

## Microclimatic boundary conditions for activity of soil lichen crusts in sand dunes of the north-western Negev desert, Israel

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### Summary

Photosynthetic activity of soil crust lichens was thoroughly investigated. Its interrelations with microclimatic boundary conditions was measured during two field experiments in the central part of the sand dune field in the north-western Negev Desert. After nocturnal rainfall the lichens were active well until noon when they dried out finally. However, over most of the year dewfall seems to be the primary controlling factor for activation as in other lichen communities. The microclimatic conditions for activity were determined in detail. It was found that after sunset terrestrial radiation leads to a progressive development of a stable air layer above ground accompanied by decreasing temperatures and wind speed. Well before midnight dewpoint temperature differences drop below 1.0 K and leaf wetness sensors indicate the formation of dew. It is exactly in this situation when lichen activity starts. Maximum activity, however, is reached a few hours later when cumulative dewfall exceeds 0.1 mm at dewpoint temperature differences around 0 K. In nights with advective labilization and subsequent dewfall evaporation, no lichen activity was observed. Even a heavy foggy night did not lead to any activity at the soil surface.

Key words: Biological crust, cryptogamic crust, chlorophyll fluorescence, dewfall, microclimate, photosynthesis

### Introduction

Lichens are able to grow in areas with low rainfall, but with high amounts of atmospheric moisture. In the fog deserts of the world, e.g. in parts of the Chilean Atacama, the South-West African Namib and the South African Succulent-Karoo, lichens cover large areas (WALTER & BRECKLE 1986; LANGE et al. 1992; SCHIEFERSTEIN & LORIS 1992; LANGE et al. 1994).

In the sand dunes of the north-western Negev desert large areas of sand dunes are covered by biological soil crusts (YAIR 1990; LANGE et al. 1992; DANIN 1996; VESTE 1995; VESTE & BRECKLE 2000; VESTE et al. 2001). These crusts (also called microbiotic, microphytic or cryptogamic crusts) are composed of cyanobacteria, green algae, mosses, fungi as well as lichens (e.g. WEST 1990). They are important communities in arid and semi-arid ecosystems and influence the ecosystem mosaic and processes (cf. reviews by WEST

1990; JOHANSEN 1993; ELDRIGE & GREENE 1994, VESTE et al. 2001). After the mobile sand is stabilized by a physical rain-crust, cyanobacteria are the first colonizers. Filaments of cyanobacteria which exude mucilaginous material and the rhizoids and protonemata of mosses stick together the sand grains and enhance the topsoil stability. Only in later stages of the succession soil lichens are able to colonise the stable biological crust (ELDRIGE & GREENE 1994). The biological soil crusts decrease infiltration rates and, thus, run-off could be observed even in a sandy area when covered by a biological crust (YAIR 1990). In addition to the influence on the hydrological conditions, the biological crust also stabilises the topsoil, reduces soil erosion, and enhances the nitrogen pools by nitrogen fixation (SHIELDS et al. 1957; WEST 1990; BELNAP & HARPER 1995; VESTE et al. 2001). An examination of soils along a 40 km long transect from the northern to the southern margin of the Sinai-Negev sand field revealed different crust types

associated with different sections of an ecological and rainfall gradient. Development of a dense cover of soil crust lichens occurs only in the northern part of the dune field (VESTE et al. 2001). LANGE et al. (1992) previously studied the CO<sub>2</sub> exchange of the biological crusts from the Negev sand dunes near Nizzana under constant laboratory conditions. However, no information has been gathered on the microclimatic boundary conditions of this biological crust activity *in situ*, i.e. specific thresholds of microclimatic parameters such as the radiative energy budget, specific humidity or dewpoint temperature difference (the difference of actual air temperature and dewpoint temperature) for the onset and termination of lichen photosynthetic activity.

Dew is a phenomenon where water vapour condenses on a substratum and transforms into liquid water once the saturation pressure at the temperature of the substratum is lower than the saturation pressure at air temperature (BEYSENS 1995; LITTMANN et al. 2001). It is an important water source for the photosynthetic activity of poikilohydric cryptogams in deserts and is seasonally more important than rainfall (EVENARI et al. 1982; ZANGVIL 1996). This conclusion has been doubted recently (KIDRON et al. 2000), a result possibly based on inappropriate field measurements.

In fact, only few long-term field investigations were carried out to measure the interrelation between microclimatic conditions during the night and lichen activity (KAPPEN et al. 1979; HAHN et al. 1989; SCHROETER et al. 1991; LEISNER et al. 1997). A better understanding of the microclimatic processes of nocturnal dewfall and its impact on the activity of biological soil crusts is needed. Therefore, the main goal of our field investigations in March 1996 and March 1999 was to analyze the interrelation of microclimatic parameters and the activity of a soil lichen crust over several nights and under varying weather conditions.

## Material and methods

### Habitat Description

The experimental site is located in the north-western Negev about 33 km inland from the Mediterranean Sea within the most eastern extension of the continental Sinai-Negev sand field, the Haluza sand dunes (E 34° 20' 50'', N 31° 2' 30'') (VESTE 1995; VESTE & BRECKLE 2000). The local climate is determined by a sharp gradient from the Mediterranean coast to the arid climate of the Negev (LITTMANN & KALEK 1997). The rainfall season is limited to the winter season (October to March) and average annual rainfall decreases from around 170 mm at the northern edge of the sand field to 90 mm near Nizzana (ATLAS OF ISRAEL 1985; LITTMANN & KALEK 1998). Most parts of the sand dunes are vegetated and stable. *Artemi-*

*sia monosperma*, *Thymelaea hirsuta*, *Retama raetam*, *Lycium schweinfurtii*, *Moltkiopsis ciliata* and *Echiochilon fruticosum* are dominant species in the northern sand dune area.

### Lichens

The interdunes in the Haluza sand field are fully covered with soil lichen crusts. This lichen community is composed by *Fulgensia fulgens* (Sw.) Elenkin (Teloschistaceae), *Squamarina cartilaginea* (With.) P. James; syn. *S. crassa* (Huds.) Poelt (Lecanoraceae), *S. lentigera* (Weber) Poelt, *Diploschistes diacapsis* (Ach.) Lumbsch; syn. *D. steppicus* Reichert (Diploschistaceae), *Collema spec.* (Collemaaceae) and other cyanobacterial lichens. In most of the interdunes the cyanobacterial lichens are dominating the soil crusts. Locally *Fulgensia fulgens* could be found on north-west facing slopes and interdunes, where *Fulgensia* covered between 15–85% of the area. The cover of the lichens of the genus *Squamarina* in this locality was between 5–8%.

### Chlorophyll Fluorescence Measurements

A MINI-PAM modulated fluorescence system (Heinz Walz GmbH, Effeltrich, Germany) with a 6 mm diameter standard fibre optic was used for the measurements of the lichen activity (see SCHROETER et al. 1992). The fibre optic was fixed at a distance of 10 mm from the surface of lichen and at an angle of 60° to avoid shading the thallus. During the night a red light beam (680 nm, < 1 μmol m<sup>-2</sup> s<sup>-1</sup>) was operated continuously so that both the steady state fluorescence yield F<sub>0</sub> in the night and F during daytime could be determined. Standard routine programmes within the MINI-PAM were used to determine effective quantum yield of photosystem II (ΔF/F<sub>m</sub>') in the light on a photosynthesizing sample (for nomenclature of fluorescence signals used, see GENTY et al. 1989; SCHREIBER et al. 1994). The time interval between sequential measurements was between 20 and 30 minutes. After onset of a modulated measuring light, a saturating pulse of white light (6000 μmol m<sup>-2</sup> s<sup>-1</sup>) was applied. All chlorophyll fluorescence parameters were instantly calculated, displayed on a LCD-screen and stored on an internal data logger. PPFD was determined with a calibrated light sensor (Heinz Walz GmbH, Effeltrich, FRG) connected with the MINI-PAM unit. Fluorescence signals were corrected for the temperature dependence of the PAM-fluorometer (WALZ 1992). The linear electron transport rate for photosystem II (ETR) can be calculated with the following equation by multiplying the effective quantum yield of PSII (ΔF/F<sub>m</sub>') and the incident PPFD (GENTY et al. 1989):

$$ETR = \Delta F/F'_m \times PPFD \times 0.5.$$

The light absorption for the investigated lichens is not known and, consequently, the ETR can only be a relative measure. Due to the differences in light absorption between the various lichens species the ETR values can not be compared (SCHROETER 1994). The ETR was used because of its expected direct relationship to the photosynthetic rate of the lichens (GENTY et al. 1989; LANGE et al. 1996). During the first experiment in March 1996 the field measurements started at sunrise and con-

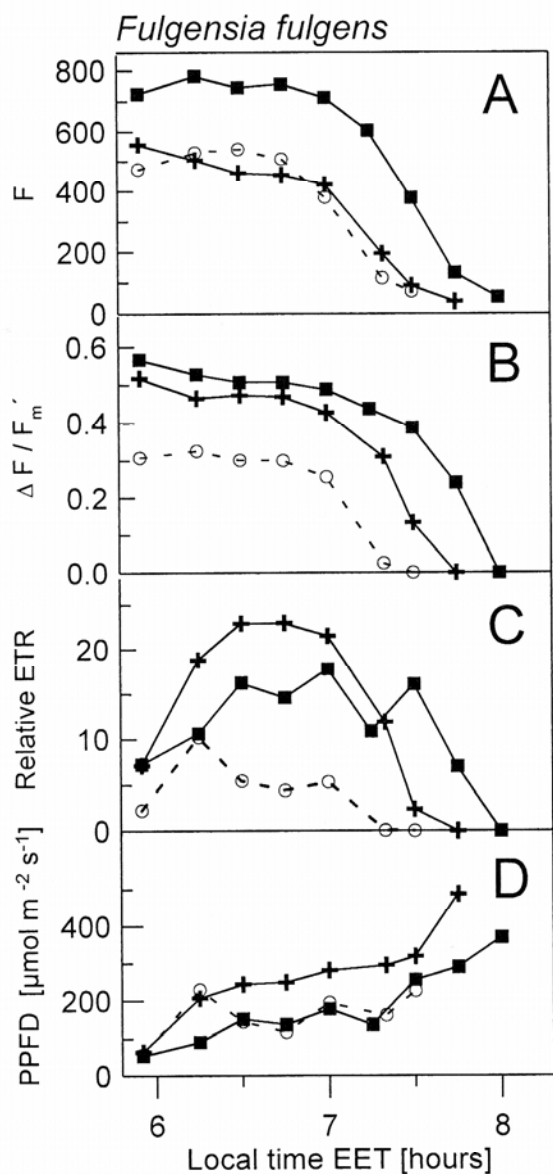


Fig. 1. Fluorescence yield  $F$  (A), effective quantum yield of the photosystem II  $\Delta F/F_m'$  (B) and relative electron transport rate ETR (C) of three different thalli of *Fulgensia fulgens* after nocturnal dewfall. (D): Photon flux density (PPFD). Date: 01 April 1996

tinued until the lichens dried out. In March 1999 the second field experiment focussed on continuous measurements of lichen activity and microclimatic parameters. Calculated values were discarded when absolute fluorescence levels were too low. The individual dates of the field measurements are shown in Figs. 1–6.

## Microclimate

Microclimatic parameters were recorded at a mast supplied with a Campbell CRX10-datalogger (Campbell Scientific, Logan, Utah, USA) about 2 m from the MINI-PAM measurement site. Air temperatures at 2 m and 0.2 m above ground were measured with Pt 100 thermoresistor probes (Campbell 107-L, Campbell Scientific, Logan, Utah, USA), specific humidity was calculated from relative humidity measurements at 2 m (Vaisala HMP35C-L, Helsinki, Finland), net radiation data at 2 m were gathered using a REBS Q7.1-L net radiometer, soil heat flux at a depth of 0.15 m was measured with a heat flux plate (REBS HFT3-L). For wind parameter measurements, we used a wind sentry for wind speed and wind direction at 2 m above ground, at 0.2 m a mini cup anemometer (03101-L, R. M. Young, USA). The duration of dewfall may be approximated by leaf wetness sensor measurements at 0.2 m; this instrument yields a low resistance signal when the surface is wetted by droplets. All individual data collected by the sensors were processed into hourly means over the observational period.

## Results

### Photosynthetic activity after sunrise

Chlorophyll fluorescence and activity of three sun-exposed *Fulgensia fulgens* thalli after sunrise is shown in Fig. 1. After nocturnal dewfall the electron transport rate (Fig. 1C) increases with increasing light intensity

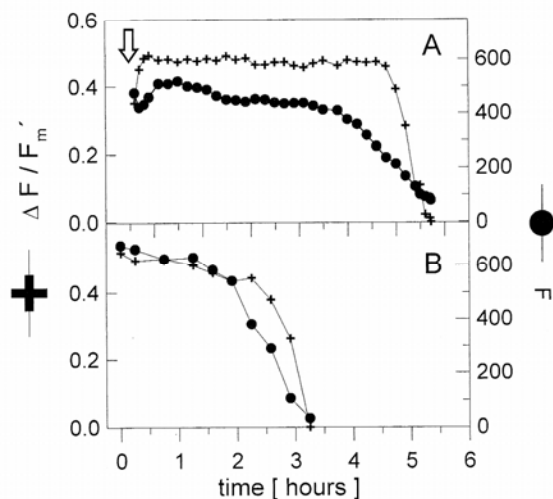


Fig. 2. Effective quantum yield of the photosystem II  $\Delta F/F_m'$  (+) and fluorescence yield  $F$  ( $\Delta$ ) in *Fulgensia fulgens* after artificial wetting (indicated by an arrow) under constant light regime (A) and in the field after nocturnal dewfall (B).

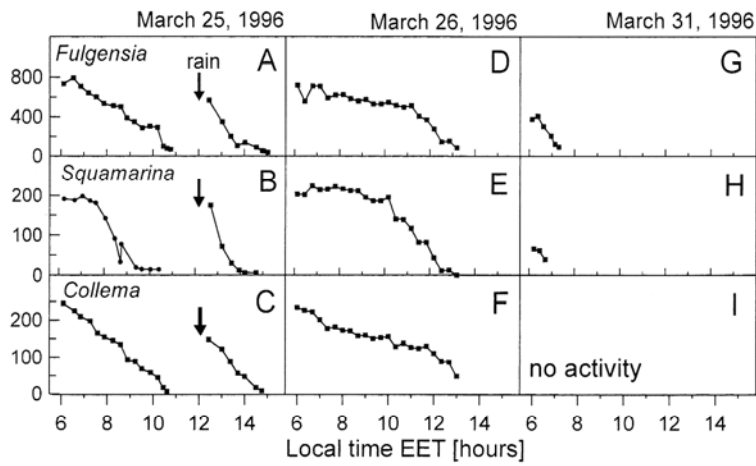


Fig. 3. Measurements of fluorescence yield  $F$  after sunrise in *Fulgensia fulgens* (A, D, G), *Squamarina lentigera* (B, E, H) and *Collema* spec. (C, F, I) after rainfall (A–F) and nocturnal dewfall (G–I).

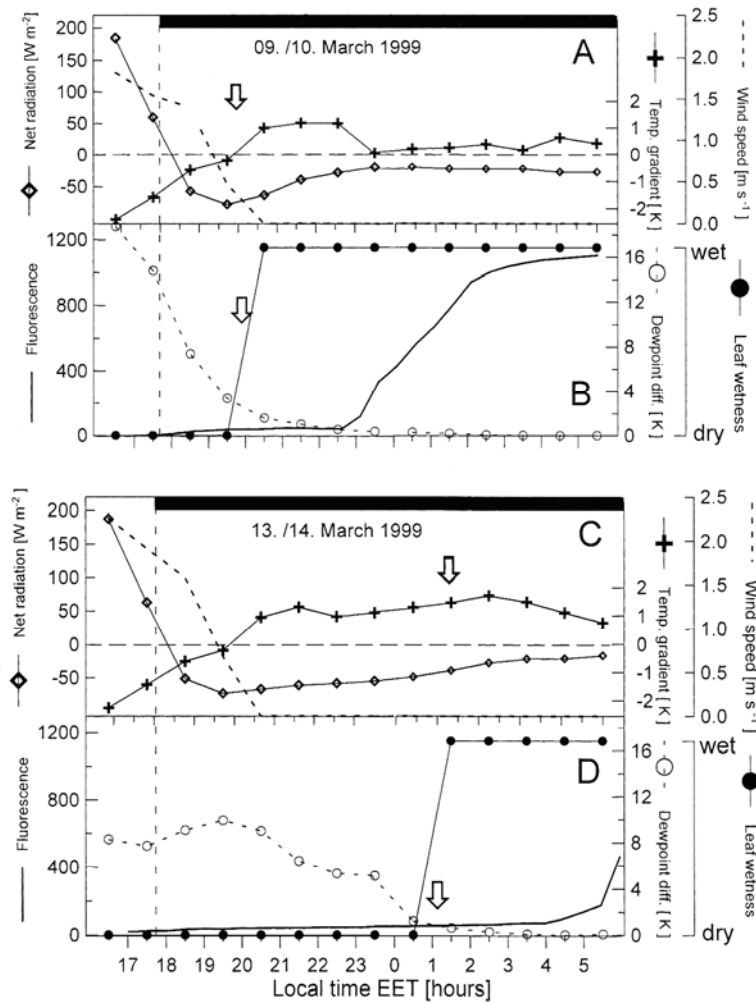


Fig. 4. Microclimatic boundary conditions (net radiation, dewpoint difference, wind speed at 20 cm height, temperature gradient between 20 cm and 2 m height and leaf wetness) after sunset and chlorophyll fluorescence of *Squamarina lentigera*, March 1999. Dewfall is indicated by an arrow.

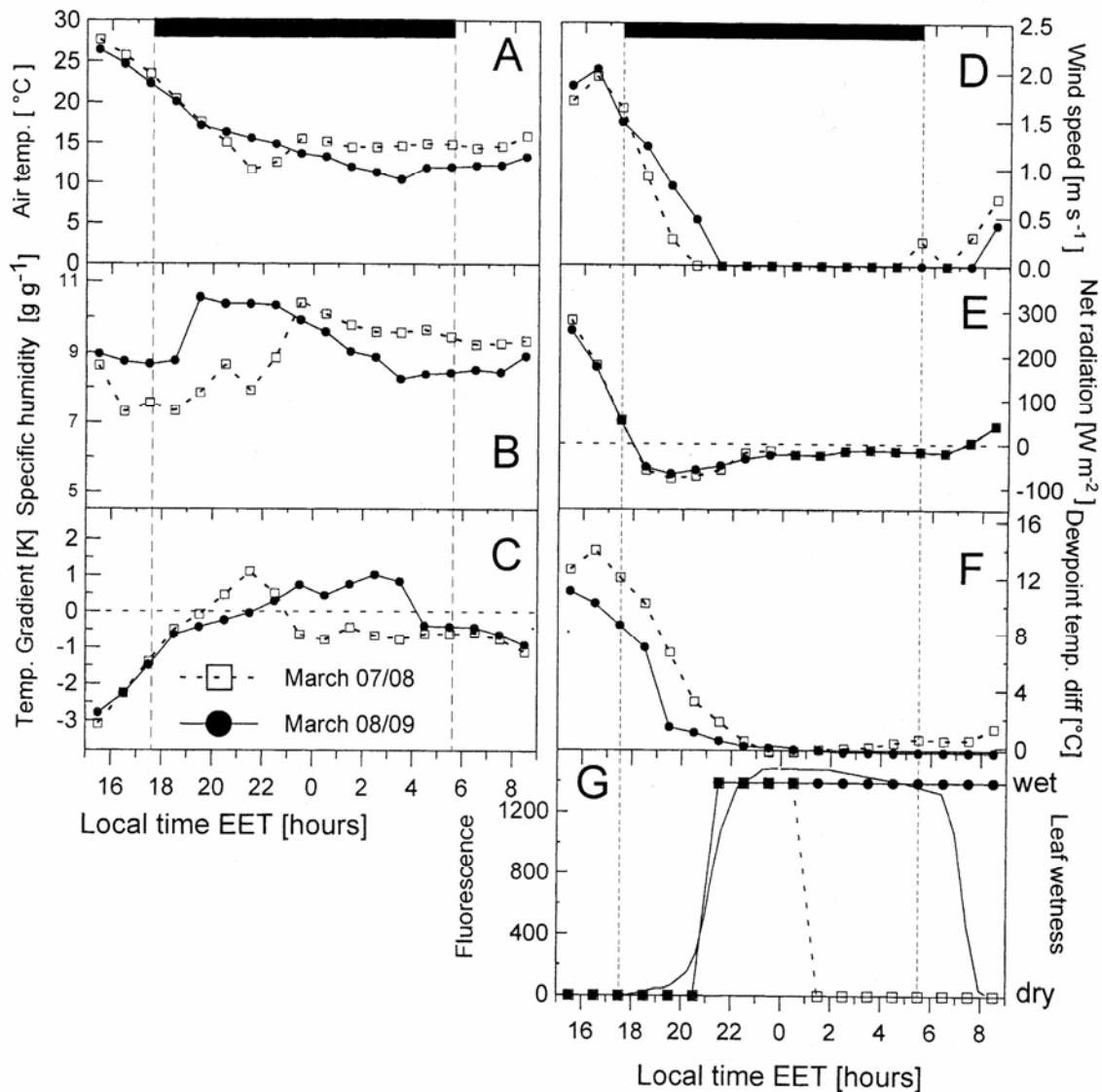


Fig. 5. Microclimatic boundary conditions (air temperature, specific humidity, net radiation, temperature gradient between 20 cm and 2 m height, wind speed at 20 cm height, net radiation, dewpoint difference and leaf wetness) during nights either with (March 08/09, 1999) or without lichen activity (March 07/08, 1999). Activity of *Squamarina lentigera* is shown (solid line in panel G).

(Fig. 1D). With rising temperature and light intensity the lichens start to dry out and fluorescence yield  $F$  (Fig. 1A), effective quantum yield of photosynthesis  $\Pi \Delta F/F_m'$  (Fig. 1B) and maximal fluorescence yield ( $F_m'$ ) (data not shown) decrease rapidly. Small differences in the exposure of the lichens influence the duration of the activity. The duration of activity of these thalli of *Fulgensia fulgens* differed by 20 to 35 minutes (Fig. 1). The

decline of the fluorescence signal during desiccation was more pronounced for the fluorescence yield  $F$  than for the effective quantum yield  $\Delta F/F_m'$ . Under constant light and temperature conditions the  $F$ -signal started to decline 45 minutes before  $\Delta F/F_m'$  was reduced (Fig. 2A). Even under field conditions the  $F$ -signal responded earlier to the desiccation than the effective quantum yield of PSII (Fig. 2B).

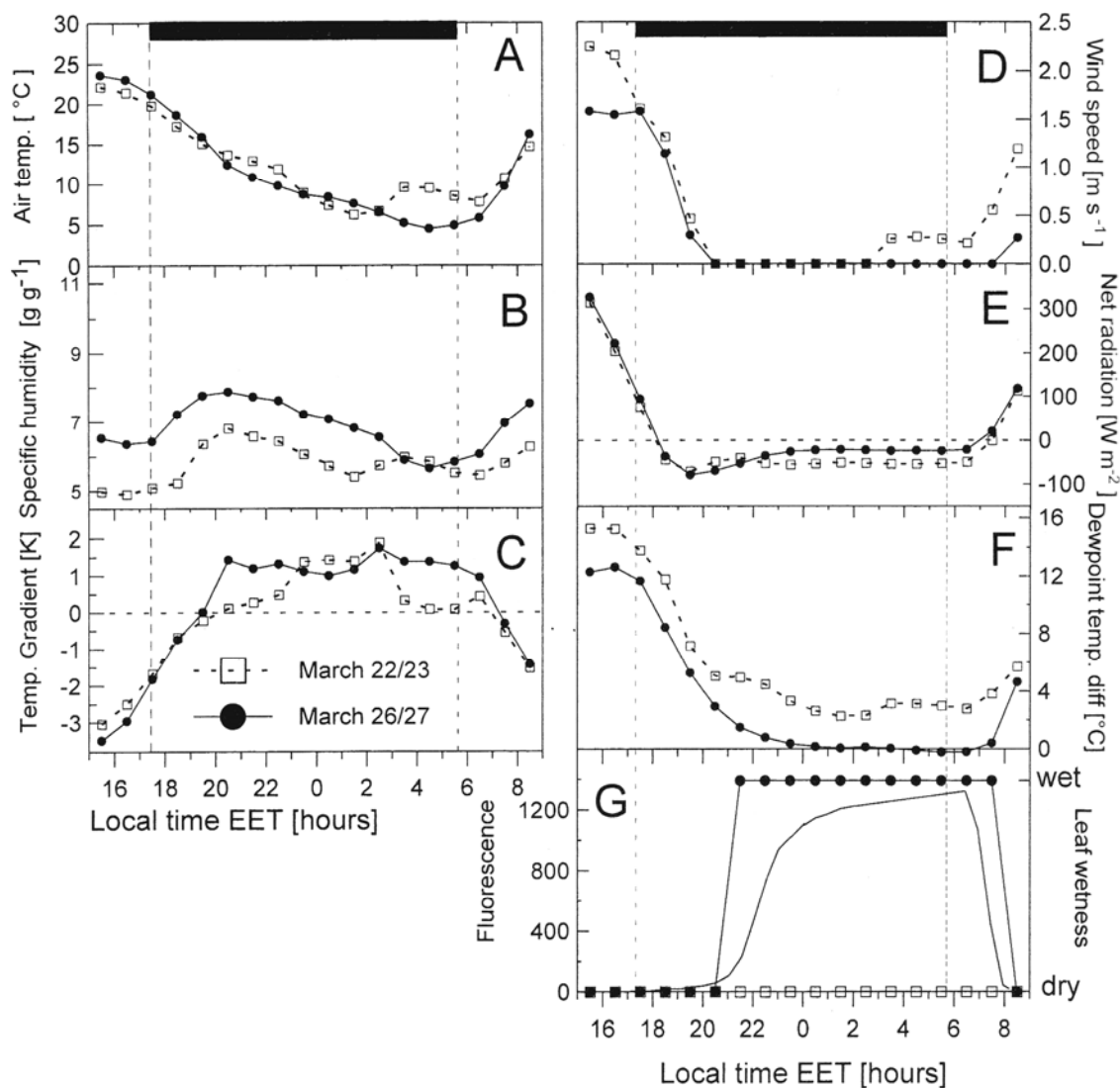


Fig. 6. Microclimatic boundary conditions (air temperature, specific humidity, net radiation, temperature gradient between 20 cm and 2 m height, wind speed at 20 cm height, net radiation, dewpoint difference and leaf wetness) during nights either with (26/27 March 1999) or without lichen activity (March 22/23, 1999). Activity of *Squamarina lentigera* is shown (solid line in panel G).

The lichens were either activated by rain or by nocturnal dewfall (Fig. 3). The amount of precipitation and subsequent evaporation influenced the duration of activity. After rainfall in the night, the investigated lichens were active until 9:15–10:30 (March 25, 1996) and 13:00 (March 26, 1996). Due to cloudy weather the evaporation was low and reduced the water loss from the thalli. On March 25 additional rainfall around 12:20

activated the lichens again for nearly 2 hours. After nocturnal dewfall (0.1 mm) only *Fulgensia* and *Squamarina* were active for 45 minutes until 75 minutes after sunrise, whereas *Collema* was still inactive (e.g. March 31, 1996, Fig. 3). The reaction of *Fulgensia* to dewfall was more pronounced than that of *Squamarina lentigera* or *Collema*. Due to the differences in light absorbance by the different lichen species, the absolute chlorophyll

fluorescence data can not be compared between the species. Under normal nocturnal dewfall conditions of  $>0.1$  mm the activity of *Fulgensia fulgens* and *Squamaria lentigera* varied between 40 and 90 minutes after sunrise.

### Nocturnal re-wetting

For the periods in March 1999 where crustal photosynthetic activity after nocturnal dewfall was measured we found fairly consistent interrelations with a large set of microclimatic parameters under conditions without rainfall (Fig. 4–6). Immediately after sunset, terrestrial radiation from the surface leads to large negative net radiation values over 2 to 3 hours and a respective radiative cooling of the near-ground air layer. Therefore we could observe the build-up of an extremely stable layer at the height of 0.2 m around 20:00 local time coinciding with the onset of crustal activity (March 8, 26, Fig. 5, 6) or anteceding it (March 9, 13, Fig. 4 C, E) and expanding towards 2 m and above a few hours later. Once the stable layer is developed, wind speeds at 0.2 m decrease towards  $0 \text{ m s}^{-1}$  and even at the height of 2 m we found only calm situations or extremely light veering winds. Under such conditions the difference between air and dewpoint temperature drops below 1.0 K and the leaf wetness sensors simultaneously indicate dew condensation. This phenomenon is consistent with the observation that in each night specific humidity slightly increased directly after sunset, which was caused by downward vapour flux in a converging near-ground boundary layer and decreased immediately after the onset of stable conditions, indicating vapour removal from the air layer in terms of condensation at the respective surfaces. It should be noted that in two cases the leaf wetness sensor surfaces did respond exactly in coincidence with the first fluorescence signal of lichen activity (20:00 on March 8, 21:00 on March 26, Fig. 4 B, H) while the dewfall signal set in 3 to 6 hours earlier on March 9 and 13.

During nights when the chlorophyll fluorescence measurements did not detect any activity of the crust, we observed also a different microclimatic situation. During the night of March 7/8 (Fig. 5), a few hours of stability were followed by an advective increase in temperature and specific humidity, labilization and subsequent evaporation of dewfall from the leaf wetness sensors. In fact, that night was a typical fog situation where moist air was advected under westerly to north-westerly wind directions from the Mediterranean. However, it is important to note that the dense fog that could be observed until well after sunrise on March 8 did not lead to conditions at the surface inducing lichen activity but, contrarily, prevented it by dew evaporation

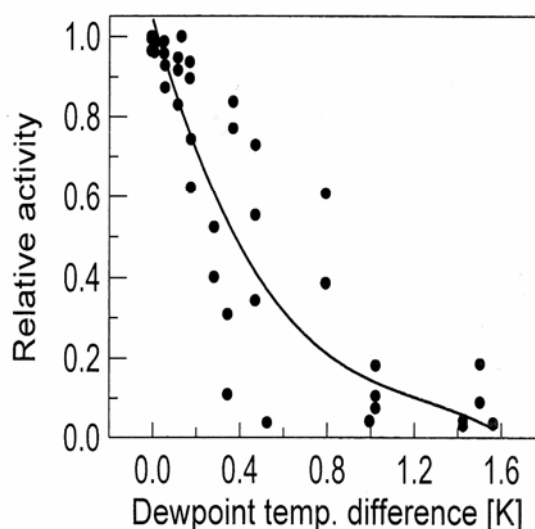


Fig. 7. Crustal activity measured as fluorescence yield (in relative units) vs. difference between air and dewpoint temperatures.

beneath the foggy air layer. An exclusively advective situation with a warm south-westerly wind flow inhibited dewfall on March 24/25, while on March 22/23 (Fig. 6) the dewpoint temperature difference did not drop below the critical threshold. As a consequence, there was no leaf wetness sensor signal. On the other hand, March 23/24 showed 5 hours of condensation but crustal activity may have been restricted by exceptionally low dewfall amounts.

In general, maximum activity (starting around 23:00 on March 9, at 4:00 on March 10, 14 and 27) always occurred when the dewpoint temperature difference reached 0 K (Fig. 7). In this situation the leaf wetness sensors indicated a cumulative wetting by the condensational removal of water vapour in a downward flux under extremely stable conditions. On March 4 and 27 morning photosynthetic activity ceased at 8:00 (i.e. during the first 2 hours after sunrise; Fig. 5, 6). In this situation the dewpoint temperature difference increased to values  $>1.0$  K and the leaf wetness sensors showed a fast evaporation of dewfall within the same time.

Following a model approximation of monthly dewfall in arid regions (LITTMANN & VESTE, unpublished), dewfall at the experimental site in March 1999 was only 1.4 mm, observed over 22 nights that showed hours with a critical dewpoint temperature difference  $<1.0$  K. Assuming a more or less constant condensation rate, average dewfall should have been around 0.06 mm per night. However, there were only 7 nights where dewfall reached approximately 0.1 mm (6 of them also indicated

by a tipping bucket rain gauge signal of 0.1 mm), three of them coinciding with observed activity nights of the crust (March 8/9, 9/10, and 26/27).

## Discussion

The application of the fluorescence technique to determine the activity of soil lichen crusts *in situ* has provided important information on nocturnal wetting as explained by microclimatic processes. The data presented here demonstrate consistent interrelations of activity and microclimatic parameters. It became obvious that boundary conditions controlling the entire activity phase are characterized by dewpoint temperature differences < 1.0 K. This coincided with a coherent leaf wetness sensor signal and the development of a near-ground stable air layer after sunset with no airflow present. Onset of lichen activity only occurs after the maximal radiative cooling of this stable layer. However, activity reaches its maximum values only if the dewpoint temperature difference is exactly 0 K, i.e. when a few hours of cumulative dewfall within an extremely stable layer have re-wetted the lichens sufficiently. Crustal activity, as measured by chlorophyll fluorescence, was only recorded during nights in which the dewfall was  $\geq 0.1$  mm and could be recorded by the tipping bucket rain gauge. Our *in situ* measurements indicate that maximum  $F_0$ -values were reached 2.5 to 5.5 hours after the initiation of dewfall. In the fruticose lichen *Ramalina maciformis* the maximum water content of the thalli was reached 35 to 404 minutes after sunset. The annual mean period of nocturnal dew imbibition, sufficient to induce respiration was 8.8 hours (KAPPEN et al. 1979).

In general, the outcome of this *in situ* dewfall measurements on different crusts and lichens indicates that activity may vary considerably because of different hygroscopy and growth form. Once vapour is deposited on the surface by downward flux it will be thermodynamically stable only in case of droplet formation which requires large thermal fluctuations to overcome the cost in free energy of forming a liquid-vapour interface, i.e. to overcome interfacial tension (BEYSENS 1995). Natural surfaces tend to lower the barrier of free energy availability by their physical and chemical properties, such as hygroscopy that results in lower saturation pressure and small dewpoint temperature differences (ROEDEL 1992), and specific wetting conditions that depend on the contact angle of the droplet on the surface (BEYSENS 1995).

*Fulgensia* and *Squamarina* showed a more pronounced response to low dewfall amounts than *Collema*. LANGE et al. (1992) demonstrated in an experiment under laboratory conditions that biological crusts

composed by cyanobacteria and green algae are active at a precipitation of >0.1 mm. This is similar to our findings under field conditions for the soil lichen crusts in the northern Negev dune field. The average dewfall amount per event varies between 0.06–0.12 mm, but strong dewfall in the Negev desert has been reported to reach values between 0.2 and 0.32 mm (EVENARI et al. 1982; ZANGVIL 1994; KIDRON 2000). The annual dew amount in the Nizzana sand dunes may be as high as 25 mm (south-facing slopes) and 49 mm (north-facing slopes), respectively (LITTMANN & KALEK 1998) and in the Central Negev Highlands (Avdat) 29.7 mm–33 mm (KAPPEN et al. 1979; EVENARI et al. 1982).

In general, the moisture compensation point of green-algal soil-crust lichens is lower in comparison with cyanobacterial lichens such as *Collema*. This lichen needs liquid water and greater quantities of water for the activation of photosynthesis (LANGE et al. 1993; LANGE et al. 1998). This may explain the different response to dewfall of *Fulgensia* and *Squamarina* in contrast to *Collema*, but also the different micro-scale distribution of the lichens within the interdune area. The green-algal lichens *Fulgensia fulgens* and *Squamarina lentigera* develop mainly on small mounds, while the cyanobacterial lichens predominantly occur in channels for run-off water. Similar zonation of green-algal and cyanobacterial lichens can be found on inselbergs in Southern Africa, where the cyanobacterial lichens also occur in run-off channels (WESSELS & BÜDEL 1989).

However, wetting of the crusts by rainfall does not necessarily mean photosynthesis for all soil crust lichen species. At very high thallus water contents the  $CO_2$  uptake of *Fulgensia fulgens* is depressed due to an increase of the thalli diffusion resistances (LANGE et al. 1995), but this effect is less pronounced in *Squamarina lentigera* (LANGE et al. 1997a). *Diploschistes diacapsis*, like other *Diploschistes* species, shows no depression of net photosynthesis under a high water content (LANGE et al. 1997a). The optimal water contents for net photosynthesis in *Fulgensia fulgens* and *Squamarina lentigera* are 0.25 and 0.42 mm precipitation equivalent, respectively, while in *Collema* it is 1.1–1.3 mm and in *Diploschistes* there is no distinct optimum (LANGE et al. 1997a; LANGE et al. 1998). The suppression of  $CO_2$  uptake by high water contents in some lichen species clearly shows that  $CO_2$  exchange and photosynthesis can not be related directly to the quantum yield measured by chlorophyll fluorescence. The chlorophyll fluorescence measurements give information only on physiological activity and not on the photosynthesis rates of the lichens species investigated in this paper. A combination of  $CO_2$  uptake measurements and chlorophyll fluorescence (LANGE et al. 1997b) is required to get unequivocal information on the photosynthesis and C gain of those lichens under natural conditions.



Desiccation in poikilohydric cryptogams is disadvantageous in terms of the sufficiency of photosynthesis during the light period. Light saturation of photosynthesis in well-hydrated *Fulgensia fulgens* is between 1000–1200  $\mu\text{mol m}^{-2} \text{s}^{-1}$  (data not shown). However, under field conditions the nocturnal wetting of soil crusts is only sufficient for photosynthesis for 1–2 hours after sunrise, during which time the optimal light intensity is not reached. Wetting of the lichen and activity time for photosynthesis depends also on slope aspect and shading of the thallus surface. In winter dew is present for longer periods on north-facing slopes than on south-facing slopes because of longer periods of shading (LITTMANN & KALEK 1998). Also shading around shrubs reduces evaporation from topsoil and prevents lichens from desiccation for a longer period of time compared to unshaded surfaces exposed to sunlight immediately after sunrise. No significant difference in the drying process could be observed between the black cyanobacterial lichen *Collema*, the yellow *Fulgensia* and the white *Squamarina*. Cloudy weather after sunrise, especially after nocturnal rainfall, reduced evaporation and extended the duration of crustal activity for several hours.

It may be concluded that the activity of soil crusts can be clearly related to nocturnal dewfall and associated microclimatic processes in a desert environment. The combination of the *in situ* measurements of cryptogamic activity by chlorophyll fluorescence and its interrelations with the complex microclimatic boundary conditions will provide a tool for the calculation of long-term activity in different habitats. In this field experiment it is clearly shown that a calculation of lichen activity only based on the dewpoint differences will not provide enough information. Appropriate information about the stability of the air layer near the ground and water fluxes are also necessary for the modelling of annual courses of re-wetting of biological crusts and lichens. Only the combination of the detailed microclimatic data with information on the  $\text{CO}_2$  exchange under laboratory conditions or in the field (KAPPEN et al. 1979; SUNDBERG et al. 1997; LANGE et al. 1997b) may allow us to finally estimate the overall productivity of cryptogams in such ecosystems.

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## References

- ATLAS OF ISRAEL (1985): The survey of Israel, Tel Aviv and Macmillan Publishing Company, New York, London.
- BELNAP, J. & HARPER, K. T. (1995): Influence of cryptobiotic soil crusts on elemental content of tissue of two desert seed plants. – *Arid Soil Res. Rehabil.* **9**: 107–115.
- BEYSENS, D. (1995): The formation of dew. – *Atmospheric Research* **39**: 215–237.
- DANIN, A. (1996): Plants of Desert Dunes, Adaptations of Desert Organisms, Springer, Berlin-Heidelberg-New York.
- ELDRIGE, D. J. & GREENE, R. S. B. (1994): Microbiotic soil crusts: a review of their roles in soil and ecological processes in the rangeland of Australia. – *Aust. J. Soil Res.* **32**: 389–415.
- EVENARI, M.; SHANAN, L. & TADMOR, N. (1982): The Negev, The Challenge of a Desert, Harvard University Press, Cambridge, Massachusetts.
- GENTY, B.; BRIANTAIS, J. M. & BAKER, N. (1989): The relationship between the quantum yield of photosynthetic electron transport and quenching of chlorophyll fluorescence. – *Biochim. Biophys. Acta* **990**: 87–92.
- HAHN, S.; SPEER, D.; MEYER, A. & LANGE, O. L. (1989): Photosynthetische Primärproduktion von epigäischen Flechten im „Mainfränkischen Trockenrasen“, I. Tagesläufe von Mikroklima, Wassergehalt und  $\text{CO}_2$ -Gaswechsel zu verschiedenen Jahreszeiten. – *Flora* **182**: 313–339.
- JOHANSEN, J. R. (1993): Cryptogamic crusts of semiarid and arid lands of North America. – *J. Phycol.* **29**: 140–147.
- KAPPEN, L.; LANGE, O. L.; SCHULZE, E.-D.; EVENARI, M. & BUSCHBOM, U. (1979): Ecophysiological investigations on lichens of the Negev desert. – *Flora* **168**: 85–108.
- KIDRON, G. J. (2000): Dew moisture regime of endolithic and epilithic lichens inhabiting limestone cobbles and rock outcrops, Negev Highlands, Israel. – *Flora* **195**: 146–153.
- KIDRON, G. J.; BARZILAY, E. & SACHS, E. (2000): Microclimate control upon sand microbiotic crust, western Negev desert, Israel. – *Geomorphology* **36**: 1–18.
- LANGE, O. L.; KIDRON, G. J.; BÜDEL, B.; MEYER, A.; KILIAN, E. & ABELIOVICH, A. (1992): Taxonomic composition and photosynthetic characteristics of the biological crusts covering sand dunes in the western Negev. – *Funct. Ecol.* **6**: 519–527.
- LANGE, O. L.; BÜDEL, B.; MEYER, A. & KILIAN, E. (1993): Further evidence that activation of net photosynthesis by dry cyanobacterial lichens requires liquid water. – *Lichenologist* **25**: 175–189.
- LANGE, O. L.; MEYER, A. & BÜDEL, B. (1994): Net photosynthesis activation of a desiccated cyanobacterium without liquid water in high air humidity alone. Experiments with *Microcoleus sociatis* isolated from a desert soil. – *Funct. Ecol.* **8**: 52–57.

- LANGE, O. L.; MEYER, A.; ZELLNER, H. & HEBER, U. (1994): Photosynthesis and water relations of lichen soil crusts: field measurements in the coastal fog zone of the Namib Desert. – *Funct. Ecol.* **8**: 253–264.
- LANGE, O. L.; REICHENBERGER, H. & MEYER, A. (1995): High thallus water content and photosynthetic CO<sub>2</sub> exchange of lichens. In: DANIELS F. J. A.; SCHULZ, M. & PEINE J. (eds.) – Festschrift für Gerhard Follmann, 139–153. Botan. Inst., Univ., Köln.
- LANGE, O. L.; GREEN, T. G. A.; REICHENBERGER, H. & MEYER, A. (1996): Photosynthetic depression at high thallus water content in lichens: Concurrent use of gas exchange and fluorescence techniques with a cyanobacterial and a green algal *Peltigera species*. – *Bot. Acta* **109**: 43–50.
- LANGE, O. L.; BELNAP, J.; REICHENBERGER, H. & MEYER, A. (1997a): Photosynthesis of green algal soil crust lichens from arid lands in southern Utah, USA: role of water content on light and temperature responses of CO<sub>2</sub> exchange. – *Flora* **192**: 1–15.
- LANGE, O. L.; REICHENBERGER, H. & WALZ, H. (1997b) Continuous monitoring of CO<sub>2</sub> exchange of lichens in the field: short-term enclosure with an automatically operating cuvette. – *Lichenologist* **29**: 259–274.
- LANGE, O. L.; BELNAP, J. & REICHENBERGER, H. (1998): Photosynthesis of the cyanobacterial soil-crust lichen *Collema tenax* from arid lands in southern Utah, USA: role of water content on light and temperature responses of CO<sub>2</sub> exchange. – *Funct. Ecol.* **12**: 519–527.
- LEISNER, J. M. R.; GREEN, T. G. & LANGE, O. L. (1997): Photobiont activity of a temperate crustose lichen: long-term chlorophyll fluorescence and CO<sub>2</sub> exchange measurements in the field. – *Symbiosis* **23**: 165–182.
- LITTMANN, T. & KALEK, J. (1997): Geländeklimatische Strukturen in einem ariden Dünenökosystem (nordwestlicher Negev, Israel). – *Annal. Meteorol.* **34**: 59–60.
- LITTMANN, T. & KALEK, J. (1998): Mikroklimatische Strukturen als Steuergröße für Ökosystemprozesse in einem ariden Dünengebiet (nordwestlicher Negev, Israel). – *Hallesches Jahrb. Geowiss.* **20**: 77–92.
- LITTMANN, T.; STEINRÜCKE, J. & BÜRGER, M. (2001): Elemente des Klimas. Grundlagen und Anwendungen. Reihe „Geographie Kompakt“, Klett-Perthes, Gotha, in press.
- ROEDEL, W. (1992): Physik unserer Umwelt, Die Atmosphäre, Springer, Berlin–Heidelberg–New York.
- SCHIEFERSTEIN, B. & LORIS, K. (1992): Ecological investigations on lichen fields of the Central Namib, I. Distribution patterns and habitat conditions. – *Vegetatio* **98**: 113–128.
- SCHREIBER, U.; BILGER, W. & NEUBAUER, C. (1994): Chlorophyll fluorescence as a noninvasive indicator for rapid assessment of *in vivo* photosynthesis, In: E.-D. SCHULZE & M. M. CALDWELL, eds., *Ecophysiology of Photosynthesis*, Ecological Studies 100: 49–70, Springer, Berlin–Heidelberg–New York.
- SCHROETER, B. (1994): In situ photosynthetic differentiation of the green algal and the cyanobacterial photobiont in the crustose lichen *Placopsis contortuplicata*. – *Oecologia* **98**: 212–220.
- SCHROETER, B.; KAPPEN, L. & MOLDAENKE, C. (1991): Continuous in situ recording of the photosynthetic activity of antarctic lichens – established methods and a new approach. – *Lichenologist* **23**: 253–265.
- SCHROETER, B.; GREEN, T. G. A.; SEPELT, R. D. & KAPPEN, L. (1992): Monitoring photosynthetic activity of crustose lichens using a PAM-2000 fluorescence system. – *Oecologia* **92**: 457–462.
- SHIELDS, L. M.; MITCHELL, C. & DROUET, F. (1957): Algal and lichen-stabilized surface crusts as soil nitrogen sources. – *Amer. J. Bot.* **44**: 489–498.
- SUNDBERG, B.; PALMQVIST, K.; ESSEEN, P.-A. & RENHORN, K.-E. (1997): Growth and vitality of epiphytic lichens. II. Modelling of carbon gain using field and laboratory data. – *Oecologia* **109**: 10–18.
- VESTE, M. (1995): Structures of geomorphological and ecological units and ecosystem processes of the linear dune ecosystem near Nizzana/Negev. – *Bielefelder Ökol. Beitr.* **8**: 85–96.
- VESTE, M. & BRECKLE, S.-W. (2000) Negev – pflanzenökologische und ökosystemare Analysen. – *Geogr. Rdsch.* **9/2000**: 24–29.
- VESTE, M.; LITTMANN, T.; BRECKLE, S.-W. & YAIR, A. (2001): The role of biological crusts on desert sand dunes of the northern Negev, In: BRECKLE, S.-W., VESTE, M. & WUCHERER, W., *Sustainable Land-Use in Deserts*, 357–367, Springer, Berlin–Heidelberg–New York.
- WALTER, H. & BRECKLE, S.-W. (1986): *Ecological Systems of the Geobiosphere, Tropical and Subtropical Zonobiomes*, Vol. 2, Springer, Berlin–Heidelberg–New York.
- WALZ, H. GMBH (1992): Temperaturabhängigkeit der Emitter-Detektoreinheit 101-ED, Walz News 2, 3.
- WESSELS, D. C. J. & BÜDEL, B. (1989): A rockpool lichen community in northern Transvaal, South Africa: composition and distribution patterns. – *Lichenologist* **21**: 259–277.
- WEST, N. (1990): Structure and function of microphytic soil crusts in wildland ecosystems of arid to semi-arid regions. – *Adv. Ecol. Res.* **20**: 179–223.
- YAIR, A. (1990): Runoff generation in a sandy area – processes in the Nizzana sands, eastern Negev, Israel. – *Earth Surface and Landforms* **15**: 597–609.
- ZANGVIL, A. (1996): Six years of dew observations in the Negev Desert, Israel. – *J. Arid Environ.* **32**: 361–371.