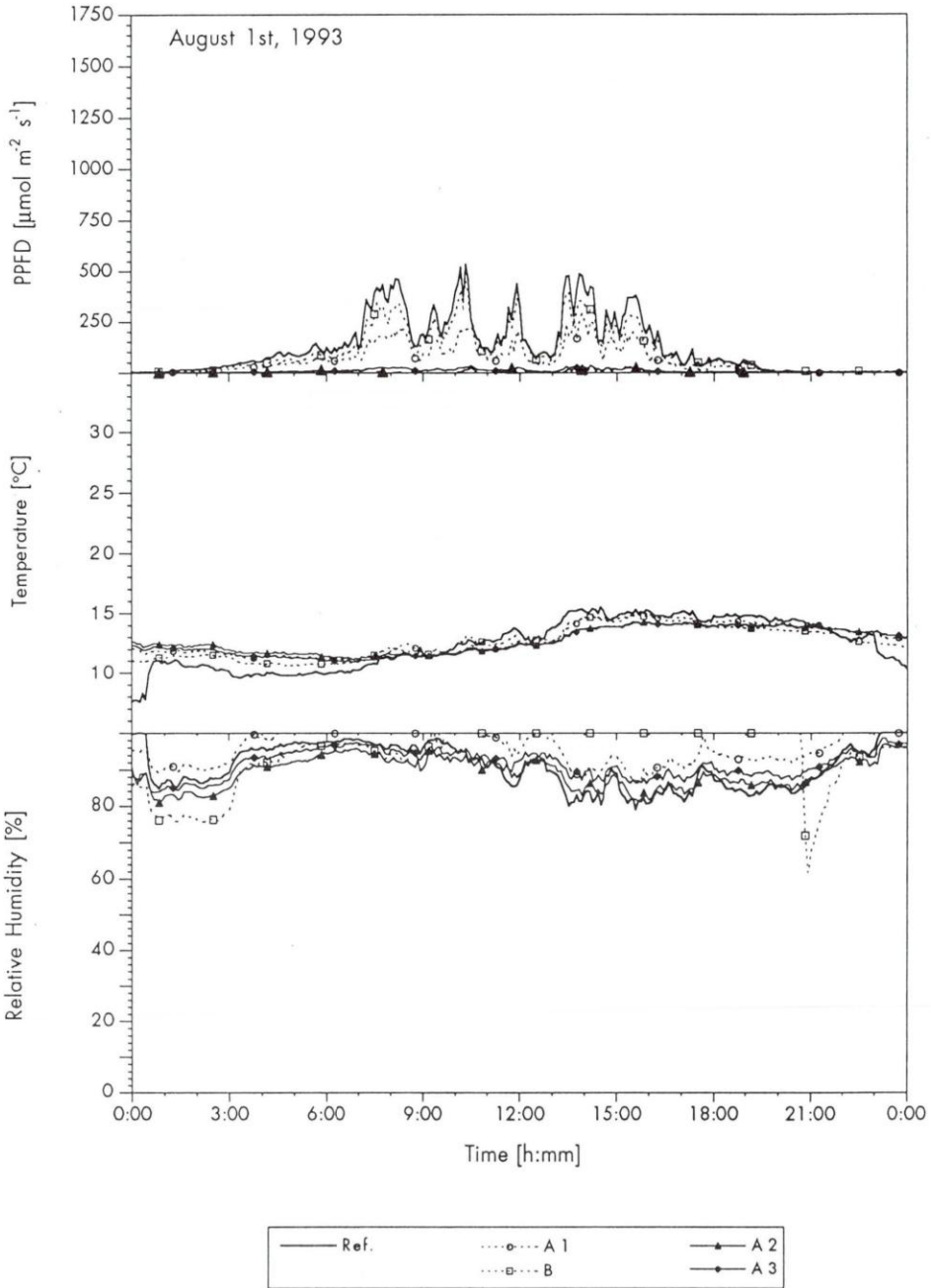


Fig.4: Diurnal courses of the microclimatic conditions during a rainy and moist day (August 1st, 1993). A1 and B: subapical plots; A2 and A3: plots on the overhang.

and wetted A2. When A2 was entirely wet, the water ran down to A3, where it generally formed narrow stripes. Most of these stripes corresponded to the distribution of the widely spaced lichen thalli of the open community.

Apparently the likelihood of water supply by rainfalls from NW during autumn is one of the most important factors of the microclimate shaping these communities. The seasonal specificity of the mode of the water supply, its frequency and duration for different epilithic crustose lichen communities on a calcareous boulder in southern France was also shown by ROUX (1980).

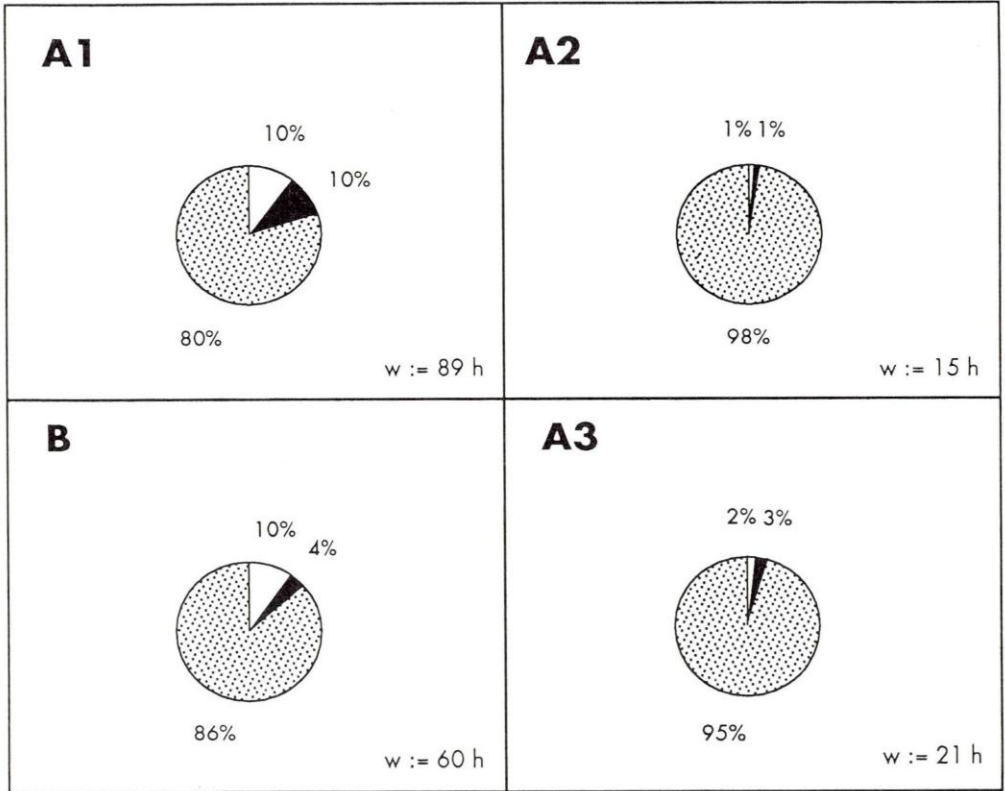


Fig. 5: The duration of the potentially active (> 95 % rel. humidity) and dry (<95 % rel. humidity) period for the lichens during the summer season (measurements taken between June 24th and August 14th 1993).

potentially active, "wet": = light (> 10 µmol m⁻²s⁻¹ PPFD)
 dark (< 10µmol m⁻²s⁻¹ PPFD)
 potentially anabiotic, "dry": =
 w: = sum of the potentially active time period [h] in the light and in darkness

However, if the microclimatic conditions in A1 and B are related to the communities at these plots, the NW-rainfall events in autumn cannot be decisive. Both plots got equally wetted during these situations, although A1 (*Rhizocarpon inarense* and *Orphniospora moriopsis*- dominated) had a different species composition and canopy structure than B, which was characterized by the dominance of *Rimularia impavida*, *Rhizocarpon inarense*, and *Porpidia melinodes*, the comparatively high cover of foliose and fruticose lichens, and the presence of free-living algae.

The communities of A1, A2 and A3 comprise many species which are described by CREVELD (1981) as being chionophobous, among these are all of the dominant species of the plots. Within community A1 13 species are listed as being chionophobous, while the situation of plot B seems to be more inherent. The community incorporates chionophobous species, e.g. *Rhizocarpon inarense*, but has an equally high number of species with a wide ecological amplitude (8 : 9 species), comprising most of the foliose and fruticose lichens and the mosses. *Porpidia melinodes* is appraised by own observations as being fairly to very chionophytic. Thus it is supposed, that a longer duration of the snow cover at site B compared to the other plots and perhaps a nutrient-enrichment caused by birds that use to sit on the peak of the boulder might be more influential to the differences between plot B and A1.

The observations and the results of the measurements suggest that the summer conditions are not decisive for the elaboration of the community pattern on the rocks. In accordance with this are the results found by ROUX (1980) and JAHNS & FRITZLER (1982), who describe that autumn and winter conditions were more important for the communities and species studied than the summer microclimate. However, COXSON & KERSHAW (1983a,b) found for *Rhizocarpon superficiale* that its alpine habitats provide favourable conditions for metabolic activity equally throughout the year.

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