Effects of Biological Soil Crust Succession on Surface Soil Nutrients and Microbial Community Composition in Sandy Areas: Postprint

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Date: 2024-12-03T00:00:00+00:00

Abstract

Biological soil crusts are important components of dryland ecosystems, playing a significant role in the interactions between biotic and abiotic factors at the soil surface. This study investigated the physicochemical properties, microbial community composition, and enzyme activities of different types of biological soil crusts and their underlying 0–2 cm and 2–5 cm soil layers at the southern edge of the Tengger Desert, and analyzed the variation characteristics of soil microbial community composition and enzyme activities with crust succession and their relationships with soil physicochemical properties. The results showed that: (1) With crust succession toward moss-dominated communities, organic carbon, total nitrogen, total phosphorus, electrical conductivity (EC), and silt-clay particle content in the crust layer and underlying soils showed a significant increasing trend, but decreased significantly with increasing soil depth; pH, bulk density, and sand particle content showed the opposite trend. (2) Total PLFAs, bacterial PLFAs, and fungal PLFAs in the crust layer all exhibited the pattern of moss crust > lichen crust > algal crust, with increases of 24%, 15%, and 39%, respectively, in moss crust compared with algal crust; the fungi-to-bacteria PLFA ratio (F:B) in moss crust increased by 20% compared with algal crust. The microbial community composition in the 0–2 cm and 2–5 cm soil layers beneath the crusts showed similar patterns, but all parameters decreased significantly with increasing soil depth. (3) The activities of invertase, catalase, cellulase, amylase, polyphenol oxidase, peroxidase, urease, and alkaline phosphatase in the crust layer and its underlying 0–2 cm and 2–5 cm layers all increased significantly with crust succession, but their activities all decreased significantly with increasing soil depth. (4) Soil microbial community composition and enzyme activities were significantly positively correlated with soil organic carbon, total nitrogen, total phosphorus, EC, and silt-clay content, but significantly negatively correlated with pH, bulk density, and sand content. Structural equation

modeling analysis indicated that changes in soil chemical properties triggered by crust succession were the key driving factors for microbial communities and enzyme activities.

Full Text

Effects of Biological Soil Crust Succession on Surface Soil Nutrients and Microbial Community Composition in Sandy Areas

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Abstract

Biological soil crusts (BSCs) represent a critical component of dryland ecosystems, mediating important interactions between biotic and abiotic factors at the soil surface. This study investigated the physicochemical properties, microbial community composition, and enzyme activities of different BSC types and their underlying soil layers (0–2 cm and 2–5 cm) at the southern margin of the Tengger Desert. We analyzed how soil microbial communities and enzyme activities change during BSC succession and examined their relationships with soil physicochemical properties. The results demonstrated that as BSCs progressed toward moss-dominated communities, the contents of organic carbon, total nitrogen, total phosphorus, electrical conductivity (EC), and silt-clay particles in both the crust layer and underlying soil increased significantly, while these parameters decreased markedly with soil depth. Conversely, pH, bulk density, and sand content showed opposite trends. Total phospholipid fatty acids (PLFAs), bacterial PLFAs, and fungal PLFAs all exhibited the pattern: moss crust > lichen crust > algal crust, with moss crust showing increases of 24%, 15%, and 39% respectively compared to algal crust. The fungal-to-bacterial PLFAs ratio in moss crust was 1.2 times that in algal crust. The underlying 0–2 cm and 2–5 cm soil layers displayed similar patterns, though all parameters decreased significantly with depth. Enzyme activities—including sucrase, catalase, cellulase, amylase, polyphenol oxidase, peroxidase, urease, and alkaline phosphatase—increased significantly with BSC succession in both the crust and underlying layers, but decreased with soil depth. Microbial community composition and enzyme activities were significantly positively correlated with soil organic carbon, total nitrogen, total phosphorus, EC, and silt-clay content, and significantly negatively correlated with sand content. Structural equation

modeling revealed that changes in soil chemical properties induced by BSC succession were the key drivers of microbial community composition and enzyme activities.

Keywords: microbial community; enzyme activity; biological soil crusts; succession; desert region

1 Introduction

1.1 Study Area

The study area is located at Mingshazui in Gulang County, Gansu Province (37°33 N, 103°41 E, elevation 1557 m), which belongs to a desertified grassland ecosystem with aeolian sandy soils. The region experiences a mean annual temperature of 7.8 °C, with extreme maximum and minimum temperatures of 36.6 °C and -27.3 °C, respectively. Annual precipitation averages 175 mm, concentrated between June and September, while mean annual potential evaporation reaches 3038.5 mm. The woody vegetation is dominated by shrubs including *Artemisia ordosica*, *Artemisia sphaerocephala*, *Caragana roborovsky*, and *Nitraria tangutorum*. Herbaceous species primarily consist of *Stipa breviflora*, *Eragrostis poaeoides*, *Bassia dasyphylla*, *Cleistogenes songorica*, and *Chloris virgata*. The inter-shrub spaces are covered by biological soil crusts with total coverage reaching 85%, comprising algal-, lichen-, and moss-dominated crusts.

1.2 Research Methods

In July 2022, we established 10 m × 10 m quadrats at 10 m intervals for vascular plant community surveys. Within each quadrat, we selected inter-shrub areas dominated by algal, lichen, or moss crusts and set up 1 m × 1 m sub-quadrats for soil sampling. Soils were collected from the crust layer (0–2 cm) and the underlying layer (2–5 cm) using a five-point sampling method. Samples from the same crust type and soil layer within each sub-quadrat were combined into composite samples, yielding 18 total samples. All samples were transported to the laboratory and sieved (2 mm) to remove roots and debris. Each sample was divided into two portions: one air-dried at room temperature for physicochemical analysis, and another stored at -80 °C for microbial community and enzyme activity analyses.

Soil particle size distribution was measured using a Microtrac S3500 laser particle analyzer, bulk density by the coating method, organic carbon by dichromate oxidation, total nitrogen by semi-micro Kjeldahl digestion, and total phosphorus by molybdenum-antimony colorimetry. Soil pH was determined in a 2.5:1 water-to-soil extract using a pH meter, and electrical conductivity (EC) was measured in the same extract with a portable conductivity meter. Chlorophyll *a* content was extracted with 95% ethanol and measured spectrophotometrically (UV-2450, Shimadzu, Japan). Microbial community composition was ana-

lyzed using phospholipid fatty acid (PLFA) analysis. Briefly, 8 g of freeze-dried soil was extracted with a chloroform-methanol-citrate buffer mixture (1:2:0.8 v/v/v), shaken at 250 rpm for 2 hours, and centrifuged at 4000 rpm for 10 minutes. The supernatant was collected, and the extraction was repeated. The combined extracts were evaporated, and non-polar lipids were removed with 10 mL acetone. PLFAs were separated, converted to fatty acid methyl esters via alkaline methanolysis, and analyzed by gas chromatography (Agilent 6890N) with MIDI identification software.

Soil enzyme activities were measured following standard methods. Sucrase, amylase, and cellulase activities were determined by 3,5-dinitrosalicylic acid colorimetry; catalase by $KMnO_4$ titration; peroxidase and polyphenol oxidase by pyrogallol colorimetry; urease by indophenol blue colorimetry; and alkaline phosphatase by disodium phenyl phosphate colorimetry.

1.3 Data Analysis

Two-way ANOVA was used to compare differences in physicochemical properties, microbial community composition, and enzyme activities among crust types and soil layers, with least significant difference (LSD) tests for post-hoc comparisons ($\alpha = 0.05$). Pearson correlation analysis quantified relationships between microbial parameters, enzyme activities, and soil properties. Structural equation modeling (SEM) was performed in AMOS 21.0 to evaluate direct and indirect effects of soil physicochemical properties on microbial communities and enzyme activities. All statistical analyses were conducted in SPSS 25.0.

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2 Results

2.1 Soil Physicochemical Properties

As BSCs progressed toward moss dominance, significant changes occurred in the physicochemical properties of both crust and underlying soils . Crust layer silt-clay content followed the pattern: moss crust > lichen crust > algal crust, with significant differences among all types. Moss crust exhibited 30% and 28% higher silt-clay content than algal and lichen crusts, respectively. Soil organic carbon, total nitrogen, total phosphorus, and EC showed similar trends, with moss crust values 3.1, 1.3, 1.3, and 1.9 times higher than algal crust, respectively ($P < 0.01$). Conversely, sand content, bulk density, and pH showed opposite patterns, decreasing by 33%, 21%, and 6% in moss crust compared to algal crust. The underlying 0–2 cm and 2–5 cm layers exhibited similar trends, though silt-clay, organic carbon, total nitrogen, and total phosphorus contents decreased significantly with depth ($P < 0.001$), while sand content, bulk density, and pH increased ($P < 0.001$). Two-way ANOVA indicated that crust type, soil depth, and their interaction significantly affected most physicochemical properties ($P < 0.001$), except for their interaction effect on silt content .

2.2 Soil Microbial Community Composition

Microbial community composition changed significantly with BSC succession [Figure 1: see original paper]. Total PLFAs, bacterial PLFAs, and fungal PLFAs in the crust layer all followed the pattern: moss crust > lichen crust > algal crust, with moss crust values 24%, 15%, and 39% higher than algal crust, respectively ($P < 0.001$). The fungal-to-bacterial PLFAs ratio in moss crust was 1.2 times that in algal crust. The 0–2 cm and 2–5 cm soil layers showed similar patterns, though all PLFA parameters decreased significantly with depth ($P < 0.001$). Crust type and depth significantly affected microbial communities ($P < 0.001$), but their interaction did not ($P > 0.05$).

2.3 Soil Enzyme Activities

Enzyme activities related to carbon, nitrogen, and phosphorus cycling increased significantly with BSC succession [Figure 2: see original paper]. All eight measured enzymes—sucrase, catalase, cellulase, amylase, polyphenol oxidase, peroxidase, urease, and alkaline phosphatase—showed the pattern: moss crust > lichen crust > algal crust, with moss crust activities 25.7%, 52.2%, 26.0%, 33.6%, 66.9%, 40.7%, 54.4%, and 42.9% higher than algal crust, respectively. The 0–2 cm layer exhibited similar trends, with moss crust enzyme activities 10.5%–31.3% higher than algal crust ($P < 0.001$). All enzyme activities decreased significantly with depth ($P < 0.001$). As depth increased, differences among crust types diminished for polyphenol oxidase, catalase, urease, and alkaline phosphatase, but increased for sucrase, cellulase, and amylase, with moss crust 2–5 cm layer activities 42.9%–243.0% higher than algal crust.

2.4 Relationships Between Microbial Communities, Enzyme Activities, and Soil Properties

Pearson correlation analysis revealed that microbial community composition and enzyme activities were significantly positively correlated with soil organic carbon, total nitrogen, total phosphorus, EC, and silt-clay content, and significantly negatively correlated with sand content, bulk density, and pH . Structural equation modeling showed that BSC succession had significant direct and indirect effects on microbial communities and enzyme activities, explaining 62.8% and 52.0% of their variation, respectively [Figure 3: see original paper]. Changes in soil chemical properties (organic carbon, nitrogen, phosphorus) were the primary drivers, explaining 60.1% of microbial community variation and 92.8% of enzyme activity variation. Physical properties also significantly influenced both parameters, explaining 11.5% and 16.1% of variation, respectively.

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3 Discussion

The type and quality of ecosystem services provided by BSCs are closely linked to their species composition and richness, making BSC development a key indicator of ecosystem health. As BSCs progress from algal- to moss-dominated communities, their structural complexity increases, profoundly altering both crust properties and underlying soils. In our study area, silt-clay content in BSCs and underlying soils increased significantly with succession. Initially, cyanobacteria mechanically entangle soil particles with filaments and chemically bind them with exopolysaccharides, reducing wind erosion and capturing fine particles from atmospheric dust. Lichen thalli and moss plants further enhance capture of silt-clay particles, improving topsoil texture. Concurrently, soil organic carbon and nutrients increased significantly with succession, primarily due to carbon and nitrogen fixation by cryptogams. Chlorophyll *a* content increased markedly during succession, and previous studies have shown that carbon fixation rates in lichen- and moss-dominated crusts are 2–3 times higher than in algal crusts. Notably, different BSC types vary in their capacity to capture atmospheric dust, with later-successional stages more effectively trapping dust and promoting elemental accumulation. As BSCs mature, surface soil stability increases, wind erosion decreases, and the crusts better retain fine particles, nutrients, and vascular plant litter.

Microbial community composition changed significantly with BSC succession. The dominant photoautotrophic groups in different BSC types employ distinct adaptive strategies that influence environmental conditions (light, temperature, moisture), fostering development of specific microbial communities that shift from generalist to specialist taxa during succession. Our SEM analysis identified chemical property changes as the key driver of microbial community variation. The accumulation of organic carbon and nutrients during BSC development provides abundant substrates, promoting growth of organic matter-decomposing microbes. Maier et al. (2018) found that BSCs harbor higher abundances of chitin- and cellulose-degrading microbes than bare soils. In nutrient-poor dryland soils, nitrogen and phosphorus accumulation during BSC development alleviates microbial nutrient limitation and enhances nutrient use efficiency, promoting microbial growth. Notably, soil microorganisms respond differently to carbon sources; later-successional stages contain abundant dead plant residues rich in low-molecular-weight organic compounds (sugars, amino acids, organic acids) that stimulate rhizosphere-associated bacteria and increase microbial diversity. Microbial PLFAs were significantly positively correlated with chlorophyll *a* and negatively correlated with pH. Higher chlorophyll *a* may increase microbial metabolic quotient and substrate utilization, while lower pH promotes microbial activity. Improved soil texture also drives microbial communities, as finer particles create favorable growth conditions and effectively adsorb substrates and microbes. Lower pH in later-successional stages favors fungal growth, and fungi are more adept at decomposing recalcitrant carbon than bacteria, which prefer labile carbon. Thus, increasing recalcitrant carbon during succession

likely promotes fungal proliferation.

Soil microbes secrete extracellular enzymes that catalyze organic matter decomposition and transformation. All eight enzyme activities increased with BSC succession, indicating enhanced metabolic capacity. SEM revealed that changes in soil chemical properties were the primary driver of enzyme activity, which is closely linked to increased microbial activity and abundance during succession. Additionally, abundant simple compounds secreted by later-successional BSCs provide rich substrates that promote enzyme activity. The increases in organic carbon, nitrogen, and phosphorus specifically enhanced enzymes related to elemental cycling. Enzyme activity was also linked to cryptogam characteristics, as lichen thalli and mosses secrete more enzymes through rhizines and litter, increasing activities in both crust and underlying soils. Furthermore, darker pigments in later-successional stages absorb solar radiation, elevating soil temperature and enhancing extracellular enzyme activity.

Microbial community composition and enzyme activities exhibited clear vertical stratification, decreasing significantly with soil depth. BSC colonization creates a layered soil structure, concentrating organic matter and nutrients in the crust layer and resulting in stratified microbial communities and enzyme activities. Additionally, the crust layer experiences frequent and intense fluctuations in moisture and temperature plus strong UV radiation, favoring pigmented fungi, cyanobacteria, and stress-tolerant taxa. In contrast, underlying soils harbor less stress-tolerant communities, leading to differentiation in extracellular enzyme activities and organic matter decomposition rates between layers.

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4 Conclusions

Biological soil crust succession toward moss-dominated communities in sandy regions promotes changes in microbial community diversity and enzyme activities. (1) As BSCs progress to moss-dominated communities, bacterial and fungal PLFAs and the activities of sucrase, catalase, cellulase, amylase, polyphenol oxidase, peroxidase, urease, and alkaline phosphatase increase significantly. Fungi become increasingly dominant in the microbial community, and all parameters decrease from the crust layer to underlying soils. (2) Changes in cryptogam composition and improvements in soil physicochemical properties driven by BSC succession are the key factors regulating microbial communities and enzyme activities.

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