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RESEARCH ARTICLE

A comparative study of soil nutrient availability and enzyme activity under biological soil crusts in different erosion regions of the Loess Plateau, China

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Abstract

Purpose The influences of biological soil crusts (BSCs) on soil properties have been investigated extensively. However, few studies have compared soil properties under different types of BSCs in different erosion regions.

Methods Three erosion regions (water erosion, wind-water crisscross erosion, and wind erosion regions) were identified in the Loess Plateau, and we collected subsoil samples of cyanobacteria and moss crusts in each region (crust coverage > 95%), respectively. The variations of soil nutrient content and enzyme activity were evaluated, and the most influential soil properties were determined.

Results Most of the tested soil properties were significantly affected by erosion and crust types ($p < 0.05$). Soil pH was significantly higher, while soil electrical conductivity (EC) was substantially lower in the water erosion region than the water-wind crisscross erosion and wind erosion regions ($p < 0.05$). Soil nutrient content and enzyme activity were higher in the water erosion region compared to the wind erosion and wind-water erosion regions ($p < 0.05$). In the subsoil below BSCs, most of the soil nutrient availability and enzyme activity was higher under moss crusts than cyanobacteria crusts ($p < 0.05$).

Conclusion Our results suggested that there were differences in the effects of two types of BSCs on the soil nutrient availability and enzyme activity across the three typical erosion regions in the Loess Plateau, and the magnitude of these effects followed the order of: water erosion regions > wind erosion regions > wind-water erosion crisscross regions, and moss crusts > cyanobacteria crusts.

Keywords Soil erosion · Cyanobacterial crusts · Moss crusts · The Loess Plateau · Soil nutrient · Soil enzyme activity

Abbreviations

BSCs	Biological soil crusts
SOC	Soil organic carbon
TN	Total nitrogen
TP	Total phosphorus
TK	Total potassium
AN	Available nitrogen
AP	Available phosphorus
AK	Available potassium
EC	Electrical conductivity
CAT	Catalase

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DHA,	Dehydrogenase
SUC	Sucrase
URE	Urease
TPF	Triphenylformazan
SD	Standard deviation
ANOVA	Analysis of variance
PCA	Principal component analysis

Introduction

In arid and semiarid environments, sealing and crusting of soil surfaces plays a vital role in ecosystem processes, especially when soil is exposed to water or wind flows, and these processes are therefore of fundamental importance for landscape structure and function (Eldridge et al. 2000). Biological soil crusts (BSCs) are communities that mainly consist of cyanobacteria, algae, lichens, mosses, bacteria, and fungi. They bond with soil particles in the uppermost few centimeters of the soil surface, cover the interspaces of vascular plants in arid and semiarid regions (Belnap et al. 2016; Eldridge and Greene 1994). Biological soil crusts cover more than 40% of the earth's terrestrial surface, and reaching up to 70% of the living cover in some parts of the world (Delgado-Baquerizo et al. 2016). According to the composition of the dominant organisms, BSCs can be classified into three different successional stages of cyanobacteria crusts, lichen crusts, and moss crusts (Darby et al. 2010; Lan et al. 2017).

In arid and semiarid ecosystems, BSCs are known as "ecosystem engineers" and have important ecosystem functions, such as influencing soil properties and behavior by altering soil stabilization, water runoff, infiltration, soil porosity, soil water evaporation, soil water erosion, and wind erosion (Castillo-Monroy et al. 2010; Gao et al. 2020a; Kakeh et al. 2020; Li 2012). Kakeh et al. (2020) reported that the higher soil water content and infiltration in BSCs than bare soil, resulted in a higher spatio-temporal variation of soil properties, while Xiao et al. (2019a) demonstrated that BSCs inhibited soil water infiltration under tension and ponding conditions in dryland ecosystems. Moreover, BSCs increase soil fertility by enhancing carbon sequestration and nitrogen fixation, with the nitrogen fixation activity of BSCs being in the range of 2.5–62.0 μmol C_2H_4 m^{-2} h^{-1}. They have also been reported to increase the total surface soil carbon content by 300% (Belnap 2003; Housman et al. 2006; Muñoz-Rojas et al. 2018; Su et al. 2011), change the soil nutrient distribution and soil physical–chemical properties by extruding polysaccharides and other organic components (Concostrina-Zubiri et al. 2013), and promote biodiversity by supplying suitable habitats and nutrients/foods for vascular plants and soil animals (Castillo-Monroy et al. 2011; Li et al. 2011; Song et al. 2020). Therefore, BSCs colonization and rehabilitation are critical for combating soil erosion (Rossi et al. 2017).

Biological soil crusts are generally considered to stabilize soil and reduce soil erosion (wind and water erosion) (Meng et al. 2021). Previous studies have indicated that the erosion modulus, sand-transport rate, and wind erosion decrease due to BSCs, which can separate the soil from the airflow (Griffiths et al. 2012; Bu et al. 2015a, b; Luo et al. 2020). The wind erosion rates measured on bare sand were 46, 21, and 17 times the erosion rates on soil with 90% crust cover at velocities of 18, 22, and 25 m s^{-1}, respectively, highlighting the protective effect of BSCs (Langston and Neuman 2005; Zhang et al. 2006). Some studies have focused on the effect of different BSCs under different wind erosion conditions (disturbances, coverage rates, and distribution patterns) and with different underlying wind erosion control mechanisms (Belnap and Gillette 1998; Bu et al. 2015a, b; Eldridge and Leys 2003; Zhang et al. 2022). Compared to wind erosion studies, there are many different aspects included in studies of how BSCs influence water erosion. For example, soil erosion by water is more closely associated with the level of development, disturbances, coverage, and spatial distribution of BSCs (Belnap et al. 2016; Emilio 2014; Liu et al. 2016; Rodriguez-Caballero et al. 2013). The impact of BSCs on soil water erosion can be determined by applying modified models, which are based on adaptations to algorithms related to soil erodibility and soil surface cover factors (Gao et al. 2017, 2020b). Biological soil crusts (especially late-developed moss crusts) have a significant controlling effect on both water and wind erosion, where high levels of moss crust coverage can significantly reduce soil erosion from rainfall, aeolian processes, and sediment emissions and transport during hydrological and aeolian processes (Zhang et al. 2006; Zhao et al. 2014). The underlying mechanism is that BSCs reduce water and wind erosion by increasing the surface cover and roughness, improving soil aggregates, changing rainfall infiltration, and altering surface soil moisture (Belnap and Gillette 1998; Chamizo et al. 2015; Fick et al. 2020). The influence of BSCs on soil erosion may be ultimately reflected in soil properties (such as a higher soil organic carbon (SOC) content, nutrient availability, microbial activity and soil moisture).

The influences of BSCs on soil properties have been investigated extensively, with most studies focusing on the uppermost few centimeters of the soil profile (Young et al. 2017). Many studies have suggested that BSCs are beneficial to the growth of the underlying soil (Li et al. 2010). Niu et al. (2017) revealed that BSCs significantly ameliorate the physical–chemical and biological properties of the subsoil, such as the soil organic matter content, soil enzyme activity and soil microbial biomass. Xu et al. (2020) found that BSCs could accelerate soil nutrient accumulation compared with bare soil, and Wu et al. (2013) reported that the development of BSCs increased soil nitrogen and phosphorus availability. Furthermore, numerous studies have indicated that the way BSCs modify soil properties depends largely on the types of BSCs, and that the physical–chemical properties of the underlying soil improve with BSCs succession (Chamizo et al. 2012). For example, infiltration in soils dominated by moss crusts is better than in those dominated by cyanobacterial crusts (Eldridge et al. 2010; Kidron et al. 2003). The soil organic matter content underlying BSCs is notably improved, and is higher in soil underlying moss dominated crusts than under cyanobacteria dominated crusts (Gao et al. 2017). However, to the best of our knowledge, few studies have compared soil properties under different types of BSCs in the different erosion regions of the Loess Plateau.

The Loess Plateau covers an area of 640,000 km^2 and is one of the most severely eroded regions of the world (Bao et al. 2019a; Xin et al. 2008). The average rate of annual soil erosion is 5000–10,000 mg km^{-2} per year due to the interactive effects of natural factors and human activities, and over 60% of the land in the Loess Plateau has suffered from soil erosion (Wang et al. 2015). The soft soil, concentrated rainfall (mainly in July to September), and low vegetation cover has resulted in severe soil severe erosion in this region (Fu 1989). Generally, there are three main types of erosion region: water erosion, wind-water erosion crisscross, and wind erosion regions (Zheng and Wang 2013). The naturally recovery of BSCs was noticed within a few decades following the implementation of the "Grain for Green" ecological project in 1999, with coverage reaching above 70% in the region (Bao et al. 2019b). Previous studies have investigated the distribution of BSCs (Bu et al. 2016) and the influence of BSCs on soil properties, especially hydraulic properties (Wang et al. 2017), in this region. There are changes in the species composition in each developmental and succession stage of BSCs, with cyanobacteria often occurring in the earlier BSCs successional stages, and lichen and moss crusts appearing later (Bowker 2007). The controlling effect on both water and wind erosion varies for the different types of BSCs, with the order being moss crusts > lichen crusts > cyanobacteria crusts (Li et al. 2007; Zhang et al. 2022).

This study explored the effects of two different types of BSCs (cyanobacteria and moss crusts, which form different stages of the BSCs succession) on soil nutrient availability and enzyme activity across three typical erosion regions in the Loess Plateau (water erosion, wind-water erosion crisscross, and wind erosion regions). We proposed the hypothesis that these effects differed among erosion and BSCs types, with the magnitude of the effects following the order of: water erosion regions > wind erosion regions > wind-water erosion crisscross regions, and moss crusts > cyanobacteria crusts. To test the above hypothesis, we collected 0–5 cm subsoil samples under two types of BSCs (cyanobacteria and moss) in three different erosion regions of the Loess Plateau. The variations in soil nutrient content and enzyme activity under different BSCs in different erosion regions were evaluated, and the most influential soil properties in the different erosion regions were explored. These results provide a reference for soil improvement and the restoration of degraded ecosystems in the arid and semiarid regions of north China.

Materials and Methods

Description of the study area

Three representative erosion regions (water erosion, wind-water erosion crisscross, and wind erosion regions) from the southeast to the northwest of the Loess Plateau region were selected (Fig. 1). The

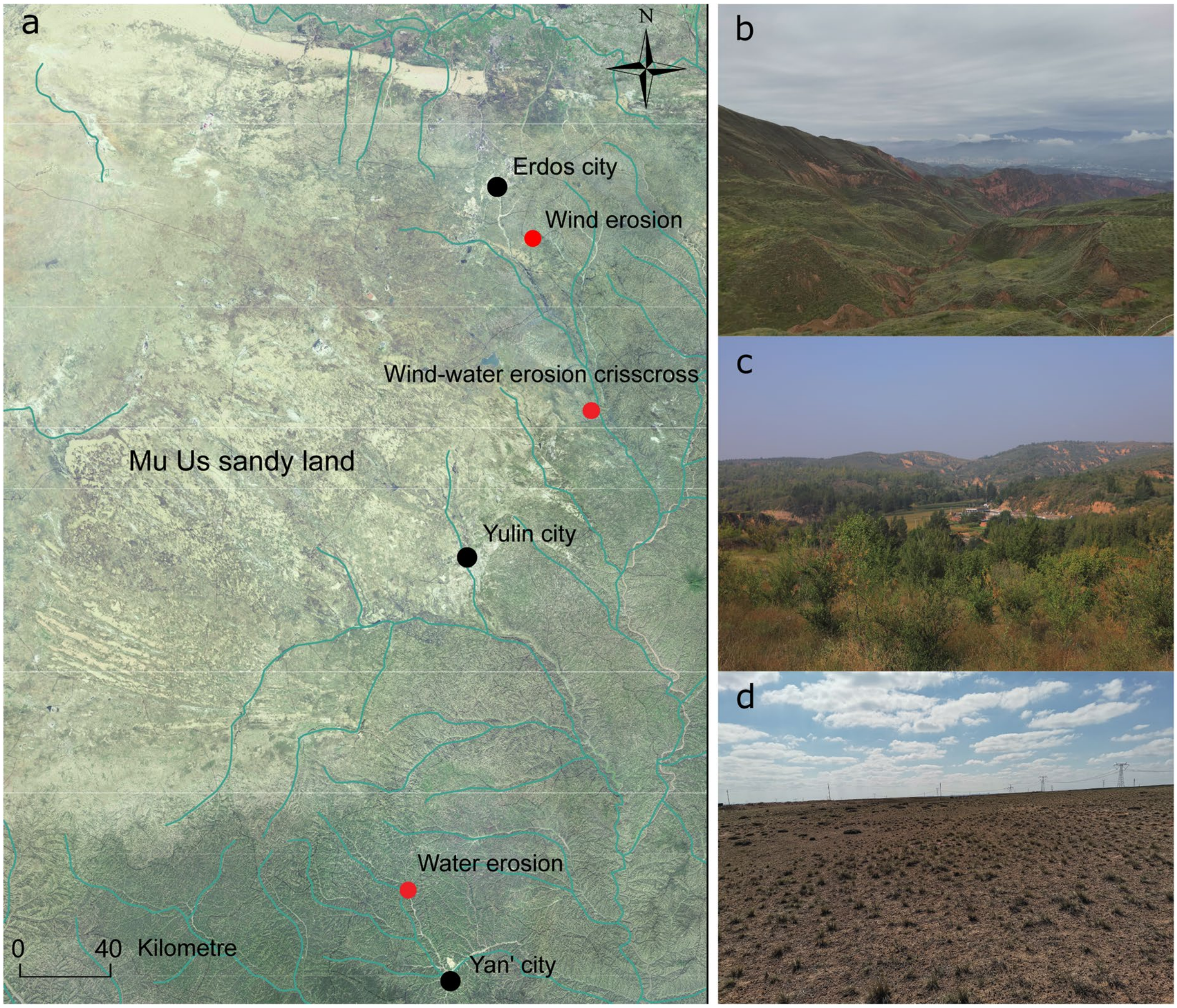


Fig. 1 The three study sites in the Loess Plateau

details of the study areas were as follows. (1) Ansai Comprehensive Experimental Station of Soil and Water Conservation (36°51′ N, 109°18′ E), Chinese Academy of Sciences (CAS). The study site is located in Ansai County, Yan′an City (Site 1). The study site is a warm temperate semi-arid continental monsoon climate, with a mean annual temperature of 8.8 °C, and the evaporation capacity is above 1000 mm (Sun et al. 2016). The study area was a typical water erosion region due to severe soil erosion caused by heavy rainfall with a short duration (Liu et al. 2020). The average annual precipitation is about 505 mm, of which 70% falls during June to September (summer months). The precipitation usually occurs as heavy storms with a short duration, which favors the rapid formation of runoff and greatly increases water erosion and flooding (Sun et al. 2016; Wu et al. 2016). In this research area, *Oscillatoriaceae* and the genus *Oscillatoriaare* are the dominant cyanobacteria species, and *Didymodon tectorum* and *D. vinealis* are the predominant moss species in BSC communities (Zhao et al. 2014). (2) Shenmu Erosion and Environment Research Station (38°46′–38°51′ N, 110°21′–110°23′ E), Institute of Soil and Water Conservation, CAS, which is situated in Shenmu County, Yan′an City (Site 2). This study area is a transitional zone of the Plateau toward the Mu Us Desert and the Loessial hilly region toward the Ordos Plateau, which is representative of the transitional belt and is subjected to both water and wind erosion (Jia et al. 2011; Ge et al. 2020). This region has a temperate semi-arid continental climate with a mean annual temperature of 8.4 °C and a mean annual evaporation of 785 mm (Jia et al. 2011). As a typical wind–water erosion crisscross zone of the Loess Plateau, this region is characterized by drought and wind-blown sand in winter and spring, and a rainy season in summer and autumn (Ge et al. 2020). The average annual precipitation is about 409 mm in this region, where some precipitation falls as snow in winter, but 77% of the total precipitation occurs as rainfall from June to September (Fu et al. 2010, 2012). Biological soil crusts in the area are dominated by cyanobacteria and moss. The moss crusts are dominated by *Bryum arcticum* (R. Brown) B.S.G. and *D. vinealis* (Brid.) Zander, with coverage reaching 70–80% (Xiao et al. 2010). (3) Ordos Sandy Land Ecological Research Station (39°29′ N, 110°11′ E), CAS. This study area is located in Yijinhuoluo Banner, Ordos City (Site 3). The study site has a temperate continental monsoon climate with remarkable seasonal and diurnal temperature variations and low rainfall. The annual mean precipitation is about 350 mm (about 93% of annual precipitation is from April to October), with an annual mean evaporation of 2,535 mm (Jin et al. 2007). This area was historically a highly productive grassland, but the landscape is now seriously desertization (Zhang, 1994). In this region, erosion by wind occurs frequently during the whole year, with over 40 days per year in this area having a wind speed exceeding 8 on the Beaufort scale (Zhang 1994; Xu et al. 2009). Cyanobacteria and moss dominate the BSC communities, and the common moss species are *B. argenteum* (Hedw.) and *D. vinealis* (Fang et al. 2015). Table 1 summarizes the major properties of each study area (Hu et al. 2019; Sun et al. 2016; Xiao et al. 2019b; Yu et al. 2017).

Collection of soil samples

During 24–30 September 2020, three sampling areas (each about 2 × 2 km) were established in the central areas of the water erosion (site 1), wind-water erosion crisscross (site 2), and wind erosion regions (site 3) of the Loess Plateau, respectively. Five 100 × 100 m subsample plots (distance between each plot > 1 km) were set up in each erosion area, which ensured sufficient amounts of the two types of BSCs (cyanobacteria and moss crusts) and representative samples. In each subsample plot, a soil drill was used to randomly collect 0–5 cm subsoil samples under the cyanobacteria and moss crusts, where the coverage of BSCs was over 95%. There were five replicates (five subsample plots) for each erosion area. In total, 30 soil samples were collected from the three research regions. Each sample was divided into two parts, one part was air dried and hand-sieved through a 2 mm screen for the measurement of soil organic carbon (SOC); total nitrogen (TN); total phosphorus (TP); total potassium (TK); available nitrogen (AN); available phosphorus

Table 1 The details of the study area

Sampling sites	Erosion type regions	Climate	Elevation (m)	Annual average temperature (^{0}C)	Annual average precipitation (mm)	Soil types	Soil texture
Site 1	Water erosion region	Warm temperate semi-arid continental monsoon climate	1200	8.8	505	Loessal soil	Silt loam soil
Site 2	Water-wind erosion crisscross region	A temperate semi-arid continental climate	1081–1274	8.4	409	Aeolian sandy soil	Silt loam soil
Site 3	Wind erosion region	A temperate continental monsoon climate	1296	6.0–8.5	350	Aeolian sandy soil	Sandy loam soil

(AP); available potassium (AK), and other physical properties, i.e., pH and electrical conductivity (EC)). The remainder of the fresh soil samples were ground, passed through a 2 mm sieve, and immediately stored in a car refrigerator (-20ºC). At the end of sampling (about one week), fresh soil samples were transported to the laboratory for the determination of soil enzyme activity, i.e., catalase (CAT), dehydrogenase (DHA), sucrase (SUC), and urease (URE).

Soil nutrient content and the analysis of other physical properties

The SOC content was estimated by the potassium dichromate oxidation spectrophotometric method (Nelson and Sommers 1996), the TN content was measured by the semi-micro Kjeldahl procedure, the TP content was determined using spectrophotometry after H_2SO_4-$HClO_4$ digest-colorimetry, the TK content was determined by the NaOH fusion-flame spectrometric method (Bao 2000; Olsen and Phosphorus 1982), the AN content (mainly refer to hydrolysable nitrogen) was assessed by the alkaline $KMnO_4$ method following the method described by Liu et al. (2015), the AP content was determined from $NaHCO_3$ extracts by Mo-Sb colorimetry, and the AK content was evaluated in NH_4OAc extracts by flame photometry (Li et al. 2013). Soil pH and EC were determined in a soil water suspension (1:5, w/v) by a calibrated pH meter and a portable conductivity meter, respectively (Chen et al. 2017).

Measurement of soil enzyme activity

Soil enzyme activity was assayed according to Guan et al. (1991). In detail, soil CAT (1.11.1.6) activity was titrated over 20 min based on a standard solution of 0.02 M $KMnO_4$ in the presence of H_2SO_4, and the absorbance value at 240 nm was determined through colorimetry. The CAT activity was expressed as µmol $KMnO_4$ g^{-1} 24 h^{-1}. Soil DHA (1.1.1.1) activity was assessed according to the 2,3,5-triphenyltetrazolium chloride (TTC) method, which was determined by the reduction of TTC to triphenylformazan (TPF). The released TPF was extracted with acetone and analyzed at 485 nm in a spectrophotometer. The data were expressed as µg TPF g^{-1} 24 h^{-1}. Soil SUC (3.2.1.26) activity was determined by 3, 5-dinitro salicylic acid colorimetry with sucrase as the substrate. The amount of 3-amino-5-nitro-salicylic-acid released over 24 h was determined by measuring the reducing sugars as glucose to determine soil sucrase activity, and then the color was determined at 578 nm using a spectrophotometer. The results were expressed as mg glucose g^{-1} 24 h^{-1}. Soil URE (3.5.1.5) activity was measured by indophenol colorimetry with urea as the substrate. The amount of NH_4^+ released was assayed using a spectrophotometer at 578 nm and expressed as µmol NH_4^+-N g^{-1} 24 h^{-1}.

Statistical analysis

Data are presented as the mean ± standard deviation (SD) of five replicates. The variations of soil nutrient content and enzyme activity under BSCs in different erosion regions were evaluated by a one-way analysis of variance (ANOVA), according to Duncan's test in the SPSS 16.0 statistical package (SPSS, Chicago, IL, USA). A two-way ANOVA was conducted to evaluate the effects of different erosion types, different crust types, and the interaction between them on soil properties. Significant results were defined at $p < 0.05$. A principal component analysis (PCA) was conducted using R version 3.5.1 in the vegan package, which was used to determine the most influential soil parameters based on the soil physical–chemical properties and soil enzyme activity that were strongly correlated with different erosion regions.

Results

Soil pH and EC

Soil pH was significantly affected by erosion and crust types, and EC was affected by the interaction of erosion and crust types (Table 2, $p < 0.05$). Significant differences in soil pH and EC under the cyanobacteria and moss crusts were observed in the water erosion, water-wind erosion crisscross, and wind erosion regions (Fig. 2, $p < 0.05$). Soil pH increased significantly from water erosion to wind-water erosion crisscross and wind erosion regions, and the maximum pH values were 8.736 and 8.862 under the cyanobacteria and moss crusts, respectively (Fig. 2a). Conversely, the soil EC under the two types of BSCs gradually decreased from the water erosion to wind-water erosion crisscross

Table 2 Results of a two-way analysis of variance (ANOVA) of the effect of different erosion types, different crust types, and the interaction between them on soil properties

Soil properties	Erosion types F-values	Crust types F-values	Erosion types × Crust types F-values
pH	134.554***	14.231***	0.011
Electric conductivity (EC)	62.475***	41.361***	4.246*
soil organic carbon (SOC)	52.130***	1271.804***	40.337***
Total nitrogen (TN)	17.242***	409.835***	8.318**
Total phosphorus (TP)	53.269***	12.475**	4.495*
Total potassium (TK)	32.567***	3.269	3.074
Available nitrogen (AN)	1.654	22.818***	0.347
Available phosphorus (AP)	247.226***	16.794***	8.698***
Available potassium (AK)	38.352***	82.337***	2.019
catalase (CAT)	18.362***	36.850***	3.092
dehydrogenase (DHA)	20.655***	1.162	0.054
sucrase (SUC)	28.705***	5.178*	2.441
urease (URE)	22.843***	56.123***	2.015

***, **, and * indicate a significant influence at 0.001, 0.01, and 0.05 levels respectively

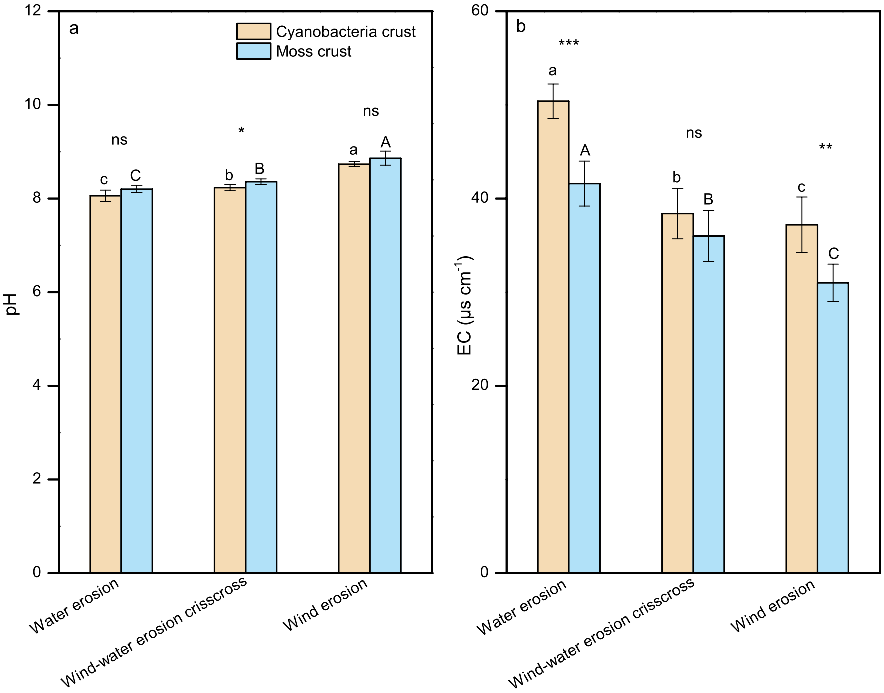


Fig. 2 Variations of soil pH and EC under the cyanobacteria and moss crusts in different erosion regions. Bars represent the mean ± SD (n = 5) and the different letters denote significant differences at $p < 0.05$ under cyanobacteria crusts (lowercase letters) and moss crusts (capital letters) in the different erosion regions according to Duncan's tests. ns indicates no significant influence, and *, **, and *** indicates a significant influence at the 0.05, 0.01, and 0.001 levels between cyanobacteria and moss crusts, respectively

and wind erosion regions, reducing from 50.4 to 37.2 µs cm^{-1} for the underlying soil of cyanobacteria crusts, and from 41.6 to 31.0 µs cm^{-1} for the underlying soil of moss crusts (Fig. 2b). In addition, soil pH values under the moss crusts were significantly higher than under the cyanobacteria crusts in the water-wind erosion crisscross region (Fig. 2a, $p < 0.05$), while the reverse pattern was observed for soil EC in the water erosion and wind erosion regions (Fig. 2b, $p < 0.01$).

Soil nutrient content

The SOC, TN, TP, and AP contents were significantly affected by erosion types, crust types, and their interaction (Table 2, $p < 0.05$). The AK content was significantly affected by both the erosion types and crust types, and TK and AN contents were significantly affected by the erosion types and crust types, respectively (Table 2, $p < 0.05$). The soil nutrient content differed among the different erosion regions (Fig. 3). There were significant significances in SOC, TN, TP, TK, AN, AP, and AK contents in subsoils of cyanobacteria and moss crusts. Among the three research areas, the SOC, TN, TP, TK, AN, AP, and AK contents under the cyanobacteria and moss crusts were highest in the water erosion region, and had intermediate levels in the wind erosion region, with the lowest levels in the wind-water erosion crisscross region (Fig. 3, $p < 0.05$). In general, compared to the wind-water erosion crisscross and wind erosion regions, the water erosion region had a higher soil nutrient availability in the subsoil under cyanobacteria and moss crusts (Fig. 3, $p < 0.05$). Moreover, the content of all soil nutrients under the moss crusts were higher than in the soil under the cyanobacteria crusts. The SOC, TN, and AK under the moss crusts were significantly higher than in cyanobacteria crusts in the three types of erosion regions (Fig. 3a, b, g, $p < 0.01$). The TP and AP under the moss crusts were also significantly higher than under cyanobacteria crusts in the wind-water erosion crisscross and water erosion regions, respectively (Fig. 3c, f, $p < 0.001$). While the AN content was higher in both the wind-water

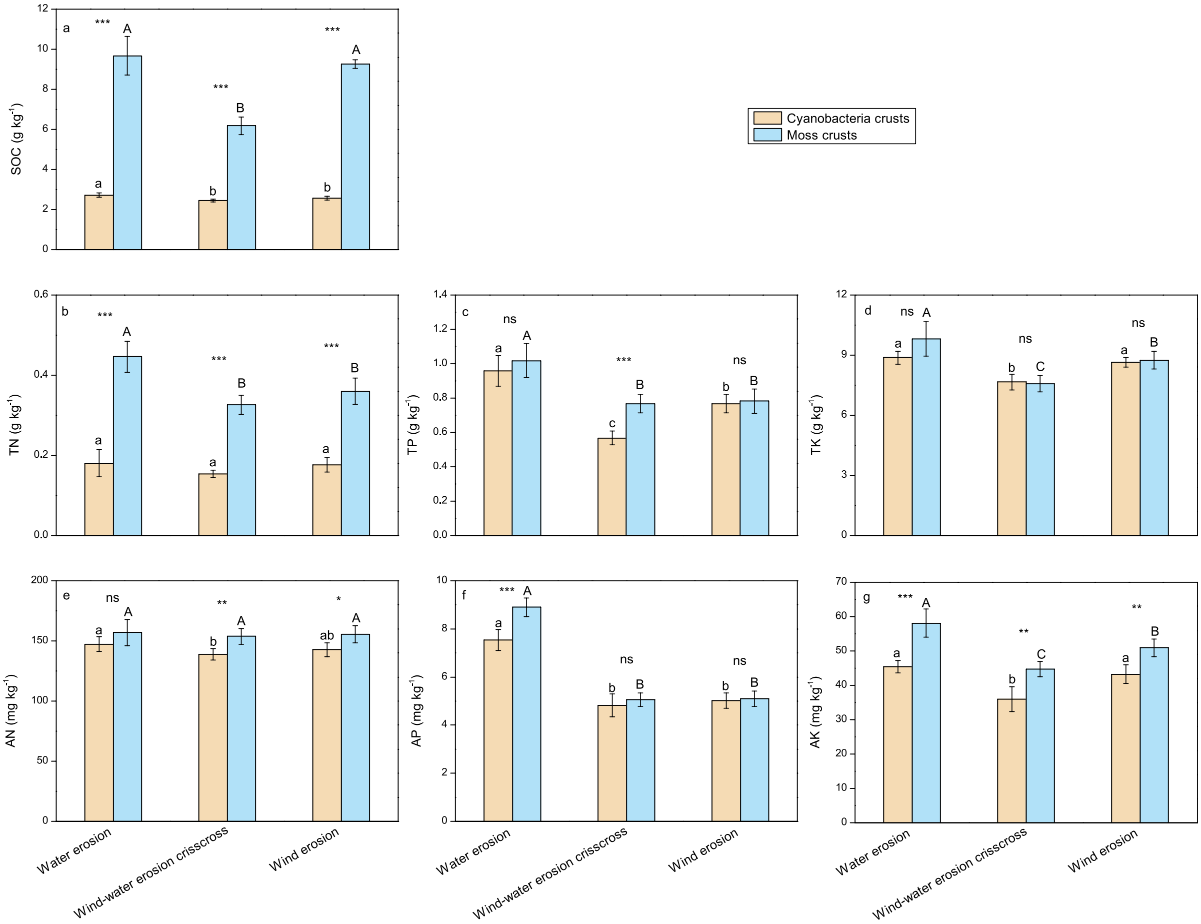


Fig. 3 Variations of the soil nutrient content under the cyanobacteria and moss crusts in different erosion regions

erosion crisscross and water erosion regions (Fig. 3e, $p < 0.01$).

Soil enzyme activity

All soil enzyme activity was significantly affected by erosion types and crust types (Table 2, $p < 0.05$), except for DHA in crust types ($p > 0.05$). There were differences among the three different erosion regions for soil enzyme activity in the subsoil under cyanobacteria and moss crusts (Fig. 4). As expected, the overall trends of the activity of most soil enzymes were similar to those of the soil nutrient content. The soil enzyme activity under cyanobacteria and moss crusts was highest in the water erosion region, intermediate in the wind erosion region, and lowest in the wind-water erosion crisscross region. With the exception of the SUC activity in the subsoil of cyanobacteria crusts, the enzyme activity followed the order of water erosion > wind-water erosion crisscross > wind erosion. In comparison with the wind-water erosion crisscross and wind erosion regions, the CAT, DHA, SUC, and URE activities in the subsoil of cyanobacteria and moss crusts were shown significantly increases in the water erosion region (Fig. 4, $p < 0.05$). Furthermore, in the BSCs subsoil of the three different erosion regions, moss crusts had a higher soil enzyme activity than cyanobacteria crusts. The URE activity was significantly higher under moss crusts in all three erosion regions, while CAT activity was significantly higher in the water erosion and wind erosion regions, and SUC was significantly higher in the wind region (Fig. 4a, c, d, $p < 0.05$).

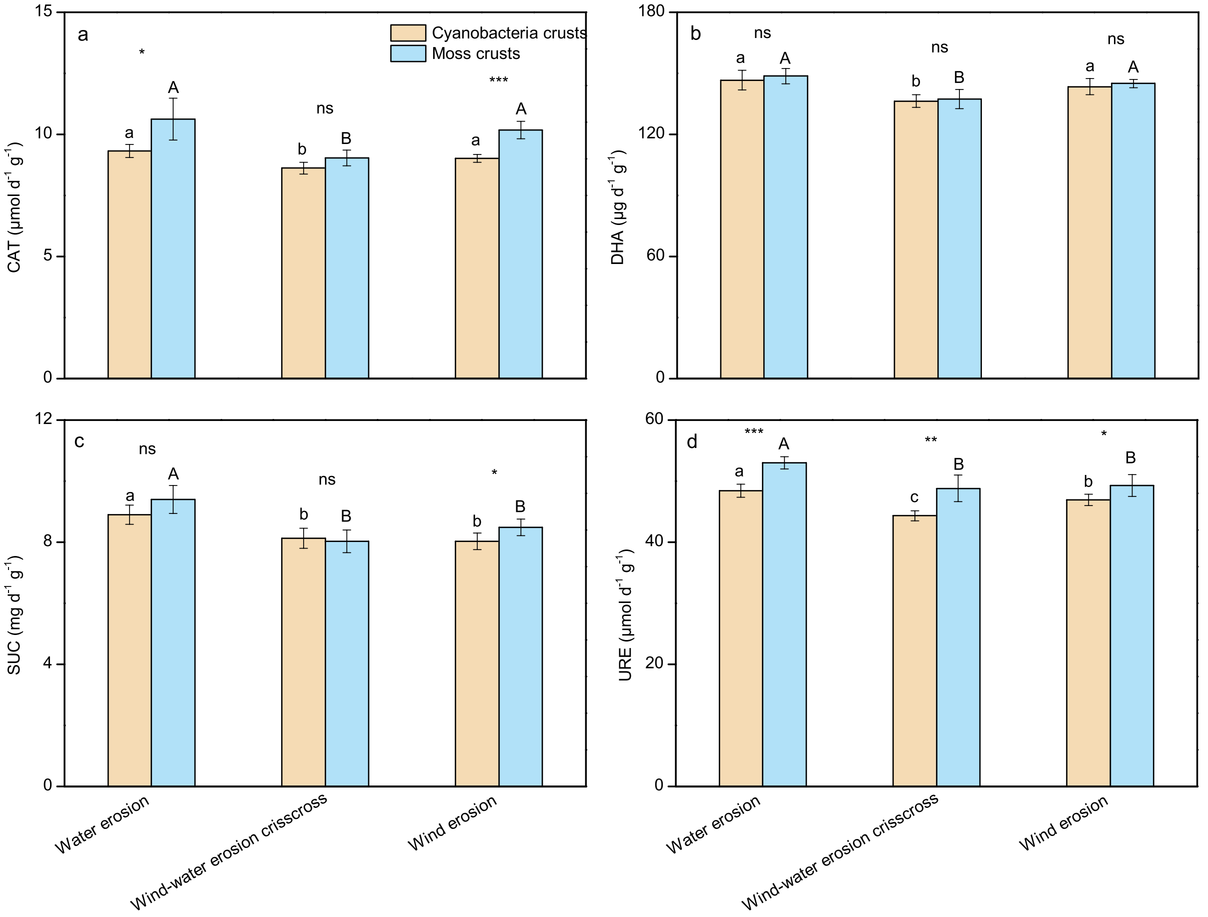


Fig. 4 Variations of soil enzyme activity under the cyanobacteria and moss crusts in different erosion regions

Principal component analysis (PCA) of the soil nutrient content and enzyme activity

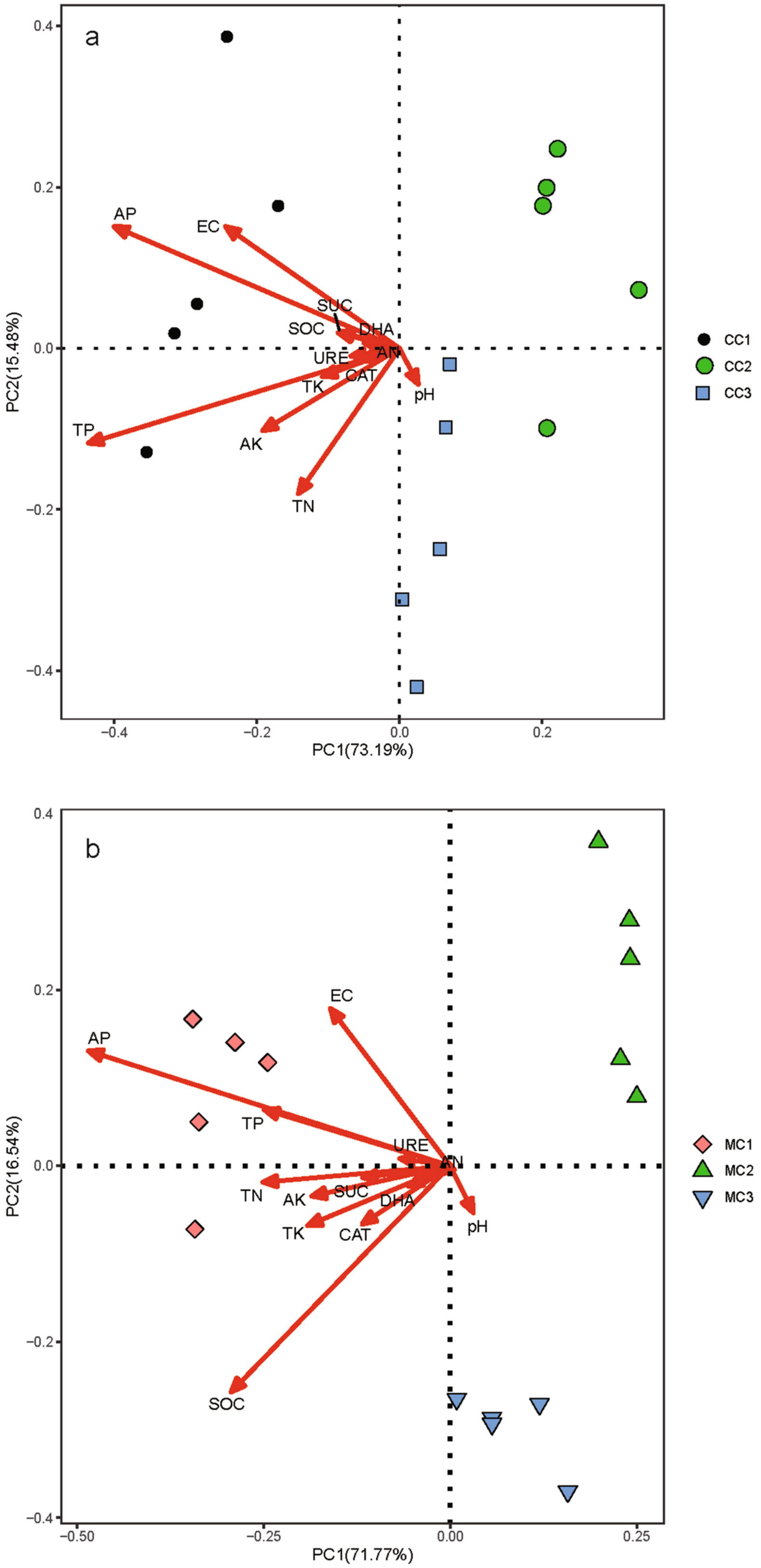
A PCA analysis of the soil nutrient content and enzyme activity under the cyanobacteria and moss crusts in different erosion regions was conducted. The cumulative variance of 88.67%/88.31% could be explained by the first principal component 1 (PC1) representing 73.19%/71.77% and the second principal component 2 (PC2) representing 15.48%/16.54% (Fig. 5). In the subsoil under the cyanobacteria crusts, EC, TP, and AP contributed most to the variability in PC1, and pH made the second largest contribution in PC2. In the subsoil under the moss crusts, TN, TP, and AP contributed most to the variability in PC1, and pH, EC, and SOC made the second largest contribution in PC2. Most of the soil physical–chemical parameters and soil enzyme activity in the water erosion region for the soil beneath the cyanobacteria and moss crusts (CC1, MC1) displayed higher PC1 scores than the corresponding parameters in the wind-water erosion crisscross and wind erosion regions for the soil under the cyanobacteria and moss crusts (CC2, CC3, MC2, MC3) (Fig. 5). This variance was dominated by specific major contributors to the PC1 scores, including higher values of EC, TN, TP, AP, and AK in the water erosion region for the subsoil under the cyanobacteria crusts (Fig. 5a), and higher levels of EC, SOC, TN, TP, TK, and AP in the water erosion region for the subsoil under the moss crusts (Fig. 5b).

Discussion

The soil nutrient content and soil enzyme activity under the BSCs were significantly higher in the water erosion region compared to the wind erosion and water-wind erosion crisscross regions. These results support our hypothesis that effect of BSCs on soil properties follow the order of water erosion regions > wind erosion regions > wind-water erosion crisscross regions, and indicated that both moss crusts and cyanobacteria crusts can maintain a higher soil nutrient availability in water erosion regions than in wind erosion or wind-water erosion regions under the same crust coverage (> 95%). This difference may be explained by the different soil erosion processes that occur during water erosion, wind erosion, and wind-water erosion. Wind is an important erosive force in desert ecosystems due to the lack of soil-surface protection offered by the sparse coverage of vascular plants (Belnap 2001). When the wind velocity exceeds a certain value, soil fine particles, litter, and large sand particles will be eroded (Williams et al. 1995). This sediment movement can ultimately result in many direct and indirect soil and nutrient losses. Unlike wind erosion, water erosion leads to soil and nutrient losses through the detachment, transport, and deposition of soil materials due to the erosive forces of raindrop impact and overland flow runoff (Hao et al. 2019; Shi et al. 2010). The different responses of BSCs to water and wind erosion may explain why BSCs can maintain a higher soil nutrient availability in water erosion regions than wind erosion regions for the same level of coverage. Our results indicated that soil nutrient availability was lower in wind-water erosion crisscross regions than in water or wind erosion regions. Although wind and water can cause serious decreases in the nutrient content of soils on the Chinese Loess Plateau, wind and water erosion occur at different temporal and spatial scales, resulting in a complex pattern of erosion (Tuo et al. 2018). Wind erosion is usually a larger component of net soil redistribution than water erosion, and clearly has the capacity to intensify water erosion (Tuo et al. 2016; Van Pelt et al. 2017), and therefore wind-water erosion crisscross regions may therefore experience more serious soil nutrient losses than water and wind erosion regions.

The succession of BSCs improved most soil physical–chemical and biological properties, and the soil under the moss crusts had higher levels of soil nutrients than the soil under the cyanobacteria crusts. The ability of BSCs to improve soil quality increased with the succession of BSCs. Moss crusts influence the soil nutrient content by capturing dust particles and promoting photosynthesis; thus, they improve the soil nutrient content, leading to the subsoil under the moss crusts having a higher nutrient content in comparison with the subsoil of cyanobacteria crusts (Housman et al. 2006). The results revealed higher levels of soil nutrients under the moss crusts than under the cyanobacteria crusts (Figs. 2 and 3). These results agreed with those of a previous study, which demonstrated that the succession of BSCs could improve soil stability, increase soil organic matter inputs, and lead to carbon and nitrogen immobilization (Plaza et al.

Fig. 5 Principal component analysis (PCA) of the soil nutrient content and enzyme activity under the cyanobacteria and moss crusts in different erosion regions. CC1: soil under the cyanobacteria crusts in the water erosion region; CC2: soil under the cyanobacteria crusts in the wind-water erosion crisscross region; CC3: soil under the cyanobacteria crusts in the wind erosion region; MC1: soil under the moss crusts in the water erosion region; MC2: soil under the moss crusts in the wind-water erosion crisscross region; MC3: soil under the moss crusts in the wind erosion region



2004; Zhang et al. 2015), all of which were beneficial to the amelioration of the soil environment. This finding was consistent with the results of Niu et al. (2017), who reported that BSCs significantly improved soil physical–chemical properties, with moss crusts producing a more significant improvement than cyanobacteria crusts. Yang et al. (2019) also revealed that BSCs increased the accumulation of organic carbon into soil, and the average SOC content under the moss crusts was approximately 1.3–2.0 times that under the cyanobacteria crusts. Furthermore, the crust types could influence water erosion, wind erosion, and wind-water erosion by impacting on the infiltration, runoff, the threshold wind velocity, and surface storage capacity of both water and loose erodible material (Aubault et al. 2015). Therefore, the soil nutrient content and stability were significantly increased in the BSCs and underlying soil as the crusts developed (i.e., from physical crusts, to cyanobacterial, lichen, and moss crusts). Soil erodibility was improved, with soils having a notably greater strength, roughness, and reduced sediment losses when compared to soils with physical or incipient BSCs (Aubault et al. 2015; Chamizo et al. 2012).

Soil enzyme activity is commonly used as an indicator of soil quality. The CAT, DHA, SUC, and URE activities increased simultaneously with the succession of BSCs from the cyanobacteria to the moss crusts (Fig. 4). Zhang et al. (2015) found that the activity of most soil enzymes increased with the succession of BSCs and higher levels occurred in soil under moss crusts than in soil covered by cyanobacteria crusts. Generally, water is a limiting factor for the activity of most soil enzymes (Brockett et al. 2012), and this can be affected by BSCs types. The distribution of moss and cyanobacteria crusts is related to soil moisture, with moss crusts usually more abundant in moist microenvironments (Gutiérrez et al. 2018). This results in higher levels of soil enzyme activity under moss crusts than under cyanobacteria crusts. Soil enzyme activity has also been reported to be positively associated with soil nitrogen content (Ghiloufi et al. 2019). In our study, contents of SOC, TN, and AN were higher in the soil under moss crusts than in the soil under cyanobacteria crusts, which showed the important influences that the crusts had on the levels of soil nutrients. Soil enzymes can accelerate soil nutrient transformation and cycling and improve soil properties, with many studies shown that soil enzyme activity had positive relationships with the available soil nutrients (Zhang et al. 2015). The increased soil enzyme activity also means that moss crusts were desirable for the reproduction and growth of underlying soil microorganisms (Mager and Thomas 2011), which are closely related to soil biogeochemical properties. Soil microorganisms play an important role in the ability of BSCs to facilitate soil nutrient transformation (Glaciela et al. 2010). Zhao et al. (2020) showed that soil microorganisms under BSCs contributed to the soil carbon and nitrogen cycles in arid ecosystems, further improving the soil quality. This was consistent with our soil nutrient content measurements (Fig. 3).

Our results also indicated that the water erosion region had a significantly lower soil pH than the wind erosion and water-wind erosion crisscross regions. This may be related to different influences of wind and water erosion on soil salt accumulation (Na^+ and Cl^-). In the wind erosion region, the rate of soil evaporation increased as wind speed and duration of windy conditions increased, which was also strongly coupled with rainfall, thermal radiation, and the hydraulic properties of soil (Davarzani et al. 2014; Fu et al. 2018). Increases in soil evaporation may cause salt to accumulate in top soils, resulting in high soil pH values. Unlike wind erosion, water erosion is unfavorable for top soil salt accumulation. Both infiltration and runoff caused by water erosion may remove salt and decrease the soil pH value. The water erosion region had a significantly higher soil EC than the water-wind erosion crisscross and wind erosion regions. The increased water content was responsible for the higher EC in the water erosion region because EC is positively correlated to the soil water content (Singer and Shainberg 2004).

Conclusions

In the subsoil under BSCs, the nutrient content and enzyme activity were higher in the water erosion region than in the wind erosion and water-wind erosion crisscross regions, which indicated that both moss and cyanobacteria crusts could maintain a higher soil nutrient availability in water erosion regions than in wind erosion or wind-water erosion regions under same crust coverage (> 95%). These results indirectly indicated that the subsoil under BSCs may keep higher fertility and stronger soil nutrient conversion when faced with water erosion compared to wind erosion or water-wind erosion crisscross regions. Moreover, the subsoil under moss crusts had a higher nutrient content and enzyme activity than the soil under cyanobacteria crusts in all three soil erosion regions. These results imply that the effect of BSCs on subsoil conditions increased with the succession of BSCs, with moss crusts better able to affect the soil's response to the erosive forces of wind, water, or combined water-wind action. Our results suggested that there were differences in the effects of the two BSCs on soil nutrient availability and enzyme activity across three typical erosion regions in the Loess Plateau, and the magnitude of the effects followed the order of: water erosion regions > wind erosion regions > wind-water erosion crisscross regions, and moss crusts > cyanobacteria crusts. This provides a reference for soil improvement and the restoration of degraded ecosystems in the arid and semiarid regions of north China.

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Authors' contributions All authors contributed to the conception and design of the study. Investigation, sample collection, and measurement, data collection and analysis were performed by Rong Hui, Huijuan Tan, Xinrong Li, Ruiming Zhao and Haotian Yang. The first draft of the manuscript was written by Rong Hui and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

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Data availability The datasets generated during and/or analyzed during the current study are available from the corresponding author on reasonable request.

Declarations

Competing interests The authors have no relevant financial or non-financial interests to disclose.

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