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REGULAR ARTICLE

What stabilizes biological soil crusts in the Negev Desert?

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Abstract
Aims Biological soil crusts (biocrusts) are widespread in many drylands, where plant growth is limited due to water scarcity. One of their most important functions is the stabilization of the topsoil, particularly in regions with sandy soils prone to desertification. Since the mechanisms playing a role in soil stabilization are poorly understood, this study aims to shed light on the connection between crust stability and different cementing agents.
Methods We measured the penetration resistance and the concentrations of different cementing agents of biocrusts in the Israeli Negev Desert. Structural equation modelling was performed to examine the direct and indirect effects of the variables analyzed and identify variables that are best able to explain the observed patterns of penetration resistance.
Results All observed variables showed a high variability within and between sites. Structural equation modelling revealed that the main parameters explaining penetration resistance are the content of fines and the electrical conductivity, while carbonates and organic carbon only have an indirect effect.
Conclusions Our results suggest that adding silt and clay to (natural or induced) biocrusts is very likely to produce stronger, more stable crusts, which will be more effective in combating desertification and improve their ability to survive trampling by livestock.

Keywords Penetration resistance · Biocrust · Surface stability · Grazing potential · Desertification · Structural equation modelling · Ecosystem restoration

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Introduction

Biological soil crusts (biocrusts) consist of different microscopic (cyanobacteria, green microalgae, fungi, bacteria) and macroscopic (lichens, mosses) organisms, which live on, or in, the uppermost millimeters of many soils, binding the mineral particles together. They are the dominant soil cover in many drylands, where higher vegetation cannot thrive due to water scarcity (Belnap et al. 2016). Because of their poikilohydric nature, most crust organisms are able to adapt to even the harshest environmental conditions (Sancho et al. 2016) and survive long periods without water. This makes them suitable elements for restoring degraded dryland ecosystems (Antoninka et al. 2016). Stabilizing formerly

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mobile sediments, which initiates pedogenetic processes, is one of the most important functions of biocrusts (Lan et al. 2014; Belnap and Büdel 2016), particularly in arid regions that are prone to desertification. The first biological cementing agents in early stage biocrusts are the extracellular polymeric substances that many crust organisms excrete (Van Ancker et al. 1985; Hu et al. 2002). They are the first source of organic carbon during initial soil development (Mager 2010), and prevent the top millimeters of the soil from being eroded. Following the initial stabilization of the soil surface, other mechanisms start to play a role in the stabilization process, such as the input of fine dust via atmospheric deposition. In the Negev Desert, Israel, this input has been shown to have a strong effect on the nutrient balance of the soils (Littmann and Schultz 2008). The dust is composed of calcareous and siliceous particles of the clay and silt fraction, which also affect soil surface stability by enhancing soil aggregation (Totsche et al. 2017). Various studies have demonstrated the high potential of biocrusts to immobilize unstable sandy soils and consequently, increase their stability and fertility (Lan et al. 2014; Xiao et al. 2015; Zaady et al. 2016). In these studies, the researchers added cyanobacterial (or bryophyte) inoculum and detected an increase in soil stability, but did not analyze the mechanisms that were responsible for the increased stability. To our knowledge, no study exists that reports the effects of different stabilizing agents on biocrust stability. Therefore, information on the mechanisms responsible for cementing the sand grains in natural crusts is not available. Shedding light on those mechanisms and furthering our understanding of the process of (early) soil stabilization is crucial if we are to realize the full potential of biocrusts as tools for restoring ecosystems and combatting desertification.

The contribution of biocrusts to landscape stability can be assessed in various ways, such as measuring their effect on wind and water erosivity by conducting rainfall and wind tunnel experiments (e.g. Brungard et al. 2015; Chamizo et al. 2017). However, when investigating landscape stability in terms of the carrying capacity of pastoral land use (i.e. grazing potential), the variable of interest is the breaking point of the crusts, measured as penetration resistance. This can be determined in various ways. The breaking point describes the maximum amount of pressure that a biocrust can withstand before breaking when, for example, grazing animals walk upon the crust. This breaking point can be determined in the laboratory, using, for example, a simple balance (as described by McKenna Neuman et al. 1996) or with a more modern, high-resolution loading frame for material testing. To measure crust stability in situ, however, one needs smaller and more portable devices, for example a simple pocket penetrometer, such as that used by Chamizo et al. (2015). Another option for obtaining high-resolution, and depth-related, penetration resistance data is the electronic micropenetrometer described by Drahorad and Felix-Henningsen (2012). While the high-resolution that is possible with the electronic micropenetrometer is desirable in many cases, it is not applicable for the purpose of this study. The reason for that is that the micropenetrometer gives depth-related penetration resistance data at a sub-millimeter scale (39 μm vertical resolution), and we could not sample the crust in the field with this high precision in order to determine the variables of interest and correlate them to the penetration resistance at each respective depth. Furthermore, a very important reason why the electronic micropenetrometer is not well suited for large-scale studies is that single measurements are time consuming, which is a major drawback when working in military areas with restricted access. Thus, for our study we used a simple, hand held manual penetrometer for the top layers, as this allowed us to take multiple measurements relatively quickly. In this manuscript, we ask whether changes in crust stability are reflected in changes in soil characteristics by measuring penetration resistance in relation to the most likely cementing agents (carbonates, salts, organic carbon, and fines) on natural occurring crusts using structural equation modelling.

Material and methods

Study sites and sampling

Our study sites are located in the NW Negev Desert, Israel and lie directly along the political border between Israel and Egypt. Along this border, we established sampling plots in three study sites (from south to north); Nizzana-south, Nizzana-84 and Nizzana-69. The area is subdivided into two large sand fields, the Haluza Agur Sands (containing the study sites Nizzana-84 and Nizzana-69) and the sand dunes of Sde Hallamish (containing the study site Nizzana-south) and is characterized by a steep rainfall gradient. Along this gradient, the amount of annual rainfall increases from approx.

90 mm in the southernmost study site (Nizzana-south) to about 170 mm in the northernmost site (Nizzana-69), which has a strong effect on the development and characteristics of the biocrusts in the region (Yair et al. 2011). Sampling took place at the beginning of the dry season in 2011. In each of the sites, we sampled one plot of 1 m^2 at three different relief positions. We chose to sample at the mid slopes of the north- and south- facing dunes as well as in the interdune (resulting in three plots per site) in order to account for microclimatic differences and cover a wide range of different crust types (Fig. 1). A more detailed description of the study sites can be found in Keck et al. (2016). The sampling design was one square of 100 × 100 cm, which we then divided into 25 sub-squares of equal size (20 × 20 cm, or 400 cm^2) that served as pseudo-replicates. Although pseudo-replication should be avoided if possible (Freeberg and Lucas 2009), in our case this was due to the limited time that we were allowed to enter the sites. Notwithstanding any issues of pseudo-replication, we believe that our study can still improve our understanding of biocrust stability (cf. Davies and Gray 2015). In each of the smaller squares, we measured the penetration resistance by pushing the penetrometer probe into the soil to a depth of 4 cm. After the penetration resistance measurement, we sampled the complete crust without the underlying soil in each of the squares to obtain enough soil material for all analyses. Depending on the thickness (between 1 and 4 cm) and bulk density of the crust, this resulted in different amounts of soil, which is the reason why we could determine texture for only 193 of the 225 samples. Crust coverage was almost 100% for all plots with the exception of a few annual plants. Any annual plants were avoided for both penetration resistance measurements and soil sampling. Since the water content (or, more precisely, the water tension) of the soil has a strong effect on the penetration resistance, one either has to measure the water content (or matrix potential) and include a correction factor (e.g. Chamizo et al. 2015), or measure on dry soils, as we did in the present study.

Penetrometer

We used a simple manual hand penetrometer, Type IB (Eijkelkamp Agrisearch Equipment 2009) to measure biocrust penetration resistance. The penetrometer consists of a steel probe with a conical tip and steel springs of different strengths, it is relatively quick to assemble and simple to handle, which allowed us to measure many repetitions in a short time. For this study, we used the 50 N spring and the 0.5 cm^2 cone in order to realize the highest sensitivity of the penetrometer.

Soil analysis

Iron oxides are not a significant cementing agent in the Negev Desert because of the low amounts of amorphous iron oxides coating sand grains in the region (Blume et al. 2008; Roskin et al. 2011). Hence, the most relevant cementing agents are the contents of $CaCO_3$, salts, organic carbon (TOC) and fines (silt and clay). After sampling, the soil was air dried at 40 °C, sieved to 2 mm according to ISO 11464 and partially fine ground for the

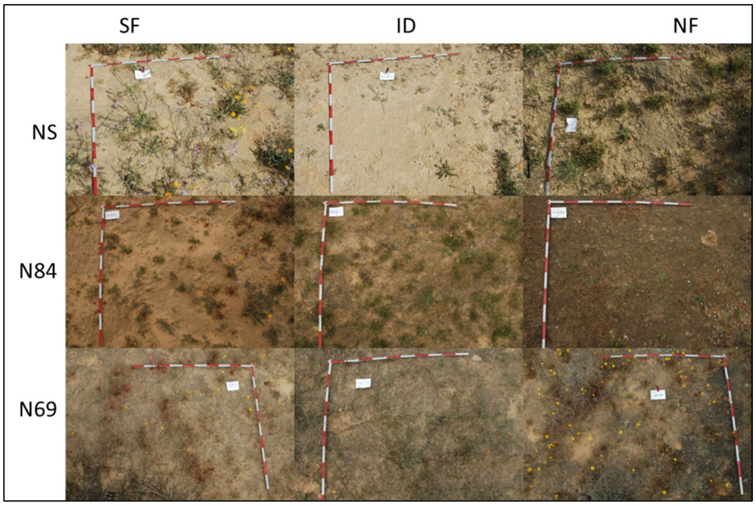

Fig. 1 Different biocrust types at the three study sites (Nizzana-south (NS), Nizzana-84 (N84) and Nizzana-69 (N69)) and in the three relief positions (south-facing (SF), interdune (ID), north-facing (NF))

determination of $CaCO_3$ and TOC. After sieving any remaining snail shells (which contain $CaCO_3$, but do not affect penetration resistance) were removed using tweezers. Soil $CaCO_3$ content was measured with a Scheibler apparatus according to ISO 10693. The content of salts was measured as EC according to ISO 11265 in a 1:5 water extract. The content of TOC was measured after dry combustion according to ISO 10694, and the content of fines (mineral particles <63 μm) was determined by wet sieving according to ISO 11277 after the destruction of organic substances with H_2O_2 and $CaCO_3$ with HCl. To examine whether differences in clay mineral composition between the two main sand fields influenced the effects of fines on crust stability, we analyzed the composition of clay minerals using X-ray diffraction analysis from both sand fields. In each case, we took samples of the crust (0–2 cm), topsoil (2–10 cm) and subsoil (30–40 cm) from seven profiles of the interdune area and the north-exposed footslope in Nizzana-south and Nizzana-84, respectively. After pre-treatment of bulk samples from the total crust with 10% HCl and H_2O_2 (see above), the samples were mechanically dispersed in water after adding drops of NaOH with a shaker for 2 h. Dispersed clay from the gravimetrically separated soil suspension was flocculated with $MgCl_2$. Oriented specimen of the natural clay fraction and after fumigation with ethylene glycol, K^+-saturation and heating for 1 h to 450 °C and 550 °C, respectively, were investigated by XRD with Cu Kα radiation. Intensities (peak areas) and d-spacings were evaluated with the software X-Pert High Score plus. The intensities of the individual types of clay minerals were weighted by factors presented by Niederbudde et al. (2012), in order to estimate their relative proportion.

Statistical analysis

The direct and indirect effects of $CaCO_3$, EC, fines, and TOC on penetration resistance were analyzed using structural equation modeling (SEM). This tool evaluates the roles of multiple factors in a single analysis, has been widely used for the analysis of ecological problems (Grace and Pugesek 1998; Grace and Keeley 2006) and successfully applied in the last years in a number of biocrust studies (Eldridge et al. 2010; Rodríguez-Caballero et al. 2013; Bowker and Antoninka 2016; Chamizo et al. 2017). The basis of the analysis is to test the degree of fit between the data and a theoretical model designed a priori by the investigator based on the knowledge about the expected relationships among the variables included in the model (Bollen 1989). The SEM compares observed covariances among variables with the expected covariances based on hypothesized relationships, and provides estimations of the direct, indirect, and total effects of a predictor variable on predicted variables (Grace et al. 2000). The effect size is given by the path coefficient, which is comparable to a partial correlation coefficient, and the proportion of variance (R^2) for each response variable explained by the factors included in the model is also estimated (Grace 2006).

Our hypothesized model for the causal relationships among the soil variables analyzed is shown in Fig. 2. In particular, we related the variation in penetration resistance to four soil properties: i) fines, ii) organic carbon, iii) electrical conductivity and iv) carbonates. We hypothesized that fines and organic carbon would be correlated, and that fines would also affect carbonates, while both organic carbon and carbonates would influence electrical conductivity. According to our knowledge of the soils in the study area, we also predicted that organic carbon would influence carbonates. The degree of fit between the observed and predicted covariances among variables was assessed with a maximum-likelihood goodness-of-fit test. Contrary to most statistical tests, in this test the non-significant *p*-value associated with the χ^2-test indicates no discrepancy between model and data. We also used the comparative fit index (CFI) (Bentler 2006) to evaluate the goodness of the model. CFI values over 0.90 indicate a good fit. We processed structural equations using AMOS 5.0 (AMOS Development Corp., Mount Pleasant, South Carolina, USA). Mean values of the individual plots were compared by ANOVA and Bonferroni *post-hoc* test using IBM SPSS Version 24.

Results

Soil characteristics

The results show a high variability between the sites and within the relief of individual sites for most of the parameters (Table 1). However, a general trend of increasing salt and organic carbon content can be observed with decreasing distance to the Mediterranean Sea. Further, carbonate content and fine content exhibit comparable trends, with similar values in all plots of

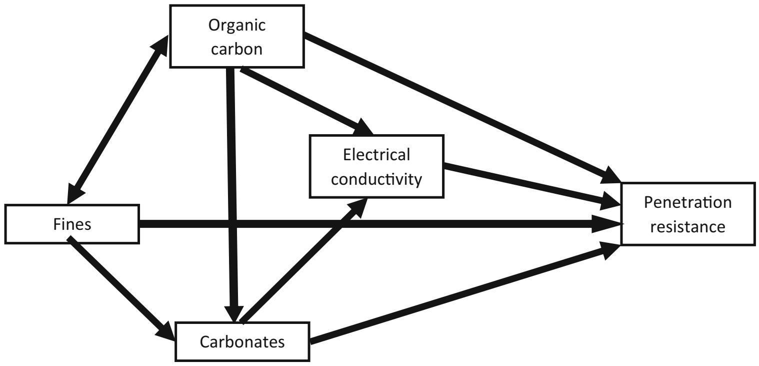

Fig. 2 A priori structural equation model of the causal relationships between penetration resistance, carbonates, organic carbon, electrical conductivity and fines. Variables shown in boxes are the individual measured variables. Double-headed arrows represent correlations between variables, while single-headed arrows represent one-directional dependence relationships

Nizzana-south and an increasing content towards the northern sites. This corresponded to the patterns in penetration resistance, but we could not observe a clear trend within the dune relief of each site. That is, the plot with the lowest value was a different one in each site (interdune in Nizzana-south, north-facing in Nizzana-84 and south-facing in Nizzana-69), whereas the highest values for penetration resistance were found in the interdune of the two latter sites (Table 1). Thus, the site with the most similar crust properties for all plots was Nizzana-south, while the site with the highest variability was Nizzana-84, which is very likely connected to the more complex dune relief.

The clay mineral composition was dominated by illite and smectite, and their composition was relatively consistent among sites and depths (Table 2). Overall, the

Table 1 Mean values and standard errors of penetration resistance (PR), electrical conductivity (EC), carbonate content ($CaCO_3$), organic carbon (TOC) and fines (< 63 μm) of all nine plots. With the exception of the fine content, all parameters have n = 25. Different upper case numbers denote significant differences between the same plots in different sites and different letters denote significant differences within one site (at $p < 0.05$)

Site	Relief		PR [kPa]	EC [dS m^{-1}]	$CaCO_3$ [weight-%]	TOC [weight-%]	< 63 μm [weight-%]
Nizzana-south	SF	mean	664.49^{1,a}	0.193^{1,a}	9.82^{1,a}	1.66^{1,a}	22.73^{1,a}
		SE	*25.71*	*0.004*	*0.17*	*0.03*	*0.58 (n = 25)*
	ID	mean	382.45^{1,b}	0.143^{1,b}	9.15^{1,a}	1.42^{1,a}	19.72^{1,a}
		SE	*23.50*	*0.005*	*0.33*	*0.08*	*1.19 (n = 25)*
	NF	mean	440.12^{1,a}	0.172^{1,a,b}	9.61^{1,a}	1.73^{1,a}	22.51^{1,a}
		SE	*30.16*	*0.006*	*0.23*	*0.08*	*0.88 (n = 25)*
Nizzana-84	SF	mean	465.22^{2,a}	0.190^{1,a}	5.64^{2,a}	1.35^{1,a}	14.13^{2,a}
		SE	*32.11*	*0.010*	*0.19*	*0.05*	*0.85 (n = 24)*
	ID	mean	1416.86^{2,b}	0.437^{2,b}	14.03^{2,b}	3.23^{2,b}	40.07^{2,b}
		SE	*50.82*	*0.014*	*0.56*	*0.25*	*2.03 (n = 17)*
	NF	mean	283.21^{1,a,c}	0.268^{2,c}	4.02^{2,a,c}	2.01^{1,c}	14.06^{2,a}
		SE	*26.74*	*0.008*	*0.18*	*0.11*	*1.01 (n = 11)*
Nizzana-69	SF	mean	473.85^{2,a}	0.216^{1,a}	4.81^{2,a}	1.56^{1,a}	15.36^{2,a}
		SE	*44.52*	*0.011*	*0.32*	*0.07*	*1.09 (n = 23)*
	ID	mean	1186.21^{3,b}	0.248^{3,a}	9.86^{3,b}	2.47^{3,b}	32.12^{3,b}
		SE	*67.78*	*0.013*	*0.34*	*0.10*	*1.04 (n = 21)*
	NF	mean	881.81^{2,c}	0.265^{2,b}	9.02^{1,3,b}	3.20^{2,c}	32.92^{3,b}
		SE	*52.90*	*0.011*	*0.32*	*0.15*	*1.36 (n = 22)*

Table 2 Average mineralogical composition of the clay fraction for Nizzana-south and Nizzana-84. Results (mean values and standard errors) are given as mass-%, with $n = 7$ for all cases

Depth	Site		Mixed layer Basal spacing	Smectite	Illite	Kaolinite
			< 1.8 nm	1.8 nm	1 nm	0.72 nm
BSC (0–2 cm)	Nizzana-south	mean	5	25	59	11
		SE	*2.6*	*2.4*	*2.6*	*0.9*
	Nizzana-84	mean	4	31	55	10
		SE	*1.1*	*2.0*	*3.3*	*0.6*
Topsoil (2–10 cm)	Nizzana-south	mean	6	22	62	10
		SE	*1.8*	*1.9*	*2.6*	*0.9*
	Nizzana-84	mean	3	27	60	10
		SE	*1.4*	*3.5*	*2.9*	*0.9*
Subsoil (35–40 cm)	Nizzana-south	mean	4	24	63	9
		SE	*1.4*	*2.0*	*0.9*	*0.5*
	Nizzana-84	mean	3	25	64	8
		SE	*1.5*	*4.2*	*3.9*	*0.6*

fine material is mainly comprised of 2:1 layered clay minerals (up to 90%) with likely strong effects on aggregation, as well as nutrient and water fixation.

Drivers of penetration resistance

The resulting SEM yielded a χ^2 of 0.001 ($p = 0.980$) and showed a very good overall fit with a CFI of 1. The variance in penetration resistance explained by the model was 60% (Fig. 3). The content of fines had a direct positive effect on both organic carbon and carbonates and was also the variable with the greatest effect on penetration resistance (path coefficient = 0.66). Electrical conductivity also showed a direct positive effect on penetration resistance, but this effect was much weaker than for fines (path coefficient = 0.23). We found no direct effect of carbonates or organic carbon on penetration resistance, but indirect positive effects, mediated by changes in electrical conductivity. Organic carbon was negatively correlated with carbonates.

Discussion

The measured concentrations of salts, fines, carbonates, organic carbon and the penetration resistance all show a very high variability in the dunefields of the NW Negev Desert. This is not surprising, since the crust types and hence their characteristics change along the gradient and within the dune relief, both due to macro- (rainfall gradient) and microclimatic (shading, runoff) differences (Yair et al. 2011; Kidron and Vonshak 2012). Moreover, the dunefield is characterized by changes in dune morphology and therefore differences in dust deposition rates along the gradient (Littmann and Schultz 2008), which is strongly linked to nearby areas of loess from the Beer Sheva region and carbonate-rich material from the Wadi Nizzana and the Negev Highlands in the southern part of Israel (Littmann and Schultz 2008). The amount of fines changes the original texture of the dunes from a pure sand (fines <10%) to a loamy sand or even sandy loam. Indeed, our model analyzing the effects of different soil properties on penetration resistance revealed that the content of fines was the major driver of penetration resistance in the biocrusts from the Negev Desert. Higher fine content promoted higher penetration resistance, which is in accordance with other studies from the region. For example, Zaady et al. (2016) also demonstrated a positive effect of an increased content of fines on crust development by testing the effect of fly coal ash on the establishment of induced biocrusts. They found that the crust was more vital and stable when inoculum was combined with coal ash. This was concluded to be the effect of an increased availability of water (i.e. a higher field capacity) caused by the fine-grained coal ash and confirmed the results of Rozenstein

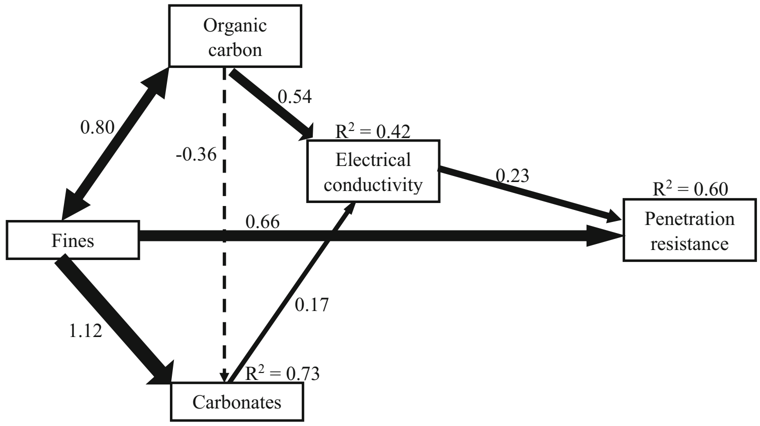

Fig. 3 Results of the SEM model. Numbers associated with paths between the observed variables represent standardized path coefficients. Continuous lines show positive effects, while dashed lines show negative effects. Arrow widths are proportional to the size of the standardized path coefficients. Non-significant paths have been omitted (see Fig. 2 for our hypothesized model). R^2-values associated with electrical conductivity, carbonates and penetration resistance describe the amount of variance explained

et al. (2014), who also found that crust establishment on fine-grained substrates was quicker than on coarse-grained sands. The results of our study also clearly show that silt and clay are the most important cementing agents responsible for the stabilization of biocrusts in the Negev. This is very likely linked to the fact that about 90% of the clay minerals show a high surface reactivity (2:1 minerals) and therefore are promotors of aggregation and able to build organo-mineral-associations (Tisdall and Oades 1982). The smectites and mixed-layer minerals are of comparatively high layer charge and derive from marine sedimentary rocks, while illites and kaolinites were mainly inherited from saprolitic, pre-weathered sandstones, which occur in some of the source areas of the dusts in North Africa, as reported by Ganor (1991), Goudie and Middleton (2001) and Sandler (2013). The homogeneity of the clay fraction in both dune fields (and with depth) indicates that dust deposition was the main source for the clay minerals and that soil forming processes did not change the primary composition of the clay fraction. This means that the degree to which clays stabilize the crust and cement the sand grains is the same in all crusts and it is therefore sensible to assume that an increase in fines causes a proportional increase in crust stability for all study sites. Organic carbon is another important factor often affecting soil penetration resistance. In unconsolidated sands or uncrusted soils, attachment of soil particles by biocrust organisms and cyanobacterial exopolysaccharide secretions contribute to increasing soil strength and resistance (Thomas and Dougill 2007). Surprisingly, our SEM model showed no direct effect of organic carbon on penetration resistance (Fig. 3), but it showed a strong correlation between organic carbon and fines (Fig. 3). While correlation does not imply causation (Munroe 2009), the model does illustrate a positive feedback between these two variables (resulting in an indirect effect of organic carbon on penetration resistance via the positive effect on fines). This feedback can act in the following way: an increase in the amount of fines facilitates the entrapment of carbon-enriched dust, for example by creating shrinkage cracks that cause a higher dust-trapping potential. At the same time, the increase in organic carbon (and related polymeric substances) favor fine particle attachment. Thus, it is very plausible that microbial extracellular polymeric substances are also contributing to crust stability (Czarnes et al. 2000), but that penetration resistance is a variable that is not sensitive enough to reflect their direct influence (at least when measured with the low-resolution hand penetrometer that we used for this study). The negative effect of organic carbon on carbonates as revealed by SEM is a result of the geological and climatological properties of the area. In the southernmost site, which receives the lowest amount of annual rainfall (Littmann and Berkowicz 2008), organic carbon content is lower and the input of carbonates is highest due to the proximity to the limestone Negev (Felix-Henningsen et al. 2008; Littmann and Schultz 2008). In contrast to that, biocrusts in the northern study sites, which receive more precipitation, show higher contents of organic carbon. The higher content of organic carbon in the moister sites is likely linked to a release of organic acids after pulsed water events and the subsequent rapid mineralization of organic matter, which is a common phenomenon in arid and semiarid ecosystems (Austin et al. 2004) and lowers the pH of the soil solution, reducing the carbonate content. Previous studies have shown the important effect of $CaCO_3$ on penetration resistance (Drahorad and Felix-Henningsen 2013; Chamizo et al. 2015). For instance, Maleki et al. (2016) showed that application of bacteria results in the formation of a biofilm on the soil surface that facilitates the precipitation of calcium carbonate crystals, which markedly increased the penetration resistance of the surface layer. In contrast, our model did not show a significant effect of carbonates on penetration resistance. Despite the fact that neither organic carbon, nor $CaCO_3$ showed a direct effect on penetration resistance, they had an indirect effect on penetration resistance mainly through two paths, which are i) the aforementioned positive relationship between organic carbon and fines, and ii) the positive effect of organic carbon and carbonates on salts (measured as electrical conductivity) which had a positive direct effect on penetration resistance. As reported by Drahorad and Felix-Henningsen (2013), high inputs of salts from the Mediterranean Sea may have a stabilizing effect on the sand grains in the Negev desert by cementing the contact points between sand grains on the soil surface. Higher penetration resistance was also reported in crusts from the Natural Park of Cabo de Gata, than in the Tabernas Badlands, both in SE Spain, partially attributed to the closer distance of the former site to the Mediterranean Sea and thus, a higher input of salts (Chamizo et al. 2015). In general, values reported in this study were higher than those reported in other previous studies. Maximum penetration resistance in rainfall-induced crusts in Irish and Iraqi soils with contrasting texture and organic carbon content ranged from 50 to 500 kPa (Hussain et al. 1985). In southern New Mexico (USA), maximum penetration resistance in rainfall-induced physical crusts was 78 kPa (Neave and Rayburg 2007). On silty and sandy loam soils from SE Spain, maximum penetration resistance of the crusts was 265 kPa and 373 kPa, respectively (Chamizo et al. 2010, 2015). In the Soebatsfontein district in South Africa, crust penetration resistance was, on average, 200 kPa (Dojani et al. 2011). A high variability of maximum penetration resistance has also been reported for the crusts in the Negev Desert, with values of 77 kPa at the Hallamish dune field (Kidron et al. 2010), and between 680 kPa in Nizzana-South and 1110 kPa in Nizzana-69 (Drahorad and Felix-Henningsen 2013). The fact that our results for penetration resistance are much higher than the ones given by Kidron et al. (2010) for the same study sites, but on the other hand smaller that our own results of a previous study (Drahorad and Felix-Henningsen 2013) highlight the very limited comparability of penetration resistance studies. This is surely a methodological problem related to the different devices used or differences in the soil depth to which penetration resistance was measured.

Our model analyzing the effects of different soil properties on penetration resistance has allowed the identification of the main factors that drive crust penetration resistance, revealing the important role of fine particles on the stabilization of the sand dunes in the Negev desert. Though other proxies for soil surface stability, such as resistance to wind and water erosion or aggregate stability may be better suited to show the influence of salts, $CaCO_3$ and TOC as stabilizing substances, with respect to grazing potential, our results underline the importance of fines for the carrying capacity of the crusts. This finding may be exploited for ecosystem restoration by artificially enhancing the stability of (natural or induced) biocrusts through the addition of fine particles of the silt and (especially) clay fraction.

Conclusions

As the combination and intensity of pedogenetic processes change within the relief of each dune valley and along the rainfall gradient (i.e. with the relative degree of aridity), so do the mechanisms that stabilize the crust in the NW Negev. The results of our structural equation modelling showed that the main variable that was able to serve as a good predictor for penetration resistance of biocrusts in the Negev was the content of fines and, to a smaller degree, the electrical conductivity. The contents of TOC and $CaCO_3$ showed an indirect effect on penetration resistance by increasing the content of fines (in the case of TOC) and electrical conductivity (both TOC and $CaCO_3$). This indicates that the stability of biocrust-covered soils in the Negev is to a large degree linked to a high input of dust. An increasing amount of airborne particles induces an increase in overall stability by i) increasing the amount of clay minerals that cement the contact points of the sand grains and ii) by creating favorable habitats with an increased availability of water for microorganisms, which allows them to be active for a longer time. Although our model does not reflect a direct effect of organic carbon or carbonates on penetration resistance, which can possibly be attributed to the low resolution of the hand penetrometer, it still provides useful implications for the use of biocrusts in ecosystem restoration. Namely, the increase of silt and clay content as a promising measure for generating more stable and vital crusts when applying cyanobacterial or bryophyte inoculum to combat desertification and for increasing the carrying capacity of the Negev sand dunes for livestock grazing.

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