Soil Biology & Biochemistry 103 (2016) 213–220

Contents lists available at ScienceDirect

Soil Biology & Biochemistry

journal homepage: www.elsevier.com/locate/soilbio

Successional biocrust stages on dead shrub soil mounds after severe drought: Effect of micro-geomorphology on microbial community structure and ecosystem recovery

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ARTICLE INFO

Article history:
Received 1 July 2016
Received in revised form
22 August 2016
Accepted 24 August 2016

Keywords:
Climate change
Cyanobacterial crust
Heterotrophs
Phototrophs
Semi-arid
Slopes

ABSTRACT

A drought- induced massive shrub death event was observed in a semi-arid region of the Negev Desert, leaving bare soil mounds in place. Hypothesizing that the absence of shrubs would allow biocrust expansion to cover the bare soil mounds, we followed the development of biocrusts on the south and north-facing slopes of the soil mounds over three years. Only after six years, when the mounds were totally flattened, were the water infiltration capacity and soil compaction properties of the developing biocrusts similar to those of the surrounding mature biocrusts. The prokaryotic community structure was exposed by pyrosequencing of 16S rRNA gene amplicons. A principal component analysis indicated that the development of microbial community on the soil mounds was affected at multiple scales, including biocrust successional stage, seasonal effect and the micro-geomorphology of the mound (north vs. south slopes). While the phototroph community structure was most associated with the biocrust successional stage, the heterotroph community structure was mostly season-associated. Compared to the north slope, the south slope exhibited delayed development in all determined parameters; with the addition of lately observed establishment of new shrubs in this site, the results emphasize the importance of the micro-geomorphology in the recovery of the affected ecosystem.

1. Introduction

Hyper-arid, arid and semi-arid zones together make up some 40% of the Earth's terrestrial surface area and are considered the most sensitive ecosystems to climate change (Maestre et al., 2012). Semi-arid landscapes are characterized by patchy vegetation in which shrub patches consist of annuals and shrubs, which create soil mounds beneath them (Garner and Steinberger, 1989; West, 1989; Schlesinger et al., 1990; Allen, 1991; Zaady et al., 1996), and alternate with inter-shrub spaces occupied by bare soil or covered with biological soil crust (biocrusts). There are functional source-sink relationships between the two patch types. The shrubs are sinks for the soil, nutrients and water (Eldridge and Greene, 1994; Shachak et al., 1998) that leak from the biocrust cover nearby, creating what are termed “fertility islands” (Schlesinger and Pilmanis, 1998; Bergkamp et al., 1999; Schlesinger et al., 1999; Shachak et al., 2008). The distribution of soil microorganisms' biomass has been reported to follow the spatial pattern of resource availability, where the improved fertility and environmental conditions under the shrub canopy create hot-spots of microbe-mediated ecosystem processes (Goberna et al., 2007; Schade and Hobbie, 2005; Loreau, 2001; Ben-David et al., 2011). The shrub patches also serve as sites for water infiltration, thus affecting the hydrology of the ecosystem (Eldridge et al., 2000, 2002; Bhark and Small, 2003). Biocrusts are top-soil microphytic communities consisting of cyanobacteria, green algae, lichens, mosses and other microorganisms that are cohesively attached with soil particles (Belnap and Lange, 2001; Garcia-Pichel, 2002). Biocrusts are crucial biotic components in dry ecosystems worldwide. They constitute “mantles of fertility” (Garcia-Pichel et al., 2003), functioning as ecosystem engineers (Jones et al., 1997;

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http://dx.doi.org/10.1016/j.soilbio.2016.08.028
0038-0717/

Bowker et al., 2005) and supplying many of the ecosystem services that are provided by higher plants in more mesic climates, such as primary production, soil erosion prevention, element lixiviation (Belnap and Lange, 2001; Beraldi-Campesi et al., 2009), soil conditioning, and soil fertilization with newly fixed C and N (Johnson et al., 2007).

After enduring several years of drought, a mass death of the dominant shrubs in the northern Negev Desert was observed (Sher et al., 2010), an event that can be related to the phenomenon named *global-change-type drought vegetation die-off*, a part of the desertification syndrome (Breshears et al., 2005; Gitlin et al., 2006; Miriti et al., 2007). Following the shrub death and decomposition, bare soil mounds were left at these sites (De Falco, 2012). The expected consequences of shrub death on ecosystem functions are not only the result of the net loss of shrub-mediated functions, but also of the weakened inter-relationships between the two patch types, namely shrub and inter-shrub biocrusted patches. It is reasonable to assume that nutrient cycling, distribution and fate (biomass production or leakage) will be altered (Sher et al., 2010). However, it is also reasonable to assume that a significant expansion and development of biocrust structures will take place and be the main ecosystem service providers of fixed C and N. Biocrusts are initiated by the growth of pioneer cyanobacteria during episodic events of available moisture, with the subsequent entrapment of mineral particles by a network of cyanobacterial filaments and a matrix of extracellular slime (Belnap and Lange, 2001; Zaady et al., 2010). Eventually, undisturbed development leads to multi-species assemblages that harbor bacterial, archaeal, fungal, algal and even lichenic and moss populations (Nagy et al., 2005; Bates and Garcia-Pichel, 2009; Soule et al., 2009). It is anticipated that after the elimination of the shrubs, the biocrusts will take over the soil mounds in the following growing seasons, starting with fast-growing, pioneer cyanobacteria of the filamentous type (Garcia-Pichel and Wojciechowski, 2009) that will cover the soil mound, followed by a typical successional colonization of other biocrust organisms, mosses and lichens (Belnap and Lange, 2001; Zaady et al., 2010). The development and structure of the biocrusts should principally depend on the rainfall regime in the affected area and the micro-geomorphology of the mounds. The establishment and recovery of disturbed biocrusts is a long-term process that may take 5–20 years (Belnap and Lange, 2001). However, to the best of our knowledge, the time-scale and patterns of biocrusts' succession on bare soil mounds remaining after shrub death, and surrounded by mature biocrusts, has not been previously studied. In this research, we studied the prokaryotic microbial community structure of developing biocrusts on bare soil mounds after shrub death in a semi-arid ecosystem of the Negev Desert, during a period of three years.

2. Materials and methods

2.1. Study site

The study was conducted in Sayeret Shaked Park (31°17′N, 34°37′E), a Long-Term Ecological Research (LTER) area located in the semi-arid region of the northern Negev Desert, Israel. Major rainfall events occur between November and March, with a long-term average annual rainfall rate of 200 mm (Stern et al., 1986). The soil is sandy clay loam with 59% sand, 27% silt and 14% clay (Teomim, 1990). Air temperature ranges from 23 °C to 35 °C during the summer and 10 °C to 21 °C during the winter (Zaady et al., 2013). The dominant shrubs in this region are *Noaea mucronata*, *Atractilis serratuloides* and *Thymelaea hirsute* (most of which died in the year 2008, Sher et al., 2010; De Falco, 2012).

2.2. Collection of crust samples and treatment

Five sampling campaigns were conducted, beginning in October 2011, when the soil mounds of the dead shrubs could still be easily identified (remains of the dead shrubs still can be seen on top of mounds), and continued until the mounds flattened (Fig. S1). In this stage the soil is loose and the mounds were about 40–50 cm in width and 15–20 cm high (Zaady et al., 1996; Fig. 1). On-site measurements and biocrust sample collections were performed in a location in which most (90%) of the shrubs had died (Fig. 1A). Samples were collected from inter-shrub patches (ISPD), from the north-facing (north dead, ND) and south-facing (south dead, SD) slopes of the soil mounds and, in one of the campaigns, also from the top of the mound (TOM) (Fig. 1B). During some campaigns, biocrust sample collection and on-site measurements were also performed in the inter-shrub patches (ISPL) from an adjacent location in which most of the shrubs had survived (Fig. 1A). Henceforth, the ISPL and ISPD biocrusts will be referred to as the "mature" biocrusts, while the ND and SD biocrusts will be referred to as "developing biocrusts." The number of biocrust samples collected in each campaign, rainfall data and relative water content of the samples are summarized in Table 1. Each sample (30–40 gr) was a composite of two subsamples. For the ISPL, samples were collected from spots that were at least 5 m apart and at a distance of

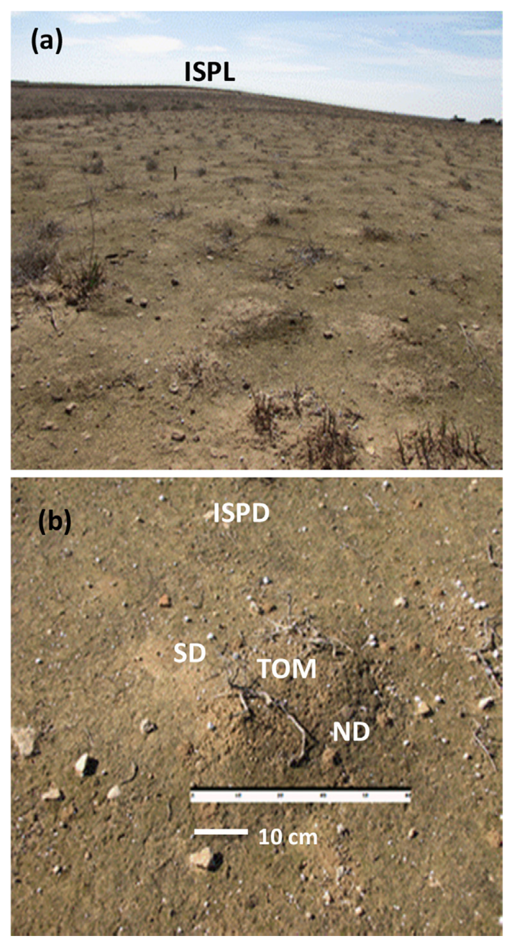

Fig. 1. A) A view of the research site. In the background area, most shrubs have survived. Biocrusts were sampled from inter-shrub patches (ISPL). In the foreground area, more than 90% of the shrubs have died. B) The sampling sites on and around the soil mounds. Biocrust samples were collected from the inter-shrub patches (ISPD), from the north (north dead, ND) and south (south dead, SD) facing slopes of the soil mounds and from the top of the soil mounds (TOM).