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Causes of two patterns of lichen zonation on cobbles in the Negev Desert, Israel

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Abstract: Two patterns of lichen zonation on cobbles were observed in the Negev Desert, Israel: growth on the top of the cobble and growth on the cobble margins. The causes of the different patterns are examined. Microscopic examinations did not reveal any textural or structural differences between the top and the margins of each cobble, excluding the possibility that mineralogical differences are responsible for the patterns observed. Field measurements have, however, shown a significant difference in the quantities of average daily dew, with the top of the cobbles receiving approximately double the quantity received at the margins. These results were consistent on all cobbles examined, loose as well as partially embedded cobbles. In addition, field observations following rain noted a greater moistness at the margins of partially embedded cobbles. This phenomenon, also observed following sprinkling experiments, was explained by water capillary rise. Whilst the top dwelling pattern may be explained by the significantly larger quantities of dew on the top of the cobble, the margin-dwelling pattern may be explained by greater moistness at the cobble-soil interface due to water capillary rise. Providing that the threshold moisture duration is met, lichen colonization may be expected. An estimated annual daylight moisture duration of approximately 260–320 h is thought to be necessary for lichen growth in the Negev. The findings may assist in evaluating weathering rates and paleoclimate reconstruction.

Introduction

Data concerning the causes of lichen zonation on rocks are scarce. Zonation has been attributed to differential rock properties (Wetmore 1970; Brodo 1973), preferential accumulation of nutrients (Scott 1967), or differential microclimatological conditions, controlling the availability of rain (Topham 1977) or dew (Danin & Garty 1983). In fact, owing to their poikilohydric nature, the availability of water to lichens is largely determined by microclimatological conditions. This is especially so in arid areas such as the Negev Desert where dew is a major water source for lichens (Lange *et al.* 1970*a*; Kappen *et al.* 1979). The accumulation of dew is largely affected by the properties and position of the substratum (Kidron 1998; Kidron *et al.* 2000), and owing to more rapid and more efficient nocturnal radiative cooling, preferential accumulation may occur at certain loci such as rock heaps, crests and loose cobbles (Kidron 1988). Kidron (1988, 2000*a*) found highly significant differences in the quantities of dew deposition obtained between loose cobbles and adjacent rock surfaces in the Negev Highlands. The cobbles were totally covered by lichens with over 90% being endolithic species, predominantly *Caloplaca alociza* (A. Massal.) Mig. and *Rinodina bischoffii* (Hepp) A. Massal. (cf. Kushnir *et al.* 1978).

Two patterns of zonation by endolithic lichens were observed on limestone cobbles at Nizzana, in the western part of the Negev: those with a marginal zone and those with a zone on top of the cobble (Fig. 1A & 1B). Whilst the marginal pattern was almost always restricted to partially embedded

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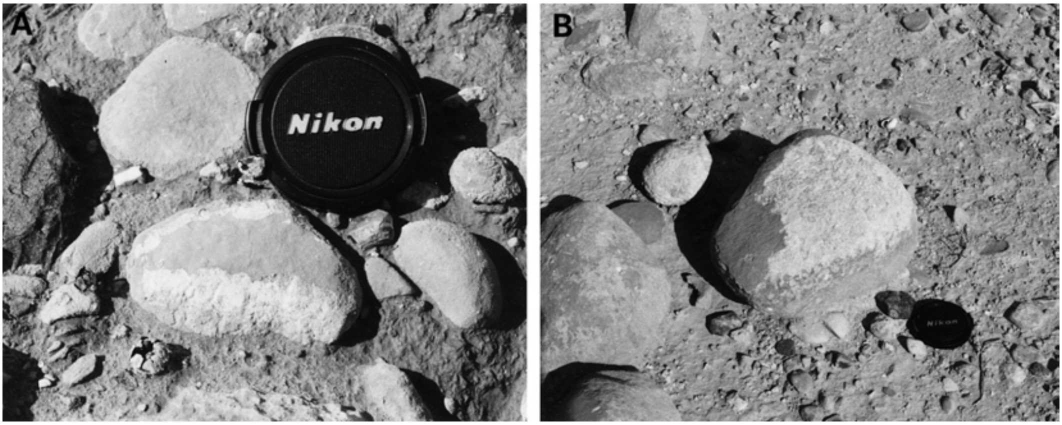

FIG. 1. Cobbles with margin -(A) and top-dwelling (B) lichen at Nizzana.

cobbles and was very common in Nizzana, the much less frequent top-dwelling pattern was restricted to loose cobbles, usually >5 cm above ground. The top-dwelling pattern was, however, common on loose cobbles at the southern parts of the Negev, south of the Negev Highlands.

Variability in the quantity of rainfall intercepted directly was ruled out as a possible explanation for the patterns observed (Topham 1977) due to the widespread occurrence of the phenomenon, regardless of cobble location or aspect. The differential availability of nutrients from an external source (i.e. rain, dust or soil splash which may supply much of a lichen's mineral and nutrient supply, see Jenkins & Davies 1966) was also ruled out owing to the fact that both growth patterns were found in the same area. Differences in substratum properties (Brodo 1973) and dew variability (Danin & Garty 1983; Kidron 1988), however, could have accounted for the differences observed. In addition, capillary rise may also provide a possible source of water.

The aim of the current investigation was to evaluate the possible role of substratum properties, dew and capillarity in determining the two patterns of zonation observed.

Research sites and methods

Observation and collection of cobbles showing both patterns of lichen zonation, i.e. on the top of the cobbles and on the margins, and dew measurements were made at Nizzana, western Negev Desert (Fig. 2). Cobbles with the top dwelling pattern were also collected from two additional sites located 6 km and 15 km east and southeast, respectively, of Mizpe Ramon in the Negev, within and south of the erosion cirque (Fig. 2). The cobbles collected from these two sites together with those collected from Nizzana were thin sectioned and examined under a light microscope for possible structural and textural differences between the top and margins.

The dew measurements were carried out at Nizzana during the late summer and fall of 1992 for 58 days, a period when the heaviest dews form in the Negev (Evenari *et al.* 1971; Zangvil & Druian 1980; Zangvil 1996). The measurements were made at the top of a hill, 245 m above m.s.l., consisting of alluvial deposits (Ahuzam conglomerate) with unconsolidated cobbles of which 85–90% are limestone. Mean annual precipitation is *c.* 95 mm (Rosenan & Gilad 1985).

Eight cobbles with lichen cover were chosen for dew measurements:

a. four flat cobbles (8–15 × 5–10 × 2–5 cm) exhibiting preferential growth around the margin (cobbles: 1–4);

b. two loose cobbles (15–20 × 10–15 × 10–15 cm) exhibiting preferential growth on the top (cobbles: 5 & 6);

and c. two loose cobbles (10–15 × 10–15 × 8–12 cm) totally covered by lichens which served as a reference (cobbles: 7 & 8).

The dew was measured using two pairs of 2·0 × 2·0 × 0·15 cm velvet-like cloths (Universal Company, Germany), attached with adhesive stickers, to the top of the cobbles, to the margins (a term used in relation to partially embedded cobbles) or to the sides of the cobbles (a term used in relation to loose cobbles) each afternoon. The cloths were collected during the early hours of the following morning, approximately half an hour after sunrise, placed in flasks and sealed immediately, then weighed for moisture content (to the nearest 0·1 mg). At this time dew quantities were maximal

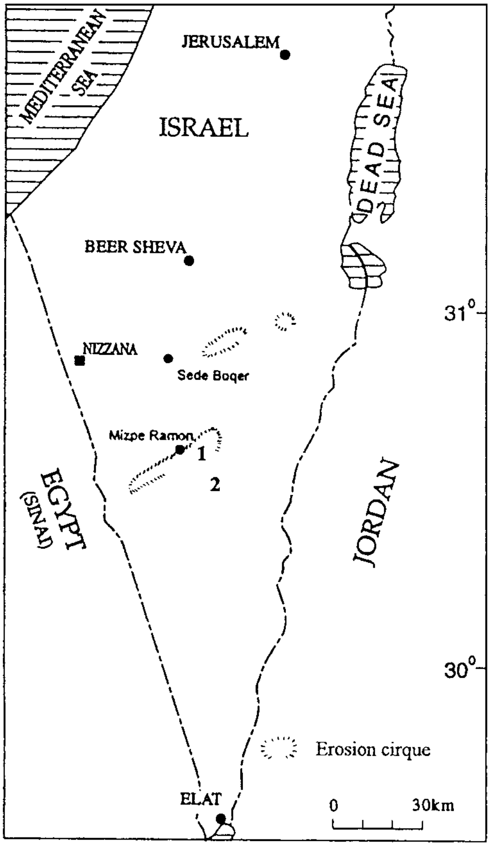

FIG. 2. Location of the Nizzana research site, and the two sites 6 km east (1) and 15 km southeast (2) of Mizpe Ramon.

(Kidron 1998). In addition, three glass plates (10 × 10 × 0·2 cm) attached on top of plywood (10 × 10 × 0·5 cm) were used as an independent uniform substratum for dew measurements. Cloths, 6 × 6 × 0·15 cm, were attached in the afternoon to the centre of each of the plates and collected during the early morning hours into flasks, and later weighed to determine their moisture content (Kidron 1998).

In addition, three field experiments were conducted in February 1997 in order to assess capillary rise. Smooth cobbles were inserted into the ground and their surrounding area, approximately 20 cm in diameter, was sprinkled with distilled water, equivalent to approximately 10 mm rainfall, during the late afternoon. The water level and duration of capillary rise was measured at 2 and 4 hours intervals during the following day time and night time, respectively.

Results

From data based on three 30 m transects at Nizzana, 87·8% of all limestone cobbles were inhabited by lichens, of which 56·5% of the cobbles were entirely covered, 35·0% were covered only at the cobble margins, and 8·5% were only inhabited by lichens on the top of the cobble. Whereas the cobbles with a marginal zone were mostly flat, usually 8–12 cm diameter and <5 cm height above ground and for the most part slightly embedded within the soil, all other cobbles lay loosely on the surface. A very sparse cover (usually <5%) of cyanobacteria was sometimes noted on top of the lichen-covered cobbles. The dominant species inhabiting the cobbles was *Caloplaca alociza*, the only endolithic species covering all types of cobbles. A number of loose cobbles also supported an epilithic species, *Diplotomma venustum* (Körb.) Körb. However, the relative cover of this species was very low, usually ⩽1%, and rarely exceeding 2% of the area covered by lichens.

A comparison of thin rock sections showed no apparent difference in structure or texture between the inhabited and non-inhabited parts of the cobbles just below the colonized zone (Fig. 3). These results were consistent for all cobbles examined from Nizzana, whether with margin dwelling (Fig. 3A), or top-dwelling lichens (not shown), and also for other types of calcareous cobbles examined with top-dwelling lichens, from 6 km east and 15 km southeast of Mizpe Ramon (Fig. 3B and 3C, respectively).

During the 58 day monitoring period, dew occurred on 39 days on glass plates, but of these days only 28 yielded dew on the cobbles. The discrepancy may be explained by the different thermal properties of glass in comparison to the rock (Kidron 1998). During the 28 days with dew deposition on the cobbles, top sections of the cobbles with either top or margin-dwelling lichens showed consistently and significantly larger ($P<0·05$) quantities of dew than the sides or margins (Fig. 4). Thus, whereas the top of partially embedded cobbles had an average daily dew deposition of 0·06–0·07 mm, the quantity at the margins was 0·03–0·04 mm (Fig. 5A), and the top of loose cobbles with top-dwelling lichens received 0·14–0·16 mm

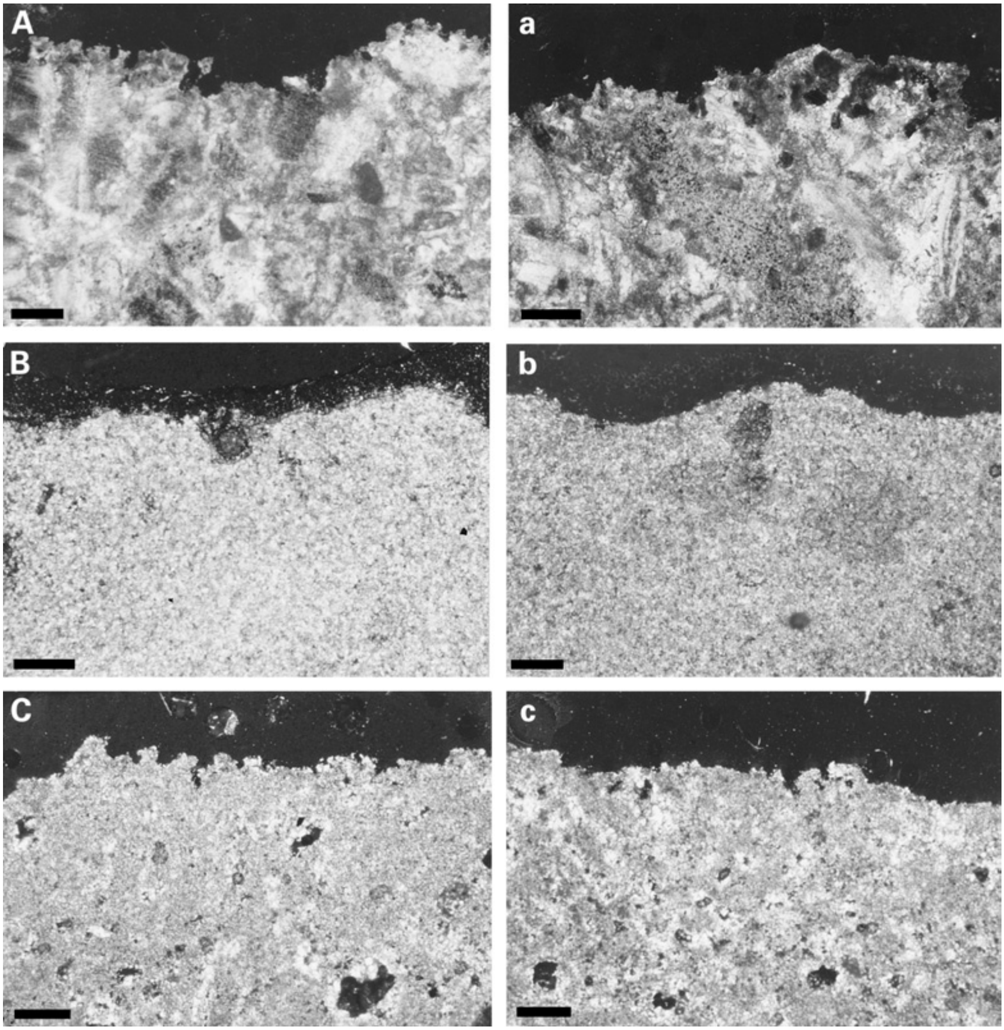

FIG. 3. Thin section micrographs of the inhabited (A, B, C) and uninhabited (a,b,c) surface of three carbonate cobbles with differential patterns of lichen zonation. A, a biomicritic, fossiliferous limestone, characterized by a margin-dwelling lichen at Nizzana; B, a biomicritic, homogenic chalk with top-dwelling lichen, 6 km east of Mizpe Ramon; C, a micritic limestone with rhombic spar lining pores with top-dwelling lichen, 15 km southeast of Mizpe Ramon. Scales = 500 µm.

compared to only 0·07–0·09 mm on the sides. These results show that the top and sides of loose cobbles receive approximately twice as much dew as the top and margins of partially embedded cobbles. Those entirely covered by lichens (reference) received a daily average of 0·07–0·14 mm (Fig. 5B & C).

A moist band, usually 1–2 cm wide (with lower rock angles having wider belts), was noted during cool, cloudy days, at the margins of partially embedded cobbles following rainstorms. These moist belts were confined to cobbles that had good contact with the surrounding surface, and usually persisted, presumably as a result of capillary rise, as long as the upper soil surface was moist.

Capillary rise was clearly observed following three sprinkling experiments on cobbles inserted in the ground. During one of the

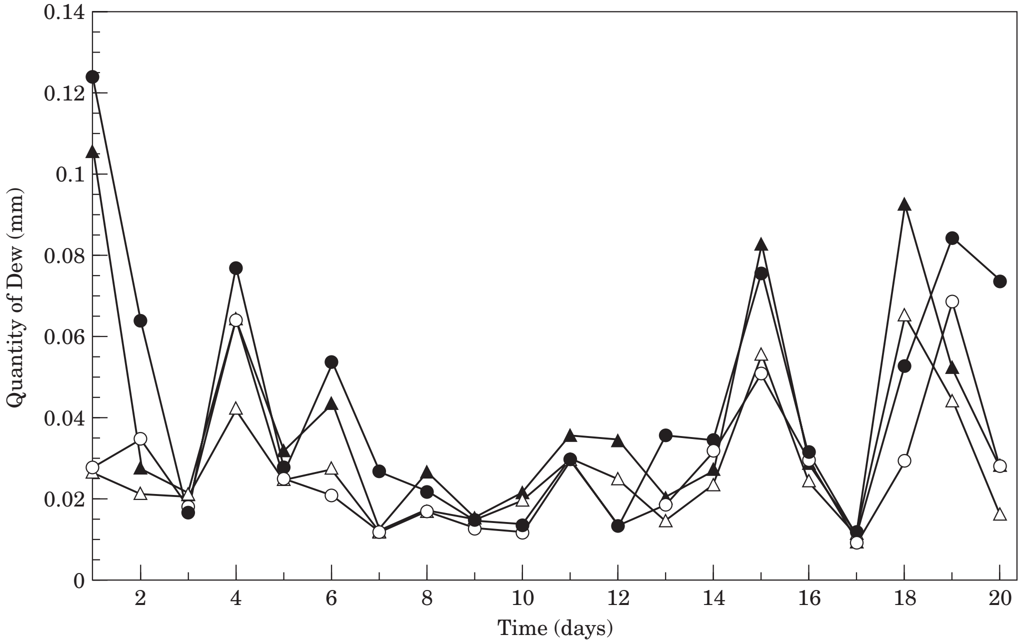

FIG. 4. Twenty days of contemporaneous dew measurements on top and at the margins of two partially embedded cobbles with margin-dwelling lichen; cobble 1: top ▲, margin △; cobble 2: top ●, margin ○.

experiments, beginning during the afternoon of 25 February 1997, the sky was partially cloudy. During the day following the sprinkling, a moist band, 1–2 cm wide, was clearly visible at the cobble-soil interface. North-facing margins were moist during the entire day following the experiment (Fig. 6), maintaining their moistness until midday on 27 February, some 40 h after sprinkling, providing approximately 20 h of daylight moistness. However, the south-facing margins dried up during midday on 26 February, but were rewetted during the early morning hours of 27 February, providing 12–14 h of daylight moistness. The results obtained during the two other experiments were similar.

Discussion

The similarity in the structure and texture of the inhabited and uninhabited parts of cobbles suggests that the two patterns of zonation are not the result of of differential rock properties. This conclusion is in agreement with Galun (1963) who did not find variation in lichen communities on variable carbonate rocks such as crystal, lithographic limestone, flinty limestone or dolomite. Clearly other factors are determining the patterns of zonation observed.

The quantities of dew on the top and sides of the loose cobbles were approximately double the amounts received on the top and margins of the partially embedded cobbles, respectively. These data were in agreement with dew values measured during the fall of 1987 and 1988 on top of loose and partially embedded cobbles in Sede Boqer, with loose cobbles exhibiting almost twice the amount as partially embedded cobbles of the same height (Kidron 1988, 2000*a*).

The larger quantities of dew obtained on the loose cobbles can be safely attributed to better ventilation (Kidron 1988; Danin & Garty 1983), and consequently to lower nocturnal temperatures (Kidron 1988, 2000*a*). The larger quantities of dew on the top of the cobbles in comparison to the margins or sides is explained by the larger

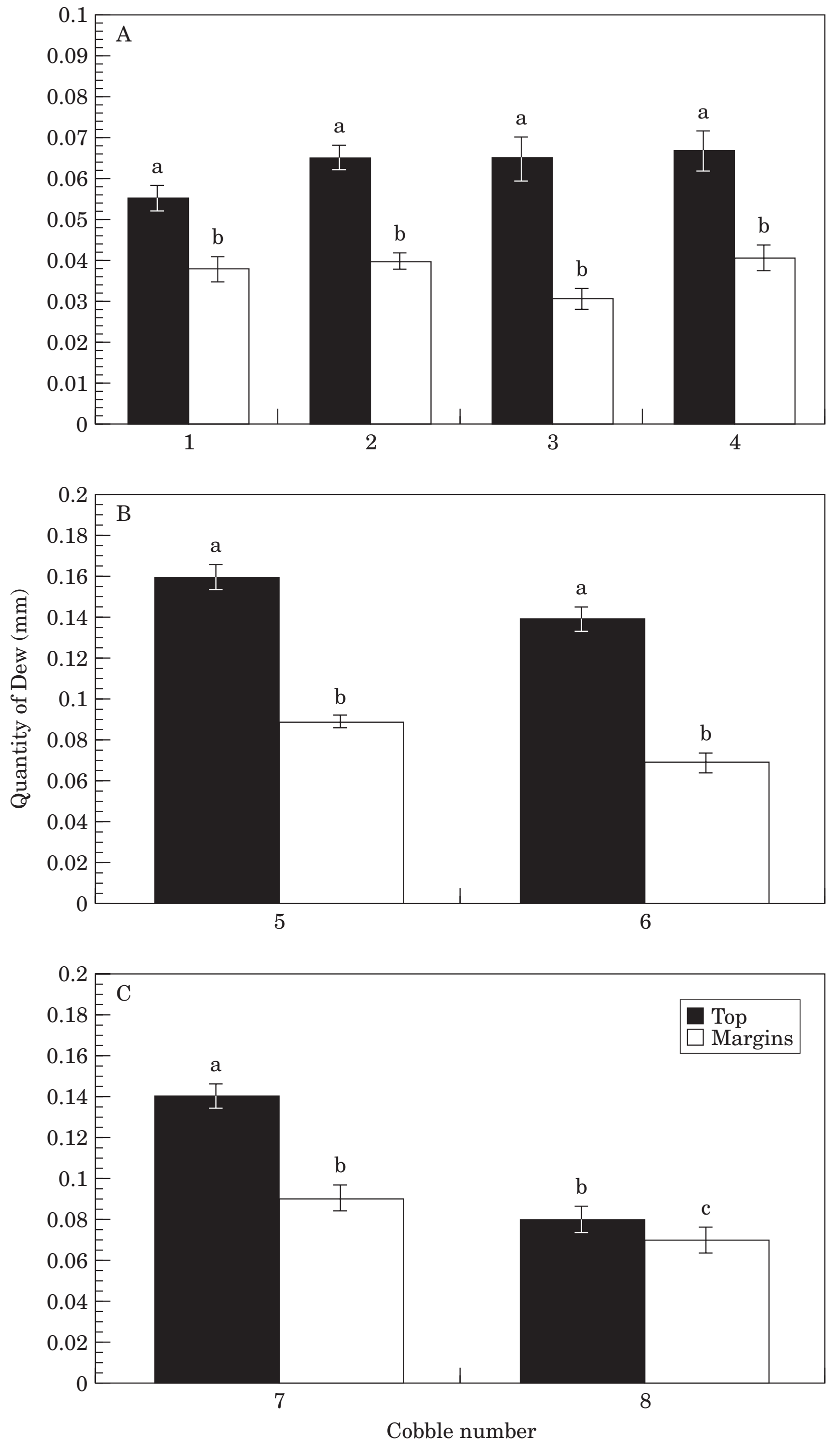

FIG. 5. Average daily dew quantities on top and margins of cobbles. A, four partially embedded cobbles with margin-dwelling lichen (cobbles 1–4); B, two cobbles with top-dwelling lichen (cobbles 5 & 6); C, reference cobbles with total lichen cover (cobbles 7 & 8). Different letters indicate statistically significant differences (paired t-test, $P<0{\cdot}05$).

FIG. 6. Water capillary rise on partially embedded cobbles (arrow) during the afternoon of 26 Feburary 1997, following surface moistening during the afternoon of the preceding day.

proportion of sky 'seen' by the relatively horizontal top sections of the cobbles i.e. the Sky View Factor (SVF) (Oke 1978). Both factors, ventilation and the SVF, may enhance outgoing radiational cooling (Oke 1978), resulting in lower nocturnal surface temperatures that will in turn promote dew condensation (Monteith 1957). Thus, while more efficient ventilation may explain the larger quantities of dew received on the loose compared to partially embedded cobbles, differences in the SVF may explain the larger deposition on the top of the cobbles in comparison to the sides or margins. Similar results, with horizontal surfaces receiving larger quantities than sloping surfaces, were also obtained by Angus (1958), and experiments with wooden boxes have shown that the quantity of dew condensed on the top of a box was approximately 4–5 times larger than that condensed on its side, normal to the ground (G. J. Kidron, unpublished). Whereas the differential rates of dew formation might explain the 'top' pattern of lichen zonation, it cannot provide a satisfactory explanation for the marginal pattern of zonation found on the partially embedded cobbles.

The quantities of dew characterizing the sides of the loose cobbles with top dwelling and the sides of the reference cobbles both fall within the range of 0·07–0·09 mm, indicating that these parts of the cobbles may have passed the moisture threshold necessary for lichen colonization. However, since the duration rather than quantity of dew may be the paramount factor in lichen establishment (Lange *et al.* 1970*a*, 1977; Kappen *et al.* 1980), a calculation of the annual estimated daylight activity available for each habitat was performed. The calculation was based on: (i) average dew deposition of 0·2 mm in Sede Boqer and 0·1 mm in Nizzana during periods of 94 and 53 days, respectively (Kidron 1999) and (ii) the surface moistness at a dune field, 6 km north of Nizzana, monitored for three years. The mean annual daytime surface moistness durations of dune sand and of a silty playa following rain were 250 h and 120 h, respectively. Assuming that the sandy loam, which characterizes the research site, may experience intermittent moistness for approximately 200 h, then this will in turn facilitate approximately 200 h of annual daytime moistness duration due to capillary rise.

Preliminary estimates of moistness duration on the cobbles, based on the above, is provided in Table 1. Whereas moistness duration on the top sections of the cobbles was assumed to last for 2 h, in accordance with the findings of Lange *et al.* (1970*b*), it was assumed that the sides or margins of the cobbles experienced shorter duration, in view of the close link between quantities of dew deposited and their duration (Kidron *et al.* 2000). The data suggest that the margins of partially embedded cobbles, and the top sections of loose cobbles, may enjoy an annual daylight activity of *c.* 320 h. The top sections of partially embedded cobbles may experience only 190–200 h of activity, whereas intermediate values of *c.* 260 h may be available to the sides of loose cobbles. Between 260–320 h are available to the reference particles, indicating that the moistness threshold necessary for lichen establishment may lie in the range of these values.

The values estimated here are similar, although somewhat lower, than those proposed for lichens inhabiting cobbles in Sede Boqer (Danin & Garty 1983), and are in

TABLE 1. *Estimated annual moistness duration for lichens inhabiting cobbles (in daylight hours)*

Source of moisture	Cobbles				
	Loose		Partially embedded		Reference
	Top	Sides	Top	Margins	Top and Sides
Rain[1]	60	60	60	60	60
Capillary Rise				200[2]	
Dew[3]	260[4]	200[5]	135[6]	55[7]	200–260
Total	320	260	195	315	260–320

1. Direct rain, based on an average of three years of measurement (1992–1994) with a tipping bucket rain recorder at the dune field, 6 km north of Nizzana (20 h)+estimated daylight moistness duration following rain (40 h).
2. The calculation is based on the estimated annual daylight time duration during which a flat sandy loam surface is wet.
3. Dew calculations here include fog and condensation.
4. Whereas dew precipitation was measured on the glass plates for 39 days, dew condensation during these days occurred only for 72% of the days on the cobbles. And thus, out of the 180 days assumed to be dewy in Nizzana, 130 days may supply moisture to the top of the cobbles. Based on an average period of photosynthetic activity of 2 h per dewfall event (Lange *et al.* 1970*b*), 260 h of moistness are expected at the top of the cobbles following dew.
5. Only 24 days out of 39 days of measurements, resulted in dew at the sides of the cobble, i.e. 110 dewy mornings with approximately 1·8 h of duration, i.e. 200 h.
6. Only 20 days out of the 39 yielded dew on these cobble sections, i.e. 90 days, with approximately 1·5 h of duration, i.e. 135 h.
7. Only 12 out of 39 dewy mornings resulted in dew on these cobble sections, i.e. 55 days, with approximately 1·0 h of duration, i.e. 55 h.

agreement with the lower dew deposition in Nizzana compared to Sede Boqer.

If this analysis is correct, then the threshold for lichen growth lies between 260 and 320 h. It is not clear yet whether the lower range of 260 h may suffice to initiate lichen growth. It may, however, suffice to sustain an already established population. According to this analysis, colonization of the top section of the partially embedded cobbles (with margin-dwelling lichens) may not be possible or may be extremely slow as long as the cobbles remain partially embedded and dew deposition on the top of the cobble is low. However, once loosened and detached from the surface, larger quantities of dew are predicted to be condensed on the top of the cobble as a consequence of better ventilation leading to a faster cooling rate and to lower nocturnal temperatures (Kidron 1988). Whereas the contact with soil may hinder outgoing radiational cooling of embedded cobbles, loose cobbles will lose their heat faster. This process was hypothesized to be accelerated by the afternoon breeze in the Negev leading to better ventilation (Kidron 2000*b*; Kidron *et al.* 2000).

Cobbles with top-dwelling lichens in Nizzana were not entirely covered by lichens, although they received similar quantities of dew to the reference cobbles. This could be owing to cobbles being relatively newly exposed and given sufficient time they may become totally covered in lichens. Alternatively, the reference cobbles currently entirely covered by lichens may have been re-positioned. According to this model, these cobbles were also once characterized by top-dwelling lichens, but owing to animal and human disturbance, they have been re-positioned, allowing the top section to become a side section and vice versa. In their new position, the top sections receive a preferential dew regime sufficient for lichen establishment and the cobble sides will receive less dew but still enough to sustain the existing population. Lichens that are re-positioned to the undersurface of disturbed cobbles will die, as clearly observed in the field and pointed out by other researchers (Danin 1986).

Field observations support the notion that cobbles with either top- or margin-dwelling lichens may eventually be completely covered by lichens. Indeed cobbles of similar size, some covered entirely by lichens, and others with top- or margin-dwelling lichens only, commonly occur at the same site. Whether an expansion of cover is solely a function of time or only occurs following a change in the cobble position (leading to a change in dew deposition) is not known. Another question yet to be answered is whether a gradual expansion occurs from the already colonized surfaces to bare sections or whether the mode of total cobble colonization in Nizzana follows a two stage pattern: (a) an initial top or margin colonization; (b) a concomitant colonization over all the bare areas following a sudden increase in dew deposition. Whilst both modes of colonization may concomitantly take place, field observations point to the paramount role of the gradual expansion mode. Both processes may however be slow, due to the low growth rates of lichens and the overall low rates of dew deposition at Nizzana.

Endolithic lichens cover over 95% of the surface area of cobbles in Sede Boqer, but only approximately 50–60% in Nizzana. The difference in lichen cover is probably a reflection of the lower average daily dew deposition measured in Nizzana (0·1 mm) compared to Sede Boqer (0·2 mm) (Kidron 1999, 2000*a*). It may also reflect the different lithology. Unlike the relatively massive strata of bedrock that characterizes Sede Boqer, the alluvial deposits (conglomerates) in Nizzana are made up of a mixture of cobbles and loessial sediments. Following erosion and anthropogenic disturbance, bare cobbles are continuously being exposed, resulting in new colonization.

Within the erosional cirque (Makhtesh Ramon) and south of the cirque, 6 km east and 15 km south-east of Mizpe Ramon, only top-dwelling lichen communities were observed. These sites receive lower rainfall and experience higher evaporation rates than Sede Boqer and Mizpe Ramon, which are located in the Negev Highlands north of the erosion cirque (Fig. 2). Being 350–400 m lower in elevation and further away from the Mediterranean Sea, the southern Negev is characterized by lower rainfall, lower quantities of dew, and higher evaporation rates (Zangvil & Druian 1980; Rosenan & Gilad 1985). It is suggested that here the current climatic conditions are too dry to sustain full lichen cover or to allow prolonged wetness due to capillary rise, and lichen growth is therefore confined to the top of the cobbles, receiving larger quantities of dew. It is also suggested that in the less arid parts of the Negev, such as the Negev Highlands, capillary rise may play a significant role in supplying water to lichens dwelling on top of small and partially embedded desert pavement pebbles, and may also explain narrow bands of cyanobacteria that occur frequently above the rock soil interface on rain-sheltered, and consequently otherwise barren, sections of cliffs.

Understanding the causes of lichen zonation may promote studies concerning the impact of moisture availability upon weathering and paleoclimate reconstruction. Thus, studies concerning dew weathering, yet to be assessed (Goudie 1989), and weathering due to capillary rise, may be feasible. Furthermore, since endolithic lichens leave a unique jigsaw puzzle-like weathering pattern on the rock surface (Danin *et al.* 1982), old weathering patterns of ancient lichen communities may serve as paleoclimate indicators (Danin 1985, 1986). While patterns of paleo top-dwelling lichens may indicate higher dew deposition, patterns of paleo margin-dwelling lichens may imply capillary rise due to longer hours of surface moistness.

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