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Linkages between biocrust development and water erosion and implications for erosion model implementation

Liqian Gao[a], Matthew A. Bowker[b], Hui Sun[a,c], Jun Zhao[a], Yunge Zhao[a,*]

[a] State Key Laboratory of Soil Erosion and Dryland Farming on the Loess Plateau, Institute of Soil and Water Conservation, Northwest A & F University, Yangling 712100, Shaanxi, China

[b] School of Forestry, Northern Arizona University, Flagstaff, AZ 86011, USA

[c] College of Forestry, Northwest A & F University, Yangling 712100, Shaanxi, China

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ABSTRACT

Biological soil crusts (biocrusts) are an important factor influencing water erosion on slopes, but they are not represented sufficiently in erosion models, which limits the reliability and accuracy of these models. Determining the predictor that can represent the effects of biocrusts on water erosion and the relationship between this predictor and water erosion is the key to solving this problem. Accordingly, we sampled 20 undisturbed biocrust samples from 10 slopes in the Loess Plateau region of China, representing a developmental sequence and used rainfall simulation to explore the effects of biocrust development on soil loss under water erosion. The results showed that the moss percentage cover was a better predictor than cyanobacterial or moss biomass to predict the resistance of biocrust covered soil to water erosion. As expected, there was a strong negative relationship between sediment concentration and moss cover. Effect of biocrust development on water erosion can be divided into two stages, based on a threshold moss cover of 35% beyond which water erosion was completely prevented. Where moss cover was below 35%, sediment concentration decreased logarithmically along with the increase of moss coverage. Biocrusts controlled water erosion through two tightly correlated mechanisms, decreasing erodibility (the *K* factor) and enhancing cover of the soil surface (the *C* factor). Increasing moss cover appears to induce a cascade of changes in soil organic matter, texture and organic carbon. All of these factors jointly control water erosion. Accounting for the effect of biocrusts in the Revised Universal Soil Loss Equation is essential, and we recommend that the most practical way of doing so is to ensure that the effect of biocrust cover, particularly moss cover, is more effectively and consistently taken into account when estimating the *C* factor. The results of this study will provide a scientific basis for the selection of parameters considering the biocrust effects in soil erosion models.

1. Introduction

Biological soil crusts (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 are ubiquitous living covers in many arid and semiarid ecosystems. It is now widely accepted that biocrusts exert a profound influence on soil stabilization and erosion prevention (Belnap et al., 2014; Belnap et al., 2012; Faist et al., 2017; Munson et al., 2011; Rodríguez-Caballero et al., 2014; Zhao and Xu, 2013). Therefore, some researchers have suggested that biocrusts must be represented explicitly in models that aim to predict and manage soil loss to improve their accuracy (Bowker et al., 2008a; Gao et al., 2017; Rodríguez-Caballero et al., 2015; Zhao et al., 2014). Furthermore, determining the predictor that can represent the effects of biocrusts on water erosion and how to parameterize the biocrust effects is a prerequisite for solving this problem.

Biocrusts in different successional stages or levels of biomass have shown varied capacity for erosion prevention. For example, earlier successional cyanobacterial biocrusts exert lesser effects than the later successional lichen or moss biocrusts on soil stabilization (Bowker et al., 2008b; Pietrasiak et al., 2013; Zhao and Xu, 2013). Further, there is a strong relationship between soil stability and chlorophyll *a* ($R^2 = 0.77$) which increases as biocrusts develop and accumulate biomass (Belnap et al., 2008). For instance, the stability of soils containing > 0.014 mg chl *a* g^{-1} soil to wind erosion was twice that of those whose chlorophyll contents was below that value, and high moss and lichen cover completely protected soil from wind erosion (Belnap

* Corresponding author at: Institute of Soil and Water Conservation, Northwest A&F University, No. 26 Xinong Road, Yangling 712100, Shaanxi, China.
E-mail address: zyunge@ms.iswc.ac.cn (Y. Zhao).

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et al., 2014). Additional studies have also corroborated that late-developed biocrusts could control water erosion completely (Belnap et al., 2012; Rodríguez-Caballero et al., 2013; Zhao et al., 2014). Given this, there may be a negative relationship between biocrust successional development and water erosion and a minimum threshold of biocrust coverage for total resistance to water erosion. Finding such a threshold should be a key step to enhance performance of water erosion models at hillslope scale.

Biocrusts affect soil stability and erosion resistance though multiple mechanisms. These can be conceptualized using the terms of the Revised Universal Soil Loss Equation (RUSLE). In RUSLE, the *K* factor describes erodibility of soils and is determined by inherent soil properties such as texture and organic matter content. The *C* factor describes the degree to which the soil is covered by vegetation and other protective elements, which is in turn often strongly related to management practice. Biocrusts modify numerous physicochemical soil properties with strong implications for soil erosion, such as soil organic matter, soil particle size distribution (through retention and accumulation of fines), soil bulk density and so on (Gao et al., 2017). According to these mechanisms, soil erodibility (*K* factor) decreases significantly as biocrusts develop from cyanobacteria to mosses, and the effects of biocrusts on soil erodibility may be highly informative when estimating and predicting soil loss (Gao et al., 2017). However, Bowker et al. (2008a) concluded that for soils covered by cyanobacterial biocrusts, chlorophyll *a* was a moderate to excellent predictor of soil stability. This effect was interpreted to be more strongly conceptually linked to the *C* factor than the *K* factor because the abundance of biocrusts, and therefore chlorophyll *a*, is dynamic and fluctuates with management and disturbance. Given these two distinct ways in which biocrusts may interact with an empirical erosion model, we asked which one is primary, the *C* factor or *K* factor, or both? This could be a key to parameterize erosion models to include the influences of biocrusts.

The Loess Plateau in China is one of the most severely eroded regions of the world, especially due to water erosion. To prevent the severe soil erosion in the region, the “Grain for Green” ecological project was implemented in 1999 across a large portion of the region, in which both cultivation and grazing on slopes steeper than 25° were prohibited. Soil loss was thus reduced drastically (Chen et al., 2007; Wang et al., 2012; Wang and Zhuo, 2015; Zheng, 2006). Biocrusts spontaneously and widely developed in response to the cessation of disturbance and functioned as a major contributor to the observed reduction in erosion rates across the Loess Plateau (Ran et al., 2011; Zhao et al., 2014; Zhao and Xu, 2013). Natural establishment of biocrusts was observed within a few years after cropping and grazing cessation, and the coverage is now up to 70% of the land area (Zhao et al., 2006a). Mosses generally dominate biocrusts by the fourth year after cessation of disturbance, and their density and coverage increase over time. Moss dominated biocrusts can eventually control soil loss totally after cessation of disturbance for about 13 years (Zhao and Xu, 2013).

The change in land use brought about by the “Grain for Green” project, and the subsequent expansion of biocrusts, provided us an opportunity to explore the linkage of biocrust development on water erosion in this region. Therefore, we evaluated the influence of biocrust development on water erosion across the region using an extensive field survey and rainfall simulation experiments. The study thus addressed two questions: (1) What is the specific linkage between biocrust development and water erosion? And (2) What is the dominant mechanism of biocrust control over water erosion? The results of this study may improve the explicit consideration of biocrust effects in erosion models, and thereby improve reliability and accuracy of the models.

2. Materials and methods

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. The topography varies locally in a complex of loessial hills and gullies, with an approximate mean altitude of 1200 m. The climate in the study area, which has been defined as typical continental semiarid, has an average annual temperature of 8.8 °C and a mean annual precipitation of 505 mm, 60% or more of which falls between July and September, typically in high-intensity and short-duration rainstorms. Mean annual potential evapotranspiration is 1617 mm (Ansai Research Station, unpublished data, record period 1998–2015).

The soil is classified as a typical loessial soil, which is highly susceptible to erosion, with an erosion rate of over 10,000 t km^{-2} year^{-1} before the “Grain for Green” ecoproject begun (Zhang et al., 2011). After the implementation of this ecological project, *Artemisia capillaris* dominated initially and peaked in biomass between five to ten years, while *Artemisia sacrorum* became dominant after ten years of cropland abandonment.

In the study area, the biocrust community is dominated by cyanobacteria and mosses. Moss biocrusts usually occur on north-facing slopes, which have better moisture conditions, and the dominating species are *Didymodon tectorum* and *Didymodon vinealis* (Zhao et al., 2014). Cyanobacteria are mainly distributed on south-facing slopes and formed in the first year after cropland abandonment. *Phormidium angustissimum* and *Phormidium tenue* were the dominant cyanobacterial species, with *Nostoc* spp. slightly less abundant (Yang, 2013). Lichens can be found in biocrusts ten years after abandonment, and eighteen species have been observed, including *Solorinella asteriscus*, *Fulgensia fulgens*, *Endocarpon pusillum*, and *Psora* spp.. Lichen coverage, however, seldom reaches 10% (Wang et al., 2016b) and since most of the decline in water erosion occurs before the arrival of lichens, we thus focus on cyanobacterial and moss biocrusts in this study.

2.2. Sample preparation

We selected 10 naturally recovering slopes with varying ages of abandonment of cropping and grazing, which biocrusts ranged from cyanobacteria to moss dominated. After a thorough field survey of biocrust coverage and composition, two undisturbed biocrust samples were collected in each of these slopes using plastic boxes, which were 30 cm (length) × 20 cm (width) × 5 cm (depth), a total of 20 undisturbed biocrust samples (Table 1). In addition, three undisturbed bare soil samples from the slope farmlands were collected as a type of control; these had been kept undisturbed for only about two months prior to sampling. Because biocrust development is fast in this ecosystem, a very recent disturbance is needed to enable sampling of a very low biocrust state. Even with the recent cropping, there was a slight degree of cyanobacterial colonization on the soil surface and their content of chlorophyll *a* ranged from 2.0 to 2.9 μg g^{-1}. After sampling biocrusts and control soil surfaces, two soil samples directly adjacent to each undisturbed biocrust sampling site were selected to measure soil physicochemical properties. At each sampling location we sampled at the depth of the biocrusts and from 0 to 2 cm underlying the biocrusts. Then, the two samples of the same depth were collected and thoroughly mixed. After collection, the samples were sent to the laboratory and air dried, sieved to 1 and 0.25 mm so as to measure soil organic matter and particle size distribution. Also, two biocrust samples directly adjacent to each undisturbed biocrust sampling site were collected with petri dishes of 9 cm diameter and 1 cm depth to determine the chlorophyll *a* content of cyanobacteria and biomass of mosses. Soil bulk density was also measured used a soil ring cutter.

The soil organic matter was measured by the Walkley Black method (Nelson and Sommers, 1982). Soil particle size distribution was performed using a laser-diffraction method (Mastersizer 2000, Malvern, UK). For the sample preparation details, please see Gao et al. (2017). Moss biomass was represented by dry mass of mosses per unit area (g dm^{-2}) (Gao et al., 2017). Chlorophyll *a* per unit soil mass (μg g^{-1})

Table 1
Characteristics of the sampling plots.

Sample plots	Cyanobacterial cover (%)	Moss cover (%)	Chlorophyll *a* (μg g^{-1})	Moss biomass (g dm^{-2})	Bare soil cover (%)
Control-1	–	0	2.0	0	100
Control-2	–	0	2.8	0	100
Control-3	–	0	2.9	0	100
1	61	33	23.1	0.64	2
2	54	25	11.7	0.42	21
3	10	85	7.6	10.65	5
4	8	75	6.6	7.65	15
5	37	57	9.4	1.32	5
6	15	69	8.6	4.43	11
7	43	43	8.7	1.1	11
8	51	48	7.6	2.34	1
9	71	4	30.4	0.14	17
10	64	7	15	0.16	24
11	66	19	32.3	0.31	5
12	70	24	7.9	0.4	6
13	61	9	8.7	0.18	25
14	71	15	17.1	0.25	6
15	61	31	27.1	0.58	7
16	61	33	17.9	0.67	4
17	10	77	6.2	7.23	12
18	6	80	4.3	9.32	14
19	50	37	10.3	0.83	13
20	45	47	9	1.68	8

was measured as a proxy for cyanobacterial biomass. Chlorophyll *a* was double extracted with ethanol and measured on a spectrophotometer at wavelengths 665 nm and 750 nm (Castle et al., 2011). Before the chlorophyll *a* extraction, traces of mosses were removed when present in the cyanobacterial biocrust samples.

2.3. Rainfall simulation

The simulated rainfall studies were conducted in the Simulation Rainfall Hall of the State Key Laboratory of Soil Erosion and Dryland Farming on the Loess Plateau in the Institute of Soil and Water Conservation, Chinese Academy of Sciences and Ministry of Water Resources in China. The height of the rainfall simulator nozzle is 16 m, which can achieve the terminal speed of natural rainfall. The intensity of the simulated rainfall can be adjusted from 30 mm h^{-1} to 200 mm h^{-1}, and it can be precisely adjusted to the target intensity ($\pm$ 2.7 mm h^{-1}) by controlling the aperture of the nozzle and the water pressure. The raindrop size distribution ranges from 0.6 to 3.0 mm. The raindrop uniformity of simulated rainfall is > 80%, which is similar to natural rainfall in both raindrop size and distribution (Zheng and Zhao, 2004).

We filled an experimental box, with the dimensions of 100 cm (length) × 60 cm (width) × 10 cm (depth), with loess soil with uniform bulk density (1.3 g cm^{-3}) to support the undisturbed biocrust samples and simulate the prevailing natural condition of the soil beneath biocrust samples. The fill soil was collected from sloping farmland in the study area. During each measurement, one of the undisturbed biocrust samples was set on the surface of the soil in the box. The surface of the fill soil was lightly disturbed and loosened with a small shovel to improve contact between the fill soil surface and the bottom of the undisturbed biocrust sample.

All biocrust samples had been previously air-dried to a moisture content of approximately 3.0%. A small frame with the dimensions of 30 cm (length) × 20 cm (width) × 15 cm (depth) and an outlet on the side of the frame, was then set around the undisturbed biocrust sample. The frame was pressed into the soil approximately 5 cm deep forming a micro-plot for rainfall simulation to collect runoff and sediment from the outlet. After assembly of this system, the slope gradient of the box was set at 25°, which was the minimal revegetated gradient in the 'Grain for Green' ecological project. The rainfall intensity was set as 120 mm h^{-1}, which was equal to extreme rainfall intensities of monsoon rainstorms experienced in the study area (Wang et al., 2016a). In the process of the experiment, both the time to runoff yield and biocrust breakage caused by the simulated rain were recorded. The simulated rainfall lasted for 30 min after the initiation of runoff. If biocrusts were not broken in the process of simulated rainfall, the time to biocrust breakage by rainfall was recorded as the rainfall duration, that was the sum of the time of runoff initiation and 30 min. Compared with the true resistance time, this approach may underestimate, to some extent. Nonetheless, the time to biocrust breakage can still provide a conservative estimate of the resistance capacity of biocrusts to water erosion. Runoff was collected continuously in three-minute increments at the outlet with plastic buckets. After the rain, the runoff in each bucket was weighed and then allowed to stand for > 24 h to separate the sediment from the supernatant. The supernatant was discarded, and the sediment was dried and weighed. We used this information with runoff yield to calculate sediment concentration (g L^{-1}).

2.4. Statistical analyses

As a preliminary step, we used Spearman correlation to determine which biocrust variables were most closely linked with sediment yield and time to biocrust breakage. In order to fully quantify the relationship between biocrust succession and development and water erosion, we created regressions of the relationship between the most informative biocrust measurements and sediment yield. We used these regressions to determine if thresholds existed. We considered a threshold to be the x value in the regression beyond which the sediment yield was indistinguishable from zero.

We used a partial regression analysis to detect and partition unique effects of our predictors on sediment concentration (Legendre and Legendre, 2012). We will first illustrate the process with an example. To determine if moss cover has a detectable unique effect on sediment concentration, that *is independent of* the effects of silt, we first fit a regression of sediment concentration as a function of silt. We removed the effect of silt by saving the residuals of this regression. We then tested the Pearson correlation between these residuals and moss cover. The strength of this correlation, and its probability value allowed us to determine if a unique effect of moss cover could be distinguished from the effect of silt. This same process was extended to tests for unique effects of moss cover from the other predictors (bulk density and organic matter). Further, we also conducted the same type of test to determine if moss cover had unique effects distinguishable from all possible combinations of the other predictors. In total, we conducted seven such tests for unique effects of moss cover. We repeated the same exercise to determine if we could detect unique effects of: 1. Organic matter, independent of moss cover, bulk density and silt, 2. Bulk density, independent of moss cover, organic matter, and silt, and 3. Silt, independent of moss cover, organic matter and bulk density. Prior to these tests, we conducted a log transformation of all variables, including sediment concentration, because this linearized the relationships between the various predictors and sediment concentration. We used this method in an attempt to elucidate the dominant mechanism(s) of biocrust-mediated control over water erosion, and determine the relative influence of expressions of the *C*-factor and *K*-factor. All statistical analyses were completed using SPSS 18.0 (SPSS, USA).

3. Results

3.1. Biocrust indicators of sediment concentration

Moss cover and biomass were more strongly and negatively correlated to sediment concentration than cyanobacterial biomass or cover (Table 2). Cyanobacterial cover was strongly positively correlated to

Table 2
Spearman correlations between sediment concentration and biocrust cover and biomass.

Variables	Cyanobacterial cover	Moss cover	Cyanobacterial biomass	Moss biomass
Moss cover	−0.93****			
Cyanobacterial biomass	0.74***	−0.72***		
Moss biomass	−0.92****	0.99****	−0.73***	
Sediment concentration	0.72***	−0.85****	−0.07	−0.85****

Note: *** and **** indicate significant differences at $P < 0.001$ and $P < 0.0001$, respectively.

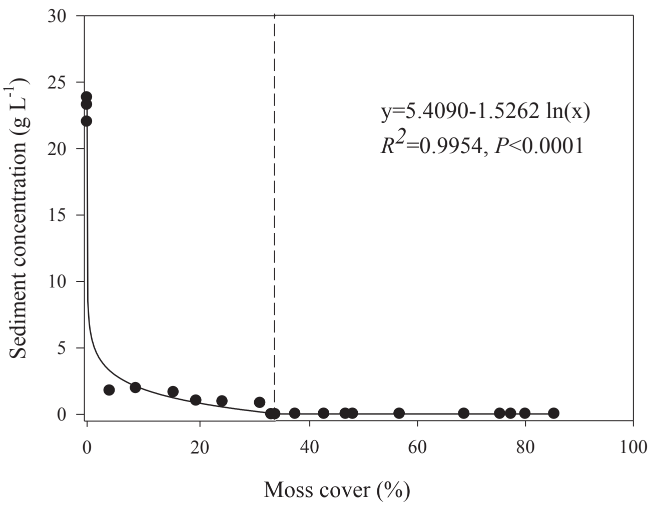

Fig. 1. Effects of moss cover on sediment concentration.

sediment concentration, while cyanobacterial biomass was a weakly negative correlate (Table 2). Cyanobacterial indicators were also consistently negatively correlated with moss indicators, whereas the two moss indicators were nearly perfectly positively correlated (Table 2). Based on these results, we pursued regression analysis of water erosion as a function of moss cover.

3.2. Soil loss as a function of moss cover

Sediment concentration was nearly perfectly described as a negative logarithmically function of moss cover ($R^2 = 0.9954$, $P < 0.0001$; Fig. 1). Only 8% of moss coverage was associated with an 87% decrease in sediment concentration compared to recently cropped samples with 0% moss cover. Sediment concentration further declined to was zero when moss coverage was > 35%. Samples low in moss coverage were visibly altered by soil loss (Fig. 2). They clearly showed the development of breakage of the soil surface, new rills and variation in microtopography; in contrast, samples with > 35% moss cover showed no evidence of breakage, surface soil loss or roughened topography.

The time to biocrust breakage by raindrops increased significantly with the successional development of biocrusts (Fig. 3). Cyanobacterial biocrust with only 7% moss cover, an early successional community, took about 3 times as long to break as recently disturbed controls with 0% moss cover. Biocrusts with > 35% moss cover were not broken by rainfall under experimental conditions, thus their true time to breakage under extreme rainfall intensity is likely underestimated. Nevertheless, this model suggests that biocrusts with > 35% moss cover can withstand high rainfall intensities > 10 times longer than recently disturbed soils.

3.3. Effects of biocrust development on soil properties

Soil organic matter content increased clearly with biocrust development (Fig. 4A). The soil organic matter content of biocrusts in the late developmental stage (moss cover > 80%) was 1.9 times higher than that in the early developmental stage, which moss cover was < 10%. Soil bulk density of biocrusts decreased obviously with biocrust development (Fig. 4B). The soil bulk density of biocrusts with a moss cover > 80% in the late developmental stage was 22.3% lower than that in the early developmental stage with a moss cover < 10%. However, soil particle size distribution did not differ strongly among biocrust development (Fig. 4C).

3.4. Unique and combine effects of biocrusts and soil inherent properties on water erosion resistance

In order to clarify the mechanism of biocrust control of water erosion, we attempted to distinguish the direct effects of biocrust cover and the indirect effects mediated through biocrust-induced changes in inherent soil properties (organic matter, bulk density, silt) (Table 3). The overarching result was that moss cover, silt, organic matter, and bulk density did not exert unique effects that could be partitioned. Moss cover did have an effect on sediment concentration that was distinguishable from the effect of silt ($r = -0.73$, $P < 0.0001$); however, this effect was not detected when changes in organic matter or bulk density were taken into account (Table 3). On the contrary, we detected no effect of silt that was independent of moss cover (Table 3). The effects of organic matter and bulk density on sediment concentration were independent of the effects of silt, but could not be distinguished from each other or the effects of moss cover (Table 3). The effects of silt were distinguishable when either organic matter or bulk density were accounted for but were not detectable when both of those variables were accounted for (Table 3).

4. Discussion

4.1. Biocrust succession and its effects on water erosion resistance

In the successional pathway of many but not all biocrust communities, the pioneers in colonizing the soil surface are the cyanobacteria, followed by mosses and lichens (Belnap et al., 2012; Eldridge and Greene, 1994; Weber et al., 2016). In dry desert regions, the succession of biocrusts is often reported as being slow, possibly requiring multiple decades (Belnap, 1993; David et al., 1982). Recovery estimates in drylands are also highly variable, and recovery rates ranging from a few years to millennia have been suggested in the literature (Weber et al., 2016). In the Loess Plateau region, however, cyanobacterial biocrust can be formed after farmland abandonment of less than one year, as evidenced by our finding of incipient cyanobacterial biocrusts on croplands that had been disused for only 2 months and experienced only a few rain events. This finding is not unlike those of Dojani et al. (2011) who showed that biocrusts recovered only one rainy season after their complete removal. In our study system, cyanobacterial biocrusts then go on to strongly dominate the soil surface in the first few years of succession, after which coverage decreases logarithmically as cyanobacteria are replaced by mosses (Fig. 5). Mosses generally dominate biocrusts by about the sixth year after cropping and grazing cessation, and the density and coverage increase as time since abandonment increases. A similar successional sequence and rate was also documented in the same study region by Zhao et al. (2006b). Biocrusts in the Loess

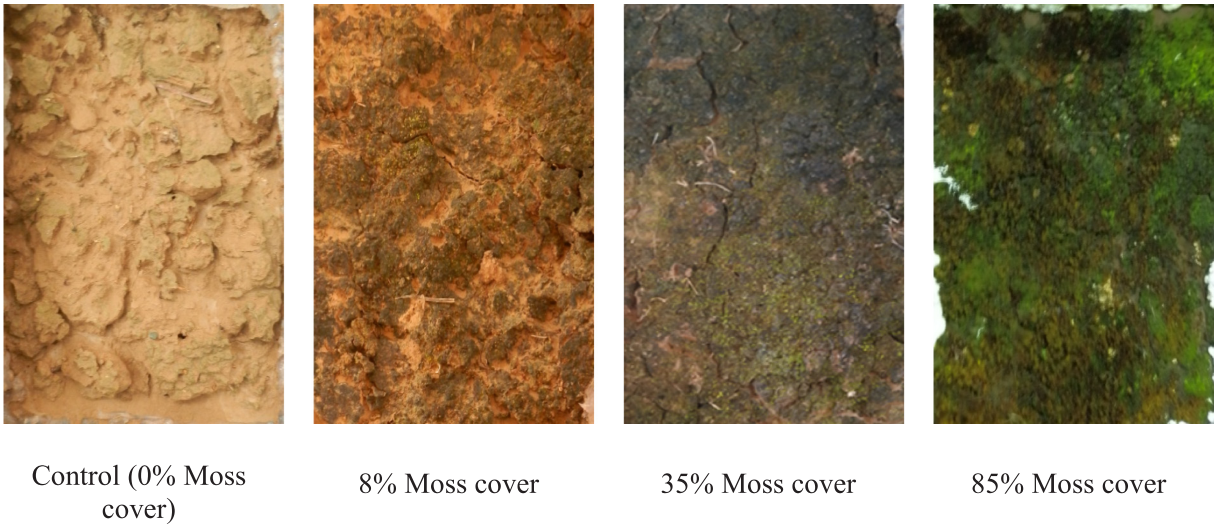

Fig. 2. Simulated rainfall induced soil erosion from biocrusts with different moss coverage.

Plateau region take only 13 years to reach a late-development stage, with > 60% moss coverage. The recovery rate of biocrusts on the Loess Plateau is among the fastest reported. The reason may be greater annual precipitation than most studied regions (mean annual precipitation is 505 mm), in addition to a pronounced rainy season that can generate long hydration periods for growing biocrust organisms. The present study investigates some of the outcomes for erosion potential of this rapid successional process.

The developmental stage of biocrusts appeared to be one factor determining local water erosion, a result also demonstrated by Belnap et al. (2012). The change of sediment concentration was correlated with biocrust indicators (Table 2). Moss cover and biomass were more strongly correlated with sediment concentration than cyanobacterial cover, whereas the two moss indicators were nearly perfectly positively correlated and thus interchangeable (0.99). We thus concluded that moss cover is the best single indicator of water erosion, at least in our study region, which is also a more economical shortcut to obtain quality data for use in erosion models.

As expected, there was a strong negative relationship between soil loss by water and moss coverage (R^2 = 0.9954). Biocrusts contribute to the stability of the soil surface in the face of the erosive forces of raindrops and runoff. Where larger biocrust organisms such as mosses cover the soil surface, they actually protrude above the soil surface and add relatively deep (up to 5 cm) anchoring structures within the soil (Belnap and Büdel, 2016). Raindrops are unable to directly impact the soil surface and detach soil particles (Zhao et al., 2014). As a consequence, sediment concentration decreased dramatically with the development of moss biocrusts.

It is worth noting that the effect of biocrust development on water erosion is a threshold-based nonlinear function (Fig. 1). That is, there are values of biocrust development beyond which erosion is completely omitted. We found that sediment can totally be controlled by biocrusts with > 35% moss coverage (Fig. 1). Moreover, this threshold value is close to the coverage value (40%) of the moss biocrust when it begins to dominate biocrusts (Fig. 5). The higher the biomass in late successional biocrusts, the more stable the soil particles are against water erosion

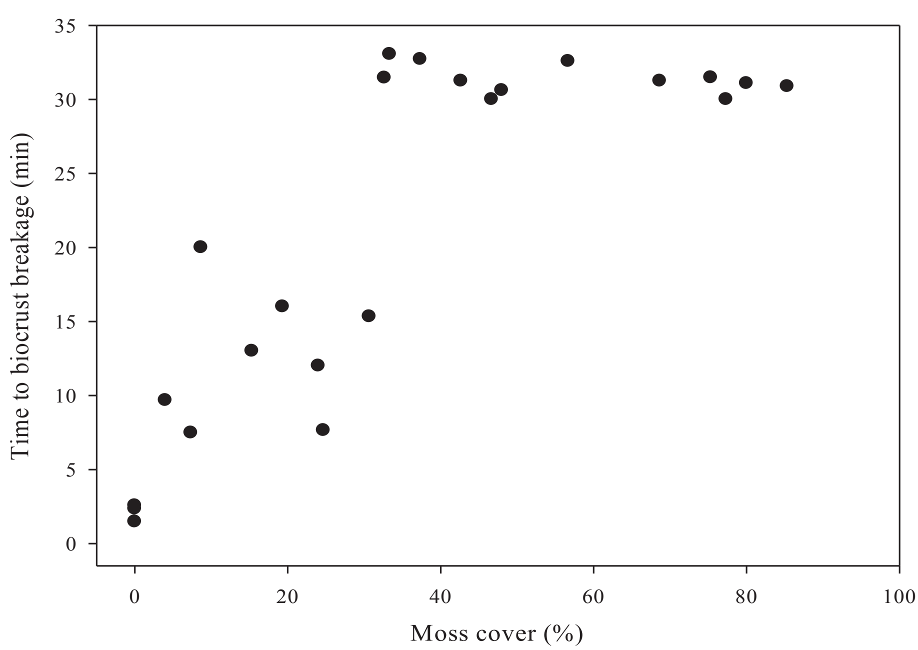

Fig. 3. Effect of moss cover on the time to biocrust breakage under simulated rainfall condition.

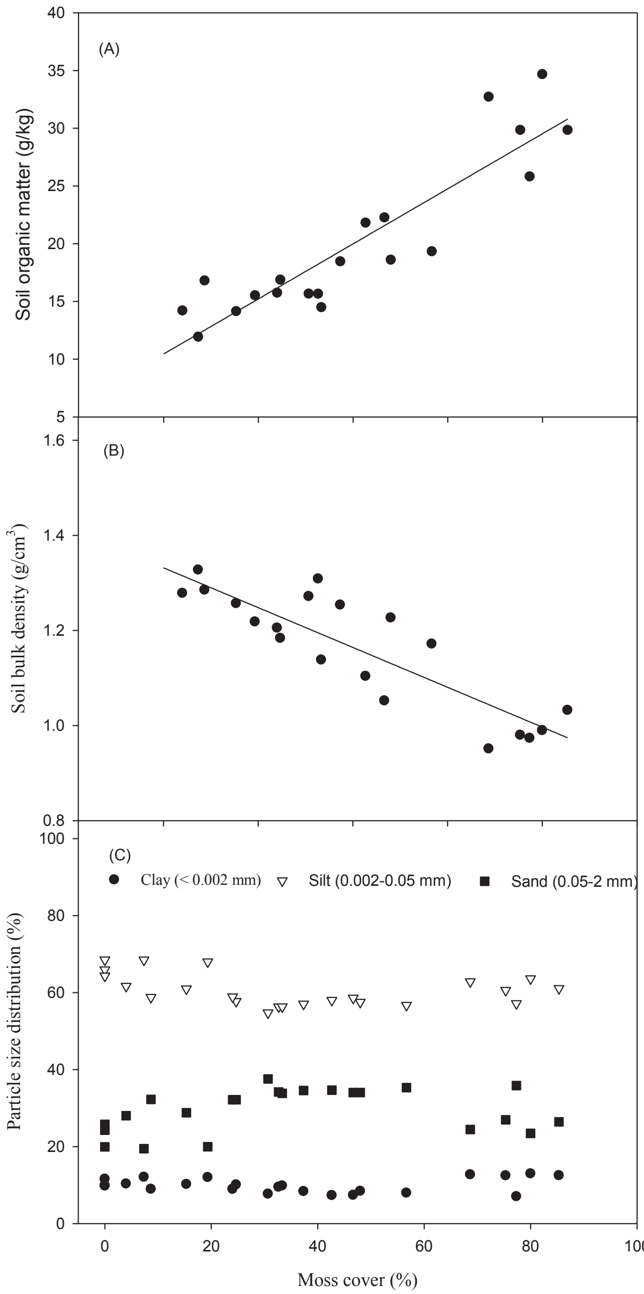

Fig. 4. Effects of biocrust development on (A) soil organic matter, (B) soil bulk density and (C) soil particle size distribution.

(Belnap and Gillette, 1997). There is also evidence that the relationship of biocrust development to soil stability and erosion resistance follows a threshold behavior. Many studies have also corroborated that late-developed biocrusts containing moss and lichens could control water erosion completely (Belnap et al., 2012; Rodríguez-Caballero et al., 2013; Zhao et al., 2014). Accordingly, determining the threshold value of biocrust development to control soil erosion completely and the quantitative relationship between biocrust development below this threshold and soil erosion in different climate zones is the basis for parameterizing the effects of biocrusts into soil erosion models. Based on the above, we seem to be able to preliminarily establish an equation of sediment concentration based on moss cover (Fig. 1):

$$y = \begin{cases} 5.4090 - 1.5262\ln(x)\ (0 \le x \le 35) \\ 0\ (35 \le x \le 100) \end{cases} (R^2 = 0.9954, P < 0.0001) \quad (1)$$

Table 3
The unique effects of predictors on sediment concentration.

Predictor	Combinations of other predictors	Correlation coefficient (r)[a]	*P*
Moss cover		**−0.95**	**< 0.0001**
Moss cover	**Silt**	**−0.73**	**0.0001**
Moss cover	Organic matter	−0.34	0.1172
Moss cover	Bulk density	−0.42	0.0684
Moss cover	Silt + organic matter	−0.20	0.3622
Moss cover	Silt + bulk density	−0.30	0.2011
Moss cover	Organic matter + bulk density	−0.36	0.1182
Moss cover	Silt + organic matter + bulk density	−0.22	0.3548
Organic matter		**−0.84**	**< 0.0001**
Organic matter	Moss cover	0.04	0.8641
Organic matter	**Silt**	**−0.78**	**< 0.0001**
Organic matter	Bulk density	−0.12	0.6011
Organic matter	Moss cover + silt	−0.02	0.9269
Organic matter	Moss cover + bulk density	−0.01	0.9576
Organic matter	Silt + bulk density	−0.16	0.5064
Organic matter	Moss cover + silt + bulk density	−0.05	0.8416
Bulk density		**0.60**	**0.0053**
Bulk density	Moss cover	−0.25	0.2793
Bulk density	**Silt**	**0.53**	**0.0152**
Bulk density	**Organic matter**	**−0.46**	**0.0400**
Bulk density	Moss cover + silt	−0.18	0.4576
Bulk density	Moss cover + organic matter	−0.20	0.3950
Bulk density	Silt + organic matter	−0.34	0.1387
Bulk density	Moss cover + silt + organic matter	−0.21	0.3859
Silt		**0.64**	**0.0009**
Silt	Moss cover	0.21	0.3299
Silt	**Organic matter**	**0.60**	**0.0024**
Silt	**Bulk density**	**0.50**	**0.0250**
Silt	Moss cover + organic matter	0.18	0.4182
Silt	Moss cover + bulk density	0.22	0.3411
Silt	Organic matter + bulk density	**0.54**	**0.0147**
Silt	Moss cover + organic matter + bulk density	0.23	0.3223

Note: [a]Correlation coefficient (r) represented the Pearson correlation between the predictor and sediment concentration when there was only a predictor. And when there were other combination predictors, r represented the Pearson correlation between the predictor and the residuals of regression of sediment concentration by the predictors.
Bold indicated significant differences at P < 0.05.

where, y represents sediment concentration (g L^{-1}); x represents moss cover (%). Soil loss on the biocrusts sloping surface may be a similar function of biocrust coverage, which needs further confirmation.

One might errantly infer from our results that cyanobacterial biocrusts enhance sediment yield, because cyanobacterial cover across the whole dataset is positively related to sediment yield. This result indicates only that cyanobacterial biocrusts are *relatively* less able to constrain erosion *compared to mosses*. Compared to truly bare soil immediately after the cessation of cropping, cyanobacterial biocrusts are more erosion resistant (an 87% decrease in sediment concentration; Figs. 1 and 2). Zhao et al. (2014) showed that the resistance capacity of cyanobacterial biocrust to raindrop erosivity was 15 times higher than that of bare soil, however it was only 4% that of completely moss-dominated biocrust. Consequently, given variable erosion resistance, the coverage of cyanobacterial biocrusts may be highly informative when estimating and predicting soil loss by water in cases where the successional development is below the threshold value at which erosion ceases (35% moss cover).

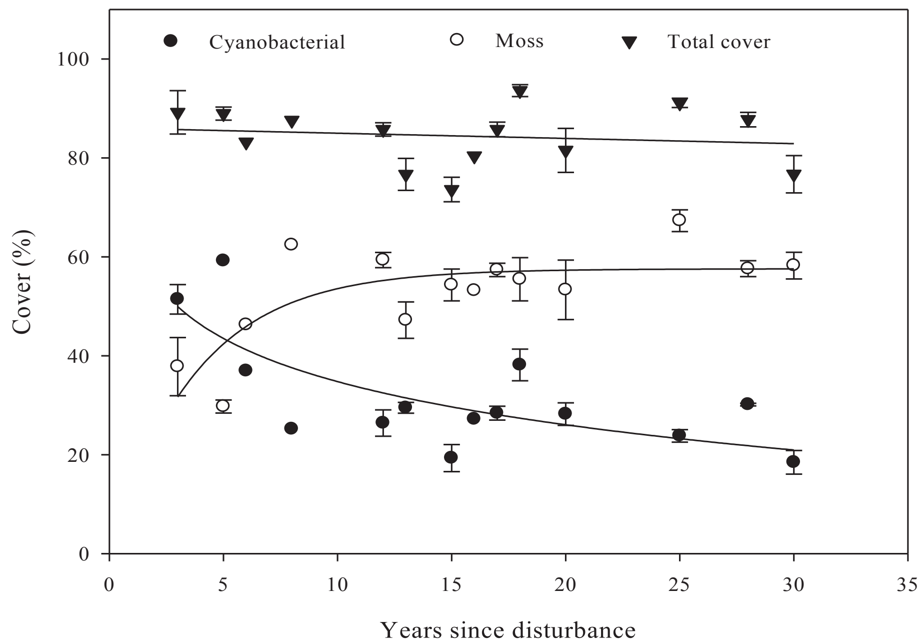

Fig. 5. Changes in the components of biocrusts over time in the Loess Plateau region.

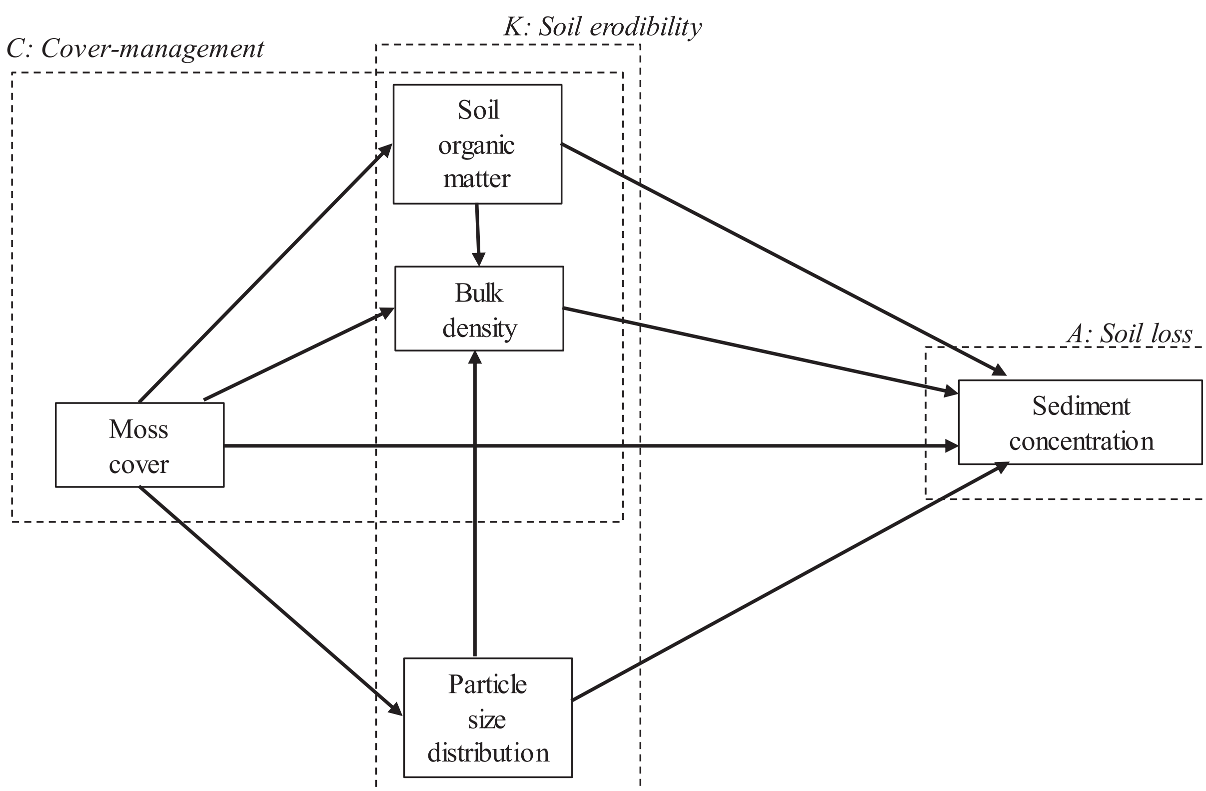

Fig. 6. A hypothetical diagram illustrating inextricable biocrust-driven linkages between the *C* and *K* factor. Two *K* factor indicators are essentially inseparable from the *C* factor. Dashed boxes and associated text indicate components of the revised universal soil loss equation that are strongly conceptually linked to the variables here. Rectangles represent measured variables. Single headed arrows represent hypothetical causal relationships.

4.2. Dominant mechanism of biocrusts control water erosion and implications for erosion model implementation

Biocrusts stabilize soils directly from erosive forces (such as wind and water) due to their own morphology entwining and binding and covering of soil particles, and indirectly by modifying inherent soil properties such as organic carbon content, bulk density, and texture. These direct effects traditionally fall under consideration as part of the *C* factor in RUSLE, whereas the indirect effects fall under consideration as part of the *K* factor. A study of the effects of biocrusts on soil detachment capacity (D_c) by overland flow on Loess Plateau showed that surface cover of the early successional cyanobacterial biocrust contributed 54.5% to the reduction of D_c, while that of moss biocrust contributed 76.7% (Liu et al., 2017). This seemed to suggest that the direct contribution of biocrusts were primary. Our results showed that direct effects were mostly inseparable from indirect effects and appeared to change nearly in lockstep (Table 3). Our estimates of unique effects seem to suggest that the influence of texture is somewhat distinguishable from the influence of organic matter-bulk density, two effects that cannot be disentangled ($r = 0.46$, $P = 0.0400$). None of the effects can be distinguished from the effect of moss cover. This led us to hypothesize that moss cover strongly and rapidly induces the other effects (Fig. 6). If so, the *C* factor has a strong causal influence on the *K* factor and thus some indicators may be indicative of both factors (Fig. 6). This would also mean that the *K* factor is much more dynamic than commonly characterized, as evidenced by the significant decrease (21%) in soil erodibility with the development of biocrusts (increase of moss biomass) in another study by Gao et al. (2017).

How should our findings be applied in erosion modeling? Given that *C* and *K* factors effects were inseparable, and that moss cover (a *C* factor indicator) is likely the ultimate cause of the variation in both factors in our system, we suggest that the most practical means of applying our findings is to ensure that the effects of mosses and other biocrusts are always accounted for in calculation of the *C* factor, which is economical shortcut to obtain quality data used in erosion models. The biocrust influence may be as strong or stronger than other soil covering elements, but biocrusts may be somewhat cryptic and more difficult to detect and are commonly overlooked. If the effects of biocrusts on soil erodibility (*K* factor) also need to be accounted in the erosion models, the elements of the *K* factor should be recognized not as inherent, with the implication that they are slow to change, but as dynamic properties that can be altered by biocrusts within a few years. The best way to apply this knowledge is to ensure that *K* is estimated using data on texture, organic matter, and bulk density at the soil surface, contemporaneous with the period in which soil loss is being measured, rather than relying solely on surveys or other static data sources.

5. Conclusions

The developmental stage of biocrusts appeared to be one factor determining local water erosion. Moss cover is the best predictor of water erosion on the Loess Plateau, providing an economical shortcut to obtain quality data used in erosion models. There was a strong negative relationship between sediment concentration and moss cover. Well-developed biocrusts containing a high cover of mosses (> 35%) can nearly completely protect soil surfaces from water erosivity. Consequently, the linkage between biocrust development and water erosion is a threshold-based nonlinear function, and the quantitative relationship between soil loss and the stage of below this threshold is crucial to revise and establish a soil loss predicting model considering biocrusts. Biocrusts enhanced soil stability by their cover directly and by modifying soil properties indirectly. However, these mechanisms were not separable. Therefore, we suggest two ways to enhance soil loss prediction using the Revised Universal Soil Loss Equation: 1. Ensure that biocrust cover is taken into account in *C* factor calculation, 2. Treat *K* factors determinants such as texture, organic matter, and bulk density as dynamic and ensure that input data is from the period of time in which soil loss is being estimated.

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