

Lithobiont-dependent ionic composition in runoff water

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Abstract: Rock dwelling organisms (lithobionts) such as cyanobacteria (prokaryotes) and chlorolichens (eukaryotes) abound in the Negev Desert, where they cover almost all calcareous bedrocks and rock particles (cobbles, boulders). In a small limestone watershed in the Negev Highlands, cyanobacteria inhabit the south-facing (SF) bedrocks, epilithic lichens (accompanied by endolithic lichens) inhabit the north-facing (NF) bedrocks, while endolithic lichens cover most of the cobbles and boulders in both aspects. In order to study their contribution to runoff water, a pair of runoff plots was established on habitats with cyanobacteria, endolithic lichens, and epilithic lichens. Rain and runoff were collected during the hydrological year 2006/07, and the chemical composition (Ca, Mg, Na, K, Cl, SO₄, HCO₃, Si) of the rain and runoff water was analyzed. Several patterns were observed: (a) as indicated by Si, more dust accumulated on the bedrocks; (b) all substrates exhibited high amounts of Ca, and HCO₃; (c) while SF-bedrocks showed enrichment in K, both bedrocks (and especially the NF bedrocks), as well as the NF boulders showed an enrichment in Mg. While the enrichment in Ca and HCO₃ can be explained by the contribution of the limestone parent material, the enrichment in K and Mg can be explained by the contribution of the living lithobionts, with K being mainly contributed by the cyanobacteria and Mg mainly by the epilithic lichens. Ion enrichment may therefore be aspect-dependent, reflecting the lithobiont distribution within the drainage basin, partially explaining the enrichment in K and Mg previously recorded in runoff water from the Negev.

Keywords: Cyanobacteria; Dew; Lichens; Magnesium; Potassium; Negev Desert.

INTRODUCTION

The ionic composition of runoff water is a matter of continuous research (Bodi et al., 2014; Wang et al., 2016; Williams et al., 2001). Ions of the runoff water may reflect rock and soil weathering and erosion (Nativ et al., 1983; Vitousek, 1977), as well as contaminants, whether stemming from the atmosphere (Hagerberg et al., 2003), or from man-made fertilizers and pesticides (Durand, 1999; Rice et al., 1989; Segal-Rozenhaimer et al., 2004). The ionic composition of runoff water may affect the biota in runoff zones (Wang et al., 2016), and in springs, where they may eventually emerge (Fisher and Grimm, 1985). It is especially important in the evaluation and control of the quality of water collected in water reservoirs or reaching the groundwater table, used as drinking water and for irrigation (Knights et al., 2000; Yechieli et al., 1992).

The quality of runoff water was extensively studied in arid and semiarid regions (Al-Qudah et al., 2015; Fisher and Grimm, 1985). This was also the case for the Negev Desert (Nativ et al., 1983, 1997). When compared to rainwater, the ionic composition of runoff exhibited enrichment in all ions, especially in K (10 times higher), Na (5.4), HCO₃ (5.1), Mg (3.8), and Ca (3.5) (Nativ et al., 1997). While the enrichment of Na, and Mg is interpreted to result from the contribution of rain, the enrichment of HCO₃, Ca and K is interpreted to result from dust (Dethier, 1979), with the enrichment of K and Mg being also attributed to plant organic matter (Burg, 1998; Herwitz, 1986; Lombin and Fayemi, 1976). Although contributing large amounts of water, and therefore used also in ancient times for field irrigation (Evenari et al., 1982), the contribution of rock-dwelling organisms, such as cyanobacteria and lichens (generally known as lithobionts) to the chemical composition of runoff was not assessed.

In micro scale, almost all rocks in the Negev Highlands are covered by 'forests' of microorganisms (cyanobacteria) or small organisms (lichens). These lithobionts cover the calcareous rocks and rock particles (cobbles, boulders), serving as a buffer zone between the atmosphere and lithosphere. They may trap dust (Souza-Egipsy et al., 2004), but also increase surface weathering (Aghamiri and Schwartzman, 2002; Chen et al., 2000; Daghino et al., 2010; Hoffland et al., 2004; Viles, 1995).

The effect of lithobionts on rock weathering was long since established. This is especially so for lithic cyanobacteria (Danin and Garty, 1983; Gorbushina, 2007) and endolithic lichens (Stretch and Viles, 2002). As for epilithic lichens, no conclusive evidence was yet reported. While some scholars regard lichens, whether endolithic or epilithic, as a weathering agent (Danin and Garty, 1983), some consider epilithic lichens as providing a protective film, which plays a 'bioprotective' role. This was mainly reported from relatively soft parent materials, such as gypsum and limestone, where lichens provided a protective shield against the raindrop impact and dissolution by rainwater (Carter and Viles, 2005; Mottershead and Lucas, 2000).

Cyanobacteria, endolithic and epilithic lichens were found to have a very peculiar distribution. Within a second-order drainage basin in the Negev Highlands, cyanobacteria were found to be confined to the south- and east-facing limestone bedrocks, while epilithic and endolithic lichens inhabit the bedrocks and boulders of the sun-shaded aspects, the north- and the west-facing slopes (Kidron et al., 2014a, 2016). Endolithic lichens inhabit all rock particles, cobbles, and boulders at all slopes.

Extensive research that took place in the Negev Highlands evaluated the abiotic conditions that characterize each of the habitats. Expectedly, higher radiation was recorded at the sun-facing south-facing slope, reflected in higher daytime surface

temperatures. This was also reflected in nighttime temperatures that were by up to 5.3° higher than that of the north-facing bedrocks (Kidron et al., 2014a). Higher nighttime temperatures also characterize the east-facing bedrocks in comparison to the west-facing bedrocks. Exposed to the afternoon winds, the west-facing bedrocks were subjected to the efficient cooling effect of the western sea-breeze winds, which resulted in turn in early vapor condensation (Kidron et al., 2016). As for the rock particles, early vapor condensation due to lower nocturnal temperatures takes place on all rock particles, regardless of aspect. They also take place at the relatively shaded north- and west-facing bedrocks. Long hours of wetness duration following dew were found to explain the proliferation of epilithic lichens at the shaded habitats (Kidron et al., 2011). All in all, research in the Negev Highlands point to two main conclusions: (a) that cyanobacteria are confined to dewless habitats and as such only rely on rainwater for growth, and (b), dewy habitats are inhabited by lichens. Whereas endolithic lichens mainly inhabit the sun-exposed habitats, epilithic lichens mainly inhabit the shaded habitats (Kidron et al., 2011).

Serving as a buffer zone, and subsequently potentially affecting rain-rock relationships, we hypothesized that the lithobionts may contribute to substrate weathering and may therefore affect the ionic composition of runoff water. Moreover, albeit the fact that soil biocrusts are not water repellent in the Negev (as was the case in many other sand dunes; Dekker et al., 2001; Lichner et al., 2012), erosion and disintegration of soil biocrusts by runoff water was recorded (Kidron, 2001), pointing to the possibility that some disintegration of the lithobionts may be expected, and may therefore be reflected in the runoff water. In order to examine these hypotheses, a second order drainage basin was chosen and the rain and runoff water from the different lithobionts were analyzed for their chemical composition.

METHODOLOGY

The research site

The research site lies in the central part of the Negev Highlands, near Sede Boqer, Israel, approximately 500 m above msl (34°46'E, 30°56'N). Long-term mean rain precipitation is 95 mm, falling mainly between November and April (Rosenan and Gilad, 1985). 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).

The research was conducted in a second order drainage basin, consisting of Turonian limestone (Fig. 1a). Vegetation is low, usually below 50 cm, covering 10–20% of the surface. Lithobionts cover >95% of all rocks and rock particles. Cyanobacteria (with *Gleocapsa* sp. predominating) cover the south-facing bedrocks, while the south-facing rock particles are covered by endolithic lichens (with *Caloplaca alociza* predominating). The north-facing bedrocks and rock particles are covered by endolithic (with *Caloplaca alociza* predominating) and epilithic (with *Caloplaca aurantia*, *Aspicilia farinosa*, and *Lecanora albescens* predominating) lichens.

With cyanobacteria embedded within the upper 5 mm of the surface of the south-facing bedrocks, and engaged in boring activity and limestone dissolution (Danin and Garty, 1983; Kidron et al., 2014a), they render the surface a ragged and high microrelief (Table 1). A relatively high microrelief also characterizes the north-facing bedrocks, stemming from the relatively tall stature of the epilithic lichens. The shaded

position of the north-facing aspect allows for long hours of photosynthetic activity, subsequently resulting in high lichen biomass (Kidron et al., 2011). The high biomass of the lichens is also assisted by the stable conditions provided by the bedrocks (as opposed to cobbles or boulders that may occasionally roll down the slope) (Table 1). Alternatively, embedded within the upper 5 mm of the rock, endolithic lichens, that mainly inhabit the cobbles and boulders of the south-facing slope (but also the north-facing boulders) render a jig-saw appearance (see Danin and Garty, 1983) of relatively smooth surface. Being loose bodies and subsequently undergoing rapid nocturnal cooling, the boulders benefit from frequent vapor condensation, and relatively high amounts of dew (Kidron and Starinsky, 2019). Nevertheless, being exposed to the first sun beams, lichen activity in the south-facing slopes is relatively of short duration (Kidron, 2000a), subsequently resulting in relatively low biomass. However, benefiting also from dew, lichen biomass is nevertheless substantially higher than that of the rain-fed cyanobacteria (Table 1).

Methods

Four pairs of runoff plots (0.12–0.35 m²) were established. The plots were established on the three main groups of lithobionts: cyanobacteria, endolithic lichens, and epilithic lichens (Fig. 1b, c, d, e). As can be seen in Table 1, while cyanobacteria and mainly epilithic lichens characterize the south-facing (SF) and north-facing (NF) bedrocks, respectively, epilithic lichens mainly characterize the NF boulders, while endolithic lichens characterize the SF boulders.

For plot construction, an insulated 1.5 cm-diameter plastic-covered flexible electrical cable was used. The cable was glued with silicon to the rock surfaces. All plots were connected to 1 liter sterile plastic bottle. A dense net (with 1 mm x 1 mm opening) prevented any entry of >1 mm particles, insects and snails into the collecting bottle.

For the collection of the rain, a 40 cm-diameter funnel mounted on top of a 1.5 m-high pole was installed. The funnel led to a 1-liter sterile plastic bottle that collected the rainwater. A larger diameter rim around the funnel prevented bird landing within the funnel, and subsequently possible contamination of the rainwater by birds. A dense net (as described above) prevented contamination by insects.

Rain and runoff were collected immediately after each rain event and no later than 24 h after the event. Malfunctioning of some plots did not always allow for the collection of runoff water from both plots of each habitat. The collected water was poured into sterile 250 ml plastic bottles and then taken to the lab. The funnels were cleaned and all bottles used to collect the rainwater and runoff water were replaced with new bottles.

All samples were immediately measured for pH and electrical conductivity (EC), filtered with #42 Whatman filter papers, and stored at 4°C until processing. Calcium (Ca), magnesium (Mg), sodium (Na), potassium (K), sulfate (SO₄, as S), and silicon (Si) were measured using ICP-OES by automated Perkin-Elmer Optima-3000 radial ICP system. Chloride (Cl) was analyzed using automated Lachat instruments model QE flow injection analysis (FIA) system with colorimetric detection (Eaton et al., 1995). Bicarbonate (HCO₃) was determined by titration (with 0.02 N HCl), with BDHK #4480 as indicator. The ICP and FIA precision are smaller than 1%.

One-way ANOVA was performed in order to assess whether ionic composition is determined by the habitat location. Results were considered significant at $P < 0.05$.



Fig. 1. View on (a) the rain collector, (b) the south-facing slope with a runoff plot on the bedrock in the center, (c) epilithic lichens at the north-facing bedrocks, (d) plot with epilithic lichens on the north-facing slope, and (e) plot with cyanobacteria inhabiting the south-facing bedrocks.

Table 1. Properties of runoff plots. Values in parenthesis indicate one SE.

Plot	Area (m ²)	Angle (°)	Micro-relief (mm/cm)	Chlorophyll <i>a</i> (mg m ⁻²)	Epilithic lichens (%)
R-NF1	0.28	35	2.39 (0.25)	118.5 (24.3)	85
R-NF2	0.26	34	2.34 (0.26)	141.5 (19.5)	80
R-SF1	0.18	24	2.87 (0.30)	21.5 (9.6)	
R-SF2	0.35	24	2.95 (0.32)	17.5 (6.3)	
B-NF1	0.12	37	1.11 (0.15)	86.6 (20.5)	60
B-NF2	0.13	33	1.04 (0.19)	63.9 (15.7)	65
B-SF1	0.18	34	0.98 (0.16)	49.5 (15.8)	
B-SF2	0.26	20	1.01 (0.15)	59.8 (19.0)	

RESULTS

Precipitation during the hydrological rain 2006/07 was above average, 143.2 mm. Most storms were of low depth of < 10 mm (Fig. 2). Substantial runoff was only produced from > 10 mm storms. These included the storms of 27–28.12.2006 (with 30.9 mm of precipitation), 20–21.1.2007 (19.4 mm), 15–17.3.2007 (14.4 mm) and 13.4.2007 (38.2 mm).

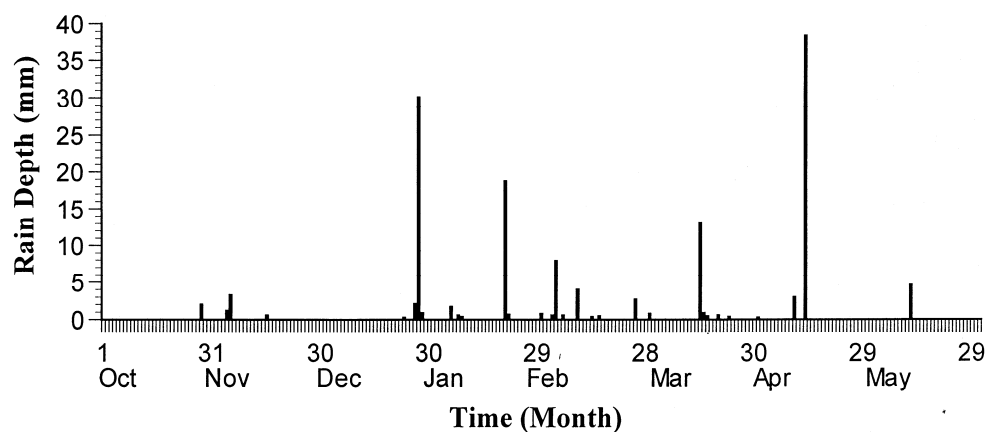
The pH, EC, and the ionic concentrations of rain and runoff from the SF and NF bedrocks and boulders are shown in Table 2. Expectedly, higher pH (7.11–7.93) and EC (0.23–0.83 mS cm⁻¹) characterized the runoff water, in comparison to the pH (7.04–7.49) and EC (0.21–0.39 mS cm⁻¹) of the rain. While

the rain was of Ca(HCO₃)₂-CaCl₂ type, the runoff was of Ca(HCO₃)₂ type.

As verified by one-way ANOVA, the ionic concentration of runoff was habitat-dependent. As can be seen in Figure 3, significant differences characterized the ionic composition of the different habitats ($P = 0.020$). This is clearly seen in Figure 4a and Figure 4b, which show the enrichment ratios for the bedrocks and the boulders, respectively. Thus for instance, NF and SF bedrocks showed an overall enrichment in almost all ions, particularly in HCO₃, Si, Ca and Mg. High enrichment in K was recorded in the south-facing bedrocks. As for the boulders, they all showed enrichment in Ca and HCO₃. Yet while SF boulders show depletion in almost all ions, NF boulders show enrichment in Ca, HCO₃ and Mg.

Table 2. Chemical composition of the rain and runoff water. TDI = total dissolved ions. nd = no data.

Date and amount of rain (mm)	Source	Na (meq/l)	K (meq/l)	Mg (meq/l)	Ca (meq/l)	Cl (meq/l)	SO ₄ (meq/l)	HCO ₃ (meq/l)	Si (mg/l)	TDI (mg/l)	EC (mS/cm)	pH
27–28.12.06 (30.9)	Rain	0.277	0.016	0.077	0.514	0.426	0.272	0.099	0.039	50.8	0.21	7.04
	R-NF1	1.967	0.036	0.647	2.679	1.601	0.889	0.840	1.489	219.1	0.31	7.49
	R-SF1	1.069	0.053	0.361	2.110	1.388	0.486	1.710	1.189	250.2	0.30	7.64
	R-SF2	1.063	0.049	0.264	1.040	1.497	0.480	0.431	0.784	152.8	0.30	7.72
	B-NF1	0.284	0.014	0.118	0.580	0.371	0.224	0.396	0.269	68.2	0.30	7.65
	B-NF2	0.197	0.010	0.078	0.540	0.240	0.146	0.436	0.293	58.9	nd	nd
	B-SF2	0.300	0.008	0.098	0.815	0.391	0.121	0.707	0.267	87.7	0.23	7.75
	20–21.1.07 (19.4)	Rain	1.369	0.035	0.322	0.780	1.636	0.490	0.370	0.282	156.5	0.35
20–21.1.07 (19.4)	R-NF1	0.840	0.021	0.330	1.270	1.144	0.369	0.938	1.351	165.1	0.37	7.68
	R-NF2	0.815	0.021	0.342	1.430	1.023	0.350	1.229	1.433	180.5	nd	nd
	R-SF2	0.567	0.050	0.235	1.330	0.700	0.536	0.940	0.889	152.4	0.39	7.86
	B-NF1	0.734	0.028	0.405	1.140	1.034	0.618	0.651	0.593	151.8	0.66	7.76
	B-NF2	0.423	0.010	0.195	1.200	0.490	0.475	0.854	0.632	128.8	nd	nd
	B-SF1	0.181	0.007	0.078	0.949	0.275	0.135	0.800	0.352	89.4	0.24	7.93
	B-SF2	0.481	0.008	0.198	1.130	0.703	0.243	0.866	0.455	125.8	0.45	nd
	15–17.3.07 (14.4)	Rain	0.136	0.013	0.050	0.540	0.189	0.244	0.302	0.356	51.9	0.38
R-NF1		0.557	0.050	0.305	2.600	0.947	0.494	2.026	1.330	251.5	0.42	7.88
R-NF2		0.702	0.056	0.359	2.640	1.176	0.494	2.079	1.273	267.9	0.43	7.86
R-SF1		0.569	0.102	0.261	2.150	0.765	0.729	1.582	1.698	222.0	0.40	7.83
R-SF2		1.111	0.137	0.342	2.400	1.369	0.902	1.706	2.052	279.1	0.48	7.86
B-NF1		0.116	0.023	0.100	1.480	0.204	0.199	1.307	0.494	131.0	0.68	7.86
B-NF2		0.121	0.025	0.076	1.191	0.234	0.179	1.070	0.361	106.3	nd	nd
B-SF1		0.273	0.039	0.112	1.620	0.372	0.343	1.324	0.487	152.1	0.83	7.80
13.4.07 (38.2)	B-SF2	0.150	0.023	0.140	1.910	0.219	0.191	1.808	1.155	171.6	nd	nd
	Rain	1.085	0.103	0.387	2.980	1.343	1.535	0.675	1.851	235.9	0.27	7.49
	R-NF1	0.703	0.076	0.357	2.620	1.149	0.673	1.929	1.660	266.7	0.39	7.94
	R-NF2	1.042	0.085	0.488	2.800	1.905	0.828	1.676	1.759	298.9	0.52	7.86
	R-SF1	0.726	0.108	0.250	2.070	0.921	0.841	1.391	1.985	223.3	0.39	7.91
	R-SF2	0.933	0.129	0.327	2.450	1.207	1.116	1.512	2.083	268.2	0.49	7.86
	B-NF1	1.271	0.113	0.668	3.170	2.213	1.315	1.682	1.357	349.6	0.26	7.98
	B-SF2	0.606	0.066	0.198	2.170	0.873	0.752	1.410	1.198	215.5	0.27	7.90

**Fig. 2.** Rain precipitation during 2006/07.

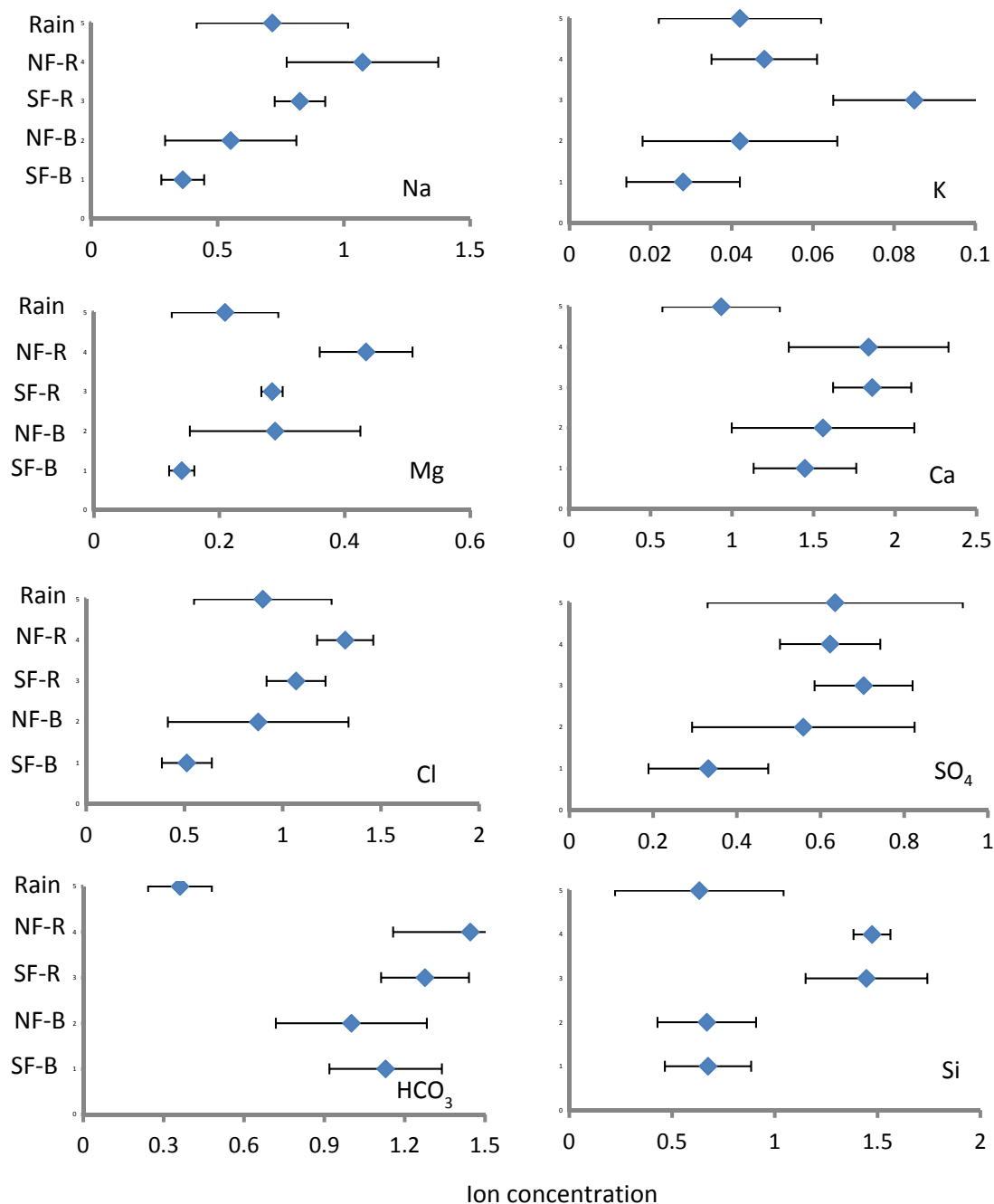


Fig. 3. Average and one standard error of the chemical composition (in meq/l, excluding Si in mg/l) of rain, and runoff at the north-facing rocks (NF-R), south-facing rocks (SF-R), north-facing boulders (NF-B) and south-facing boulders (SF-B).

DISCUSSION

The pH of the rain was similar to other reports from the Negev (commonly between 7.0 to 8.3; Herut, 1992; Nativ et al., 1983, 1997), while the EC of the rain fell within the lower values reported from the Negev (up to 0.88 mS cm^{-1} ; Nativ et al., 1983). Also the EC of the runoff was lower than that recorded of floodwater in the Negev (up to 3.5 mS cm^{-1} ; Nativ et al., 1983). This may be explained by the fact that (a) our measurements were carried out on rock surfaces while all other measurements were conducted on soil, and (b) the small plot size and therefore the short distance and traveling time, implying short duration of rain-substrate contact, and therefore lower salinity. These unique conditions of our experiment may

also explain the lower EC ratio of runoff to rain (2–3 fold higher) in comparison to floodwater values in the Negev (up to 6-fold higher; Nativ et al. 1983), or other deserts, such as the Amargosa Desert, Nevada (10-fold higher; Al-qudah et al., 2015).

Generally, while Na, Mg and Cl stem from the sea, HCO_3^- , SO_4 and K stem from land (dust) (Nativ et al., 1983). With runoff being $\text{Ca}(\text{HCO}_3)_2$, it is assumed to result from dust (Nativ et al., 1997). Higher HCO_3^- characterize also other reported runoff waters (Fisher and Grimm, 1985). As for SO_4 , it is assumed to be mainly provided from sabkhas in North Africa (Nativ et al., 1983, 1997). Overall, higher amounts of Cl than Na characterized the runoff water, which according to Nativ and Mazor (1987) may imply that some Cl is provided by CaCl_2 or MgCl_2 salts.

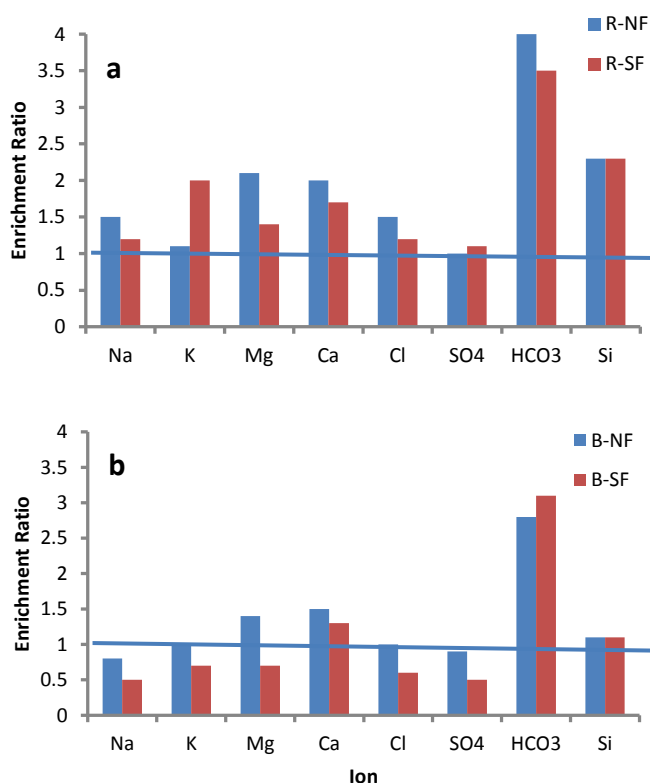


Fig. 4. The average values of the enrichment ratio (ER) of the bedrock (a) and boulder (b) surfaces of all examined ions.

When analyzed in accordance with habitat, especially high Na, Ca, Mg, Cl and Si characterize the NF bedrocks. With the parent material having only trace amounts of Si (Yaalon, 1963; Kidron et al., 2014a), the high concentration of Si in the runoff water points to accumulation of dust. Indeed, located at the shadow of the high-speed dust-laden winter winds, high amounts of dust accumulation took place at the NF slopes of the current drainage basin (Kidron et al., 2014b). Interestingly, the amount of Si in the runoff water that stemmed from the boulders was low. This can be explained by the relatively smooth surface of the boulders (especially the SF boulders), and the efficient leaching of the dust from the small-size boulders already during the low-depth rains of October, 28th (2.0 mm) and November 4–5th (4.5 mm). Apparently, unlike the boulders, the high surface area coupled with the high microrelief that characterize the NF bedrocks serve as a relatively potent sink for dust.

Both bedrocks, NF and SF, exhibited high concentration of Ca and HCO₃. Although slightly lower, high concentrations of Ca and HCO₃ were also found in the runoff water from NF and SF boulders. While some Ca and HCO₃, especially in the bedrocks, can be explained by the presence of calcite in the dust (which comprises approximately 30% of the dust composition of the Negev; Ganor, 1975; Offer and Azmon, 1994), the high Ca and HCO₃ along with the similar amounts of Si in the boulders and rainwater (indicating dust leaching from the boulders) point to limestone weathering also from the boulders. Whether due to the production of carbonic acids by the cyanobacteria and lichens or the mechanical action of the tightly attached fungi (Fry, 1924; Lee and Parsons, 1999), or following the excretion of various acids by the lichens (oxalic, citric, gluconic and lactic and also 'lichen acids'; Adamo and Violante, 2000), limestone weathering is taking place. This was verified by the high concentration of Ca and HCO₃ also at the NF bedrocks which

are inhabited by epilithic lichens. And thus, although residing on top of the rock, and seemingly not closely associated with the rock surface, bioprotection by the epilithic lichens, as suggested in some publications (Carter and Viles, 2005) was not verified by the current findings.

Of special interest are the concentrations of K and Mg. High concentration of K characterizes the SF bedrocks, while high concentrations of Mg characterize the NF bedrocks and boulders as well as the SF-bedrocks.

Enrichment in K and Mg in runoff water or throughfall was long ago noted. High enrichment ratio of Mg was reported in runoff from the Amargosa Desert, Nevada (10; Al-qudah et al., 2015); from throughfall in Israel (4–5; Burg, 1998) or runoff in the Negev (3.8; Nativ et al., 1997). The enrichment ratios reported for K were even higher. It was reported following lab experiments (2.5; Sharpley, 1985); and from runoff from North Carolina (2.4–4.2; Johnson and Swank, 1973), Nevada (10; Al-Qudah et al., 2015), Malaysia (45; Crowther, 1987), and Burkina Faso following sprinkling experiments on microdunes (110; Ribolzi et al., 2003). It was also reported from throughfall in Israel (13–19; Burg, 1998) and runoff from the Negev (10-fold; Nativ et al., 1997). Generally, these enrichments were attributed to biological activity (Johnson and Swank, 1973), or more specifically to plant and litter contribution (Burg, 1998; Herwitz, 1986; Lombin and Fayemi, 1976). Given the limited cover of plants in deserts, the contribution of the clay fraction of dust was suggested (Herut, 1992; Nativ et al., 1997; Nettleton et al., 1973; Ribolzi et al., 2003; Sharpley, 1985).

Nevertheless, meager amounts of clay in the Negev dust (Offer and Azmon, 1994), lack of correlation between Na and K (which exclude feldspar weathering), and lack of correlation between K and Si, exclude the possibility that K enrichment stems from dust. The meager amounts of K in the parent material (Kidron et al., 2014a; Yaalon, 1963) also exclude the possibility that K enrichment stems from the parent material. No satisfactory explanation was given by Nativ et al. (1997) for the enrichment in Mg. We therefore suggest that the enrichment of both cations, K and Mg, can be explained by lithobiont contribution.

With Mg being an important structural element of the chlorophyll pigment (Beraldi-Campesi et al., 2009), enrichment of Mg is expected following disintegration and erosion of algae or cyanobacteria. This may however be hindered in endolithic lichens, where the algae are well protected by the rock minerals and fungi. Cyanobacteria and especially epilithic lichens are much less protected. Residing above the rock surface and characterized by high biomass and high microrelief, epilithic lichens are relatively vulnerable to erosion, whether by the raindrop impact or runoff flow. Supporting evidence for our interpretation is data provided by Wright (1999), who reports an enrichment of Mg in a lake following cyanobacterial death and disintegration.

As for K, it plays a central role in the regulation of the turgor pressure of cells (Allison and Walsby, 1985; Meury et al., 1985). While organic molecules mainly regulate the turgor pressure of green algae and fungi (Meury et al., 1985), K is largely responsible for the regulation of the turgor pressure in cyanobacteria (Hastings and Gutknecht, 1976; Meury et al., 1985). Being preferentially accumulated within the cell, and preserving the turgor pressure during dry conditions, K is however released into the liquid media under wet conditions to prevent osmolytic rupture of the cell membrane due to excess entry of water into the cell (Kieft et al., 1987). The enrichment of K at the south-facing bedrocks can be therefore explained by the excretion of K by the cyanobacteria following wetting.

Obviously, loss of essential ions during runoff events may be possible only if these ions will be accumulated during previous occasions. Accumulation of ions implies lower concentration of ions in the runoff water in comparison to rain, and possible adsorption of certain ions to the rock minerals or absorption of necessary ions by the lithobionts. This however was not common under the current conditions. We however suspect that this will be much more common during low-depth rain events and following dew. We therefore suggest that during light rain events, which characterize most of the Negev rainstorms (Kidron and Yair, 1997), accumulation of essential ions by the lithobionts takes place. We also maintain that especially high accumulation of nutrients will take place following dew. This is facilitated by the low amounts of dew water (commonly up to 0.2–0.3 mm; see Kidron, 1999, 2000b), which are unlikely to facilitate leaching and the high concentration of nutrients characterizing the dew (Kidron and Starinsky, 2012).

As far as the substrate size is concerned, the current findings highlight the unique abiotic-biotic relationship. Although of identical lithology as the bedrocks, boulders and cobbles differentially affect the surface temperature regime (Kidron et al., 2016), triggering preferential dew accumulation (Kidron et al., 2014a), responsible in turn to different lithobiont population (Kidron, 2000b). The abiotic (dew)-biotic (lithobionts) relationship is accentuated by preferential accumulation of nutrients by the dew (abiotic). This preferential nutrient accumulation (Kidron and Starinsky, 2012) may enrich the surroundings of the boulder or cobble with nutrients (abiotic), serving (together with the addition of water through runoff) to increase microbial activity and plant biomass (biotic) in the interspace between the boulders and cobbles (Lahav and Steinberger, 2001). Massive bedrocks on the other hand may preferentially trigger dust accumulation and runoff generation (abiotic), providing water and nutrients to strips and patches of soils within the rocky slopes or at the bedrock-soil interfaces (Yair and Danin, 1980). During large rainstorms, the runoff flow along gullies and wadis may contribute water and nutrients to vascular plants (biotic) at downstream alluvial fans (BenDavid-Novak and Schick, 1997).

The current findings may explain some of the enrichments in ion concentration of the runoff flow and floodwaters in the Negev, and specifically, the enrichment in K and Mg (Nativ et al., 1997; Yair et al., 1991). They may also explain, at least partially, the high enrichment ratio in K and Mg also in the Negev groundwater (Nativ et al., 1997). As thoroughly shown during the current research, ion composition is aspect-dependent, closely linked to the type of lichens and to prokaryote-eukaryote distribution within the drainage basin.

CONCLUSIONS

Ionic composition of runoff water from many parts of the world is often reported to be enriched in Ca, HCO₃, K and Mg. This was also found in runoff water following natural rainstorms during the hydrological year 2006/07 on limestone-covered lithobionts (cyanobacteria, and endolithic and epilithic lichens) in the Negev Desert. While all rock-dwelling lithobionts (whether cyanobacteria on the SF bedrocks or epilithic and endolithic lichens on the NF bedrocks) showed an enrichment of Si (attesting to dust accumulation and subsequent leaching by runoff), all habitats exhibited an enrichment in Ca and HCO₃ (indicating calcium carbonate dissolution by all types of lithobionts). Cyanobacteria and epilithic lichens also showed enrichment in Mg, whereas a pronounced enrichment in K was

recorded at the cyanobacteria habitat. While the lack of enrichment in Mg from the SF boulders attest to the relatively high resilience of the more protected endolithic lichens to erosion, the enrichment of Mg at the cyanobacterial habitat (SF bedrocks) and that of the epilithic lichens (NF bedrocks and boulders) is attributed to chlorophyll decomposition following disintegration and erosion of some of the cyanobacteria and the epilithic lichens. Serving as compatible solutes in cyanobacteria (assisting the cell to keep the essential turgor pressure), the enrichment in K is attributed to its excretion following the onset of rain. The current findings highlight the unique abiotic-biotic relationship. The abiotic factors (aspect, type of substrate whether bedrock or boulder) affect the temperature regime and hence the type of lithobionts (whether cyanobacteria, epilithic or endolithic lichens) which in turn affects dissolution, erosion, decomposition, and subsequently ionic composition. This may explain the high variability and enrichment of the above-mentioned ions in runoff water, and may affect in turn plant nutrition and groundwater table composition.

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