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Successional stage of biological soil crusts: an accurate indicator of ecohydrological condition

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ABSTRACT

Biological soil crusts are a key component of many dryland ecosystems. Following disturbance, biological soil crusts will recover in stages. Recently, a simple classification of these stages has been developed, largely on the basis of external features of the crusts, which reflects their level of development (LOD). The classification system has six LOD classes, from low (1) to high (6). To determine whether the LOD of a crust is related to its ecohydrological function, we used rainfall simulation to evaluate differences in infiltration, runoff, and erosion among crusts in the various LODs, across a range of soil depths and with different wetting pre-treatments. We found large differences between the lowest and highest LODs, with runoff and erosion being greatest from the lowest LOD. Under dry antecedent conditions, about 50% of the water applied ran off the lowest LOD plots, whereas less than 10% ran off the plots of the two highest LODs. Similarly, sediment loss was 400 g m^{-2} from the lowest LOD and almost zero from the higher LODs. We scaled up the results from these simulations using the Rangeland Hydrology and Erosion Model. Modelling results indicate that erosion increases dramatically as slope length and gradient increase, especially beyond the threshold values of 10 m for slope length and 10% for slope gradient. Our findings confirm that the LOD classification is a quick, easy, nondestructive, and accurate index of hydrological condition and should be incorporated in field and modelling assessments of ecosystem health. Published in 2012. This article is a U.S. Government work and is in the public domain in the USA.

KEY WORDS runoff; infiltration; erosion; Colorado Plateau; RHEM; desert; dryland hydrologic cycles

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INTRODUCTION

Biological soil crusts, dominated by lichens, mosses, cyanobacteria, and microfungi, are commonly found in dryland regions. Their extent and degree of development have an important influence on ecosystem structure and processes, including nutrient cycling, soil stability, biodiversity, erosion, and runoff (Belnap and Lange, 2003). The influence of biological soil crusts on soil hydrology and erosion has been studied in drylands across the globe, principally in North America, Israel, and Australia. This research has consistently demonstrated that biological soil crusts reduce erosion and that disturbance of the crust surfaces can dramatically increase erosion rates (Loope and Gifford, 1972; Eldridge and Kinnell, 1997; Eldridge, 1998; Barger *et al*., 2006). At the same time, the relationship between biological soil crusts and runoff and infiltration is complex: Their presence can increase, decrease, or have no effect on these processes (Eldridge, 2003; Warren, 2003). The successional stage, or level of development (LOD), of crusts appears to be one factor determining local hydrological response. As crusts mature, the biomass of cyanobacteria, mosses, and lichens increases – which, in turn, increases the aggregate stability, shear strength, and roughness of the soil surface (Belnap, 2003, 2006). A six-level classification of biological soil crusts was recently developed on the basis of crust LOD – which is determined through visual assessment of colour (light to dark), presence of mosses/lichens, and soil surface roughness (Belnap *et al*., 2008).

The questions our work is intended to answer are as follows: To what extent can one use the LOD classification to infer the soil infiltrability, runoff potential, and erosion potential of areas covered with biological soil crusts? And which aspects of the classification (e.g., soil surface roughness, organismal biomass) have the greatest influence on these hydrologic processes? For the study reported on in this paper, we used small-plot rainfall simulation to systematically determine the hydrological differences between crust-covered surfaces of different LOD classes, as defined in Belnap *et al*. (2008), across a range of soil depths and pre-wetting conditions. Further, we used the Rangeland Hydrology and Erosion Model (RHEM) (Nearing *et al*., 2011) to scale up our results from the plot to the hillslope scale and to better understand how these relationships may be affected by differences in rainfall and slope gradient.

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STUDY AREA AND METHODS

Study area

Our study area is a cool desert region within the Colorado Plateau, near the Island-in-the-Sky District of Canyonlands National Park in southeast Utah. The site is located about 30 km north of Moab, Utah, at an elevation of ~1800 m. The vegetation is dominated by *Pinus edulis* (Pinyon Pine) and *Juniperus osteosperma* (Utah Juniper). The soils are fine sandy loams and well drained, having formed from residuum, colluvium, and eolian material derived mainly from sandstone. They range in thickness from 20 to 80 cm. Depending on the thickness, they are classified as Lithic Ustic Torriorthents (Rizno Series) or Ustic Haplocalcids (Anasazi Series).

Methods

Plot characterization. We simulated rainfall on 83 experimental plots, each measuring 0·5 m^2 (71 × 71 cm) (Table I). On the basis of a visual assessment of the LOD of the crusts, each plot was assigned to one of the six classes defined by Belnap *et al.* (2008). The lowest class (1) is characterized by the lightest colour (indicating a low biomass of cyanobacteria), no lichens or mosses, and little if any surface roughness. The highest class (6) is characterized by the darkest colour, indicating high cyanobacterial biomass, cover of lichens and mosses, and surface roughness (resulting from the frost-heaving of soils held together by cyanobacteria, mosses, and lichens). The plots were selected to have close to 100% coverage of biological soil crusts and no other vegetation. Any litter that would disrupt water flow was removed. The percent slope ranged from 2% to 20% and averaged between 5% and 10%. Depth to bedrock was determined by probing with a steel rod in ten places around the perimeter of the plot; soil depths were found to range from 10 to over 80 cm (Figure 1).

To elucidate which of the LOD characteristics had the most influence on the hydrological variables to be measured, we examined and noted each plot's distinctive characteristics. We estimated average soil surface roughness by carefully following the contours of the soil surface at three locations across the plot with a 20-cm-long, solid-link chain; we then measured the linear distance of the soil surface covered by the chain (Saleh, 1993). We determined average soil surface strength with a hand-held penetrometer (QSA Supplies, Alexandria, VA, USA) at five locations around the perimeter of each plot. We measured soil surface aggregate stability at three locations around the perimeter of each plot, in accordance with the method of Herrick *et al.* (2001).

Chlorophyll $\underline{a}$ was used as an indicator of cyanobacterial biomass, and glucose as a measure of microbial exopolysaccharides (thus, an indirect measure of cyanobacterial and fungal biomass). Five samples – each a combination of eight subsamples from the plot perimeter – were collected from each plot. These were combined and ground. Chlorophyll $\underline{a}$ samples were measured with high-pressure liquid chromatography analysis after acetone extraction (Karsten and Garcia-Pichel, 1996). Peak areas were integrated from photodiode array data at 436 nm and compared with a commercially obtained standard. Exopolysaccharides are also critical in the stabilization of desert soil surfaces (Mazor *et al.*, 1996) and were used as an indicator of surface soil stability. After extraction, samples were analysed with a Hewlett-Packard 8452A Diode-Array Spectrophotometer (Palo Alto, CA, USA) at 480, 486, and 490 nm (Dubois *et al.*, 1956). A standard curve of glucose solutions was obtained by plotting glucose concentration versus absorbance. Results are expressed as glucose equivalents per gram of dried sample at the 480-nm setting.

Rainfall simulation. The pre-simulation protocol differed slightly from year to year. In 2004 and 2005, no pre-wetting was carried out. In 2006 and 2007, about 10 mm of water was applied to the plots before the rainfall simulations (in 2006, with an interval of 30 min between pre-wetting and rainfall simulation and in 2007, with an interval of 24 h—. The parameters measured were runoff, infiltration, and erosion. We ran one rainfall simulation per plot location.

A nozzle-type rainfall simulator was used to apply water for at least 30 min on paired plots. The VeeJet 80/100 nozzle, installed 2 m above the soil surface, was moved across the plots every 4 s with a hand-pulley system. The target application rate was around 115 mm h^{-1}, monitored via manually recording rain gauges near the corners and adjacent to the centre of each plot. The actual application rate ranged from 80 to 140 mm h^{-1}, depending on wind conditions and other variables. In most cases, it was between 110 and 125 mm h^{-1} (Figure 1).

A triangular gutter at the downslope end of each plot channelled the draining runoff into a collector, where the runoff volume was recorded every 60 s during the simulation. Samples for measuring sediment concentration were collected at 5-min intervals. In addition, any sediment that had accumulated on the runoff tray was collected at the

Table I. Number of rainfall simulation plots by level of development (LOD) class, under various wet antecedent conditions.

Antecedent condition	LOD class						Total
	LOD 1	LOD 2	LOD 3	LOD 4	LOD 5	LOD 6	
Dry (2004–2005)	4	8	2	8	2	12	38
30 min pre-wet (2006)	2	6	3	4	2	6	23
24 h pre-wet (2007)	6	2	2	4	4	4	22
Total	12	16	8	18	8	22	83

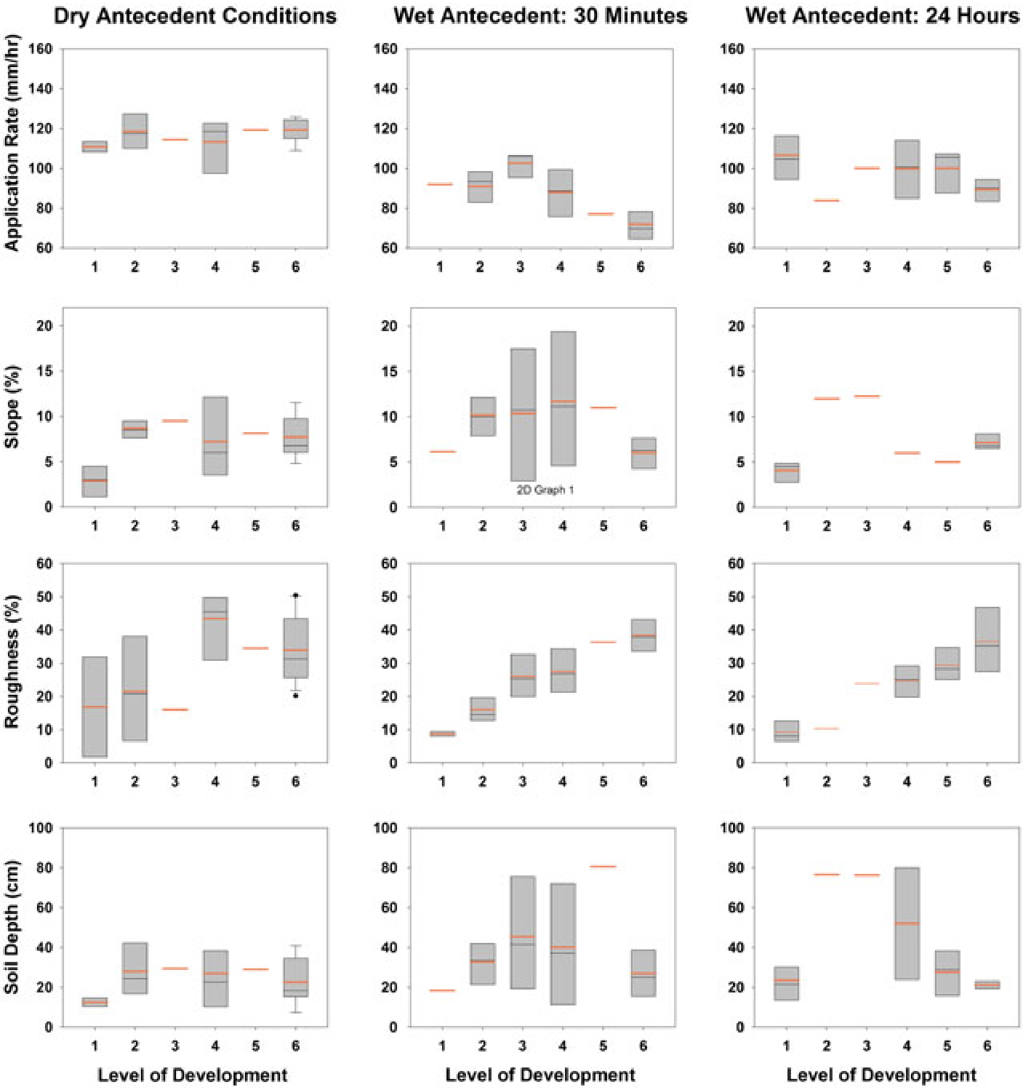

Figure 1. Box plots illustrating the range in application rates, slopes, roughness, and soil depths for each level of development class under each of the three antecedent wetness conditions. The ends of the boxes define the 25th and 75th percentiles, the black line is the median, error bars define the 10th and 90th percentiles, and the orange line is the mean.

end of the simulation and subsequently dried and weighed (Herrick *et al*., 2001).

Using the Rangeland Hydrology and Erosion Model to scale up plot data to the hillslope scale. Determining how plot-scale data from rainfall simulation can be translated to larger scales, such as the hillslope or small watershed, is challenging (Seyfried and Wilcox, 1995; Wilcox *et al*., 2003). One approach, and the one used in our study, is to simulate larger-scale conditions using a hydrologic model that has been parameterized and calibrated from the small-scale data. The RHEM is such a model; it is event-based and simulates runoff and erosion at the hillslope scale. It was developed especially for rangeland conditions (Nearing *et al*., 2011).

To simulate runoff and erosion from the small-plot infiltration experiments, 18 parameter sets were developed for RHEM, representing the six LOD classes of biological soil crusts at three soil wetness conditions. The parameterization process involved calibrating the model to cumulative runoff at 30 min, then to cumulative erosion at 30 min. For each condition, initial saturation and friction factors were set before calibration. The calibration parameters were hydraulic conductivity (K_e) for runoff, and soil erodibility (K_{ss}) for erosion.

RESULTS AND DISCUSSION

Infiltration and runoff

Infiltration and runoff were affected by both LOD and antecedent moisture conditions (Figure 2). On average, as LOD increased, infiltration increased and runoff decreased, but there was some overlap between LOD classes, as shown by the runoff box plots (Figure 2). The data seem to cluster into three main groups: LOD 1 (earliest stage) was distinct, having the lowest infiltration and most runoff; LODs 5 and 6 (the latest stages) had the greatest infiltration and lowest runoff; and LODs 2, 3, and 4 were similar and intermediate in infiltration and runoff.

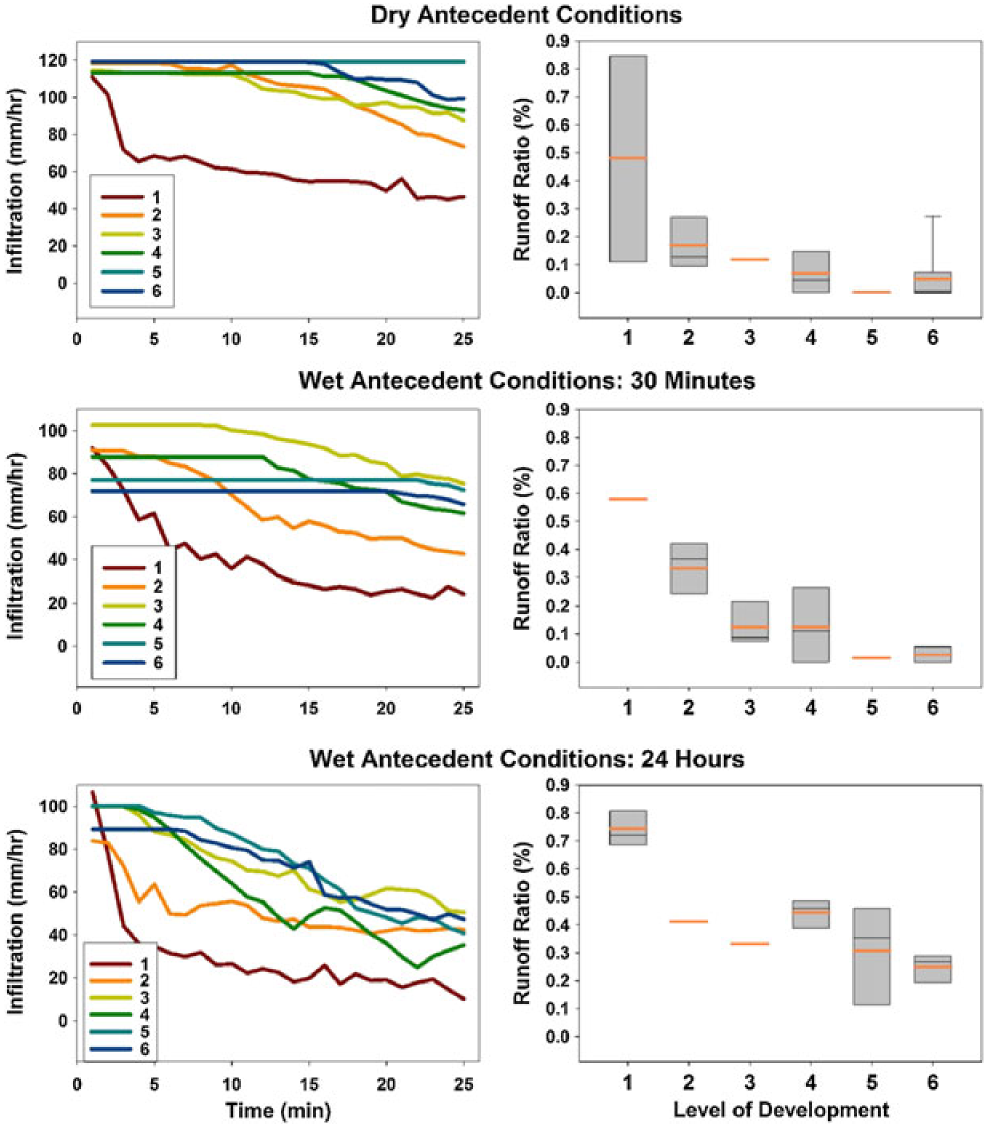

Figure 2. Infiltration rates (first column) and box plots of the percent runoff (second column) for each level of development class. The ends of the boxes define the 25th and 75th percentiles, the black line is the median, error bars define the 10th and 90th percentiles, and the orange line is the mean.

For the simulations carried out 24 h after pre-wetting, infiltration rates were lower and runoff was higher than under the other two antecedent conditions (Figure 2), except in the case of the LOD 1 plots: Under all three antecedent conditions, more than half the water applied for a period of 30 min ran off the LOD 1 plots (about 60% for the simulations carried out 24 h after pre-wetting). For the other LODs, the amount of runoff declined quite rapidly as LOD increased: 20–30% of the water ran off for the simulations carried out 24 h after pre-wetting.

Statistically significant correlations between distinctive plot characteristics and infiltration and runoff are presented in Table II. Most of these characteristics were consistently correlated with time to ponding, time to runoff, total runoff/water applied, infiltration rate, and wetting depth. Although LOD did not always show the highest R^2 value, it was still highly correlated with all the measured variables. In addition, it has the advantages of being nondestructive, the most rapid, and the most inexpensive of all the characterization measures taken. For example, soil surface

Table II. Statistically significant correlations of plot surface characteristics with hydrologic response on the plot ($p < 0.05$).

Characteristic	Time to ponding	Time to runoff	Total erosion	Total runoff	Final infiltration rate	Wetting depth
Level of development	0·94	0·83	−0·55	−0·70	0·65	0·64
Soil surface roughness	0·88	0·83	−0·6	−0·77	0·92	0·93
Soil surface shear strength	0·63			−0·52	0·64	−0·62
Soil aggregate stability	0·93	0·82		−0·69	0·83	0·88
Exopolysaccharides				−0·74	0·82	0·78
Cyanobacterial biomass	0·71	0·71	−0·64	−0·84	0·84	0·86

roughness showed a high correlation with ponding, runoff, and infiltration measures, because as roughness increases, water travels greater distances and its velocity is slowed, allowing more time for infiltration. The disadvantage of using roughness as a measure is that doing so in a nondestructive manner is very time-consuming and difficult. Other characteristics that increase with increasing LOD (soil surface strength, aggregate stability, cyanobacterial biomass, and exopolysaccharides) were both destructive and time-consuming compared with measures of LOD characteristics and did not always provide higher correlations.

It has been speculated in the literature that the higher biomass provided by biological soil crusts reduces soil porosity and thus slows infiltration and increases runoff (Avnimelech and Nevo, 1964; Campbell, 1979; Eldridge and Greene, 1994; Verrecchia *et al.*, 1995; Kidron *et al.*, 1999). In our study, however, higher organismal biomass – as indicated by both cyanobacterial biomass and LOD class – was negatively associated with runoff/water applied and positively associated with both infiltration rates and wetting depth. These findings would indicate that these earlier conclusions do not apply in this environment, perhaps because (i) frost-heaving and differential downcutting of soils create a high degree of surface roughness in the biological soil crusts, thus slowing the water sufficiently for increased infiltration despite reduced porosity (Barger *et al.*, 2006; Belnap, 2006) and/or that (ii) the soil aggregates formed by biological soil crusts increase micropore channels (which are known to increase water infiltration), thus counteracting the lowered soil porosity (Greene, 1992; Eldridge, 2003).

Erosion

For the simulations carried out under dry antecedent conditions and those carried out 30 min after pre-wetting, erosion declined as LOD increased (Figure 3). Interestingly, for the simulations carried out 24 h after pre-wetting, more sediment was produced by the LOD 2 and 3 plots than by the LOD 1 plots, in spite of the fact that runoff from the LOD 1 plots was about twice that from the LOD 2 and 3 plots. One possible explanation is that natural erosion processes may have depleted available sediment on the LOD 1 plots. Another possibility is that the biological soil crusts in LOD classes 2 and 3 are more cohesive than those of LOD 1; that is, because they are held together by more cyanobacteria, larger chunks of soil can be transported. A similar phenomenon has been observed when biological soil crusts of lower LOD classes were subjected to wind-tunnel simulations; LOD 2 and 3 classes release large chunks of material, whereas LOD 1 classes move as individual particles (Belnap, pers. obs.). Biological soil crusts in the highest classes (5 and 6) display very high cohesion, greatly reducing movement and making erosion very low.

One of the more remarkable aspects of these results is how dramatically erosion increases with greater antecedent wetness for all the LOD classes. Some of this increase can be attributed to higher runoff, but not all. For example, runoff was comparable for the simulations carried out under dry antecedent conditions and those carried out 30 min after pre-wetting, yet erosion more than doubled under the latter conditions (Figure 3). For the simulations carried out 24 h after pre-wetting, erosion doubled again. It is possible that pre-wetting caused some swelling of the crustal organisms, creating greater cohesion in the soils than when dry. Once exposed to the very high intensity rain of the simulations, the biological soil crusts may have been unable to withstand detachment and were moved as large chunks of material as opposed to individual soil particles (especially in the case of the very shallow soils).

As expected, erosion was negatively correlated with LOD, surface roughness, and cyanobacterial biomass (Table II). The ability of biological soil crusts to reduce soil loss has been well documented in over 20 studies during the past 60 years (reviewed in Belnap, 2006). As the biological soil crusts develop, so does the number of cyanobacterial and microfungal filaments, along with anchoring structures of mosses and lichens that weave through the soil surface, providing structural resistance to movement by water (Belnap and Gardner, 1993; Belnap *et al.*, 2003; Warren, 2003). Biological soil crusts also contribute significant amounts of organic carbon to soils, via carbon fixation (Beymer and Klopatek, 1991) and decay of organic matter (Danin and Ganor, 1991), both of which contribute to aggregate formation and, thus, soil stability. In addition, lichen tissue and moss tissue actually protrude above and cover the soil surface, protecting underlying soils from raindrop impact. Because cyanobacteria reside just under the soil surface, they are less protective than lichens or mosses. Therefore, crusts with higher lichen and moss biomass (higher LOD classes) provide more protection than cyanobacterial crusts (lower LOD classes). The effect can be quite dramatic, as demonstrated by Eldridge (2003), who found that soil erosion decreased by almost two orders of magnitude as biological soil crust cover increased from 0% to 100%. Other studies have also found that soil loss is reduced as biological soil crust biomass, cover, and development increase (Warren, 2003; Barger *et al.*, 2006).

Scaling up with the Rangeland Hydrology and Erosion Model

The plot attributes (average values) and key parameter values used for model calibration are given in Table III. The incorporation of these parameter values results in very close model approximations to cumulative 30-min runoff (Figure 4) and erosion. We used these parameters to simulate erosion at the hillslope scale for a variety of slope gradients and slope lengths. We found, however, that the model was relatively insensitive to changes in slope length or slope gradient.

The relative insensitivity of the RHEM model (as parameterized) to slope steepness or slope length is realistic if rill erosion does not develop on the hillslope. This would be the case for the higher LOD classes (perhaps 5 and 6).

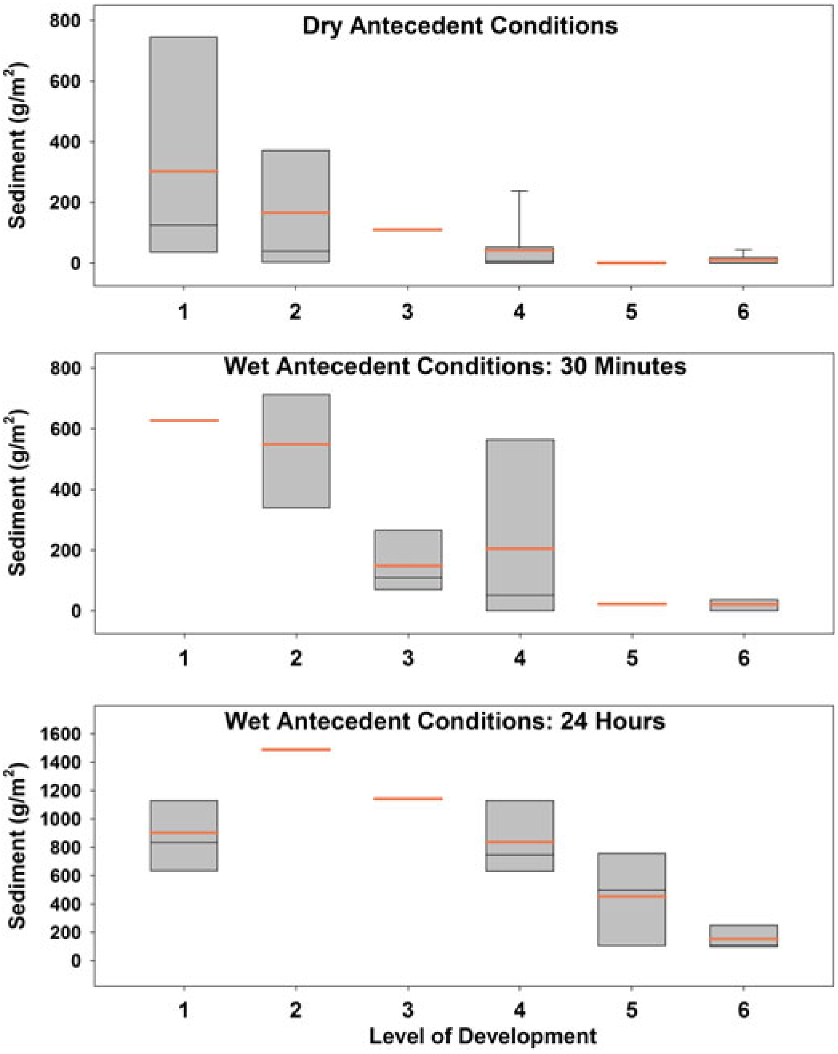

Figure 3. Box plots of sediment production (erosion) for each level of development class. The ends of the boxes define the 25th and 75th percentiles, the black line is the median, error bars define the 10th and 90th percentiles, and the orange line is the mean.

However, if rills do develop – as is likely under the more disturbed conditions typical for lower LOD classes – then erosion would logically increase as slopes become longer and steeper.

The RHEM model can be parameterized to simulate these dynamics by adjusting the concentrated flow erosion parameter (K_c) and the friction factor for erosion (f_e). These parameter values were set as recommended by the Water Erosion Prediction Project (WEPP) protocol for cultivated soils with sandy loam textures (WEPP User Summary NSERL Report #11, Table 13): K_c was set to 0·0102, and f_e was set to 2·5.

The results from this modelling, summarized in Figure 5, are encouraging because they are consistent with what we would expect. First, there is a much higher sensitivity to changes in slope for the most degraded conditions – especially the lowest LOD classes (1 and 2); for these LOD classes, predicted erosion increases as both slope length and, especially, slope gradient increase. And second, thresholds exist. For dry conditions, there appear to be thresholds in slope length and slope gradient beyond which erosion increases sharply. The slope gradient threshold is ~10%, and the slope length threshold is ~10 m. For less degraded conditions (LOD classes 4–6), the model was relatively insensitive to changes in slope length or gradient: Erosion rates increased by a factor of 10 for wet antecedent conditions.

Model simulations of runoff and erosion for different amounts of rainfall in a 30-min period are presented in Figure 6. For dry antecedent conditions, these simulations show the greatest differences between the LOD 1 plots and all the other LOD classes. In other words, very small amounts of rainfall can cause runoff and erosion when the land is in a highly degraded state. For the other LOD classes, rainfall needs to be around 40 mm in 30 min before runoff occurs if conditions are dry, but runoff can be initiated by much smaller amounts of rainfall if soils are wet.

By calibrating RHEM for each of the LODs using the plot-scale data, we were able to extend our results to larger scales – particularly for longer and steeper slopes. By coupling modelling with the small-plot simulations, we were able to address weaknesses inherent to both methods. Small-plot data alone are not sufficient as a basis for large-scale inferences (Wilcox and Wood, 1988; Wilcox and Wood, 1989; Wilcox *et al.*, 2003), and uncalibrated hydrology models often give

Table III. Plot conditions and key parameter values (italicized) used for model calibration.

	Level of development class					
	1	2	3	4	5	6
Dry (2004–2005)						
Rainfall rate (mm h^{-1})	111	119	114	112	119	117
30-min rainfall	55	59	57	56	60	58
30-min runoff (mm)	25·2	10·7	14	7·2	0·5	5·5
Erosion (g m^{-2})	302	164	109	41	1	14
Slope	3·3	8·6	9·5	5·7	8·1	6·8
Initial saturation	*25*	*25*	*25*	*25*	*25*	*25*
Friction factors	*5*	*5*	*5*	*10*	*15*	*15*
K_e	*9*	*27*	*21·5*	*32*	*47*	*35*
K_{ss}	*6 800*	*6 000*	*3 650*	*2 500*	*1 000*	*900*
30-min pre-wet (2006)						
Rainfall rate (mm h^{-1})	92	91	103	88	77	72
30-min rainfall	46	45	52	44	39	36
30-min runoff (mm)	27	15	6	6	1	1
Erosion (g m^{-2})	630	548	147	208	23	23
Slope	6	10	11	11	11	6
Initial saturation	*50*	*50*	*50*	*50*	*50*	*50*
Friction factors	*5*	*5*	*5*	*5*	*5*	*5*
K_e	*4*	*14*	*35*	*25*	*30*	*25*
K_{ss}	*16 000*	*21 700*	*9 700*	*16 000*	*8 700*	*7 000*
24-h pre-wet (2007)						
Rainfall rate (mm h^{-1})	107	84	100	100	108	89
30-min rainfall	53	42	50	50	54	45
30-min runoff (mm)	40	17	17	23	16	11
Erosion (g m^{-2})	910	1 498	1 143	843	459	155
Slope	4	12	12	7	5	7
Initial saturation	*50*	*50*	*50*	*50*	*50*	*50*
Friction factors	*0*	*0*	*5*	*5*	*5*	*5*
K_e	*1*	*10*	*16*	*10*	*21*	*18*
K_{ss}	*16 000*	*60 000*	*34 500*	*22 000*	*31 000*	*7 100*

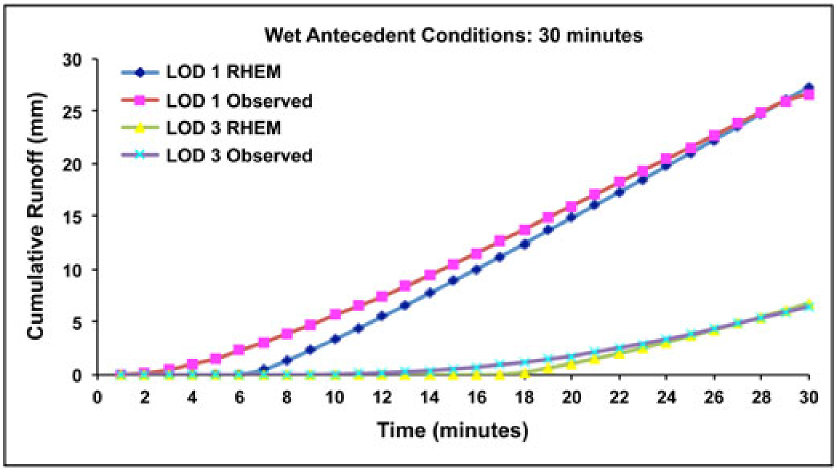

Figure 4. Predicted versus measured cumulative runoff for two biological soil crust classes (level of development (LOD) 1 and 3).

poor results, especially for rangeland conditions (Wilcox *et al.*, 1989; Wilcox *et al.*, 1990; Wilcox *et al.*, 1992).

CONCLUSIONS

The results of our study clearly demonstrate that biological soil crusts strongly influenced both surface hydrology and erosion at our study site and that the LOD of the crust determined how and to what extent those processes were influenced. In general, as LOD increased, infiltration increased and erosion decreased. Our results showed marked differences in soil infiltrability, runoff, and erosion between the low-LOD (1 and 2) plots and the high-LOD (5 and 6) plots.

For rainfall simulations carried out under dry antecedent conditions, about half of the water applied ran off the plots with the lowest LOD (1), whereas less than 10%

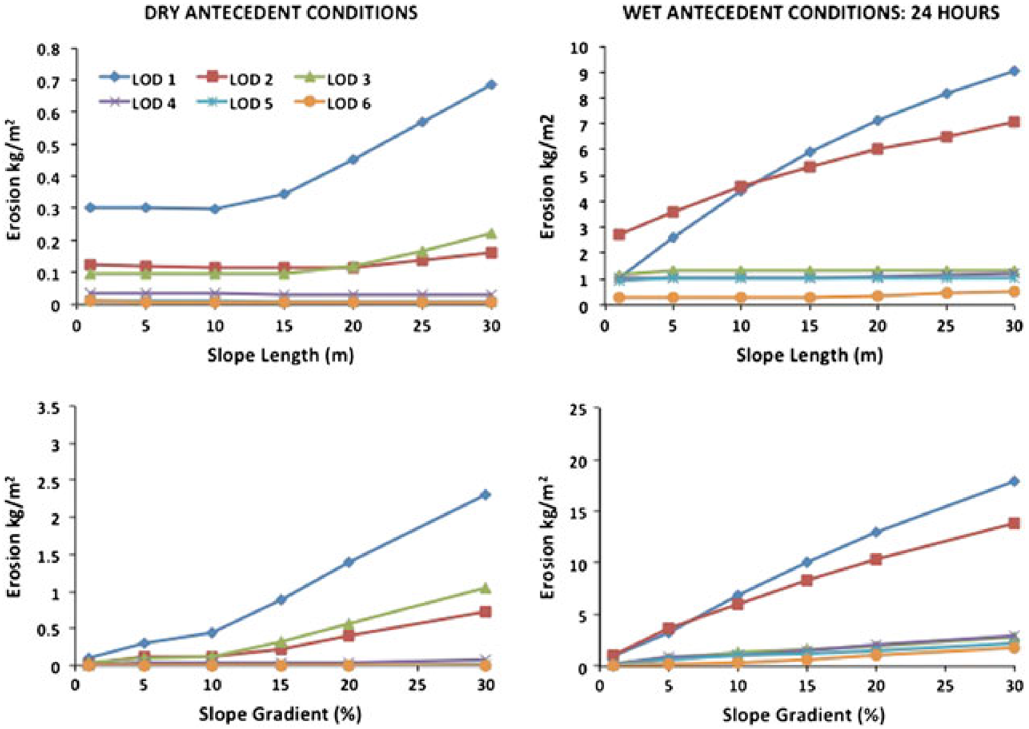

Figure 5. Predicted changes in erosion with slope length (slope gradient set at 9%) and slope gradient (slope length set at 15 m) for rainfall simulations under dry and wet antecedent conditions. The rainfall amount for both sets of simulations was 55 mm in 30 min.

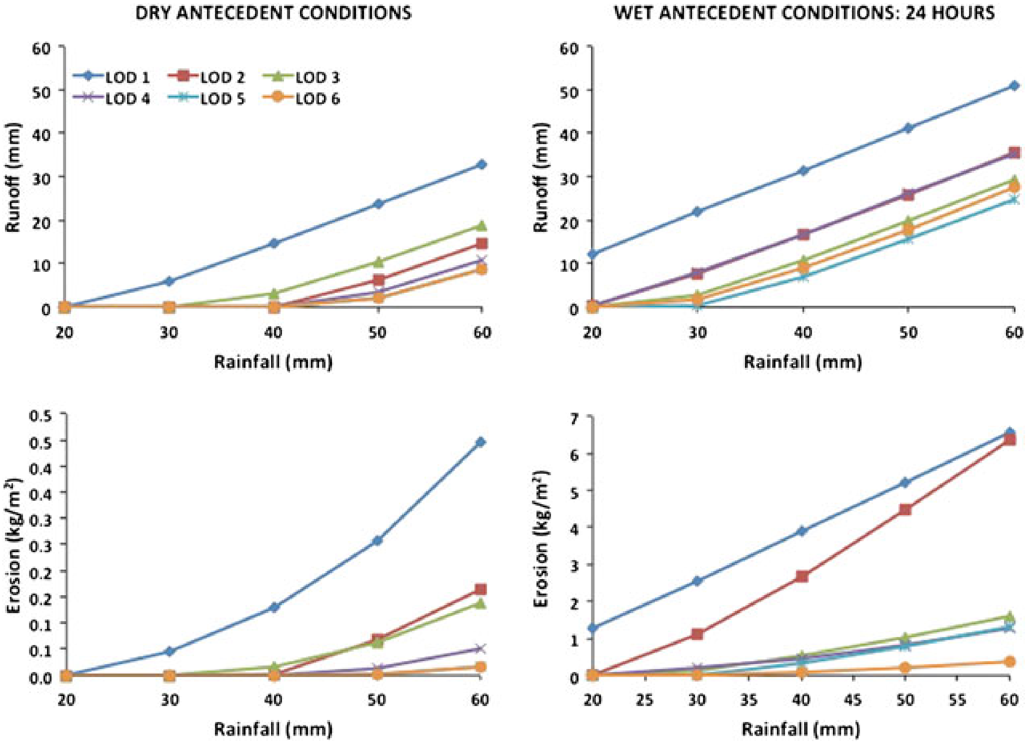

Figure 6. Predicted changes in runoff and erosion with amount of rainfall during a 30-min period for each of the level of development classes during dry and wet antecedent conditions. Slope gradient was set at 9% and slope length at 15 m.

ran off the plots having the highest LODs (5 and 6). Differences in erosion were even more profound: Around 300 g m^{-2} of sediment was lost from the LOD 1 plots, contrasted with almost zero for the LOD 5 and 6 plots, and intermediate amounts for LODs 2, 3, and 4. Our results also made clear the importance of antecedent soil water. For all the LODs, erosion rates were much greater for the plots that had been pre-wetted 24 h before rainfall simulation. Conditions of wet antecedent soil moisture are typical during the summer monsoon period in this area, but the natural rainfall events that follow are seldom so large as those applied via rainfall simulation.

The RHEM model results were enlightening, revealing that for plots covered with biological soil crusts having lower LODs (1 and 2), erosion potential increases dramatically as slope length and, particularly, slope gradient increase: Erosion potential increases by a factor of 10 as slope gradients increase from 0% to 10%. The model results also show that erosion potential rises as antecedent soil moisture levels rise.

Management agencies often rely on hydrological and erosion models such as WEPP, RHEM, or Revised Universal Soil Loss Equation for making ecological assessments. However, these models are typically parameterized on the basis of site characteristics such as soil texture and extent of coverage by vegetation, rocks, and litter. Coverage by biological soil crusts is sometimes incorporated, but rarely the LOD. Our results demonstrate that to be useful and meaningful, assessments of site health or modelling studies to predict runoff and erosion must consider not only the total coverage of biological soil crusts but also their LOD.

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