



Revisiting classic water erosion models in drylands: The strong impact of biological soil crusts

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ARTICLE INFO

Article history:

Received 15 February 2008

Received in revised form 24 April 2008

Accepted 15 May 2008

Available online 11 June 2008

Keywords:

Arid and semi-arid regions

Cryptobiotic soil crusts

Cryptogams

Cyanobacteria

Erosion modeling

Universal soil loss equation

ABSTRACT

Soil erosion and subsequent degradation has been a contributor to societal collapse in the past and is one of the major expressions of desertification in arid regions. The revised universal soil loss equation (RUSLE) models soil lost to water erosion as a function of climate erosivity (the degree to which rainfall can result in erosion), topography, soil erodibility, and land use/management. The soil erodibility factor (K) is primarily based upon inherent soil properties (those which change slowly or not at all) such as soil texture and organic matter content, while the cover/management factor (C) is based on several parameters including biological soil crust (BSC) cover. We examined the effect of two more precise indicators of BSC development, chlorophyll a and exopolysaccharides (EPS), upon soil stability, which is closely inversely related to soil loss in an erosion event. To examine the relative influence of these elements of the C factor to the K factor, we conducted our investigation across eight strongly differing soils in the 0.8 million ha Grand Staircase-Escalante National Monument. We found that within every soil group, chlorophyll a was a moderate to excellent predictor of soil stability ($R^2 = 0.21\text{--}0.75$), and consistently better than EPS. Using a simple structural equation model, we explained over half of the variance in soil stability and determined that the direct effect of chlorophyll a was $3\times$ more important than soil group in determining soil stability. Our results suggest that, holding the intensity of erosive forces constant, the acceleration or reduction of soil erosion in arid landscapes will primarily be an outcome of management practices. This is because the factor which is most influential to soil erosion, BSC development, is also among the most manageable, implying that water erosion in drylands has a solution.

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1. Introduction

Accelerated soil erosion is among the most pressing of environmental problems, resulting in degradation of ecosystem function (Ludwig and Tongway, 2000; Ludwig et al., 2006), decreased productivity and sustainability of agriculture (Diamond, 2005), and displacement of human populations (Opie, 2000). Jared Diamond's "Collapse: how societies choose to succeed or fail" examines five well known examples of past societal collapse, all of which are associated to some degree with soil erosion (Diamond, 2005). In ecosystem ecology, "leakiness" refers to an ecosystem's ability or inability to retain resources such as soil, nutrients and water and can be used as a negative index of ecosystem health

(Ludwig and Tongway, 2000; Ludwig et al., 2006). In desertification science, loss of soil stability and subsequent erosion is considered a major cause and symptom of desertification processes in the world's dry rangelands (Pierson, 2000). Plant canopy cover is low in dryland ecosystems and the soil surface is often exposed, thus, a major driver of ecosystem leakiness with regard to soil resources is the resistance of the soil surface to erosive forces. In drylands, soil particles may be aggregated abiotically by clays (Eldridge and Leys, 2003) or cementing chemicals such as CaCO_3 or gypsum (Rillig et al., 2003). Additionally, interacting biotic agents including vascular plants, and arbuscular mycorrhizal fungi (AMF) may account for a substantial proportion of soil aggregate stability (Tisdale and Oades, 1982) in most systems. But many drylands are distinctly different than other ecosystems in that there is a strong influence of biological soil crusts (BSCs), a complex community typically dominated by cyanobacteria, mosses and lichens, on soil stability (Warren, 2003; Chaudhary et al., in press). Because drylands account for $\sim 40\%$ of the terrestrial surface, and are the home to one-third of the Earth's population (Millenium Ecosystem

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Assessment, 2005), it is of global importance to understand the resistance to accelerated soil erosion and desertification. This need is reflected in an increasing number of calls for assessment and monitoring of the health of drylands used for livestock production to explicitly include information on soil aggregate stability (Tongway, 1994; Pyke et al., 2002; Herrick et al., 2005).

While wind erosion models (e.g. Webb et al., 2006) have primarily focused on drylands because they are known to be the world's primary dust sources (McTainsh and Strong, 2007), water erosion models were initially developed in cropping systems. The universal soil loss equation (USLE) was an early water erosion model, which has been repeatedly revisited (e.g. revised universal soil loss equation [RUSLE]) and has conceptually influenced most subsequent water erosion modeling activities (Croke and Nethery, 2006). RUSLE predicts the amount of soil lost due to water erosion as a function of climate erosivity (the degree to which erosive forces can result in erosion, influenced by amount and intensity of rainfall, and raindrop size), topography, soil erodibility, and cover/management (Renard et al., 1997). The soil erodibility factor (K) is primarily based upon inherent abiotic soil properties (e.g. soil texture), while the cover/management factor (C) is based on several parameters including BSC cover (Renard et al., 1997). The C factor expressed the ratio of soil erosion from a site with given cover to that of an otherwise identical bare site; it reaches zero when cover = 100% (Renard et al., 1997).

Grand Staircase-Escalante National Monument (GSENM) is a semi-arid region covering ~800,000 ha, containing diverse soils (USDA-NRCS, 2005) and high potential for colonization by BSCs (Bowker et al., 2006) making it an ideal location to study the controls on soil stability in arid regions. Biological soil crusts are ubiquitous in this region and other arid and semi-arid regions, and one of their defining characteristics is their aggregation of mineral soil into a cohesive horizontal macroaggregate at the soil surface (Belnap and Lange, 2003). This is primarily due to production of exopolysaccharides (EPS) which glue together fine soil particles (<65 μm), physically weaving soil particles together by filamentous cyanobacteria, and armoring of surfaces by mosses and lichens (Belnap and Gardner, 1993; Mazor et al., 1996). Over 50 studies from five continents provide quantitative evidence that BSCs protect soils against erosion by increasing the threshold friction velocity and decreasing sediment yield due to splash erosion or shear forces (reviewed in Belnap and Lange, 2003). The causal influence that BSCs have upon soil stability is clearly demonstrated by studies which remove (Belnap and Gillette, 1997), chemically kill (Williams et al., 1995), or add (Faust, 1970) BSCs in the field, experimentally create artificial BSCs in the laboratory (Hu et al., 2004), or apply causal modeling techniques (Chaudhary et al., in press).

To determine how important BSCs are to aggregate stability compared to the RUSLE K factor in semi-arid rangelands, we sampled a wide range of BSCs in various stages of development in eight contrasting soil groups representing the range of soil gradients found in GSENM. We compared the relative efficacy of two indicators of BSC development and activity, chlorophyll a and EPS, in predicting soil stability indicators (relevant to the C factor), and compared their influence to inherent soil physico-chemical properties (relevant to the K factor). Chlorophyll a has traditionally been used as a total biomass indicator for cyanobacterially dominated communities such as BSCs (Belnap and Gardner, 1993). Exopolysaccharide exudates are known to be one mechanism by which BSCs aggregate soil (Mazor et al., 1996). We addressed three questions in our study area: (1) How important is BSC development-activity (a C -factor component) compared to the K factor?, (2) Which indicator of BSC development-activity, chlorophyll a or EPS, is the best indicator of soil stability? and (3) How does the relationship between BSCs and soil stability change among very different soils? Because the C factor is alterable by

management practices, our study estimates the degree to which management can improve or worsen soil erosion processes in dryland regions by modifying BSCs.

2. Materials and methods

2.1. Study site and design

In 2001–2002, we sampled 43 sites in GSENM, southern Utah (USA). Long term mean annual precipitation at two nearby cities is 34.3 cm in Kanab, Utah, and 16.4 cm in Page, Arizona. In 2001 Kanab received 9% more precipitation than average, while Page received 12% less than average. In contrast 2002 was a drought year, with Kanab receiving 24% less precipitation than average, and Page receiving 38% less than average. Our sampling represented eight general soil groups developed and described in Bowker et al. (2006) and Bowker and Belnap (2008). This soil grouping system groups together over 200 soil map units over 50 ecological site types in GSENM (USDA-NRCS, 2005) based upon characteristics that are known to be important to BSC development or activity (e.g. texture, gypsum content, parent material, carbonate content, and shrink-swell potential). The soil groups are bentonitic fine soils, non-bentonitic fine soils, calcareous sandy soils, non-calcareous sandy soils, siliceous sandy soils, Kaiparowits-derived soils (an unusual sandstone parent material which develops into highly eroded badlands), limestone-derived soils, and gypsiferous soils.

At each site, we simultaneously measured surface soil stability using a field-based soil stability test kit, and two indices of "BSC development-activity": chlorophyll a and EPS (when mass of sampled soil material permitted). These variables were measured on soil surfaces lacking mosses and lichens and usually colonized by cyanobacteria to some extent. We subjectively selected patches of surface soil in varying degrees of cyanobacterial development ranging from visibly absent to those containing high biomass and late seral cyanobacterial species. Many samples with no visible crusting did in fact have some cyanobacteria, but we also recovered samples with no detectable cyanobacteria.

2.2. Soil aggregate stability

For all measures of soil aggregate stability we used a field-based test developed by Herrick et al. (2001). This method subjects dry soil peds to a timed water immersion and wet sieving regimen and assesses cohesion using an ordinal scale ranging from 0 to 6. We chose this method because it is rapidly being accepted as a useful, fast field assessment and monitoring tool (Pyke et al., 2002; Herrick et al., 2005).

We used different sampling techniques in the two years. In 2001, we sampled opportunistically while conducting more extensive surveys for Bowker et al. (2006). We conducted the soil stability test on a ped of soil, and collected an adjacent visually similar ped for chlorophyll a and exopolysaccharide analysis. Because this technique yielded only a small amount of soil for each sample, samples within a site that received the same soil stability test score were pooled into a composite sample. In 2002, we improved our sampling method. For each sample, we selected a relatively homogenous soil surface of ~16 cm² ($n = 360$). We subsampled three representative peds from this area and measured their stability (detailed below; Herrick et al., 2001). To create an average value for the 16 cm² area, we squared the soil stability test data and averaged the resulting values. This transformation was necessary because it linearizes the curvilinear relationship of data from the field soil stability test kit to percentage of stable aggregates, a laboratory measurement. Linearization of the measurement scale

of the field soil stability test allows the computation of a mean value of replicate measurements and a closer approximation of a continuous measurement of soil aggregate stability. We pooled all of the resultant data into a single data set of 385 samples with both soil stability test and chlorophyll *a* data; of these, 254 samples also had exopolysaccharide data.

2.3. “BSC development–activity” estimation

2.3.1. Chlorophyll *a*

We measured concentrations of chlorophyll *a* using quantitative and qualitative high performance liquid chromatography (HPLC) analysis according to a slightly modified version of the method of Karsten and Garcia-Pichel (1996), detailed in Bowker et al. (2002). These data have traditionally been used as a total biomass proxy for cyanobacterially dominated communities such as BSCs (Belnap and Gardner, 1993).

2.3.2. Exopolysaccharides

To extract EPS from soils we used a method similar to Mazor et al. (1996). Soil samples were hot water extracted and separated from soil particles by two cycles of centrifugation and isolation of the supernatant. Polysaccharides were precipitated from the supernatant, and concentrated *via* centrifugation. After drying, samples were reconstituted and analyzed using a Hewlett Packard 8452A Diode-Array Spectrophotometer (Palo Alto, California) at 480 nm, 486 nm, and 490 nm (Dubois et al., 1956).

2.4. Modeling the relationship between “BSC development–activity” and the soil stability test within soil groups

Some data transformations were necessary prior to modeling. First, soil stability was related to chlorophyll *a* curvilinearly in most cases. We might expect this on *a priori* grounds, because at some point soil stability should reach an asymptote with regards to addition of cyanobacterial biomass. To linearize this we used power transformations: the soil stability test data were squared (see above), while the chlorophyll *a* data were square root transformed. This improved linearity in all cases. Second, because the soil stability test reaches its maximum at “6”, which was well before chlorophyll *a* reaches its maximum in siliceous sandy soils, an artificial ceiling is created. To correct this problem in these soils, we found the chlorophyll *a* value beyond which the soil stability test was always “6” (0.038 mg g⁻¹), and removed points with higher chlorophyll *a* values. This resulted in the removal of only two points. We followed the same procedure modeling exopolysaccharide data, except that there was no need to correct the artificial ceiling problem. Linear regressions were adequate in all cases.

2.5. Interannual variation in the relationship between “BSC development–activity” and the soil stability test

In order to estimate the sensitivity of these relationships to interannual variation, we separated the data collected in the two years. We created regressions of the relationships between chlorophyll *a* or EPS and soil stability test results for 2001 data by soil group. Then using the chlorophyll *a* or exopolysaccharide data from 2002 we applied the regression equation to generate estimates of soil stability value in 2002 based upon the 2001 regression. We then compared the predicted and observed soil stability test values for 2002, and used the R^2 and slope as measures of agreement; a “perfect model” would have both slope and R^2 of 1. We repeated this exercise in reverse, using 2002 data to generate regression equations and 2001 data to validate them. Because only one non-zero chlorophyll *a* datapoint existed in the 2002 data for

bentonitic fine soils, we omitted this soil group from the analysis. Exopolysaccharide data were available for both years in only three of the soil groups; therefore the others could not be subjected to this analysis.

2.6. Modeling the relationship between “BSC development–activity” and the soil stability test among all soil groups

We used a simple structural equation model (SEM) to determine the relative importance of soil group and BSC development–activity in determining soil stability. SEM is ideal in this case because it allows: (1) a flexible combination of categorical and continuous predictors, (2) correlated predictors, (3) stronger causal inference from non-experimental data through the study of direct and indirect effects, and (4) the option of a combination of linear and curvilinear relationships. We began the modeling process with the simple *a priori* model that soil group may influence soil stability directly (e.g. due to clay content, carbonates and other abiotic factors) or indirectly *via* chlorophyll *a* (e.g. some soil groups may generally support greater BSC development). Chlorophyll *a* was expected to have a direct influence upon soil stability (e.g. chlorophyll *a* indicates greater cyanobacterial biomass, which has soil stabilizing features). We then formulated the model in AMOS 5.0 (2003 SPSS Inc.) using a composite variable in order to include the categorical predictor “soil group” (Grace, 2006). We considered modeling the chlorophyll *a* → soil stability relationship as a second order polynomial, but found that a linear model was adequate. Once the model was constructed, we used a maximum likelihood estimation technique to parameterize the model, and conducted goodness-of-fit tests (χ^2 test, Joreskog’s goodness-of-fit [GFI] index). In the χ^2 test, the *P* value indicates the probability that a model fits the data; thus, contrary to most tests, a high *P* value is desired. Other fit indices are interpreted using rules-of-thumb: $\chi^2/\text{d.f.} < 2$ and Joreskog’s GFI > 0.95 are considered to indicate a good fit (Grace, 2006).

3. Results

3.1. Relationship of chlorophyll *a* and EPS to soil stability within soil groups

In general, chlorophyll *a* was very strongly related to soil stability values (Fig. 1), and was a better predictor than EPS in all but one case. Chlorophyll *a* was a particularly strong predictor, explaining greater than half of the variance in soil stability test values, for bentonitic fine soils ($R^2 = 0.67$; Fig. 1a), non-calcareous sandy soils ($R^2 = 0.75$; Fig. 1b), Kaiparowits-derived soils ($R^2 = 0.63$; Fig. 1e), and siliceous sandy soils ($R^2 = 0.52$; Fig. 1h). In contrast, EPS was extremely inconsistently related to the soil stability test in these particular soils ($R^2 = 0.00, 0.00, 0.70, 0.35$, respectively, data not shown). The results for the other soil groups were more similar when the relationships between soil stability and chlorophyll and between soil stability and EPS were compared. In all cases, chlorophyll *a* performed better than EPS: in calcareous sandy soils, chlorophyll *a* $R^2 = 0.49$, EPS $R^2 = 0.45$; in non-bentonitic fine soils, chlorophyll *a* $R^2 = 0.49$, EPS $R^2 = 0.39$; in gypsiferous soils, chlorophyll *a* $R^2 = 0.33$, EPS $R^2 = 0.29$; and in limestone-derived soils, chlorophyll *a* $R^2 = 0.21$, EPS $R^2 = 0.11$.

3.2. Relationship of BSC development–activity to soil stability among years

Regressions generated from crust development–activity and soil stability data from one year predicted the other years soil stability data extremely variably ($R^2 = 0.01–0.89$, slope = 0.3–2.3; Table 1). In the three soil groups in which EPS could be evaluated in this way,

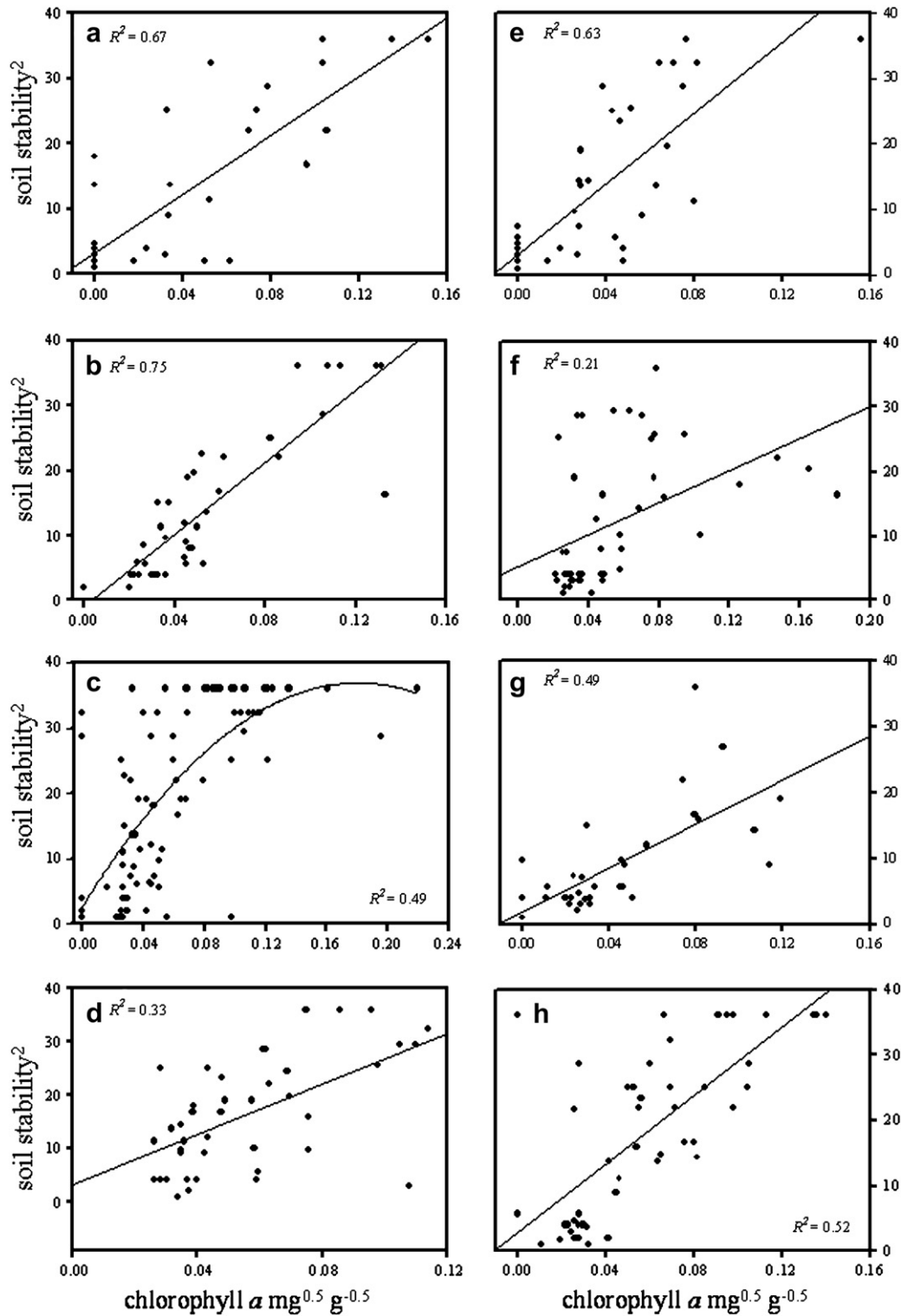


Fig. 1. Relationship between the soil stability test and chlorophyll *a* on eight soil groups (*sensu* Bowker et al., 2006; Bowker and Belnap, 2008). (a) Bentonitic fine soils, (b) non-calcareous sandy soils, (c) calcareous sandy soils, (d) gypsiferous soils, (e) Kaiparowits-derived soils, (f) limestone-derived soils, (g) non-bentonitic fine soils, and (h) siliceous sandy soils. In (f) $P = 0.001$, otherwise $P < 0.0001$ in all other cases.

EPS generally performed similarly to chlorophyll *a*. In all but one case, R^2 for the polysaccharide and corresponding chlorophyll *a* regressions were similar (the exception is an R^2 of 0.01 for the 2002 → 2001 exopolysaccharide regression). Neither chlorophyll *a* nor EPS performed appears to be less sensitive to interannual variability.

3.3. Relationship of chlorophyll *a* to soil stability among all soil groups

Our structural equation model had satisfactory fit criteria ($\chi^2 = 16.0$, d.f. = 18, $P = 0.60$; χ^2 d.f.⁻¹ = 0.89; Joreskog's goodness-of-fit index = 0.99), indicating that the causal scenario advanced in

Table 1
Interannual reliability of chlorophyll *a* and exopolysaccharides as indicators of soil stability measured using a soil stability test

Soil group	Chlorophyll <i>a</i>				Exopolysaccharides			
	2001		2002		2001		2002	
	R ²	Slope	R ²	Slope	R ²	Slope	R ²	Slope
Bentonitic fine	–	–	–	–	–	–	–	–
Calcareous sandstone-derived	0.38	1.47	0.40	0.58	0.36	0.78	0.52	1.29
Gypsiferous	0.26	1.06	0.48	0.67	–	–	–	–
Kaiparowits-derived	0.88	1.98	0.49	0.50	–	–	–	–
Limestone-derived	0.28	1.70	0.17	0.58	0.22	0.30	0.01	0.33
Non-bentonitic fine	0.54	2.34	0.57	0.42	–	–	–	–
Non-calcareous sandstone-derived	0.57	0.84	0.89	1.18	–	–	–	–
Siliceous sandstone-derived	0.21	0.69	0.55	1.04	0.26	0.77	0.49	0.88

Columns marked 2001 denote regression equations derived from 2001 data and tested with 2002 data, columns marked 2002 indicate regression equations derived from 2002 data and tested with 2001 data. Both R² and slope of each regression are listed; a theoretical "perfect" correspondence among years would be indicated by an R² and slope of 1. – = No regression was attempted, see text for explanation.

the *a priori* model is consistent with the data. In an SEM, a small probability value associated with the χ^2 test indicates a lack of fit, therefore a high *P* value is desired.

Our model explained over half of the variance in soil stability (Fig. 2). The direct effect of chlorophyll *a* upon soil stability ($r=0.67$) was more than three times that of soil group ($r=0.21$). Even when indirect effects of soil group *via* chlorophyll *a* are accounted for, the total effect of soil group ($r=0.38$) is considerably less than that of chlorophyll *a* ($r=0.67$; Fig. 2).

4. Discussion

4.1. Indicators of the soil stabilization function of BSCs

Our data represent the most comprehensive examination of BSC-based soil stability indicators to date, because they were collected across two years and eight very different soil groups (Bowker et al., 2006). This soil grouping system has previously been shown to effectively summarize 19 different chemical and physical

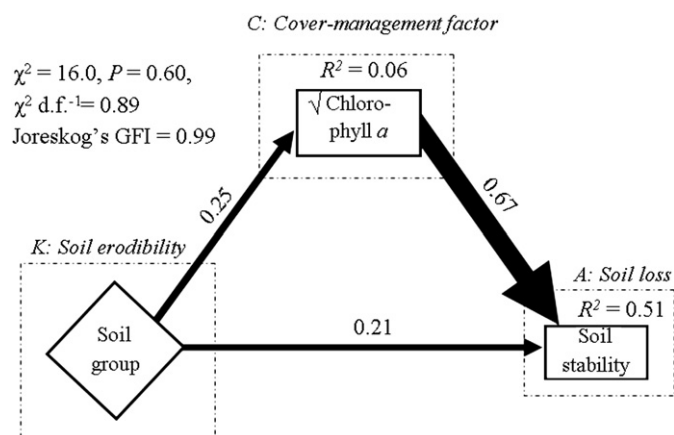


Fig. 2. A structural equation model demonstrating a much greater effect of BSC development-activity ($\sqrt{\text{chlorophyll } a}$) compared to soil physico-chemical properties (soil group) upon soil stability (soil stability test²). Dashed boxes and associated text indicate components of the revised universal soil loss equation that are strongly conceptually linked to the variables modeled here. Rectangles represent measured variables. The diamond represents a composite variable, which in this case simply allows the inclusion of a multi-level categorical variable. Arrows represent hypothetical causal relationships tested by the model. Adjacent path coefficients (equivalent to correlation coefficients or regression weights) estimate the strength of the relationship, and arrow width is proportional to the coefficient. Goodness-of-fit test statistics indicate a very strong fit of the model to the data (see text).

soil properties (Bowker et al., 2006). Additionally, approximately one-third of BSC community structure and two-thirds of BSC species richness and evenness can be explained by the soil groupings (Bowker and Belnap, 2008). Another recent work examined the relationship between an ordinal descriptor of BSC development and a modified soil stability test in five ecosite types (Belnap et al., *in press*) indicating a very strong relationship ($R^2 = 0.61$). In our data, chlorophyll *a* was a better indicator of the soil stabilizing functions of BSCs than total EPS. Total BSC cover has also been used successfully as a soil stability predictor (Chaudhary et al., *in press*).

Cyanobacteria aggregate soils both chemically and physically. Exopolysaccharide production is a key chemical mechanism, as charged surfaces of exopolysaccharides have a bonding affinity with clays and calcium compounds such as gypsum and calcium carbonate (Belnap and Gardner, 1993). Exopolysaccharides are transient compounds which are particularly important in the creation of microaggregates (Tisdale and Oades, 1982). In contrast, biological fibers such as roots, hyphae and cyanobacterial filaments and their sheaths create macroaggregates (Tisdale and Oades, 1982), which are particularly important for soil stabilization (Barthès and Roose, 2002). Total exopolysaccharide content of soil may be only indirectly related to physical mechanisms of macro-aggregation. Using wind tunnel experiments with artificial BSCs, McKenna Neuman et al. (1996) and Hu et al. (2004) demonstrated that it is primarily the larger filamentous cyanobacteria that confer resistance to the shear forces of wind erosion, suggesting that the physical enmeshment of soil particles is more important than chemical mechanisms. We might expect the same to be true of the shear forces applied by water flow.

The chemical microaggregation effects are likely primarily determined by the surface area of EPS sheaths, whereas the EPS assay measures the total amount of EPS. The physical macro-aggregation properties of cyanobacteria are likely strongly influenced by total sheath length per volume of soil, which is probably well correlated with sheath surface area. The total amount of EPS is also influenced by sheath thickness which probably does not greatly enhance micro- or macroaggregation properties. Thus we might hypothesize that chlorophyll *a* is a better assay of sheath length and surface area because it is not influenced by sheath thickness.

When resources permit, comprehensive studies of the effect of BSCs on soil stability would incorporate both EPS, chlorophyll *a* as indicators of BSC development-activity; however when only one variable can be measured to assess the cyanobacterial contribution to soil stability, our data suggest that chlorophyll *a* is the superior measurement. Combination of such information on the cyanobacterial contribution may also be complementary to cover data of moss and lichen BSC components, resulting in even better prediction of soil stability. At the present time, the best solution for the interannual variability of chlorophyll *a* is to pool data collected from multiple years to create generalized conversion equations from chlorophyll or EPS to water stable aggregation.

4.2. Comparing the C and K factor in semi-arid rangelands

The RUSLE states that

$$A = RKLSCP,$$

where *A* = computed soil loss, *R* = rainfall-runoff erosivity factor, *K* = soil erodibility, *L* = slope length factor, *S* = slope steepness factor, *C* = cover-management factor, and *P* = supporting practices factor. The *R* factor is primarily determined by the amount and intensity of rainfall. The *L* and *S* factors describe the steepness and length of slopes, and thus modify the erosivity of rainfall-runoff.

The P factor describes management practices such as conservation tillage which tend to increase infiltration and reduce runoff. This factor is irrelevant in our case. In our data, we have standardized the erosivity and all of its modifying factors (i.e. the erosion event is timed water immersion and wet sieving of approximately equal erosivity) in an experimental setting; thus, R , L , or S factors are held constant. We are left with this simplified equation to predict soil erosion:

$$A = KC.$$

Because the soil stability test approximates a measure of percentage of water stable aggregates (Herrick et al., 2001), which in turn has been experimentally demonstrated to be very closely related to soil loss ($R^2 = 0.81$; Barthès and Roose, 2002), we can also state that

$$\text{Soil stability test} \approx KC.$$

K describes inherent properties of soil which influence soil erodibility, including texture, structure, organic matter and salts. Soils high in silts are most erodible, while organic matter and salts may reduce erodibility (Caravaca et al., 2001). When applied to rangelands, C traditionally describes plant canopy cover, ground cover (including BSCs), and surface roughness (also partially determined by BSCs in many rangelands). This may be an adequate approach when BSCs are primarily composed of mosses and lichens, which are clearly visible and easily described using percent cover methods. However, in a region where BSCs are dominated by sometimes cryptic cyanobacteria, visual estimates of BSC cover such as those used in RUSLE may not adequately characterize BSC development–activity because apparently bare ground may actually be colonized by the nearly ubiquitous cyanobacteria (Belnap and Gardner, 1993). One possible consequence of underestimating or poorly characterizing the cyanobacteria is overestimation of the C factor, which approaches zero when cover of plants, rocks, BSCs and other protective agents is 100%.

To address the same conceptual information with more precision, we compared a biochemical assay which measures BSC development–activity, and compared its predictive power to the K factor. We found that BSC development–activity, although apparently only a part of the C factor, explained nearly half of the variance in soil stability, and influenced soil stability much more than the K factor. The K factor has direct influences upon soil stability, and also influences the C factor (i.e. the soil physico-chemical properties influence potential vegetation and BSC development–activity), but its total influence is only about half that of BSC development–activity indicators which are only a portion of the C factor.

These results compare well with another study in the same study region that focused on arbuscular mycorrhizal fungi (Fig. 3; Chaudhary et al., in press). Our SEM estimated a path coefficient of 0.67 describing the effect of chlorophyll a upon soil stability, whereas Chaudhary et al. (in press) estimated a path coefficient of 0.61 for the effect of cyanobacterially dominated BSC cover upon soil stability (Fig. 3). Both models estimated the same path coefficient for the effect of soil group (0.21; Figs. 2 and 3). The parallels between the two studies are striking, and both contrast with a third study in a mesic region (Jastrow et al., 1998; Miller and Jastrow, 2000). The Jastrow et al. (1998) model indicates a pervasive influence of vascular plants upon soil stability in a restored prairie, whereas the combined findings of the present study and Chaudhary et al. (in press) strongly suggest that BSCs are the most important surface soil stabilizing agent in drylands, emphasizing that determination of soil stability in arid regions is fundamentally different.

What accounts for the remaining 49% of variance in soil stability that is not explained by our model (Fig. 2)? A partial answer can be found in the Chaudhary et al. (in press) model (Fig. 3). It measures

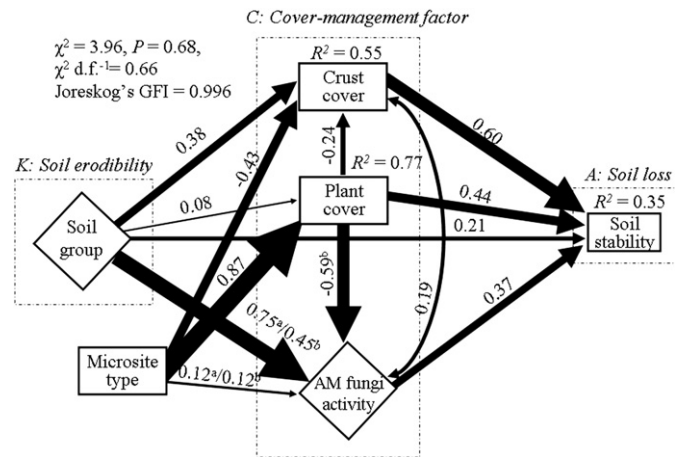


Fig. 3. A structural equation model (modified from Chaudhary et al., in press) demonstrating a much greater effect of variables related to the C factor (crust cover, plant cover, and AM fungal development–activity) compared a variable related to the K factor (soil group) upon soil stability (soil stability test). Dashed boxes and associated text indicate components of the revised universal soil loss equation that are strongly conceptually linked to the variables modeled here. Rectangles represent measured variables. The diamonds represent composite variables, which allow the inclusion of categorical variables, or the pooling of the effects of multiple measured variables. Single headed arrows represent hypothetical causal relationships tested by the model. Double headed arrows represent an unresolved covariance. Adjacent path coefficients (equivalent to correlation coefficients or regression weights) estimate the strength of the relationship, and arrow width is proportional to the coefficient. Goodness-of-fit test statistics indicate a very strong fit of the model to the data (see text).

an additional portion of the C factor, plant cover, and demonstrates that it is the second most influential variable (path coefficient = 0.41), and directly explains about 8% more variance in the soil stability test (see McCune and Grace, 2002 for the R^2 formula in SEM). Indicators of arbuscular mycorrhizal fungi are influenced strongly by plants and can explain an additional 13% of the variance. The remainder of the variance may be partially explained by variability of soil properties within soil groups and measurement error.

4.3. Implications for management and erosion modeling

While inherent properties of soils, such as texture, chemistry, and organic matter content are very important in determination of soil erodibility (i.e. the K factor), they cannot be economically altered on large scales to prevent erosion. Likewise erosivity of wind and water, and topography which modulates erosivity, cannot be managed. However, we have demonstrated here that the C factor (particularly BSC development–activity) can be considerably more influential than the K factor, and unlike the other factors are dynamic and manageable. The potential development–activity of BSCs varies spatially (Bowker et al., 2006), but departure from potential is largely a result of past and present management practices. The positive aspects of these findings are that soil erosion may often be ameliorated in drylands by management activities which promote the cover and development of BSCs, and other contributors to the C factor.

A landmark paper by Tisdale and Oades (1982) elucidated the basic mechanisms by which biota and their organic residues strongly influence soil aggregation, and revolutionized thinking about this topic. Because this study was based primarily upon studies in closed-canopy mesic areas, BSCs were not mentioned. We can say with a high degree of confidence that in the semi-arid regions that we have studied, the mechanisms proposed by Tisdale and Oades (1982) are generally consistent with our observations; however it is BSCs, *not plants*, which are the single most important

stabilizer of the soil surface. A large number of studies conducted around the world provide support that this may be a general principle in the world's drylands and other systems where BSCs attain high cover (Van den Anker et al., 1985 [Netherlands]; Belnap and Gardner, 1993 [USA]; Mazor et al., 1996 [Israel]; Marticorena et al., 1997 [USA]; Eldridge and Leys, 2003 [Australia]; Maxwell and McKenna Neuman, 1994 [Canada]; Belnap and Gillette, 1997 [USA]; Williams et al., 1995 [USA]; Hu et al., 2004 [China]; Wang et al., 2006 [China]; Knapen et al., 2007 [Belgium]; see Belnap and Lange, 2003 for additional references). Extensions of RUSLE and other water erosion models to uncropped drylands would be well informed by high quality information describing BSC development-activity. Because the slope of the relationship between chlorophyll *a* and soil stability differs by soil type, it may be prudent to account for this interaction in future modeling attempts and erosion prediction.

Recently, a simple visual index of BSC development (which quickly accounts for cover and rough community composition) has been proposed which is strongly correlated to chlorophyll *a* and exopolysaccharides ($R^2 = 0.68\text{--}0.81$; Belnap et al., in press). This may represent a more economical shortcut to obtain quality data on cyanobacterial BSC development that could be used in erosion models. In addition, remote sensing techniques of BSC development and coarse taxonomic composition are becoming increasingly refined (Chen et al., 2005). The spectral signatures of various BSC organisms are strongly related to their chlorophyll *a* content (and other pigments), making it feasible to obtain a reasonable estimate of soil chlorophyll *a* content from remotely sensed imagery (Karnieli et al., 1999). Incorporation of these information sources is highly likely to improve the prediction of soil erosion in arid and semi-arid rangelands using RUSLE and other erosion models, and even enable the mapping of these dynamic processes.

Acknowledgements

Sasha Reed, Bernadette Graham, and Patricia Ortiz developed methodology and conducted pigment and exopolysaccharide extractions. Drs. Mark Miller (U.S. Geological Survey) and Kent Sutcliffe (Natural Resources Conservation Service) provided valuable discussion and insight. Kate Kurtz and Jenn Brundage assisted with field sampling. Drs. Sasha Reed, Nichole Barger, David Eldridge and Jim Grace helped us improve earlier drafts. Funding was provided by BLM Grand Staircase-Escalante National Monument. The use of trade, product, or firm names in this publication is for descriptive purposes only and does not imply endorsement by the U.S. Government.

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