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Organic matter from biological soil crusts induces the initial formation of sandy temperate soils

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ABSTRACT

Different development stages of algae-dominated and moss-dominated biological soil crusts (BSCs) were sampled on a natural sand dune (<17 years old) and on an experimental sand dune (<8 years old) along a catena, including gradients of vegetation cover, location on the slope, as well as composition and thickness of BSC organisms in northeastern Germany. The accumulation of BSC-derived organic carbon (OC) was determined for bulk materials and fractions less than 63 μm. The OC composition was characterized by solid-state ^{13}C NMR spectroscopy and the carbohydrate-C signature. ^{14}C contents were determined to assess the origin and dynamics of OC. From the radiocarbon contents, two OC pools were differentiated: recent BSC-derived and lignite-derived "old" OC. Downward movement of OC into the underlying substrate was found only under moss-dominated BSCs at the old sand dune. BSC-derived OC was mainly composed of carbohydrate-C and, to a lesser extent, alkyl C and N-alkyl C, with considerably higher contributions of alkyl C in the young dune, indicating differences in the composition of extracellular polymeric substances produced by the BSCs with age. This is consistent with higher proportions of water-soluble OC of moss-dominated BSCs at the old dune, which is leached in the underlying substrate and initiates soil formation. Because of the channeling effect of mosses, OC depth translocation along with suspended colloidal substances may contribute to OC accumulation in substrates.

1. Introduction

Biological soil crusts (BSCs) are an association of soil particles and microorganisms (cyanobacteria, algae, bryophytes, fungi, lichens) in varying compositions that cover the uppermost and vegetation-free soil surface in many ecosystems (Belnap and Lange, 2001). As first colonizers, BSCs are important producers in many initial ecosystems (e.g., forefields of receding glaciers) as well as mature ecosystems with a sparse vegetation cover from the deserts to polar regions (Langhans et al., 2009; Schaaf et al., 2011). It is assumed that cyanobacterial and green algae BSCs are the earliest successional stage of BSCs that are replaced by lichen-dominated and moss-dominated BSCs during later stages of BSC development (Belnap, 2006; Lange et al., 1997). The period until BSCs are established on previously bare substrate has been controversially discussed and is influenced by the spatial scale of disturbance, the substrate, and the climatic conditions (Belnap and Lange, 2001). In deserts, the reported recovery time after disturbance ranges from decades to centuries (Belnap and Eldridge, 2003; Maestre et al., 2011), whereas small-scale disturbances can be colonized by cyanobacteria and green algae in 1 to 2 years (Dojani et al., 2011; Veste et al., 2001). In a temperate climate, Fischer et al. (2010a) observed the development of the BSC after 3 years on an artificial watershed.

Several studies revealed the important effect of BSCs on water availability and hydrological processes (Belnap, 2006; Fischer et al., 2010b; Maestre et al., 2002; Yair et al., 2011), plant establishment (Beyschlag et al., 2008; Prasse and Bornkamm, 2000), soil stability (Belnap and Gardner, 1993; Lázaro et al., 2008; Mazor et al., 1996), carbon and nitrogen fixation (Belnap, 2002; Beymer and Klopatek, 1991; Brankatschk et al., 2012), as well as soil fertility (Lange et al., 1992; Reynolds et al., 2001); thus, BSCs have a significant influence on ecosystem functioning, development, and health (Castillo-Monroy et al., 2011; Maestre et al., 2011; Veste et al., 2011). As photo-autotroph organisms, these microorganisms play a key role in the net carbon fluxes in microphyte-dominated ecosystems (Beymer and Klopatek, 1991; Elbert et al.,

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2012; Wilske et al., 2008). Further, BSC-dominated microsites are also an important contributor to total soil CO_2 efflux (Castillo-Monroy et al., 2011; Thomas, 2012).

Bacteria and algae produce extracellular polymeric substances (EPS) comprising a large range of different biopolymers that mediate the adhesion of EPS to mineral surfaces (Flemming and Wingender, 2010). In an incubation experiment, Miralles et al. (2013) demonstrated that the metabolic processes and the content of labile carbon in BSCs differ in dependence of the type of BSC organisms (cyanobacteria and lichens). In all crusts from this study, simple sugars (sucrose, glucose) remained at the end of the incubation period, suggesting that these sugars may play a protective role in BSCs. There is only one study (Beymer and Klopatek, 1991) that demonstrated a downward movement of organic carbon (OC) from the BSC into the underlying soil by using a $^{14}CO_2$ chamber experiment. This labile and leachable OC is considered to be an important source of nutrition to the large mass of heterotrophic soil microorganisms (Beymer and Klopatek, 1991). In addition, OC accumulation increases mineral weathering (Amit and Harrison, 1995; Chen et al., 2009; Drever and Stillings, 1997). Therefore, it can be expected that the effects of EPS on initial soil formation are more intense if EPS compounds are water-soluble and, thus, moveable into greater soil depth.

So far, the amount of BSC-derived OC input into soils and its chemical composition have been rarely investigated, especially in in situ conditions. Similarly, the effect of BSC colonization of the uppermost millimeters of the soil surface on soils beneath the BSC is still unclear.

Therefore, we investigated different development stages of BSCs (algae-dominated and moss-dominated) on a natural sand dune (ND; <17 years old) and an experimental sand dune (ED; <8 years old) in northeast Germany. Our objectives were as follows: to determine the amount of OC fixation in BSC layers and the BSC-derived OC input into the underlying substrates; to characterize the chemical composition of OC in BSCs and substrates (bulk materials and fractions <63 μm) by applying solid-state ^{13}C NMR spectroscopy and analyses of the carbohydrate signature (hydrolysis with trifluoroacetic acid); and to assess the OC dynamics and timescales of BSC establishment by using radiocarbon analysis in combination with the known ages of the sand dunes.

2. Material and methods

2.1. Study sites, sampling, and description of BSCs

We investigated one ND and one ED in Brandenburg (northeast Germany) in a temperate climate with a subcontinental character (mean annual rainfall, 560 mm; mean annual temperature, 9 °C). The sand dunes were chosen because they offered the unique possibility of studying BSC development in two sand dunes with similar substrates and known ages of the sand dunes. At each sand dune, different development stages of BSCs were sampled along a catena, including gradients of vegetation cover (mainly the grass species *Corynephorus canescens*), location on the slope, as well as composition and thickness of BSC organisms (Fig. 1). The early successional stages of the BSCs include cyanobacteria and green algae (mainly *Zygogonium ericetorum* Kützing). The moss cover consisted of *Polytrichum piliferum* Hedw. A detailed list of species occurring in European sand dunes was provided by Fischer et al. (2012). Henceforth, BSC types will be referred to as algae-

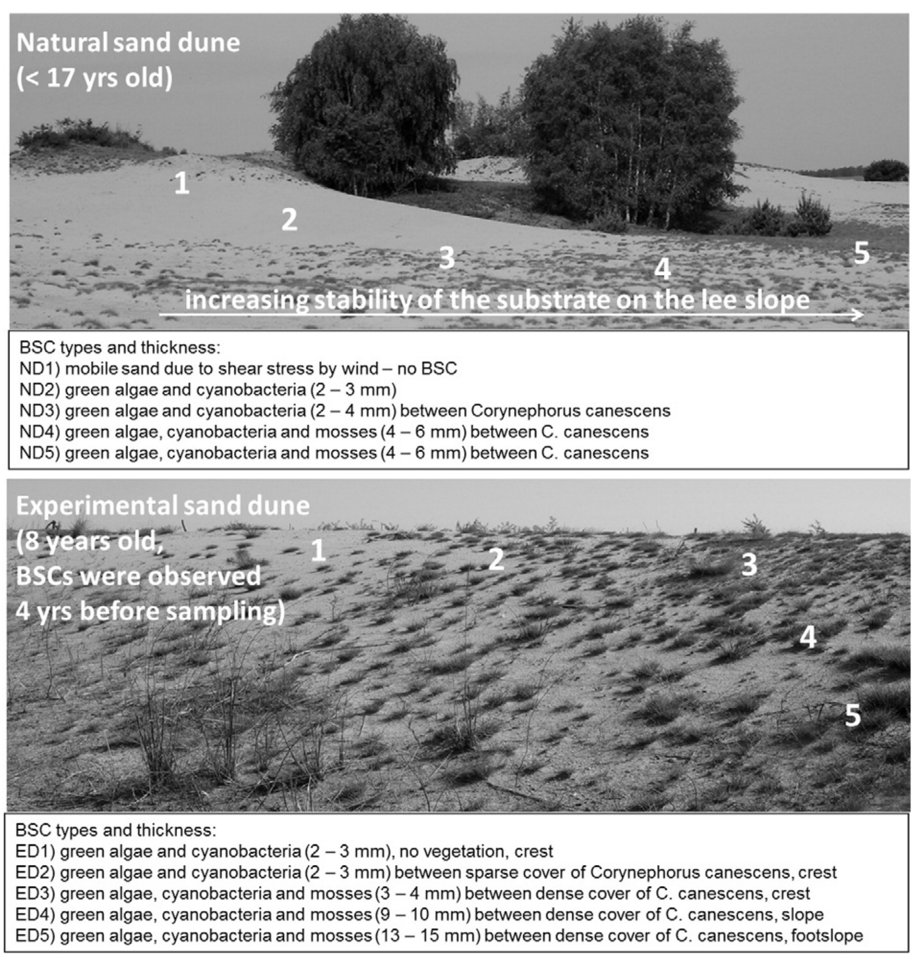

Fig. 1. The natural (<17-year-old biological soil crusts [BSCs]) and experimental (<4-year-old BSCs; length, 50 m; height, 1.5 m; width, 7 m) sand dunes with sampling sites and description of BSC types.