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Biological soil crusts of temperate forests: Their role in P cycling

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ABSTRACT

To elucidate the ecological role of biological soil crusts (BSCs) in the P-cycle and to disclose vegetation (pine vs. beech), soil horizon (A horizon vs. C horizon) and land use intensity effects, we examined BSCs collected from a temperate forest in Schorfheide-Chorin (Germany). Total C, N and P of the three sample compartments crust, crust-adhering soil underneath and crust-free soil were quantified and inorganic and organic P (P_i, P_o) contents in five sequentially extracted P fractions of the different compartments were determined. In addition, P species were characterized using P *K*-edge XANES (X-ray absorption near edge structure) and ^{31}P NMR (nuclear magnetic resonance) spectroscopy. BSC biodiversity of algae was morphologically determined using enrichment cultivation. Results showed an accumulation of total P in the BSC with high shares of P_o. Proportions of labile and moderately labile P_o pools were higher in BSC than crust-free soil in expense of residual P indicating weathering of Fe/Al-P species by BSC organisms. Vegetation affected the C/N ratio and proportion of labile P_i in total P of BSC; they were significantly higher under beech compared with pine. XANES results revealed BSC weathering of mainly Fe-P under beech and Al-P under pine. Soil horizon affected the composition of BSC organisms; there were more filamentous algae in BSCs on C horizon than A horizon. Moderately labile P_i concentrations were higher in BSC on C horizon compared with A horizon while the share of the labile P_o pool in total P was lower on C horizon than A horizon. Increasing forest management intensity decreased the share of moderately labile P and P_o in total P as well as the monoester-P/diester-P ratio in pine BSC. While in BSC under pine changes occurred in microbial diversity, under beech changes occurred in algal richness and life form. We conclude that BSCs in Central European forests are particularly involved in the transformation of P_i to P_o fractions and respond differently to management intensity depending on the predominating tree species.

1. Introduction

Worldwide, biological soil crusts (BSCs) play an important role in ecosystem function and dynamics. BSC communities consist of heterotrophic and autotrophic organisms, sticky byproducts as well as soil particles which in intimate association form a coherent soil layer in the uppermost millimeters of soil (Belnap et al., 2001a). This living layer stabilizes soil and is an important site of primary production, water retention, and manifold biogeochemical interactions and element cycling (Evans and Johansen, 1999). Due to these functions, BSCs provide the basis for further ecosystem development particularly in habitats in which soil moisture is limited or in non-vegetated or disturbed areas (Belnap et al., 2001b; Bliss and Gold, 1999). Hence, BSCs are well studied in arid and semi-arid regions from all over the world. However, much less is known on such communities in temperate regions particularly on their functional aspects (Büdel, 2001a).

From studies in arid and semi-arid regions it is well known that BSCs play a crucial role in element cycling: numerous studies report on their function in the carbon (C) cycle (e.g. Evans and Johansen,

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1999; Li et al., 2012; Yoshitake et al., 2010; Zaady et al., 2000) and nitrogen (N) cycle (e.g. Belnap, 2002; 2011; Evans and Belnap, 1999; Zaady et al., 1998). Elbert et al. (2012) estimated that BSCs are responsible for global C fixation of about 7% of the terrestrial vegetation and for N fixation of about 50% of terrestrial biological N fixation. Much of the C that is photosynthetically assimilated by BSCs is released to the underlying soil already shortly after fixation, thereby strongly increasing the total amount of C in soil (Pointing and Belnap, 2012). Similarly, N from N-fixing cyanobacteria of the BSCs such as *Microcoleus* and *Nostoc* reaches the soil (Belnap et al., 2003). In the soil, the C and N sources benefit the heterotrophs, leading to enhanced decomposition rates, thus increasing soil moisture, soil fertility and availability of nutrients to higher plants (Belnap et al., 2003).

While the role of BSC in the C and N cycle is well documented, little is known on its role in the cycle of the macro-nutrient phosphorus (P). It is assumed that already the sole presence of BSC increases potentially available P due to an increase in organic matter. The activity of BSC organisms can further increase P availability depending on BSC species composition. For instance, the excretion of H^+ during respiration or secretion of organic acids can solubilize carbonates and Fe- and Al-bound P (Belnap, 2011; Fox, 1995); an increase in pH can lead to liberation of Fe- and Al-bound P (Blume et al., 2016; Garcia-Pichel and Belnap, 1996). Also, the secretion of metal chelators (e.g. siderochromes) increases available P by maintaining metals in solution (Lange, 1974). Phosphatases, existing in cell walls and mucilaginous sheaths of most BSC organisms, hydrolyze organic phosphates liberating P (Nannipieri et al., 2011). All these different mechanisms contribute to the essential role of BSCs in accumulating and providing plant available P from organic and inorganic sources. Early studies mainly elaborated on the capacity of the BSCs in nutrient enriched dust trapping, including P (Belnap et al., 2003; Pointing and Belnap, 2012; Reynolds et al., 2001). Recently, Delgado-Baquerizo et al. (2015) showed that total P content in BSC-forming lichen thalli depended on P availability in the soil. According to Schulz et al. (2016), the total P content of BSC-free sand was the only factor that significantly influenced cyanobacterial and algal community structure of BSCs in coastal dunes. Zhao et al. (2014) reported a higher alkaline phosphatase activity in BSC compared with control soil. However, none of these studies chemically characterized P including the identification of specific P forms.

Therefore, the present study aims to elucidate P content and P-speciation in BSC (soil with phototrophic BSC organisms including their interaction effects with soil), crust-adhering soil (soil underneath BSC which could be affected by BSC) and crust-free soil (soil not affected by BSC) in two different types of temperate forest (pine vs. beech). Total P analysis as well as the P analyses of various sequential fractions after Hedley et al. (1982) should provide a detailed picture on spatial distribution of P content and P pools. Additionally, P *K*-edge XANES (X-ray absorption near edge structure) spectroscopy and solution ^{31}P NMR (nuclear magnetic resonance) spectroscopy were complementary employed to disclose the chemistry of underlying P compounds (Kruse et al., 2010; Negassa et al., 2010). While P *K*-edge XANES spectroscopy is preferred to identify the speciation of inorganic P compounds (Kruse et al., 2015), ^{31}P NMR spectroscopy is more suitable to detect organic P compounds (Cade-Menun and Liu, 2013; Doolette and Smernik, 2011). In addition, the number of algal species (richness) in the BSC as well as their life form was determined to assess the influence of their biodiversity on the P cycle.

It is hypothesized that (i) higher P concentrations with (ii) higher portions of labile P and (iii) P pools with a high organic P fraction exist in the BSC compared with crust-adhering soil underneath the BSC or even crust-free soil. Moreover, it is expected that (iv) the P-speciation reflects the influence of BSC on soil by showing a higher contribution of organic P species in BSC compared with crust-free soil. We further hypothesize that (v) due to differences in tree species, soil horizon and forest management intensity, site-specific effects for P contents, pools and speciation occur.

2. Materials and methods

2.1. Sample collection and preparation

Within the framework of the German Biodiversity Exploratories (Fischer et al., 2010), 20 BSC samples were collected from 14 different forest plots at the study site Schorfheide-Chorin (thereafter referred to as Schorfheide) in summer 2014 and 2015 (Table 1). Plots differed in the dominant tree species (Scots pine (*Pinus sylvestris* L.) or European beech (*Fagus sylvatica* L.)) and were characterized regarding land use intensity by the silvicultural management intensity (SMI) indicator taking into account tree species, stand age and aboveground living and dead wood biomass (Schall and Ammer, 2013). The SMI value increases with more intense management. BSC developed on either the A horizon (pine/A, beech/A) or exposed C horizon (on root plate after windfall of trees with root exposure; including all non-A horizons; beech/C). Soil texture was analysed by sieving and sedimentation procedures (Blume et al., 2010), pH_{CaCl2} was determined using 0.01 M $CaCl_2$ (1:2.5 w/v) (data for A horizons were provided by Ingo Schöning, data for texture of C horizons were partly provided by the Brandenburg State Agency for Mining, Geology and Raw Materials (LBGR)). The top millimeters of soil, on which BSC had been visually detected as a green cover, was manually removed from the forest using a spatula. After transport to the lab at 4 °C, samples were separated into the compartments BSC (green cover, including the upper 2 mm of the soil which still contained algae as identified using a binocular) (BSC) and crust-adhering soil (defined as soil between 2 mm and 5 mm depth) (ca) using a razor blade. Additionally, crust-free soil (cf) was sampled by manually taking the upper 5 mm of forest top soil without green cover using the spatula. The three subsamples BSC, ca and cf represent one sample set. Material of all three subsamples (excluding gravel and stones > 2 mm) was air-dried before ground to < 0.5 mm.

2.2. Total C, N, P and sequential P fractionation

Total C and N (C_t, N_t) were determined using a Vario EL elemental analyzer (Elementar Analysensysteme, Hanau, Germany). Total P (P_t) was extracted from 0.5 g dry material by microwave-assisted digestion with aqua regia solution (3:1 hydrochloric acid − nitric acid) (Chen and Ma, 2001; ISO standard 11466). Its concentration in the extract was measured by inductively coupled plasma optical emission spectroscopy (ICP-OES) (JY238ULTrace, France).

The concentrations of various P pools were determined using sequential P fractionation after Hedley et al. (1982) with modifications after Chang and Jackson (1957). In brief, 0.5 g dry material was sequentially extracted with 30 mL of distilled water, distilled water in the presence of anion exchange resin (6 × 2 cm resin membrane (55164 2S, BDH Laboratory Supplies, Poole, England), 0.5 M $NaHCO_3$, 0.1 M NaOH and 1 M H_2SO_4. Mixtures were shaken for 18 h before they were centrifuged at 2700 *g* for 20 min. In the resin-P fraction, P was removed from the resin using 1 M HCl. The concentration of P_t of the different extraction fractions was measured in the supernatants by ICP-OES while the pellet was used for the next extraction step. For undisturbed P analyses, HCO_3 of the $NaHCO_3$ extract was cleaved using 37% HCl (10:1, v:v). Molybdate-reactive P (P_i) of each extract was determined colorimetrically at