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Cyanobacteria are confined to dewless habitats within a dew desert: Implications for past and future climate change for lithic microorganisms

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SUMMARY

Although covering almost all rock outcrops around the world, little is known regarding the factors that govern the spatial distribution of lithic cyanobacteria and lichens. This is also the case in the Negev Desert, where cyanobacteria predominate on the rock outcrops of the south-facing slopes and lichens on the rock outcrops of the north-facing slopes. Hypothesizing that abiotic conditions determine their distribution, radiation, temperature, rain, dew and fog were monitored over a two-year period (2008–2010) at cyanobacteria- and lichen-dwelling habitats within a first-order drainage basin in the Negev Highlands. While non-significant differences characterized the rain amounts, substantial differences in substrate temperatures were recorded which resulted in turn in fundamental differences in the non-rainfall water regime. While dew condensed at the rock outcrops of the lichen habitat, no condensation took place at the cyanobacteria habitat. Contrary to the common belief, cyanobacteria were found to inhabit dewless habitats. As a result, cyanobacteria solely rely on rain precipitation for growth and can therefore serve as bioindicators for dewless habitats within the dewy Negev Desert. The findings may have important implications regarding Earth colonization, soil forming processes and geochemical processes following climate warming. They may explain lichen expansion and subsequent O_2 increase during the mid Neoproterozoic providing indirect support for substantial photosynthetic activity and high weathering rates during this era.

1. Introduction

As photoautotrophs, cyanobacteria and lichens (a symbiotic association between a photobiont and a mycobiont) are of outmost importance to primary production. Inhabiting the most harsh and extreme habitats, and almost all rocky substrates (Chen et al., 2000), they are primary producers of organic C and N (Evans and Lange, 2001). As such, their importance goes back to early Earth colonization, where both groups provided most of the primary production (Altermann et al., 2006; Yuan et al., 2005; Guo et al., 2011). They are also known for their high weathering capabilities (Schwartzman and Volk, 1989; Aghamiri and Schwartzman, 2002), therefore fulfilling an important role in soil formation (Wright, 1985).

Both microorganisms are widely distributed. Lithic cyanobacteria and lichens occupy all continents. They abound around the Mediterranean Sea (Albertano and Urzi, 1999; de los Rios and Ascaso, 2005), Europe (Sigler et al., 2003), North America (Gerrath et al., 2000), South America, Africa, and Australia (Büdel, 1999), the Arctic (Cockell et al., 2003) and Antarctica (Wynn-Williams et al., 1999; Casanovas et al., 2013). In light of the growing amount of evidence of past and possible present Martian life (Schulze-Makuch et al., 2005, 2008), and ongoing efforts to identify reliable biomarkers for Martian life (Jehlička et al., 2009), such as microtunnels (Fisk et al., 2006), knowledge regarding the abiotic conditions necessary for cyanobacteria and lichen growth on Earth is essential for identifying comparable conditions on Mars.

Although regarded as an extreme desert (with a mean annual precipitation of ≈90 mm), lithobiontic microorganisms including cyanobacteria and lichens occupy the bedrock of the Negev Desert Highlands, such as at Sede Boqer and Avdat (Fig. 1), subjected to extensive research (Lange et al., 1970; Danin and Garty, 1983). With epilithic lichens dwelling on top of the surface and with cyanobacteria occupying the upper several millimeters of the surface (triggering rock weathering and the subsequent formation of pits and tunnels) they render the surface a different appearance. While

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[1] Regrettably, Dan passed away during the preparation of the ms.

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epilithic lichens (with green algae as photobionts such as *Caloplaca aurantia* (Pers.) Hellb., *Aspicilia farinosa* (Flörke) Arnold, and *Lecanora albescens* (Hoffm.) Branth and Rostr. predominating) (Fig. 2a) render the north-facing slopes (NFS) smooth, cyanobacteria (with the genus *Gleocapsa* predominating, see Friedmann and Galun, 1974; Danin and Garty, 1983; Kidron et al., 2011), occupying the south-facing slope (SFS), render the surface uneven, with a ragged, pit-like microtopography (Fig. 2b and c).

The current view maintains that water provided by rain and dew is the driving force behind the growth of the cyanobacteria (Friedmann and Galun, 1974; Smith et al., 2000; but see also Danin and Garty, 1983 that report no dew condensation during two nights of measurements). In a dew desert with annual average dew and fog precipitation of ~33 mm falling during ~195 days a year, dew was assumed to be the major water source for these lithobionts (Friedmann and Galun, 1974). While lichen activity following high relative humidity and dew condensation (vapor condensation at the substrate surface) as well as fog precipitation (i.e., substrate wetting by water droplets that condensed in the air) was monitored (Lange et al., 1970), no such data were provided for the cyanobacteria and no explanation for the confinement of the cyanobacteria to the bedrocks of SFS was offered. Furthermore, as part of a larger project (Kidron, 1999), temperature measurements took place at different substrates along a north–south gradient of the Negev Desert. Temperatures of cyanobacteria-inhabited bedrocks were found to be consistently warmer by at least 3–4 °C than lichen-inhabited bedrocks, bringing about the notion that the cyanobacteria-inhabited bedrocks are subjected to much lower dew condensation. Hypothesizing that the confinement of the cyanobacteria to SFS may stem from microclimatological variables and that understanding these microclimatological conditions may explain past colonization conditions, the goal of the current research was to monitor the abiotic variables at the cyanobacteria and the lichen habitats. Towards this goal, irradiance, temperatures, rain, dew and fog were measured. Mornings with high relative humidity only were not monitored despite the fact that high relative humidity is also utilized by most lichens (Lange et al., 1986). Nevertheless, since high relative humidity culminates in dew condensation for over 90% of the nights (Kappen et al., 1979), its contribution may largely be seen reflected in the amounts of dew and fog. As for the research location, it was confined to a single drainage basin thus avoiding the introduction of multiple variables that may affect the results, such as cloudiness and lithology.

2. Methods

The research site is located in Sede Boqer in the Negev Desert Highlands, Israel (34°46′E, 30°56′N), approximately 500 m above sea level (Fig. 1). Mean annual rain precipitation is 95 mm, limited to the winter months (November–April)). Average annual temperature is 17.9 °C; it is 24.7 °C during the hottest month of July and 9.3 °C during the coldest month of January (Bitan and Rubin, 1991). Annual potential evaporation is ~2600 mm (Evenari, 1981). Vegetation is low, usually below 50 cm, covering 10–20% of the surface.

A first-order drainage basin (~5 ha), consisting of Turonian limestone (Kidron and Zohar, 2010; Kidron and Starinsky, 2012), and characterized by relatively steep slopes of up to 24° (for the mid NFS) and 31° (for the mid SFS) was chosen (Fig. 2d). A pair of plots, 2 × 2 m, was demarcated at the rock outcrops of each of the mid NFS and SFS, both of which were inhabited by distinct communities. While euendolithic cyanobacteria that actively penetrate into the upper 5–10 mm of the rock cover 88% of the bedrock at SFS (with bare surfaces with and without microcolonial fungi occupying the remaining area), epilithic lichens cover 86% of the

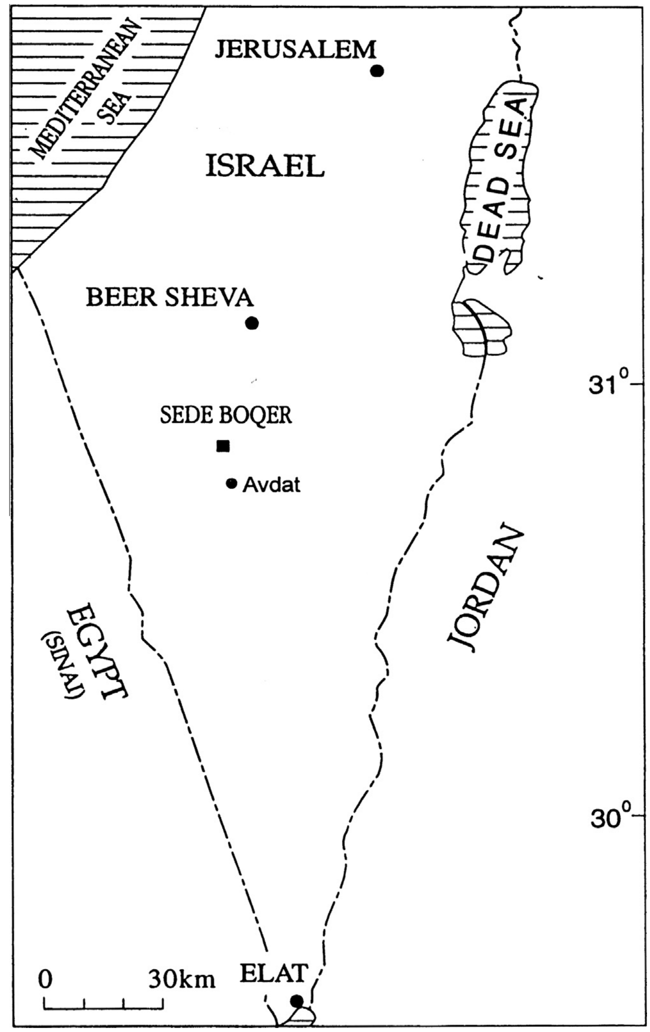

Fig. 1. Location of research site.

bedrock at NFS with the remaining area occupied by endolithic lichens (7%) or cyanobacteria (7%).

Temperatures were measured at the rock outcrops at each plot. In addition, in order to measure the actual rain reaching the slope, a small orifice rain gauge, 30 cm above ground, was installed next to each plot. Rain measurements took place following rain events with >1 mm of rain. Yet, due to technical difficulties, not all consecutive rain events, occurring within 1–3 days apart, were collected separately. Subsequently, the combined sum of the rain events was analyzed.

Dew and fog were measured manually. Periodical measurements took place during 2008–2010. In order to avoid condensation due to distillation (i.e., vapor originating from the wet ground following rain) and ensure dew condensation which solely stems from atmospheric vapor (Monteith, 1957), dew measurements were carried out only when the ground was dry.

Synthetic velvet-like 6 × 6 × 0.15 cm cloths (Universal company, Germany), directly attached to the rock surfaces with four adhesive stickers at their four corners, were used as a substrate for dew condensation. Passive absorbance of the atmospheric moisture by the lichens and the high correlation (with $r^2 = 0.88$) obtained between cloths and lichen thalii (*Ramalina maciformis* (Del.) Nyl. which abound at the site), placed next to one another on rock substrates (with *R. maciformis* mimicking epilithic lichens) (Fig. 3) justified the use of cloths for the monitoring of atmospheric moisture. The cloths, attached in the afternoon, were collected