



Biological soil crusts decrease erodibility by modifying inherent soil properties on the Loess Plateau, China



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ABSTRACT

Soil erosion and subsequent land degradation contributed to societal collapse in the past and are a leading cause of desertification in arid and semi-arid regions. Biological soil crusts (biocrusts) are ubiquitous living covers in many arid and semiarid ecosystems that have an important role in soil stabilization and erosion prevention. The “Grain for Green” ecological project improved vegetation recovery, and led to an extensive development of biocrusts across the Loess Plateau region in China, one of the most eroded regions in the world. The expansion of biocrusts was instrumental in reducing soil loss in a very large, severely eroded region of the Loess Plateau. We hypothesized that development of biocrusts would change soil organic matter (SOM) and soil particle size distribution (PSD), thereby reducing soil erodibility and soil loss. We sampled 56 sites that were passively revegetated grasslands on former croplands and 3 bare soil sites in the Loess Plateau region, and used the erosion productivity impact calculator (EPIC) model combined with simulated rainfall to test our assumption. The PSD and SOM content varied significantly among biocrust types and successional stages. The SOM content was 4 times higher in moss dominated biocrust and 1.5 times greater in cyanobacterially dominated biocrust than bare soil. More fine-particles (< 0.01 mm) and fewer coarse-particles (0.05–0.25 mm) were present in biocrusts than in bare soil. Modeled soil erodibility decreased significantly as biocrust biomass increased, mainly due to increase in SOM content, reducing the predicted soil loss by up to 90%. Finally, the prevalence of moss biocrust was a better predictor of soil erodibility than cyanobacteria in the Loess Plateau region. We conclude that biocrusts were a decisive factor for the initial reduction of soil erosion, which must be considered explicitly in models that aim to predict and manage soil loss on the Loess Plateau.

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1. Introduction

Human-accelerated soil erosion is among the most pressing of environmental problems in many parts of the world, leading to the degradation of ecosystem function (Liu et al., 1999; Lal, 2001; Ludwig et al., 2006) and decreased agricultural productivity and sustainability (Zheng et al., 2004). Although the resistance of soil to water erosion depends in part on erosivity, topography, vegetation,

and human activities (Morgan, 2005), the inherent properties of the soil, such as soil texture and soil organic matter (SOM) that influence soil erodibility, are also very important determinants. Soil erodibility defines the inherent resistance of soil to both detachment and transport by rainfall and runoff, commonly quantified measured by the soil erodibility factor (*K* value; Morgan, 2005). It is widely applied in models to predict soil erosion (Liu et al., 1999; Wang et al., 2001; Parysow et al., 2003), for example in the universal soil loss equation (USLE), revised universal soil loss equation (RUSLE2), water erosion prediction project (WEPP), and erosion productivity impact calculator (EPIC). Soil erodibility thus is an essential indicator for global land management. Soil particle size distribution (PSD) is the principal inherent soil property affecting

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erodibility. Larger particles are resistant to transport because of the greater force required to move them and fine particles are resistant to detachment because of their cohesiveness. Clay particles combine with organic matter to form soil aggregates, and the stability of these determines the resistance of the soil. The least resistant particles in size separates are silts and fine sands (Morgan, 2005). Another inherent soil property, SOM, influences soil erodibility due to its promotion of aggregate stability (Caravaca et al., 2001; Morgan, 2005). In addition, structure, permeability and salt content also influence soil erodibility (Parysow et al., 2003; Morgan, 2005; Bonilla and Johnson, 2012; Wang et al., 2013).

Stabilizing soil and preventing soil loss is the most important ecological function of biological soil crusts (biocrusts) in many ecoregions (Belnap and Lange, 2003; Eldridge and Leys, 2003; Belnap et al., 2009; Zhao and Xu, 2013). Biocrusts consist of microscopic (cyanobacteria, algae, fungi, and bacteria) and macroscopic (lichens, mosses) poikilohydric organisms that occur on or within the top few centimetres of the soil surface (Belnap et al., 2016). They also influence hydrology by determining soil surface structure and morphology (Eldridge et al., 2000; Belnap, 2006; Belnap et al., 2012), enhance soil fertility by fixing atmospheric carbon and nitrogen (Belnap, 2002, 2003; Zhao et al., 2010), and perform other functions. In one dryland region, biocrusts prevented soil loss from wind erosion even in the absence of vascular plants (Munson et al., 2011), and biocrust cover was the most important predictor of site stability (Belnap et al., 2009). Similarly, in regions experiencing water erosion, soil erosion may be decreased by 100% by well-developed biocrusts (Belnap et al., 2012; Zhao and Xu, 2013). In semiarid catchments, almost no erosion was measured in areas with biocrusts, in spite of the high runoff measured in these areas (Rodríguez-Caballero et al., 2014). In general, biocrusts exert protection against erosion that is proportional to their coverage of the soil surface, due to their ability to physically protect the erodible surface layers or through aggregate formation from their biomass (e.g., filamentous tissues). One plausible, but overlooked mechanism, is that biocrusts alter the inherent soil properties, leading to lower erodibility.

The Loess Plateau in China is one of the most severely eroded regions of the world. Preventing and controlling erosion is an urgent issue requiring resolution in the region (Fu et al., 2011). To solve this problem, the “Grain for Green” ecological project was implemented across a large portion of the Loess Plateau, in which farmers are compensated for taking land out of production and allowing passive vegetation recovery (Zhang et al., 2000). Cultivation on slopes steeper than 25° and grazing were both prohibited. The project is among the largest payment for ecosystem services programs ever undertaken. To a large degree, the program has been successful in drastically reducing sediment transport (Zheng, 2006; Chen et al., 2007; Wang et al., 2012; Wang and Zhuo, 2015). Biocrusts were a major, and unexpected, contributor to the reduction in erosion rates across the region in response to the cessation of disturbance (Ran et al., 2011; Zhao and Xu, 2013; Zhao et al., 2014). Natural recovery of biocrusts alongside grasses and shrubs was observed within a few years of implementation of the project and now cover up to 70% of the land area (Zhao et al., 2006a).

The change in land use brought about by the “Grain for Green” project, and the subsequent expansion of biocrusts, provides us an opportunity to determine the degree to which biocrusts regulate soil erosion in this ecoregion. Previous studies focus on the physical protection of soil from erosion provided by undisturbed biocrusts (Eldridge and Leys, 2003; Belnap et al., 2012; Zhao and Xu, 2013; Zhao et al., 2014), whereas we focused on biocrust-induced changes to inherent soil properties relevant to erodibility. We evaluated the influence of biocrusts on soil erodibility across the region using an extensive field survey in multiple watersheds, and

rainfall simulation experiments. In addition to the protective value of undisturbed biocrust cover (Bowker et al., 2008), and their provision of surface roughness which slows overland flow (Rodríguez-Caballero et al., 2012), biocrusts can influence erodibility (as estimated by EPIC) through two mechanisms: accumulation of silt and clay (Xiao et al., 2007), and SOM (Zhao et al., 2006b,a; Xiao et al., 2007). Therefore, our study addressed three questions: (1) How do biocrust type and successional stage influence PSD and SOM in the Loess Plateau ecoregion? (2) Do changes in PSD and SOM translate into a corresponding effect on predicted soil erodibility? (3) Can these potential effects of biocrusts on erodibility result in less sediment yield? The results will demonstrate the degree of influence exerted by biocrusts on decreasing soil erodibility, protecting soil against erosion and governing soil loss on the Loess Plateau.

2. Materials and methods

We conducted a large scale field sampling campaign to estimate biocrusts contribution to soil erodibility, coupled with an experimental demonstration of soil stabilization by biocrusts using a state-of-the art rainfall simulator.

2.1. Study region

The study was conducted on passively revegetated grasslands on former croplands and rangelands of the Loess Plateau in the northern portion of Shaanxi province, China (Fig. 1). Mean altitude of the region is approximately 1200 m, but the topography varies locally in a complex of loessial hills and gullies. The region has a typical semiarid continental climate, with an average annual temperature of 8.8 °C. Mean monthly temperatures range from 22 °C in July to −7 °C in January. Mean annual accumulated temperatures above 0 and 10 °C are 3733 and 3283 °C, respectively. Mean annual precipitation is approximately 500 mm, 60% or more of which falls between July and September, typically in high-intensity and short-duration rainstorms (Zhang et al., 2011). Mean annual potential evapotranspiration is 1617 mm. The region experiences annual averages of 157 frost-free days and 2415 h of sunshine (Ansi Research Station, unpublished data, record period 1998–2015).

The soil is classified as a typical loessial soil, representing the most common soil type on the Loess Plateau. The average thickness of the loess parent material is approximately 50–80 m, with uniform soil texture of *Calcustepts*. The soil in this region is highly susceptible to erosion, with the erosion rate of over 10 000 t km^{−2} year^{−1} before the “Grain for Green” ecoproject begun (Zhang et al., 2011).

Common vegetation in the region includes grasses such as *Bothriochloa ischaemum* (L.) Keng., *Stipa bungeana* Trin., *Artemisia capillaries* Thunb., and *Artemisia giraldii* Pamp., and shrubs such as *Cotoneaster horizontalis* Dcne., *Rosa xanthina* Lindl., *Rubus parvifolius* L., *Sophora davidii* (Franch.) Skeels., and *Artemisia sacrorum* Ledeb. The coverage of vegetation ranges from 20% to 70% where cropland was abandoned (Wang et al., 2011). *Achillea capillaries* Thunb. dominates initially and peaks in biomass between five to ten years after abandonment, while *Artemisia sacrorum* is the prime species after ten years of abandonment.

In the study area, cyanobacteria and mosses dominate the biocrust communities. Coverage of mosses may reach 80% on north-facing slopes in the Loess Plateau region (Zhao et al., 2014). Eight moss species, *Didymodon tectorum* (C. Mull.) Saito., *Didymodon vinealis* (Brid.) Zander., *Bryum argenteum* Hedw., *Bryum caespiticium* Hedw., *Bryum arcticum* (R. Brown) B.S.G., *Trichostomum crispulum* Bruch in F. A. Muell., *Crossidium squamiferum* (Viv.) Jur., and *Aloina rigida* (Hedw.) Limpr., have been identified in the

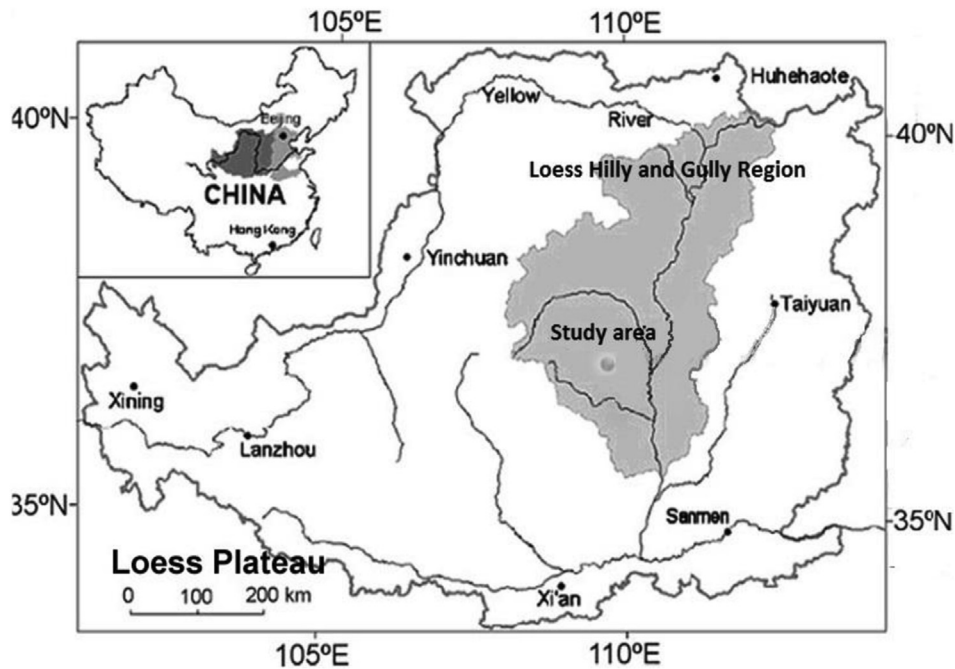


Fig. 1. Location of the study area (from Wang et al., 2011).

biocrust community (Zhang et al., 2007), but the *Didymodon* species usually dominate. Cyanobacteria are distributed on south-facing slopes and formed in the first year after cropland abandonment. *Phormidium angustissimum* West et G.S. West and *Phormidium tenue* (Menegh.) Gom are the dominant cyanobacterial species, and *Nostoc* spp. are subdominant (Yang, 2013). Mosses generally dominate biocrusts by the fourth year after cropping and grazing cessation, and biocrust density and coverage increases as the vegetation ages. Lichens can be found in biocrusts ten years after abandonment, and eighteen species have been observed. Lichen coverage, however, seldom reaches 10% (Yunge Zhao, unpublished data). The impact of lichen biocrust on soil erodibility was thus not included in this study, and instead we focus on cyanobacterial and moss biocrusts.

2.2. Large scale field study and soil sampling

We sampled a total 59 sites from three watersheds, ranging in area from 18.26 km² to 73.83 km², and 8 km - 20 km distant from one another. Biocrusts, ranging from cyanobacterial to moss-dominated, were present on 56 of the sites. Our strategy was to capture variation in biocrust type and degree of development according to the time since cessation of agricultural activities. We interviewed farmers about the age of abandonment of their fields, and then sampled depending on the number of different ages present. The dataset included fields that had not been cultivated for 3–30 years and that contained at least some biocrust, with variable productivity and species composition. We also sampled 3 recently cropped sites, devoid of biocrusts, as a bare soil control. Biocrust development was represented by moss biomass, measured as the moss mass per unit area (g dm⁻²). To illustrate the biocrust development clearly, we divided the 56 sites into six successional stages based on hierarchical cluster analysis (between-groups linkage method) and natural separations in moss biomass in our collected data (Table 1). In our successional classification, Class 1 represents earlier succession, and Class 6 represents later succession. Biocrust coverage and species diversity were measured with a

point-intercept method using a 25 cm × 25 cm gridded quadrat (Belnap et al., 2001).

After measuring biocrust cover, we collected composite soil samples at all sites above, to determine the impact of biocrust development on predicted soil erodibility. Each site (>200 m²) had a slope > 10°, except in the case of the cyanobacterial biocrust sites, which were terraces (some terraces in steeply sloping terrain were also abandoned). Due to the prevalence of mosses, location of relatively pure cyanobacterial crusts was challenging, thus we had to sample outside of sloping areas alone. At each site, five soil samples were randomly selected to insure the representativeness of samples. At each sampling location we sampled at the depth of the biocrust, and from 0–2, 2–5, and 5–10 cm underlying biocrusts. Thickness of cyanobacterial biocrust was about 1 mm, and that of moss crust ranged from 4 to 12 mm. Samples for the same depth were thoroughly mixed and placed for each depth in different bags. Then the samples were dried, sieved to 1 and 0.25 mm and then sent to the State Key Laboratory of Soil Erosion and Dryland Farming on the Loess Plateau in China to measure SOM and PSD, parameters used to estimate *K* values.

The SOM content was measured by the Walkley Black method (Nelson and Sommers, 1982). Soil PSDs were performed using a laser-diffraction method (Mastersizer 2000; Malvern, UK). The soil samples were pretreated by adding 10% H₂O₂ and heating within a sand bath until the organic matter oxidation reaction was complete. After the samples were cooled to room temperature, 10% HCl was used to dissolve carbonate. Prior to particle size analysis, soil samples were sonicated for 30 s to disperse fine particles with an ultrasonic mixer. The laser particle analyzer was used to measure soil PSD values within the size range 0.02–2000 μm (Peng et al., 2015). Mosses were collected in Petri dishes and air dried. The mosses were reactivated by watering and exposure to light before measurement. Samples of the mosses were collected with a soil corer with an area of 0.95 cm² after rewetting to obtain intact samples of uniform area. The soil on the mosses was removed by wet-sieving, and the moss plants were transferred to weighing bottles, dried in an oven at 85 °C for 30 min then at 65 °C until no

Table 1
Characteristics of the sampling sites grouped by biomass classes (mean \pm SD).

Biomass classes	Moss biomass (g dm ⁻²) (number of sites)	Cyanobacterial biomass (mg g ⁻¹) (number of sites)	Vegetation coverage (%)	Biocrust coverage (%)
Bare soil	0(3)	0(3)	0	0
1	0 ^a (4)	3.67 \pm 1.10(4)	40.0 \pm 13.5	89.0 \pm 8.9
2	1.71 \pm 0.05(9)	5.68 \pm 1.10(9)	57.3 \pm 19.6	86.0 \pm 3.0
3	2.91 \pm 0.12(17)	8.20 \pm 1.93(5)	50.6 \pm 17.6	90.7 \pm 3.1
4	3.31 \pm 0.05(13)	7.46 \pm 2.77(10)	70.0 \pm 5.0	81.7 \pm 9.3
5	4.31 \pm 0.12(9)	8.29 \pm 2.13(8)	54.5 \pm 20.5	80.5 \pm 0.7
6	8.84 \pm 0.27(4)	–	58.8 \pm 8.5	73.8 \pm 5.0

All plots were on gully slopes, except plots of Class 1 were from lever terraces.

^a Class1 contained only cyanobacteria.

further weight change was observed, after which dry masses were determined, and used to calculate biomass on a per area basis (dry mass of mosses per unit area, g dm⁻²). Chlorophyll *a* per unit soil mass was measured as a proxy for cyanobacterial biomass. Chlorophyll *a* was double extracted with DMSO and measured on a spectrophotometer at wavelengths 665 nm and 750 nm (Bell and Sommerfeld, 1987). Before the chlorophyll *a* extraction, traces of mosses were removed when present in the cyanobacterial crust samples.

2.3. Estimation of biocrust *K* values

EPIC was used to model *K* values for soils with different biocrusts and for bare soil as:

$$K = \{0.2 + 0.3 \exp[-0.0256SAN(1 - SIL/100)]\} \cdot \left(\frac{SIL}{CLA + SIL}\right)^{0.3} \cdot \left[1.0 - \frac{0.25c}{c + \exp(3.72 - 2.95c)}\right] \cdot \left[1.0 - \frac{0.7SN_1}{SN_1 + \exp(-5.51 + 22.9SN_1)}\right] \quad (1)$$

where *SAN* is the sand content (%), *SIL* is the silt content (%), *CLA* is the clay content (%), *c* is the organic carbon content (%), and *SN₁* = 1 - *SAN*/100.

Zhang et al. (2008) found that function (1) overestimated *K* values calculated by EPIC, compared to measured erosion values in the Loess Plateau region of China. A revised transformation EPIC model was formed based on their investigation. Thus, the revised EPIC model was used to estimate the *K* value (*K_{Repic}*) in this study:

$$K_{Repic} = -0.01383 + 0.51575K_{epic} \quad (r = 0.613) \quad (2)$$

where *K_{epic}* is *K* estimated by function (1).

2.4. Rainfall simulation experiment

2.4.1. Microcosm preparation

The amount of soil loss by water erosion, which is positively related to soil erodibility, was determined by simulated rainfall to experimentally confirm the effect of biocrusts on soil erodibility, independently of biocrust cover. Each microcosm was a bed of soil in a metal box, with an adjustable user-set slope incline. Soils were sourced from different types of biocrust, with the biocrust structure destroyed and mosses removed. We subjectively selected three types of biocrusts, representing three successional stages for the experiments with simulated rainfall, cyanobacterial biocrust (early successional; coverage of cyanobacteria was more than 80%), mixed cyanobacterial and moss biocrust (mid-successional; coverage of cyanobacteria and mosses were approximately 60% and 30% respectively), and moss dominated biocrust (late successional; coverage was approximately 70%). We collected the topsoil from

each of these types of surfaces to a 2 cm depth (inclusive of the biocrusts), based on their typical thickness in the study region. Soil from sloping cropland (bare soil) in the same area was used as the control. To elucidate the effect of biocrusts on soil loss caused by soil erodibility reduced, all the soil samples were dried, ground with a shovel, and sieved through 5 mm sieve, moss stems and plant roots were removed.

2.4.2. Rainfall simulation

Rainfall simulation studies were conducted in the Simulation Hall of the State Key Laboratory of Soil Erosion and Dryland Farming on the Loess Plateau at the Institute of Soil and Water Conservation, Chinese Academy of Sciences and Ministry of Water Resources in China. This facility is unique in China. The height of the rainfall simulator nozzle was 16 m, which can achieve the terminal speed of natural rainfall. The rain intensity ranges from 30 to 200 mm h⁻¹, with the drop size ranging from 0.6 to 3.0 mm. The simulated rainfall, with drop uniformity greater than 80%, is similar to natural rainfall in both raindrop size and distribution. The rain intensity can be precisely adjusted to a target intensity of ± 2.7 mm h⁻¹ by controlling the aperture of the nozzle and the water pressure (Zheng and Zhao, 2004).

The experimental boxes were 100 cm (length) \times 20 cm (width) \times 15 cm (depth). The soil bulk density in the boxes was 1.30 g cm⁻³, the same as that in the local natural grassland (Xu et al., 2014). Soil depths were uniform at 10 cm. The slope gradient was set as 20°, a common gradient on the Loess Plateau. The rain intensity was set at 2 mm min⁻¹, which was the highest intensity of monsoon rainstorms in the study area (Zhang and Zhu, 2006; Huang et al., 2011). Each type of biocrusts and bare soil had five replicates in the experiment. In the process of the experiment, plastic runoff collection buckets at the box outlet were changed every 3 min, and the rain was simulated for 30 min. After the rain, the runoff in each bucket was weighed and then allowed to stand to separate the sediment from the supernatant. The supernatant was discarded, and the sediment was dried and weighed. We used this information to calculate the soil loss per square meter per minute (g m⁻² min⁻¹) in each experimental box.

2.5. Statistical analyses

The field survey data were analyzed using two broad approaches, one maximizing contrasts in a subset of samples, and one exploiting the entire gradient of biocrust development. To analyze maximal contrasts we subjectively selected two types of biocrust (completely dominated by either cyanobacteria or mosses) in the 56 sites above to determine the impact of biocrust components on predicted soil erodibility. Four sites of each biocrust type and additional three bare soil sites were selected as controls. In these contrasts we conducted a combination of ANOVA, for univariate responses, and MANOVA, for multivariate responses (PSD), on a

subset of the data. Data were tested for normality with the Kolmogorov–Smirnov test and for equality of variance using Levene's test. We used ANOVAs with Fisher's least significant difference post hoc test (LSD) (or Tamhane's T2 if variances were statistically unequal) to analyze for differences in SOM and K_{Repic} values in two ways: 1) the same soil layer among different biocrust types or successional stages; 2) different soil layers within the same biocrust type or successional stage. GLM analysis was used to explain the interactions between biocrust biomass and soil depth in determining SOM.

Our gradient analyses consisted of ANOVA applied to analyze K_{Repic} , SOM, and PSD as a function of biocrust successional stage (see section 2.2) across the whole dataset. Concurrently, we used regression analysis to model K_{Repic} values as a function of moss biomass in 55 sites (not including cyanobacterially-dominated sites) and cyanobacterial biomass in 41 sites (not including the sites of moss coverage more than 70%) to model their effects on K_{Repic} as a continuous function to predict their trends in our research scope.

For the rainfall simulations, we used the same ANOVA analysis approach to analyze for differences in amount of soil loss among beds of disaggregated soils sourced from bare surfaces, cyanobacterial biocrust, mixed biocrust and moss biocrust. All statistical analyses were completed using SPSS 18.0 (SPSS, USA).

3. Results

3.1. Influence of biocrusts on SOM content and PSD

3.1.1. Variation in SOM content among contrasting biocrust types

In our analysis of maximal contrasts, the contents of SOM were markedly higher in both biocrust types, especially moss biocrust, than either the bare soil or the soils underlying biocrusts (Fig. 2). SOM was the highest by far in moss biocrust (2.5 times the cyanobacterial biocrust, 5 times the bare soil), followed by cyanobacterial biocrust (2 times the bare soil). The SOM content in subsurface layers was 44–73% greater under moss biocrust than under bare soil and cyanobacterial biocrust, whereas subsurface SOM was similar under cyanobacterial biocrust and bare surfaces.

Finally, within each type of sample, subsurface SOM did not vary with increasing depth.

3.1.2. SOM along biocrust development gradients

SOM content increased clearly with biocrust succession (Table 2). The SOM content of biocrust was 161% higher in the later successional Class 6 than in Class 1 ($F = 10.813$, $P < 0.0001$). As in the maximal contrast of biocrust types above, the SOM content of soil underlying biocrusts was always dramatically lower than the biocrust regardless of biomass classes, but SOM enrichment attenuated sharply below 2 cm. Δ SOM (differences between the biocrust layer and 5–10 cm layer) increased gradually with the development of biocrusts ($F = 7.648$, $P = 0.00002$). The effect of successional stage and soil depth and their interactions on SOM were all significant (Table 3), with soil depth exerting the strongest influence (Partial $\eta^2 = 0.776$) such that SOM content in biocrust layer was always higher than subsurface layers.

3.1.3. Variation in PSD among contrasting biocrust types

Biocrusts, especially moss biocrust, had more fine particles and fewer coarse particles compared to bare soil surfaces (Table 4). Fine-silt was more in both biocrusts than bare soil, especially in the cyanobacterial biocrust, which had about twice as much fine-silt as the bare soil ($F = 49.454$, $P < 0.0001$). Clay was also 25% more in the cyanobacterial biocrust, and 13% in the moss biocrust compared to bare soil ($F = 40.775$, $P < 0.0001$). Coarse-silt of the two biocrust types and bare soil did not differ. Fine-sand decreased by 41% and 15% in the cyanobacterial and moss biocrusts compared to bare soil, respectively ($F = 195.000$, $P < 0.0001$). Conversely, the coarse-sand was 5.1 times more in the cyanobacterial biocrust than in the bare soil, while there were no differences between moss biocrust and bare soil.

3.1.4. PSD along biocrust development gradients

Soil PSD did not differ strongly among biocrust successional stages (Table 5). Clay and fine-silt were about 12% and 65% more than bare soil in the biocrust successional Class 2 to Class 6, respectively, which were all fewer than Class 1 (clay, $F = 17.718$, $P < 0.0001$; fine-silt, $F = 28.478$, $P < 0.0001$). No significant

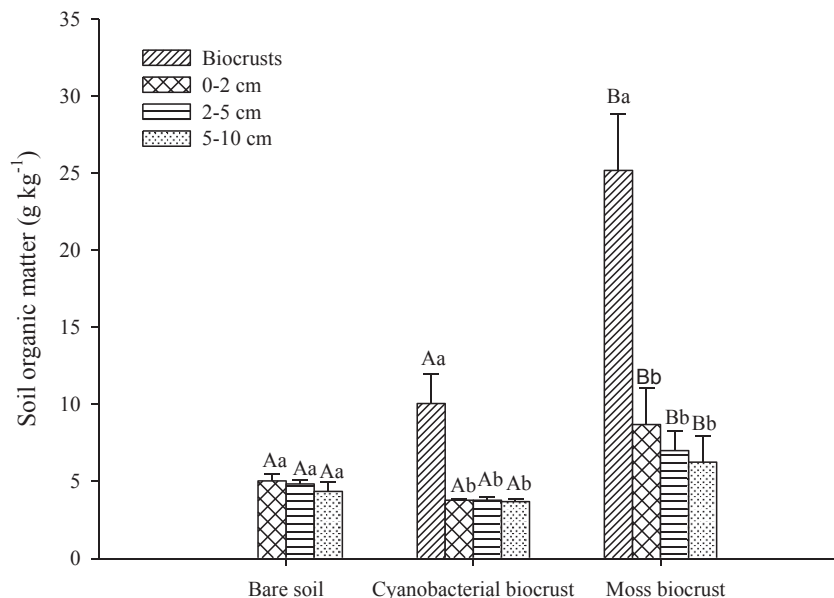


Fig. 2. Soil organic matter content (mean \pm SE) amongst soil layers and types of biocrusts collected from the field. Different uppercase letters indicate significant differences among biocrust types within the same depth; Different lowercase letters indicate significant differences between soil layers within a biocrust type.

Table 2
Soil organic matter content (g kg^{-1}) of biocrusts and soil layers among biomass classes (SOM, mean \pm SE).

Soil layers	Biomass classes						
	Bare soil	1	2	3	4	5	6
Biocrusts	–	10.05 \pm 0.96Aa	15.06 \pm 1.88Aab	18.78 \pm 1.17Ab	21.79 \pm 1.41Abc	21.46 \pm 1.49Abc	26.26 \pm 1.16Ac
0–2 cm	5.03 \pm 0.28Aa	3.78 \pm 0.04Ba	7.68 \pm 0.48Bb	8.07 \pm 0.30Bb	8.47 \pm 0.64Bb	8.33 \pm 0.55Bb	9.97 \pm 0.76Bb
2–5 cm	4.83 \pm 0.14Aab	3.78 \pm 0.11Ba	6.47 \pm 0.39Bbc	6.60 \pm 0.29Cbc	6.88 \pm 0.52Bcc	7.04 \pm 0.36Bcc	6.55 \pm 0.52Cc
5–10 cm	4.35 \pm 0.37Aab	3.69 \pm 0.08Ba	6.00 \pm 0.22Bc	5.92 \pm 0.28Cbc	5.67 \pm 0.58Cbc	6.48 \pm 0.39Cc	4.94 \pm 0.13Cb
ΔSOM^a	–	6.36 \pm 0.98a	9.05 \pm 1.93a	12.85 \pm 1.11b	16.11 \pm 1.12c	14.98 \pm 1.44bc	21.32 \pm 1.06d

^a Represents difference of soil organic matter content between biocrust and 5–10 cm. Different lowercase letters indicate significant differences among developmental stages at the same soil depth; different uppercase letters indicate significant differences among soil layers at the same developmental stage.

Table 3
Effects of moss biomass, soil depth and their interactions (by GLM analysis) on soil organic matter in field soil.

Factor	df	F	P	Partial Eta Squared
Biomass classes	6	13.010	0.0000	0.275
Soil depth	3	237.589	0.0000	0.776
Biomass classes* Soil depth	17	3.990	0.0000	0.248

Table 4
Influence of biocrust types on particle size distribution in field samples (Mean \pm SE).

Biocrust type	Clay (<0.002 mm, %)	Fine-silt (0.002–0.01 mm, %)	Coarse-silt (0.01–0.05 mm, %)	Fine-sand (0.05–0.25 mm, %)	Coarse-sand (0.25–1 mm, %)
Bare soil	10.39 \pm 0.26c	5.09 \pm 0.15c	49.86 \pm 0.31a	33.56 \pm 0.79a	1.09 \pm 0.13b
Cyanobacterial biocrust	12.95 \pm 0.16a	10.71 \pm 0.17a	49.75 \pm 0.94a	19.92 \pm 0.63c	6.67 \pm 1.34a
Moss biocrust	11.71 \pm 0.44b	8.44 \pm 0.26b	50.48 \pm 0.24a	28.41 \pm 0.87b	0.97 \pm 0.63b

Different letters within the same type of soil particle indicate significant differences at $P < 0.05$.

Table 5
Changes in the particle size distributions (Mean \pm SE) amongst the successional stages (biomass classes) of biocrusts in field samples.

Biomass classes	Clay (<0.002 mm, %)	Fine-silt (0.002–0.01 mm, %)	Coarse-silt (0.01–0.05 mm, %)	Fine-sand (0.05–0.25 mm, %)	Coarse-sand (0.25–1 mm, %)
Bare soil	10.46 \pm 0.29a	5.14 \pm 0.21a	49.92 \pm 0.39 ab	33.57 \pm 0.54a	0.91 \pm 0.13a
1	13.97 \pm 0.25c	10.49 \pm 0.18c	54.61 \pm 0.33d	19.13 \pm 0.47d	1.80 \pm 0.26a
2	11.53 \pm 0.16b	8.38 \pm 0.12b	48.94 \pm 0.22c	29.94 \pm 0.31b	1.22 \pm 0.16a
3	11.79 \pm 0.12b	8.61 \pm 0.09b	50.55 \pm 0.16b	27.89 \pm 0.23c	1.16 \pm 0.12a
4	11.55 \pm 0.14b	8.46 \pm 0.10b	49.83 \pm 0.19a	28.89 \pm 0.26bc	1.27 \pm 0.14a
5	11.93 \pm 0.16b	8.53 \pm 0.12b	50.35 \pm 0.22 ab	28.10 \pm 0.31c	1.09 \pm 0.16a
6	11.98 \pm 0.25b	8.42 \pm 0.18b	50.39 \pm 0.33 ab	28.36 \pm 0.47c	0.85 \pm 0.25a

Different letters indicate significant differences among biomass classes within the same soil particle size class.

differences were detected among Classes 2 to 6 for clay and fine-silt. Fine-sand in all the biomass classes was correspondingly 16% fewer than that in bare soil (fine-sand, $F = 76.139$, $P < 0.0001$). Coarse-silt in Class 1 was more than that in bare soil, whereas that in Class 2 was fewer; otherwise biocrust classes were reasonably comparable to bare soil. Coarse-sand did not differ across successional stages.

3.2. Effects of biocrusts on predicted soil erodibility

3.2.1. Variation of K_{Repic} values among contrasting biocrust types

In our maximal contrasts, the K_{Repic} value of moss biocrust was 17% lower than that of bare soil, while the value of cyanobacterial biocrust was 5% higher ($F = 71.610$, $P < 0.0001$) (Fig. 3). K_{Repic} values were significantly lower by 6% and 18% in the cyanobacterial and moss biocrusts, respectively, than in the soils underlying them (0–2, 2–5 and 5–10 cm). K_{Repic} of subsurface soils was highest underneath cyanobacterial biocrust, and both lower and similar under moss biocrust or bare surfaces.

3.2.2. Predicted soil erodibility along biocrust development gradients

K_{Repic} values decreased significantly with advancement of biocrust successional stage ($F = 8.433$, $P < 0.0001$) (Fig. 4a). K_{Repic} was 21% lower for the biocrust soil with the higher moss biomass than for the earlier stage (Class 1). Even a minor presence of mosses was enough to induce a detectable decrease in K_{Repic} , as observed when

contrasting Class 1 and Class 2. ΔK_{Repic} (differences between 5 and 10 cm soil and biocrusts) in biocrusts increased with the development of biocrusts (Fig. 4b). ΔK_{Repic} in biomass Class 6 was about 3 times higher than in biomass Class 1 ($F = 4.131$, $P = 0.003$), indicating that as biocrust succession progresses the K_{Repic} becomes increasingly distinct from subsurface soils.

We also simultaneously analyzed the relationship between moss and cyanobacterial biomass and predicted soil erodibility (Fig. 5). Predicted soil erodibility decreased exponentially with increasing moss biomass ($R^2 = 0.45$, Fig. 5a). However, there was a much weaker negative relationship between cyanobacterial biomass and predicted soil erodibility ($R^2 = 0.12$, Fig. 5b).

3.3. Soil loss with simulated rainfall

Soil loss was significantly lower in soil sourced from biocrusts compared to soil sourced from bare surfaces in the simulated rainfall experiments (Fig. 6). The reduction in soil erodibility by the biocrusts, even with the biocrust structure destroyed and moss tissues removed, significantly decreased soil loss by approximately 90% relative to the loss from bare soil ($F = 148.059$, $P < 0.0001$). The amount of soil lost, however, did not differ significantly among

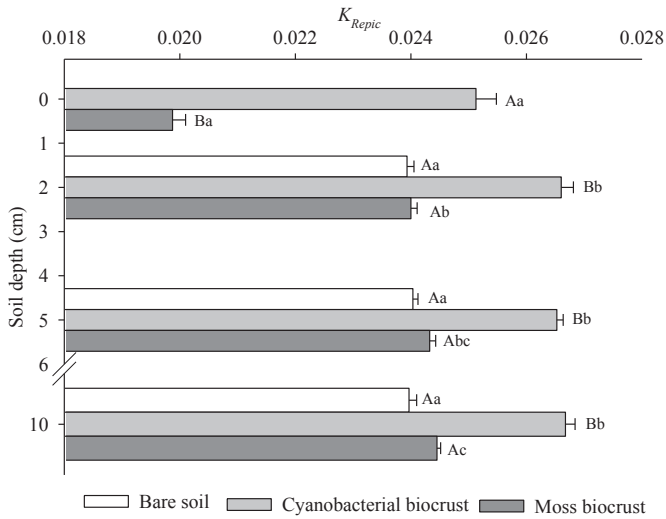


Fig. 3. Influence of the types of biocrusts on soil erodibility (K_{Repic} , mean \pm SE) in field samples. A soil depth of 0 represents the biocrust layer. Different uppercase letters indicate significant differences among biocrust types within the same depth; Different lowercase letters indicate significant differences between soil layers within a biocrust type.

cyanobacterial, moss, and mixed biocrusts.

4. Discussion

4.1. Estimation of soil erodibility

Soil erodibility is an important index to measure susceptibility of soil to erosion, and is an essential parameter for prediction of soil loss. The direct measurement of soil erodibility, however, is limited by many conditions, such as the requirement of long-term erosion monitoring, which is costly and time-consuming. Therefore, techniques have been developed to estimate the K values from readily available data on soil properties for soil erosion prediction and conservation planning. A soil erodibility nomograph, which relates the K value to five soil and soil profile parameters (silt, sand, SOM, structure and permeability) (Wischmeier and Smith, 1978), has been widely used. However, two of its parameters, soil structure

and permeability, may not be widely available. Therefore, in the current study, we selected the EPIC model because it requires only SOM and PSD to estimate the K values in our study. In past work, K values estimated using EPIC were considerably higher than measured K values on the Loess Plateau (Zhang et al., 2008). Thus, we used the adjusted EPIC model provided by Zhang et al. (2008) in our study.

Because EPIC only uses SOM and PSD to estimate K values, it is unable to capture soil aggregation directly. One of the major effects that biocrusts have on soil is enhancement of aggregate stability (Bowker et al., 2008; Chaudhary et al., 2009), which is negatively related to soil susceptibility to water erosion (Bissonnais and Arrouays, 1997; Barthes and Roose, 2002). Thus, EPIC may overestimate K values compared to the actual soil erodibility in our study due to omission of this effect. Indeed, our past investigations suggest that EPIC overestimates K relative to USLE (data not shown). However, since we consistently used the same method to estimate K values, EPIC is still a useful tool for us to make relative comparisons within our study. The contribution of biocrusts to lowering erodibility via the mechanisms of increasing SOM and altering PSD has been understudied and EPIC provides us the opportunity to address this research gap. Future studies will be needed to more accurately and completely describe the effect of biocrusts on actual soil erodibility, via all mechanisms, in undisturbed locations.

4.2. The mechanisms underlying the biocrust effect on erodibility

Soil erodibility depends on the inherent properties of soil, including texture, SOM content, and structure (Caravaca et al., 2001). Soil texture is a relatively stable property of soils, which usually varies over geological time, but which can be changed by particle redistribution over shorter time scales. There was, in fact, a slight change in PSD with the development of biocrusts. Specifically, clay and fine-silt were enriched when biocrusts were present compared to bare soil, and fine-sand was less prevalent than when biocrusts were absent. Biocrusts may influence PSD through two mechanisms: 1) development of biocrusts can stabilize the soil surface and reduce fine particle loss by runoff (Belnap et al., 2012; Zhao and Xu, 2013); 2) biocrusts may roughen surfaces and exude gelatinous materials leading to entrapment of mobile fine sediments, concentrating clay and silt at the soil surface in this process (Danin and Ganor, 1991; Reynolds et al., 2001; Chamizo et al., 2012;

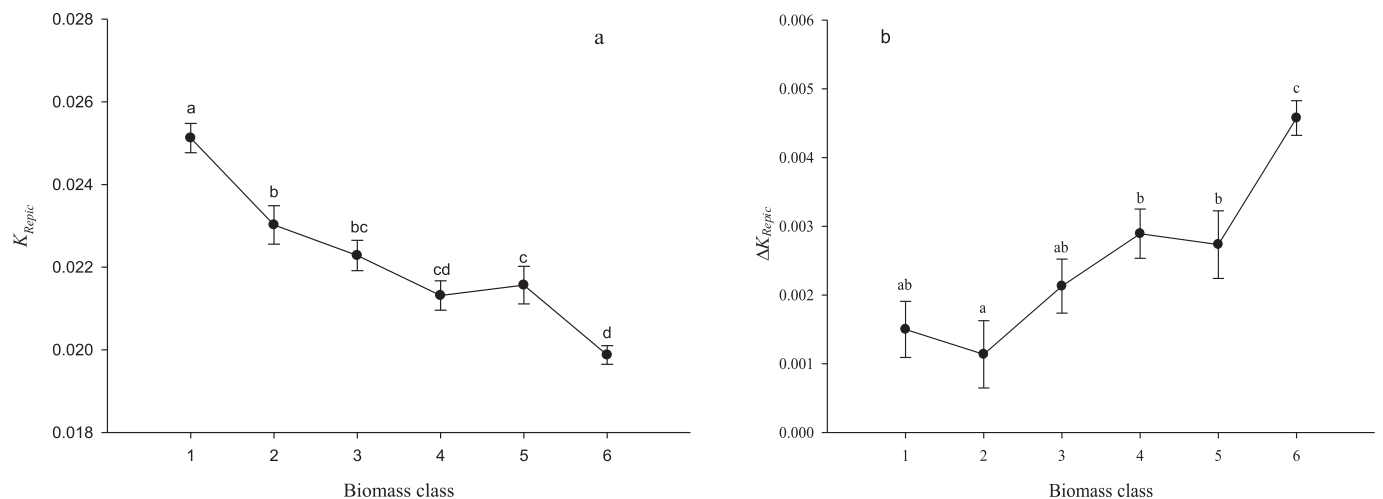


Fig. 4. (a) Influence of biocrusts with variable biomass on soil erodibility (K_{Repic} , mean \pm SE) in the field. (b) Reduction of K_{Repic} (ΔK_{Repic} , the differences between values measured at 5–10 cm depth compared to the overlying biocrusts) among biocrust biomass classes.

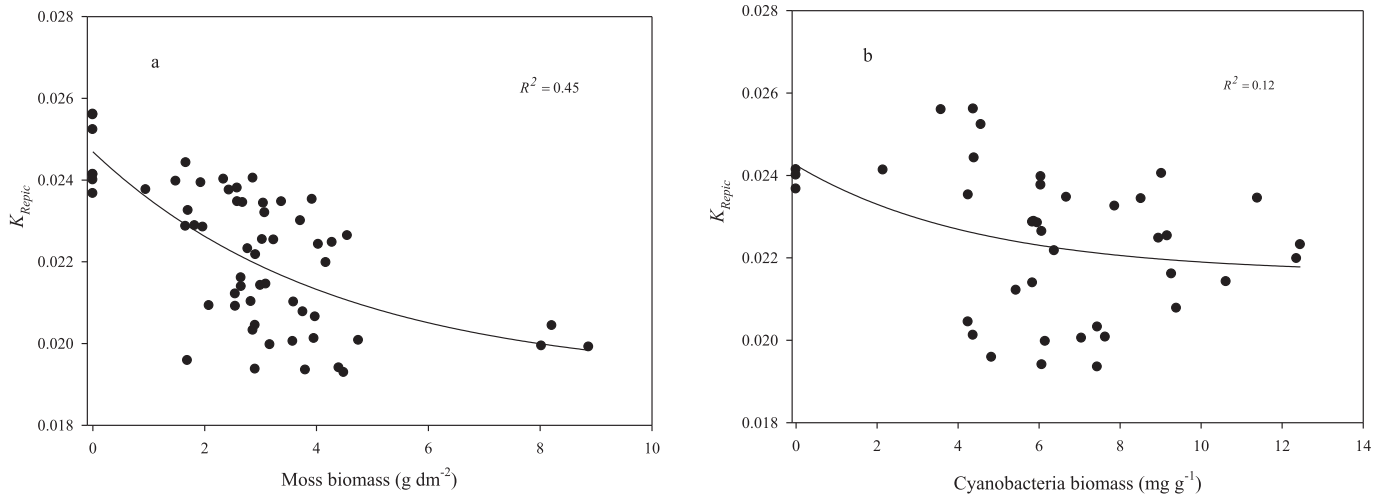


Fig. 5. Regression relationship between biocrusts development and soil erodibility in field samples. (a) Moss, (b) cyanobacteria.

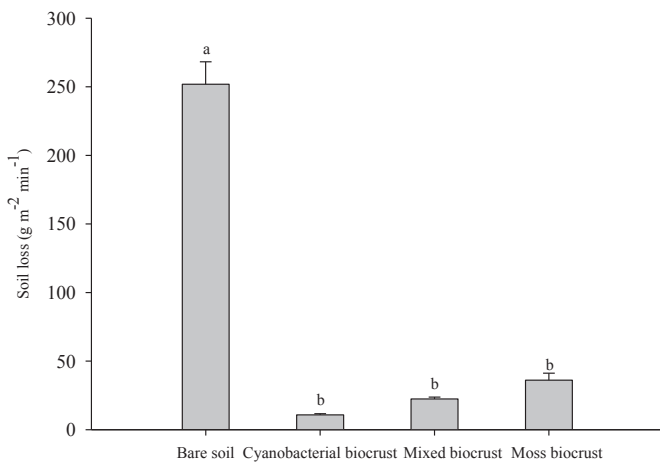


Fig. 6. Soil loss (mean \pm SE) from biocrust soil microcosms under simulated rainfall.

Chen and Duan, 2015). In this study, clay and fine-silt in cyanobacterial crust were more abundant than in moss crust, which ran counter to our expectation that mosses would function better to trap or retain fine sediments. The reason may be that the samples of cyanobacterial biocrust were collected from level terraces, while the other samples were from slopes. Sediments containing fine particles may have accumulated on the surface of terraces from upslope areas.

SOM is an important factor for soil erodibility because it interacts with other factors such as texture, aggregation and permeability (Tejada and Gonzalez, 2006; Jin et al., 2009). Biocrusts contribute significant amounts of organic carbon to soils via carbon fixation (Belnap and Lange, 2003) and decaying organic matter (Danin and Ganor, 1991), both of which contribute to aggregate formation. The relative importance, however, of biocrusts and their different ecological roles within an ecosystem is highly dependent on the relative cover of various biocrust components (Belnap and Lange, 2003). The effects of cyanobacterial biocrust on the physical and chemical properties of soil are limited compared to those of biocrust dominated by mosses (Zhao et al., 2006b,a; Gao et al., 2012; Belnap et al., 2014). Biocrusts dominated by mosses (the later successional stage) can contain nearly twice as much organic carbon as cyanobacterial biocrust (the earlier successional stage)

(Chamizo et al., 2012). Here, we found that SOM content was 1.5 times greater in moss biocrust than that in cyanobacterial biocrust (Fig. 2). The formation of biocrusts brought about an enrichment of SOM in the topsoil, and the enrichment was even more obvious with the succession of biocrusts. Soil layers differed more strongly in SOM content than different successional classes (Table 3). The improvement of SOM seems to be limited to a maximum depth of 2 cm under biocrusts because these organisms are concentrated in the uppermost cm of soil where light is available.

Based on the discussion above, as biocrusts develop, two outcomes are plausible with respect to soil erodibility. Erodibility could increase due to increase of fine particles, which are more easily eroded, or it may decrease due to increasing SOM. K_{Repic} decreased with succession of biocrust (Fig. 4). We attribute this to the very strong effect of mosses on SOM rather than their more subtle effect on PSD. Additionally, K_{Repic} values did not differ among the three soil layers under biocrusts (0–2, 2–5 and 5–10 cm) with the development of biocrusts. We thus consider the reduction in K_{Repic} values specifically to be a surface phenomenon attributable to biocrust presence. This effect is magnified by successional advancement from cyanobacterial to moss dominance, as evidenced by the fact that the reduction of soil erodibility (ΔK_{Repic}) by moss biocrust was 1.7 times that of cyanobacterial biocrust (Fig. 3). Further, we found an exponential decline of K_{Repic} with increasing moss biomass, supplying even stronger evidence that mosses may reduce erodibility through their effects on SOM or PSD.

Interestingly, the K_{Repic} value of cyanobacterial biocrust was higher than that of bare soil, suggesting that cyanobacterial biocrust increase rather than decrease erodibility. We believe this result may be an artifact because even at 10 cm depth, the soils under cyanobacterial biocrust are more erodible than counterparts under moss biocrust or in bare sites. This suggests that those locations harboring cyanobacterial biocrust as dominants simply have a siltier soil texture, which is highly plausible since they are flatter than the other sites. The correlation between erodibility and silt is higher than for the other soil particle sizes, thus silts are more easily eroded than other particle sizes (Bonilla and Johnson, 2012). Moreover, detachment decreases as particle size either decreases or increases beyond the range of 20–200 μm . Above this range, it is more difficult to detach and transport particles because of the particle mass, and below this range, cohesive forces counter particle detachment (Di and Ferro, 2002; Ampontuah et al., 2006). Indeed, when we compare K_{Repic} values of cyanobacterial biocrust

with the soils underlying it, they are lower, suggesting that cyanobacterial biocrust do reduce erodibility through effects on either SOM or PSD. Further evidence is provided by the weak, but negative, relationship of K_{Repic} to cyanobacterial biomass (Fig. 5). We therefore conclude that the prevalence of biocrusts of any kind, but especially those dominated by mosses, appears to be instrumental in determining soil erodibility in our study region.

4.3. Impacts of biocrusts on soil loss

Soil losses decreased dramatically (about 90%, Fig. 6) in biocrust-influenced soils compared to bare soil, even though the physical structure of the biocrusts had been omitted. Interestingly, soil losses were not different among soils sourced from different biocrust types, which contrasted with the modeled result that K_{Repic} in moss biocrust was lower than cyanobacterial biocrust. We simultaneously measured the runoff generation, along with sediment loss. The result showed a similar trend with soil loss, in that biocrusts experienced less runoff generation than bare soils, whereas there were no differences among biocrust types. This may be one of the reasons that sediment yield was similar among biocrust types: despite that biocrust types may differ in erodibility, they may similarly negatively influence runoff generation reducing the erosive force of runoff and therefore sediment yield. Another possible reason is that the simulated rain intensity (120 mm h^{-1}) we used was the maximum in the study region (Jiao and Wang, 2001). This intensity may have been too strong to discriminate amongst the slight variations in soil erodibility of the different types of biocrusts, a possibility that will require further investigation.

Biocrusts are a crucial factor influencing soil erosion in arid and semiarid regions where the coverage of vascular plants is limited (Eldridge and Greene, 1994; Belnap and Lange, 2003). Eldridge and Leys (2003) found soil erosion decreased by almost two orders of magnitude as biocrust cover increased from 0 to 100%. On clay and sandy soils, two to five times as much sediment, was collected from the uncrusted compared to biocrusted soils (Belnap and Büdel, 2016). Biocrusts appear to reduce erosion through several mechanisms. Soil particles are bound together (Chamizo et al., 2012; Chen and Duan, 2015), and soil aggregates are formed by polysaccharides exuded by biocrust organisms (Belnap and Gardner, 1993; Neuman et al., 1996), inhibiting water erosion. Biocrusts possess a layered structure with strong horizontal stability to protect soil from shear stresses like water erosion (Yang et al., 2012). The higher the organism biomass in late successional biocrusts, the more stable the soil particles are against water erosion (Belnap and Gillette, 1997). Well-developed biocrusts containing a high cover of mosses can nearly completely protect soil surfaces from water erosivity (Belnap and Lange, 2003; Belnap et al., 2012; Zhao and Xu, 2013). Because mosses actually protrude above the soil surface and add relatively deep (up to 5 cm) anchoring structures, later successional biocrusts are better able to withstand raindrop erosion than cyanobacterial biocrust, regardless of the cyanobacterial biomass (Zhao et al., 2014).

The above mechanisms are examples of the effect of physical protection or aggregation provided by biocrust cover, and have been the subject of most studies. Indeed, Bowker et al. (2008) concluded that for soils in a region of heterogeneous biocrust cover, the cover management (C) factor was considerably more influential than the soil erodibility (K) factor (inherent properties). Although the examples above clearly demonstrate that physical protection of biocrusts provides resistance to water erosion, potentially leading to a 100% reduction of soil loss when biocrusts are kept undisturbed (Belnap et al., 2012; Zhao et al., 2014), we found that a 90% reduction in soil loss was demonstrated in

biocrust soil compared to bare soil even with the protective cover of biocrusts removed and disaggregated. Our field study provides evidence that this effect is linked to modification of SOM and PSD induced by development of biocrusts. We therefore believe that biocrusts are necessary to consider not only for their effects on the C factor (Bowker et al., 2008), but also on the K factor when estimating, predicting, and managing soil loss due to water erosion. Despite that their influence is expressed mainly in the topsoil (about 2 cm), they are crucial because they are analogous to a kind of skin on the soil surface protecting soil from water erosion (Eldridge and Greene, 1994; Belnap and Gillette, 1997; Zhao and Xu, 2013). Soils underlying biocrusts are unlikely to be eroded unless the biocrusts layers are first destroyed, thus, the biocrusts through multiple mechanisms provide a first line of defence against erosion.

5. Conclusions

The presence of biocrust organisms, especially mosses, can be of great importance to land managers, given their critical roles in soil stability and fertility in drylands. This study on the Loess Plateau supports the general finding of previous studies that biocrusts can improve soil organic matter content and accumulate fine soil particles. Consequently, the soil erodibility of biocrusts decreases significantly, which is attributable to changes in soil properties, especially the increase of SOM.

The Grain for Green project has improved vegetation recovery and biocrust development extensively across the Loess Plateau region in China. The most direct result of that is that a very large severely eroded region has experienced drastically reduced sediment yield, and biocrusts are instrumental in this occurrence partly through their reduction of soil erodibility. Therefore, the influence of biocrusts on soil loss under water erosion is necessary to consider, specifically via effects on the K factor, when estimating, predicting, and managing soil loss both within and among watersheds.

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