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The effect of sand grain size on the development of cyanobacterial biocrusts

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ABSTRACT

Biocrusts are critical components of desert ecosystems, significantly modifying the surfaces they occupy. Although the presence of fine soil particles is known to be conducive to biocrust development and recovery from disturbance, their influence on the inceptive development of biocrusts has not been empirically studied. In this study, the effect of substrate granulometry on the development of biocrusts was explored, under controlled laboratory conditions of light, soil humidity, and temperature. A cyanobacterial inoculum of *Microcoleus vaginatus* was applied to five sand fractions in the range of 1–2000 μm. The results showed that the biocrusts developed more rapidly on the fine fraction (<125 μm) than on the coarser fractions. While the biocrust cover on the fine fraction was spatially homogenous, it was patchy and discontinuous on the coarse fractions. The difference in the pore size between the different fractions is suggested to be the reason for these discrepancies in biocrust development, since large pores between the particles of coarse soil restrict and regulate the filaments' spreading. It was found that the spectroscopic indices, the Normalized Difference Vegetation Index and the Brightness Index, were more sensitive to the biocrust development than the bio-physiological parameters of the biocrusts (polysaccharides, protein, and chlorophyll contents). The faster biocrust development on the fine fractions can explain various biophysical phenomena in aeolian environments.

1. Introduction

Drylands occupy more than 40% of the earth's terrestrial surface area (Glenn et al., 1993; Lal, 2004). Throughout the world, drylands are home to biocrusts (Belnap and Lange, 2001; West, 1990). Biocrusts are dominated by cyanobacteria and may also include lichens, mosses, green algae, microfungi, and bacteria (Belnap and Lange, 2001). In natural drylands across the world, biocrusts cover vast regions and may amount to 70% of the ground cover (Buis et al., 2009; Eldridge and Greene, 1994; Karnieli et al., 2002; Qin et al., 2006).

Biocrusts under variable conditions of aridity reach various developmental stages and function in different ways (Belnap, 2006; Zaady et al., 2014). Some of these functions include carbon and nitrogen fixation (Belnap, 2002; Burgheimer et al., 2006a,b; Shields, 1957; Wu et al., 2009; Zaady et al., 1998, 2000) and profound effects on plant germination (Boeken et al., 2004; Serpe et al., 2006; Zaady et al., 1997). Biocrusts also play a crucial role in geomorphological processes, such as aeolian (Maman et al., 2011; Meir and Tsoar, 1996; Tsoar, 1990), hydrological (Akuja et al., 2003; Eldridge et al., 2002; Ram and Aaron, 2007; Zaady et al., 2014; Zaady, 2005) and pedological processes (Eldridge and Leys, 2003; Zhang et al., 2006). Biocrusts may effectively impede wind and water erosion and water flow; however due to hydrophobic properties and extracellular polysaccharides that act to clog the surface, some biocrusts may also trigger runoff resulting in nutrient and sediment translocation (Belnap, 2006; Zaady et al., 2013). The effects of biocrusts on pedological processes are due in part to their organic matter content as well as microorganism–mineral interactions (Belnap and Lange, 2001; Breckle et al., 2008). Thus, biocrusts are critical components of desert ecosystems, significantly modifying the surfaces they occupy.

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Biocrusts are essentially composed of photoautotrophic organisms and soil granules. The composition of their photoautotrophic community is dynamic and associated with a successional process. Initially, the aggregation of soil granules is performed by metabolic extracts secreted by cyanobacteria and green algae, forms the hard crust layer. This mucilage layer allows better water retention in the soil over time by reducing evaporation and desiccation (Zaady et al., 2014). Cyanobacteria, the most common element in the desert's microphytic community, are a primary producer. Their dominance as a primary colonizer in desert areas stems from their extraordinary ability to disperse through dust and runoff water, colonizing new and disturbed areas, and then binding with soil particles to produce wind resistant surfaces. As a result of their endurance for low water potential (Brock, 1975), high temperature (Buzer et al., 1985), and radiation (Levy and Steinberger, 1986), the colonization, establishment and domination of cyanobacteria on the soil surface can occur rapidly and may take only a few weeks. The soil stabilization process begins when the initial crust is generally formed by filamentous cyanobacteria of the *Microcoleus* genera (Campbell et al., 1989). Other filamentous cyanobacteria such as *Phormidium* spp., *Oscillatoria* spp., may also appear and colonize the soil surface (Belnap, 2001; Zaady et al., 2010). Following soil stabilization, nitrogen-fixating cyanobacteria, such as *Calothrix* spp. and *Nostoc* spp., are established and enrich the soil with nutrients (Rychert and Skujins, 1974). As the successional process continues, green algae appear, followed by mosses. The latter further contribute to soil stabilization since moss rhizoids penetrate into the soil and act as a skeleton, compacting the cyanobacterial crust into the soil (Zaady, 1999). Lichens appear later as they require an established biocrust in order to develop (Belnap and Lange, 2001).

Previous studies have found links between soil texture and biocrusts (Danin, 1996; Williams et al., 2013). Topsoil texture changes with biocrust succession; as the biocrusts become more mature, they contain higher proportions of fine grained particles (Kidron, 2014; Ram and Aaron, 2007). A significant positive correlation was found between organic matter in biocrusts and the proportion of silt and clay (Danin, 1996). Further, Danin (1996) suggested a positive feedback between the biocrusts and the amount of fine particles. In addition, biocrusts are known to trap airborne dust (Danin and Ganor, 1991; Pietrasiak et al., 2014; Williams et al., 2012; Zaady and Offer, 2010). Indeed, it is this trait that was suggested to be an essential component in the formation of loess soil since biocrusts aggregate deposited dust particles into their structure and keep these particles from being eroded by water and wind (Svirčev et al., 2013). The process of enriching the topsoil with fine particles reinforces the development of biocrusts by increasing their water-holding capacity and by providing necessary mineral nutrients. Dust incorporation into the biocrusts increases the growth of cyanobacteria and strengthens the cohesion of biocrusts (Hu et al., 2002). Moreover, biocrusts cover a larger portion of the surface when the soil contains finer particles, and it was observed that at least 4–5% of clay and silt is required to support a measurable microphytic crust (West, 1990). Accordingly, cyanobacterial biocrusts are abundant on soils with fine sand and negligible rocks (Williams et al., 2013). With the succession of biocrust underway and later the establishment of mosses and lichens, biocrusts increase dust capture to form biologically mediated vesicular horizons that are finer textured than the underlying fine sands (Williams et al., 2012, 2013). Thus throughout the biocrust succession, texture, microstructures, and the potential to capture dust change with developments in biocrust composition and morphology (Felde et al., 2014; Williams et al., 2012, 2013). Following a disturbance, biocrust recovery is more rapid in fine-textured soils that form physical crusts than in coarse-textured soils that do not form physical crusts, when climate and disturbance characteristics are otherwise similar (Belnap and Eldridge, 2001). As a result, clay, silt, and fine sand particles are recognized for their importance for biocrust establishment, development, and recovery. Yet, little research has experimentally examined the impact of the soil grain size on the establishment of initial biocrusts on bare soil. Filling this knowledge gap is crucial to understanding the process of biocrust formation. Hence, the primary aim of the current investigation is to explore how the sand-grain-size distribution affects the ability of biocrusts to establish themselves. Specifically, the objective is to compare the rate and dispersal patterns of inceptive cyanobacterial biocrusts on different grain-size fractions.

2. Materials and methods

2.1. Characterization of the sand substrate

Sand was collected from Wadi Kasuy sand dunes in the southern Negev Desert in Israel (29° 59′ 14″ N; 34° 59′ 25″ E). The sand composition in this area was previously described as 60% calcite and 35% quartz (Yizhaq et al., 2012). Its grain-size distribution is polymodal with many coarse grains. The collected material was sterilized in an autoclave and sieved into five grain-size fractions following the classification of sand sizes from the U.S. Department of Agriculture (USDA): <125 μm (very fine sand), 125–250 μm (fine sand), 250–500 μm (medium sand), 500–1000 μm (coarse sand), and 1000–2000 μm (very coarse sand) (Buol et al., 2011). A grain-size distribution analysis was performed using the laser diffraction technique (ANALYSETTE 22 MicroTec Plus) that measures particles in the range of 0.08–2000 μm. The mineral composition of the sand in each fraction was determined by phase analysis using the X-ray Powder Diffraction (XRPD) method. The data were collected on a Philips 1050/70 powder diffractometer, with a graphite monochromator on a diffracted beam providing CuK α radiation (=1.541 Å) and operating at $v = 40$ kV, $I = 30$ mA. Phase identification was performed by using the Bede ZDS computer search/match program coupled with the International Centre for Diffraction Data (ICDD) Powder Diffraction File database. The amount of definite phase concentrations of the crystalline components was estimated by using the Relative Intensities Ratio (RIR) method following Hubbard and Snyder (1988) with a determination accuracy of 10%.

2.2. Controlled experiment

The experiment and all measurements described below were conducted at laboratory of the Agricultural Research Organization (ARO), Gilat Research Center, Israel. A total of 32 samples were prepared for each size fraction of the sand. Each sample consisted of 80 g of sieved sand on filter paper in a sterile Petri-dish (90 mm in diameter) with five 1-mm drainage holes at the bottom. The inoculant of the filamentous cyanobacteria (*Microcoleus vaginatus*) was isolated from the sand dunes of the northern Negev Desert, and the Accession number of the 16S rRNA gene sequence was EF667962 (Zaady et al., 2010). The cyanobacteria were grown in a synthetic growth medium up to a certain biomass in a bioreactor (Lan et al., 2014). The medium was filtered and dried at 40 °C for 48 h. The dry powder of the cyanobacterial fragments was stored at 4 °C before the experiment took place. One gram of the cyanobacterial powder was suspended in 100 ml of double-distilled water (DDW), and 1 ml of the suspension was sprayed into each Petri-dish. The growth and the incubations began by adding DDW to the soils up to a moisture content equivalent to field capacity (approximately 22%, −30 kPA) that was maintained during the experiment. The samples were kept in a growth chamber (21 °C) with continuous illumination. The samples were covered by punctured lids to prevent rapid desiccation while