

Synergic hydraulic and nutritional feedback mechanisms control surface patchiness of biological soil crusts on tertiary sands at a post-mining site

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Abstract: In a recultivation area located in Brandenburg, Germany, five types of biocrusts (initial BSC1, developed BSC2 and BSC3, mosses, lichens) and non-crusts mineral substrate were sampled on tertiary sand deposited in 1985–1986 to investigate hydrologic interactions between crust patches. Crust biomass was lowest in the non-crusts substrate, increased to the initial BSC1 and peaked in the developed BSC2, BSC3, the lichens and the mosses. Water infiltration was highest on the substrate, and decreased to BSC2, BSC1 and BSC3. Non-metric multidimensional scaling revealed that the lichens and BSC3 were associated with water soluble nutrients and with pyrite weathering products, thus representing a high nutrient low hydraulic feedback mode. The mosses and BSC2 represented a low nutrient high hydraulic feedback mode. These feedback mechanisms were considered as synergic, consisting of run-off generating (low hydraulic) and run-on receiving (high hydraulic) BSC patches. Three scenarios for BSC succession were proposed. (1) Initial BSCs sealed the surface until they reached a successional stage (represented by BSC1) from which the development into either of the feedback modes was triggered, (2) initial heterogeneities of the mineral substrate controlled the development of the feedback mode, and (3) complex interactions between lichens and mosses occurred at later stages of system development.

Keywords: Recultivation; Pyrite weathering; Bistable ecosystems.

INTRODUCTION

Open-cast lignite mines in Lower Lusatia (Brandenburg, NE Germany) create large landscape destruction. Landscape reclamation, including soil, vegetation and ecosystem management is challenging, because the material dumped is tertiary carboniferous and pyritic sands which are often poor in nutrients, have a low water holding capacity, contain high amounts of potentially toxic elements and have an extremely low pH (Schaaf and Hüttl, 2005). In this context, new land surfaces in post-mining areas can be regarded as initial ecosystems comparable to newly created landscapes by volcanic activity, to glacier retreat areas in arctic or alpine environments, or to coastal and inland sand dunes (Schaaf et al., 2011). In the early stages of the ecosystem development cyanobacteria and green algae are the first colonizers of the surface and are forming biological soil crusts (BSCs) (Fischer et al., 2010a; Lukešová, 2001; Spröte et al., 2010), while in later stages of the vegetation succession, lichens and mosses are established on the stable soil surface (Büdel and Veste, 2008; Eldridge and Greene, 1994; Felinks, 2000). Although most areas are being reclaimed with forest trees in Central Europe to accelerate the restoration processes, open landscapes, like dry grasslands or areas with sparse vegetation between the young birch and pine stands are common in the post-mining sites (Wiegand and Felinks, 2001). In such open landscapes pioneer species are common, and biological soil crusts often cover the interspaces between trees. In particular, the formation of dense surface crusts influences hydrological processes, which depend on soil physical properties and on species composition, on different ecosystem scales (Fischer et al., 2010b). On the other hand, feedback mechanisms have been described between small scale

variation of surface properties, exposition, as well as microclimatic conditions, and BSC development and structure (Fischer et al., 2012; Veste and Littmann, 2006). Such microsite differentiation due to BSC establishment is known to create safe sites and to have various impacts on spatial distribution and successional processes of higher vegetation and BSCs on initial and reclaimed sites (Beyschlag et al. 2008; Cutler et al. 2008; Elmarsdottir et al., 2003). Therefore, ecological functions of BSCs have also important implications for reclamation and restoration of devastated ecosystems, and there is still a need for more detailed studies (Bowker, 2007; Veste, 2005).

Such spatial patchiness may be a key feature of many dryland ecosystems, and such ecosystems may be a manifestation of self-organisation (Viles, 2008). Linking feedback control to self-organized patchiness of resources and their consumers, several studies demonstrated that a resource concentration mechanism explains the diversity of spatial structures in these ecosystems. Although environmental change can be slow and gradual, it may lead to sudden, often called „catastrophic“ change in the structure and functioning of ecosystems (Scheffer et al., 2001). Such changes have been attributed to the existence of two alternative states in ecosystems (Scheffer and Carpenter, 2003), which were defined as bistability. Ignoring spatial interactions, so-called mean field models predict bistability in ecosystems as a consequence of positive feedback, which has been interpreted as local bistability. In contrast, bistability at large spatial scales predicted by these spatially explicit models has been defined as global bistability, where the stable states co-exist in space. It has further been proposed that the resource concentration mechanisms fail with increasing resource availability, meaning that specific spatial structures may develop in real ecosystems

that only arise when resource availability is decreased, but not when increased (Rietkerk et al., 2004).

While a resource concentration mechanism may generate self-organized surface patchiness under resource-limited conditions, we hypothesize that surface patchiness may also be organized by distribution mechanisms for stressors. In our study, this abiotic stress arose from liberation of protons due to weathering of pyrite contained in tertiary overburden sediment after mining activities. It was the aim of our study to demonstrate that (I) two types of BSC with alternative nutritional and hydraulic feedback modes co-exist in one area and that (II) these feedback modes are synergistic, because system stability cannot be reached without either of these two modes.

MATERIAL AND METHODS

The sampling site is located in the recultivation area of the Schlabendorf-Süd open cast mine in Germany (N 51°46'11.88'', E 13°45'22.54''). According to the WorldClim (2014) database, the mean annual temperature is 9.2°C, mean annual precipitation is 569 mm (1950–2000). The biological soil crusts developed on pyrite containing clastic overburden sediments of tertiary age, which were transported by conveying bridges and deposited to the surface in 1985–1986 (LMBV,

2012), and which were classified as medium sand according to Arbeitsgemeinschaft Boden (2005). The vegetation cover consisted of scattered pine trees, which had an average height of approximately 1.3 m (Figure 1a). The topography of the sampling plot was flat with no indication of erosion, like gullies or colluvium.

Three stages of crust development and the respective subjacent mineral substrate were taken in duplicate from a 25 m² sampling plot. Samples of the non-crustured surface were taken without distinction between crust and subjacent layer in triplicate. The sites to sample were selected by expertise, trying to represent mixed sites dominated by mosses, by lichens, and by visually in the field observable surface properties (colour and crust thickness) for the non-crustured substrate and BSC1 to 3. BSC1 was sampled in the vicinity of a pine tree and was influenced by shading. In addition, lichen and moss samples which were considered to represent final stages of cryptogamic development were sampled (Figure 1b). The crust, moss and lichen patches had diameters ranging from 5 to 20 cm. The samples were taken from patches >10 cm, which was the size of the petri dishes used for sampling.

We provided a species inventory and estimated surface coverages in all samples by visual inspection using single (C 2000 Z-ADP, Olympus, Japan) and binocular microscopes

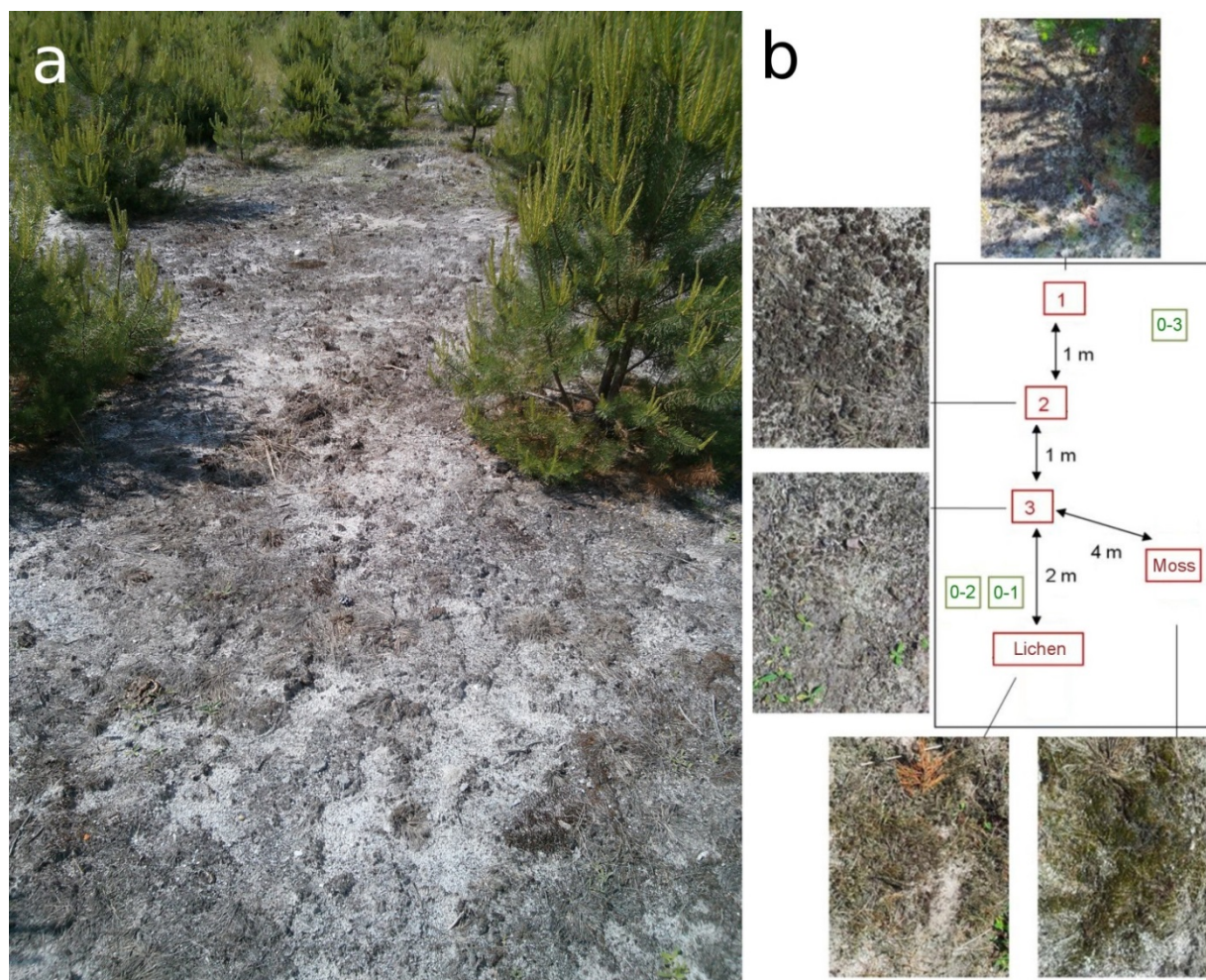
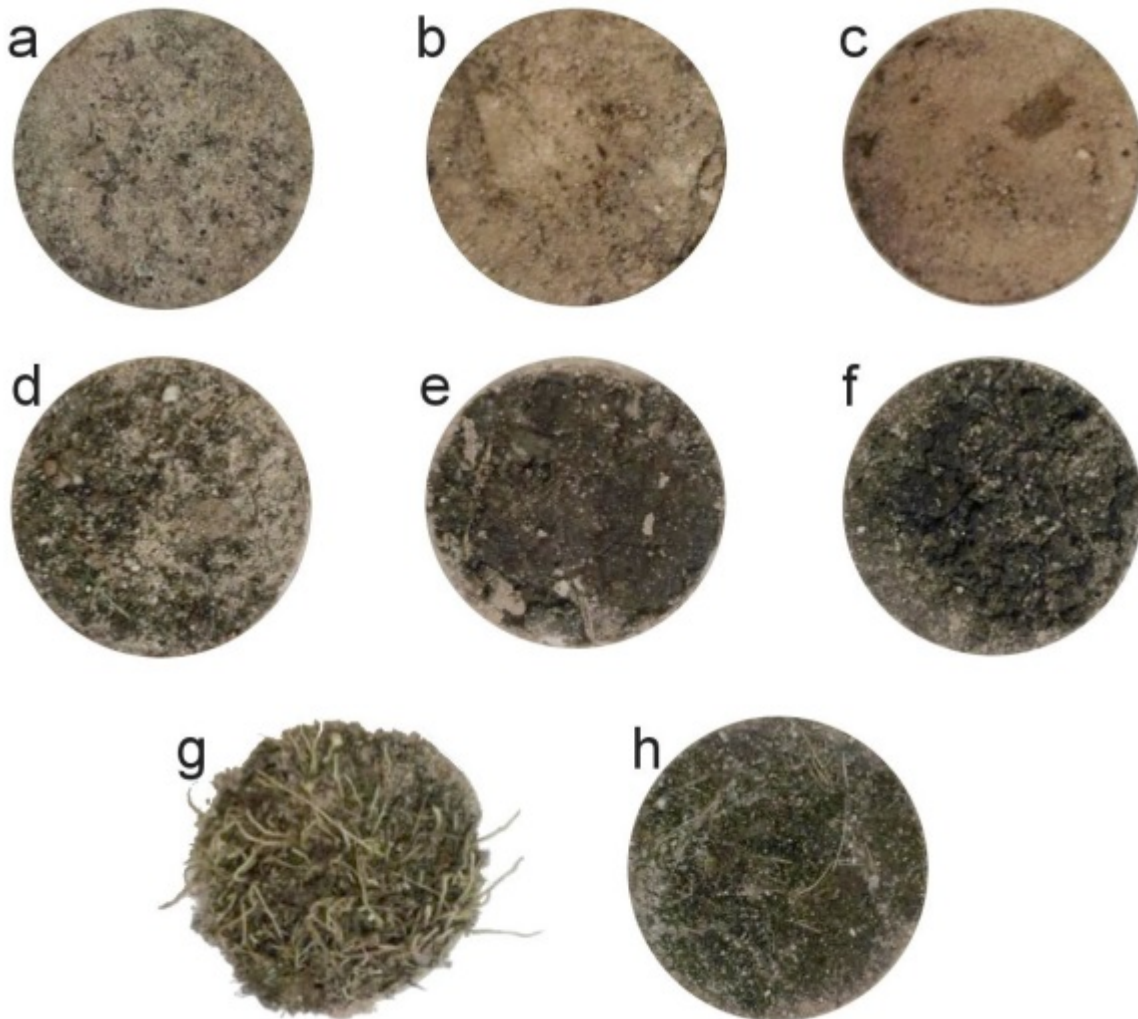


Fig. 1. Overview photograph (a) and sketch map (b) of the sampling plot. 1, 2, 3 – BSC types 1, 2 and 3, respectively, 0-1, 0-2, 0-3 – non-crustured surface samples.

Table 1. Surface coverage (%), species and genus inventory of the crust types.

	Crust type					
	substrate	BSC 1	BSC 2	BSC 3	Moss	Lichen
Green algae						
<i>Zygogonium</i> spec. (Kützing)	0.1	25	100	25	100	0
<i>Chlorella</i> spec. (Beijerinck)	0	25	75	25	5	0
<i>Ulothrix</i> spec. (Kützing)	0.1	0	0	5	0	0
<i>Haematococcus</i> spec. (Wille)	0.1	0	0	0	1	0
Lichens						
<i>Placynthiella oligotropha</i> (Laundon)	1	5	100	50	25	0
<i>Cladonia subulata</i> (Linné)	0	1	1	0	1	100
Mosses						
<i>Ceratodon purpureus</i> (Hedwig)	1	5	0	1	100	1

**Fig. 2.** Top view photographs of the samples, a – non-crusted surface sample 1 (0-1), b – non-crusted surface sample 2 (0-2), c – non-crusted surface sample 3 (0-3), d – BSC 1, e – BSC 2, f – BSC 3, g – Lichen, h – Moss. Samples d to f: one replicate of two taken shown; sample diameter: 10 cm.

(Stemi 2000-CS, Zeiss, Germany). Mosses and Lichens were determined according to Jahns (1987), Wirth (1995) and Wirth and Düll (2000), for lichens determination we also used Moberg and Holmasen (1992). Algae were determined according to Guiri (2013), Kinross (2012) and Linne van Berg et al. (2012). Deviant from vascular plant cover BSCs may develop pronounced multiple layers, for example, lichens may grow on algal mats. Therefore, total coverage may exceed 100% in our study.

Water infiltration rates (Q) and surface repellency indices (R_s) were determined using the ethanol-water micro-infiltration method (Hallett and Young, 1999). Due to dense cover with large thalli, the microinfiltrometric method was not applicable to the moss and lichen samples. Therefore, infiltrometric data were available only for the non-crust sample and the samples BSC1 to 3. Surface related chlorophyll concentrations were determined by thorough grinding and sonicating air-dried biological soil crusts with 80% acetone and UVVIS-spectroscopy (Fischer et al., 2010b). Total carbon, nitrogen and sulfur concentrations of the ground BSC and mineral substrate samples were determined by dry combustion using an elemental analyser (vario EL, Elementar, Germany). Water soluble nutrients (SO_4 , NO_3 , NH_4 , K, Mg, Ca) were determined after 1:2.5 exhaustive extraction with deionised water and membrane filtration (0.45 μm , Sartorius, Germany) using ionic chromatography (DX100 and ICS 90, Thermo scientific, USA). Total element concentrations (Mg, Al, Si, P, K, Ca, Ti, Fe) were determined using x-ray fluorescence spectroscopy (x-supreme 5000, Oxford instruments, UK). Water holding capacity of the non-crust surface samples and of the BSCs was determined by dehydration of previously water saturated 3.0 cm I.D. x 1.0 cm soil cores at a 60 hPa suction pressure on a sand bed (Eijkelkamp, The Netherlands). Five analytical replicates were used for each sample.

STATISTICS

To handle total species coverage exceeding 100% due to multiple layering in BSCs we used non-metric multidimensional scaling (NMDS) to compare microphytic communities. Unlike canonical correspondence analysis (CCA), NMDS uses rank orders and is commonly regarded as the most robust unconstrained ordination method in community ecology (Minchin, 1987). We used biplot ordination diagrams to visualize community similarities between BSC types and to relate BSC types to soil chemical, hydrological and floristic properties. Species abundances, infiltration rates, pH, total carbon, chlorophyll a, as well as water soluble nutrients (SO_4 , NH_4 , K, Mg and Ca) were used for NMDS. Because infiltration data were not available for the moss and lichen crusts (see above) and because the non-crust substrate did not undergo crust succession, only BSC1, BSC2 and BSC3 were considered for NMDS ordination analysis. The metaMDS function of the vegan package of the R software suite was used for multivariate community analysis. To evaluate the floristic similarity between the samples including the moss and lichen crusts, we used hierarchical cluster analysis based on species abundances. To evaluate the chemical similarity between the samples including the moss and lichen crusts, we used hierarchical cluster analysis based on z-transformed total carbon, chlorophyll a, water soluble nutrient (SO_4 , NH_4 , K, Mg and Ca) concentrations, as well as pH. Kruskal-Wallis rank sum test was used to prove significance of differences and Pearson's product-moment correlation coefficient was used to test significance of correlation.

RESULTS

The results of the species inventory are listed in Table 1. The non-crust samples contained minor incrustations of the lichen *P. oligotropha*, young leaflets of the moss *C. purpureus*, as well as very sparsely present individuals of the green algae *Ulothrix* spec., *Zygogonium* spec. and *Haematococcus* spec. The sample BSC1 was not entirely covered with microphytes, crust patches were smooth, and *P. oligotropha* was observed to develop on residues of *C. purpureus* and on unspecified organic detritus. BSC2 covered the surface entirely and was dominated by *P. oligotropha* and by *Zygogonium* spec. The sample BSC3 consisted of pad-like patches predominantly growing on organic residues. The moss sample was dominated by *C. purpureus* and *Zygogonium* spec. growing between the moss stemlets directly on the mineral surface, the lichen sample was dominated by *C. subulata* with sparsely scattered individuals of *C. purpureus* (Figure 2).

An overview of the results of hydrological and chemical analysis is given in Table 2. Water soluble sulfate concentrations, increased in the sequence non-crust < moss < BSC2 < BSC1 < lichen < BSC3, with the concentrations generally being higher in the crust layer as compared to the subjacent mineral substrate layer.

NMDS ordination analysis revealed that all water soluble nutrients and total carbon were closely associated with BSC3, whereas water infiltration was associated with BSC2. Chlorophyll a was negatively, but pH was positively related to BSC1, indicating a drop of pH with biomass accumulation (Figure 3a). Hierarchical cluster analysis revealed that BSC2 was floristically and chemically most similar to the moss crust, whereas BSC3 was floristically and chemically most similar to the lichen crust. BSC2 BSC3 were chemically and floristically similar to the non-crust substrate and to BSC1, respectively (Figure 3b and c).

Surface related chlorophyll a amounts increased from the non-crust samples to BSC1, further to the moss sample, BSC3, BSC2 and to the lichen sample (Figure 4a). The moss and lichen samples, as well as BSC2 and BSC3 did not differ significantly from each other (Kruskal-Wallis rank sum test, $p = 0.24$). Infiltration was highest in the non-crust substrate. Infiltration of BSC2 significantly exceeded infiltration of BSC1 and BSC3 (Tukey-Test, $p < 0.05$, Figure 4b).

Negative correlations of pH with log-transformed total and sulfate-S concentrations were estimated to be statistically significant (Figure 5).

DISCUSSION

Apart from the non-crust surface and the weakly developed BSC1, the BSCs were associated with two types of ecological feedback modes (Figure 3).

BSC 3 belongs to a **high nutrient low hydraulic feedback** mode. Both higher repellency indices, which also can be interpreted as inhibited surface wettability (Table 2), and reduced infiltration (Figures 3a and 4b) favour precipitation water running off BSC patches. A similar behaviour was observed for *Zygogonium ericetorum* mats on quaternary sands in the same geographical region (Fischer et al., 2010b). Presumably, water intercepted in the organic rich crust layer created conditions for pyrite weathering, for example by the chemolithotrophic bacterium *Acidithiobacillus ferrooxidans* (formerly *Thiobacillus ferrooxidans*, Meyer et al., 1999), leading to liberation of sulfate and protons into the soil solution

Table 2. Analytical results, WHC – water holding capacity at –60 hPa, R_i – repellency index, Q – water infiltration rate into dry soil at a pressure head of –2 hPa, ChlA – Chlorophyll a, mean arithmetic values \pm standard deviation, n.d. - not determined.

		non-crusted	BSC1		BSC2		BSC3		Moss		Lichen	
		surface	surface	sub-surface	surface	sub-surface	surface	sub-surface	surface	sub-surface	surface	sub-surface
WHC	[vol %]	8,6 $\pm 1,3$	18,8 $\pm 4,5$	n.d.	13,8 $\pm 0,9$	n.d.	23,4 $\pm 2,7$	n.d.	20,9 $\pm 1,1$	n.d.	16,8 $\pm 2,4$	n.d.
R_i		0,87 $\pm 0,11$	1,28 $\pm 0,33$	n.d.	1,11 $\pm 0,11$	n.d.	1,38 $\pm 0,06$	n.d.	n.d.	n.d.	n.d.	n.d.
Q	[mg s ⁻¹]	6,37 $\pm 1,95$	2,09 $\pm 0,89$	n.d.	3,97 $\pm 0,02$	n.d.	1,23 $\pm 0,36$	n.d.	n.d.	n.d.	n.d.	n.d.
ChlA	[mg m ⁻²]	2,41 $\pm 0,98$	6,30 $\pm 3,27$	n.d.	29,97 $\pm 5,61$	n.d.	29,62 $\pm 6,48$	n.d.	21,36 $\pm 3,45$	n.d.	30,93 $\pm 6,42$	n.d.
pH		4,64 $\pm 0,62$	4,92 $\pm 0,01$	5,20 $\pm 0,16$	4,73 $\pm 0,11$	5,05 $\pm 0,32$	4,14 $\pm 0,01$	3,03 $\pm 0,08$	4,23 $\pm 0,01$	4,20 $\pm 0,09$	4,59 $\pm 0,05$	3,70 $\pm 1,20$
total element concentrations												
N	[%]	0,03 $\pm 0,01$	0,17 $\pm 0,05$	0,06 $\pm 0,01$	0,04 $\pm 0,01$	0,02 $\pm 0,01$	0,71 $\pm 0,11$	0,23 $\pm 0,02$	0,64 $\pm 0,02$	0,09 $\pm 0,02$	0,23 $\pm 0,01$	0,03 $\pm 0,01$
C	[%]	0,70 $\pm 0,14$	3,58 $\pm 0,84$	1,20 $\pm 0,28$	1,22 $\pm 0,09$	0,70 $\pm 0,38$	19,75 $\pm 1,68$	11,83 $\pm 1,15$	27,47 $\pm 0,55$	3,76 $\pm 0,60$	6,62 $\pm 0,27$	0,66 $\pm 0,16$
S	[%]	0,02 $\pm 0,01$	0,04 $\pm 0,01$	0,02 $\pm 0,01$	0,03 $\pm 0,01$	0,02 $\pm 0,01$	0,40 $\pm 0,02$	0,38 $\pm 0,02$	0,78 $\pm 0,02$	0,10 $\pm 0,02$	0,05 $\pm 0,02$	0,02 $\pm 0,01$
Mg	[%]	0,10 $\pm 0,01$	0,07 $\pm 0,01$	0,10 $\pm 0,01$	0,11 $\pm 0,01$	0,11 $\pm 0,02$	0,05 $\pm 0,01$	0,06 $\pm 0,01$	0,06 $\pm 0,01$	0,06 $\pm 0,01$	0,05 $\pm 0,01$	0,11 $\pm 0,01$
Al	[%]	2,48 $\pm 0,14$	1,55 $\pm 0,11$	2,11 $\pm 0,54$	2,58 $\pm 0,23$	2,55 $\pm 1,26$	1,23 $\pm 0,14$	1,32 $\pm 0,01$	1,75 $\pm 0,35$	1,41 $\pm 0,30$	0,88 $\pm 0,11$	2,34 $\pm 0,50$
Si	[%]	39,87 $\pm 1,68$	27,91 $\pm 0,19$	36,88 $\pm 3,97$	33,47 $\pm 4,02$	39,17 $\pm 8,97$	14,86 $\pm 1,68$	14,77 $\pm 4,91$	23,50 $\pm 3,20$	32,04 $\pm 3,50$	28,42 $\pm 0,70$	40,34 $\pm 2,94$
P	[%]	0,12 $\pm 0,01$	0,11 $\pm 0,01$	0,13 $\pm 0,02$	0,10 $\pm 0,02$	0,12 $\pm 0,04$	0,09 $\pm 0,01$	0,08 $\pm 0,01$	0,08 $\pm 0,01$	0,09 $\pm 0,01$	0,15 $\pm 0,01$	0,14 $\pm 0,02$
K	[%]	1,10 $\pm 0,35$	0,42 $\pm 0,27$	0,81 $\pm 0,05$	1,06 $\pm 0,10$	1,00 $\pm 0,10$	0,41 $\pm 0,12$	0,32 $\pm 0,14$	0,54 $\pm 0,01$	0,52 $\pm 0,01$	0,56 $\pm 0,02$	0,56 $\pm 0,18$
Ca	[%]	0,05 $\pm 0,01$	0,09 $\pm 0,02$	0,06 $\pm 0,01$	0,06 $\pm 0,01$	0,06 $\pm 0,01$	0,11 $\pm 0,03$	0,17 $\pm 0,01$	0,14 $\pm 0,01$	0,08 $\pm 0,01$	0,08 $\pm 0,04$	0,04 $\pm 0,04$
Ti	[%]	0,12 $\pm 0,01$	0,06 $\pm 0,01$	0,06 $\pm 0,01$	0,11 $\pm 0,02$	0,11 $\pm 0,04$	0,07 $\pm 0,01$	0,05 $\pm 0,01$	0,05 $\pm 0,01$	0,05 $\pm 0,01$	0,07 $\pm 0,01$	0,14 $\pm 0,02$
Fe	[%]	0,15 $\pm 0,05$	0,15 $\pm 0,01$	0,12 $\pm 0,01$	0,20 $\pm 0,02$	0,17 $\pm 0,07$	0,55 $\pm 0,04$	0,59 $\pm 0,08$	0,39 $\pm 0,07$	0,29 $\pm 0,05$	0,08 $\pm 0,01$	0,14 $\pm 0,04$
water soluble element concentrations												
SO ₄	[mg kg ⁻¹]	23,1 $\pm 7,1$	59,1 $\pm 21,7$	34,7 $\pm 1,3$	41,9 $\pm 5,3$	22,8 $\pm 8,4$	202 ± 1	140 ± 15	50,6 $\pm 8,5$	18,8 $\pm 10,2$	123 ± 13	15,9 $\pm 3,1$
Na	[mg kg ⁻¹]	9,63 $\pm 3,08$	15,63 $\pm 0,01$	21,72 $\pm 13,92$	17,31 $\pm 2,03$	9,09 $\pm 1,28$	25,25 $\pm 0,35$	10,22 $\pm 1,46$	11,81 $\pm 2,55$	17,56 $\pm 3,30$	52,69 $\pm 1,15$	11,88 $\pm 0,01$
NH ₄	[mg kg ⁻¹]	3,54 $\pm 0,36$	17,19 $\pm 7,51$	7,19 $\pm 3,09$	2,81 $\pm 1,33$	1,56 $\pm 0,44$	30,94 $\pm 3,98$	6,56 $\pm 1,33$	3,75 $\pm 1,56$	<0,05 n.d.	55,94 $\pm 0,44$	3,44 $\pm 0,44$
K	[mg kg ⁻¹]	24,54 $\pm 2,34$	135,94 $\pm 79,11$	53,13 $\pm 2,65$	41,56 $\pm 10,16$	23,75 $\pm 2,65$	236,56 $\pm 20,77$	25,94 $\pm 0,44$	21,25 $\pm 3,83$	15,00 $\pm 2,35$	478,13 $\pm 76,01$	35,31 $\pm 3,09$
Mg	[mg kg ⁻¹]	1,79 $\pm 0,51$	8,56 $\pm 4,15$	2,06 $\pm 1,50$	4,19 $\pm 0,27$	1,69 $\pm 0,27$	27,88 $\pm 2,30$	15,50 $\pm 4,60$	7,31 $\pm 2,35$	2,38 $\pm 1,55$	29,25 $\pm 0,18$	2,31 $\pm 0,62$
Ca	[mg kg ⁻¹]	7,04 $\pm 0,29$	29,38 $\pm 4,42$	9,06 $\pm 6,63$	16,56 $\pm 2,21$	9,69 $\pm 0,44$	78,13 $\pm 6,19$	62,50 $\pm 7,07$	18,75 $\pm 2,22$	10,62 $\pm 1,85$	97,81 $\pm 13,70$	7,50 $\pm 2,65$

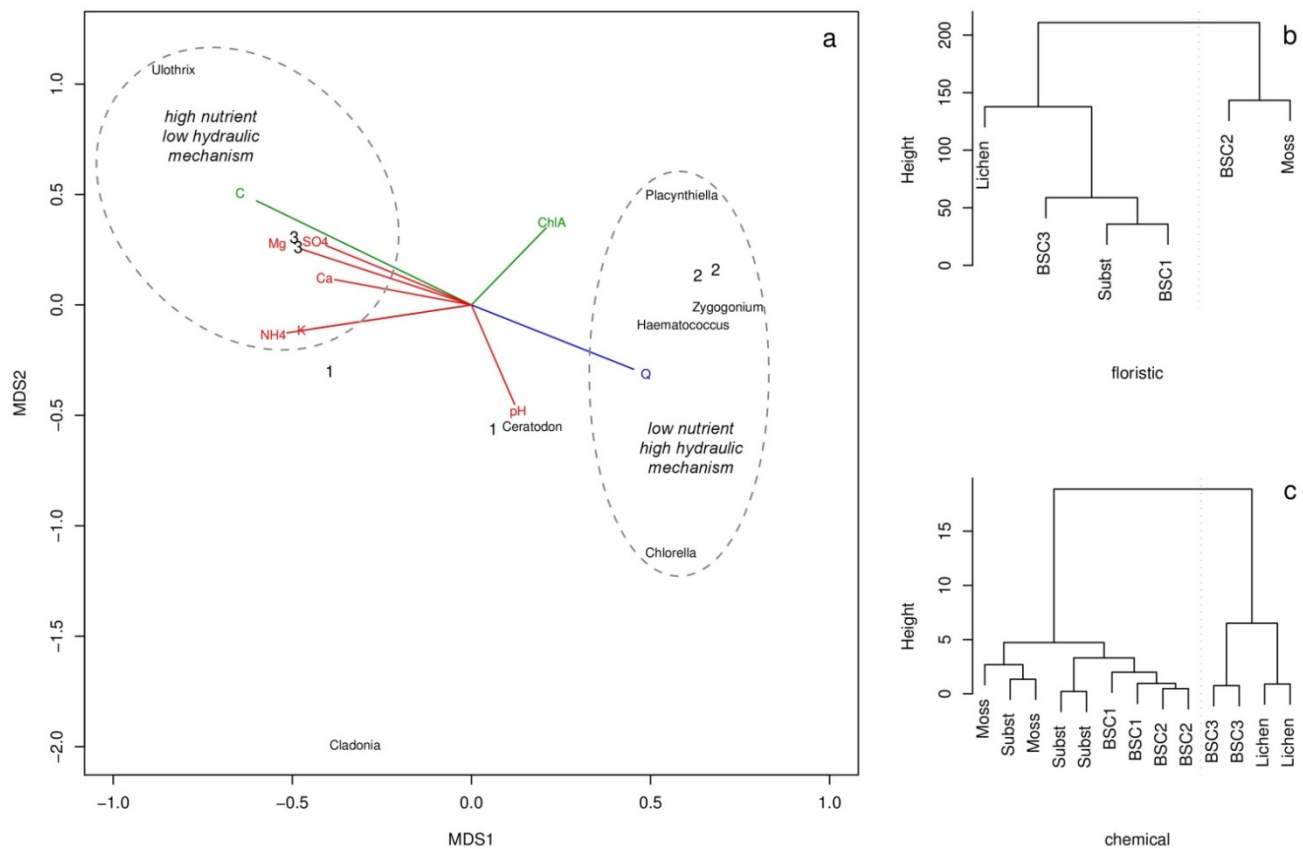


Fig. 3. (a) NMDS ordination plot. 1 – sample BSC1, 2 – sample BSC2, 3 – sample BSC3, C – Carbon, Chla – chlorophyll a, Q – infiltration rate. Colour codes (electronic version only): red – soil chemical data, green – soil biological data, blue – soil hydrological data, black – BSC samples and microphytic species, (b) hierarchical clustering of samples based on floristic similarity, (c) hierarchical clustering of samples based on chemical similarity.

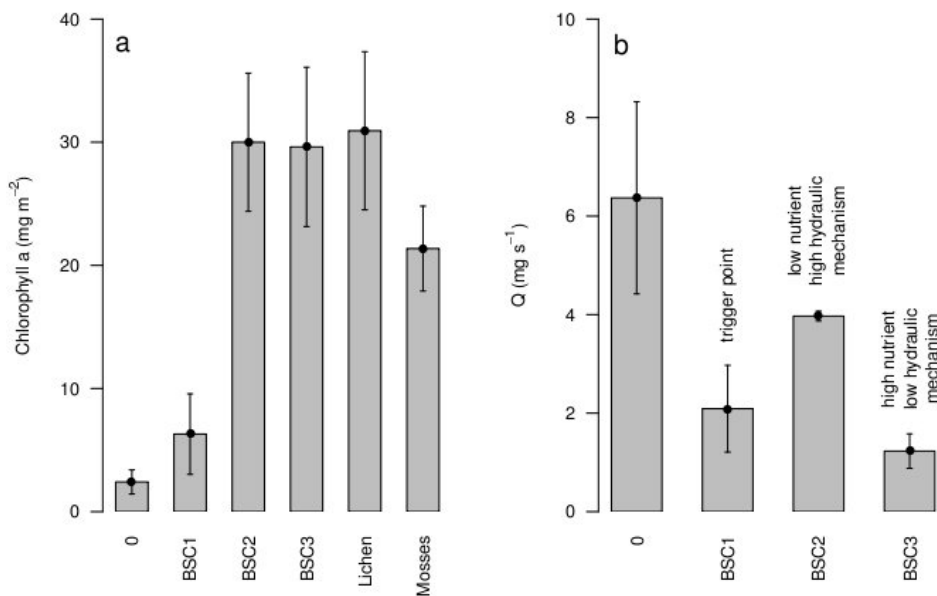


Fig. 4. Arithmetic mean values of surface related chlorophyll a concentrations (a) and infiltration Q at -2 hPa (b) of the non-crustified surface (0), the surface crust samples (BSC1 to 3, respectively), as well as the lichen and moss samples. Error bars indicate standard deviations.

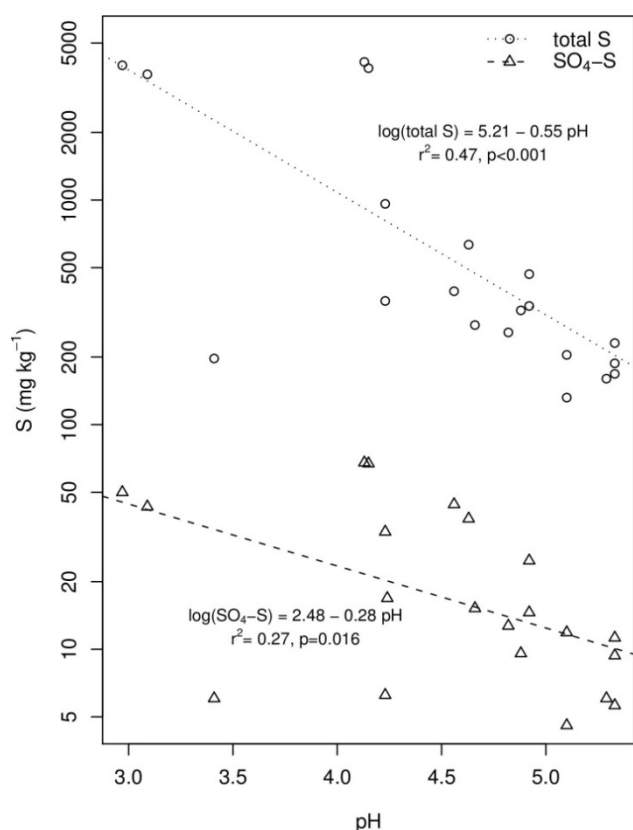


Fig. 5. Relationship between pH and log-transformed total as well as sulfate sulfur.

(Johnson, 1998). Due to diminished infiltration these products of pyrite weathering, and possibly other elements deposited from the atmosphere, were not leached into deeper soil beneath developed crusts, but accumulated in their place of production or deposition, respectively. *Ulothrix* spec., which has been reported to accompany *Zygogonium* spec. in xeric habitats in southern Brandenburg (Hoppert et al., 2004), was particularly associated with this high nutrient and low hydraulic regime. Some species of the genera *Ulothrix* have been further reported to grow in acidic environments at pH values down to 3, but also to be tolerant to high dissolved element concentrations (Das et al., 2009; Orandi et al., 2007). In this study, water soluble element concentrations were highest in the *C. subulata* dominated lichen sample and in the *Ulothrix* containing BSC3, where pH of the lower crust dropped to values of 3.70 and 3.03, respectively (Table 2). In addition, BSC3 and the lichen crust showed closest floristic and chemical similarity (Figure 3b and c). Close correlation between pH and total S, and between pH and sulfate-S (Figure 5) point to pyrite oxidation, and to common origin of sulfate and protons, respectively. Surface sealing and resulting accumulation of weathering products and nutrients may favour the development of species tolerant to low pH or high ionic strength, like *Ulothrix*, or requiring higher concentrations of nutrients, like *C. subulata*, which, in turn, progressively inhibit infiltration. Pyrite acts as a proton source, and pH stress contributed to a shift in the community structure rather than a drop of total biomass.

BSC2 belongs to a **low nutrient high hydraulic feedback** mode (Figure 3a), where the products of pyrite weathering and atmospheric depositions were leached into deeper soil. This leaching is characterized by low element concentrations in both

crust and subjacent layers (Table 2). The lichen *Placynthiella oligotropa*, as well as the green algae *Zygogonium* spec., *Chlorella* spec. (the photobiont of *Placynthiella oligotropa*) and *Haematococcus* spec. were associated with this mechanism. Although *Zygogonium* is known to form water repellent mats (Ettl and Gärtner, 1995), which might promote the high nutrient low hydraulic feedback mechanism, Fischer et al. (2010b) reported that appearance of the moss *Polytrichum piliferum* within *Zygogonium* dominated BSCs caused an increase of infiltration rates. Due to its high floristic and chemical similarity with BSC2, the moss crust can be attributed to this feedback mode (Figure 3b and c).

Area related chlorophyll concentrations, which are a very common biomass indicator for terrestrial microphytes (Belnap and Lange, 2001), do not differ significantly between BSC2, BSC3, the lichen and the moss crusts (Figure 4a, Kruskal-Wallis rank sum test, $p = 0.24$) and, hence, are not correlated with either of the two mechanisms. Different BSC types have been reported previously to reduce, to increase, or have no effect on infiltration. Reduced infiltration has been attributed to pore clogging and water repellency (Fischer et al., 2010b; Issa et al., 2009; Kidron et al., 1999), whereas increased infiltration was reported to be caused by higher porosity, enhanced aggregate stability and improved physical structure (Mager and Thomas, 2011; Menon et al., 2011; Rossi et al., 2012). No influence of BSCs on infiltration has been attributed to interfering factors, such as texture or structure, which may mask the influence of BSCs on infiltration (Williams et al., 1999). It can be concluded that the two feedback mechanisms observed do not only develop as a result of biomass accumulation, but likely also by means of community-mediated formation of the physical crust structure.

Total sulfur concentrations were high both in BSC3 and in the moss crust (Table 2), which are hypothesized to belong to different nutritional and hydraulic feedback modes. Three S fractions should be considered here: (I) immobile geogenic sulfur bound to pyrite (FeS_2), (II) relatively immobile bioaccumulated sulfur, as well as (III) highly mobile sulfate as a result of pyrite weathering. High correlation between carbon and total sulfur (Pearson's product-moment correlation coefficient = 0.96, $p < 0.001$) serves as clear indication of S bioaccumulation, which may not necessarily be related to the cryptogams (Pearson's product-moment correlation coefficient between chlorophyll a and total sulfur = 0.24, $p = 0.43$), but likely to the heterotrophic or chemoautotrophic crust community, or in the detritus. Hence, the sulfur turnover was driven by pyrite weathering, S bioaccumulation and by sulfate leaching, where – due to the high mobility of sulfate – the latter differed remarkably between the nutritional and hydraulic feedback modes described above.

A spatial setting in which cyanobacterial crusts were located upslope of moss dominated crusts can be found in arid dunes of the north-western Negev (Kidron et al., 2010; Veste et al., 2011). In this specific case extended wetness durations triggered a shift of crust types from cyanobacterial to moss-dominated crusts (Kidron et al., 2010; Veste and Littmann, 2006). These studies emphasize the importance of small-scale processes, like microclimate, wetness duration, soil properties, for the development of biological soil crusts. Even that the topography of our study site is flat compared to the Negev dunes, small-scale ecological processes play an important role for crust development in the post-mining site here. Although infiltration was reported to increase in moss dominated crusts due to their relatively low content of exopolysaccharides and their higher

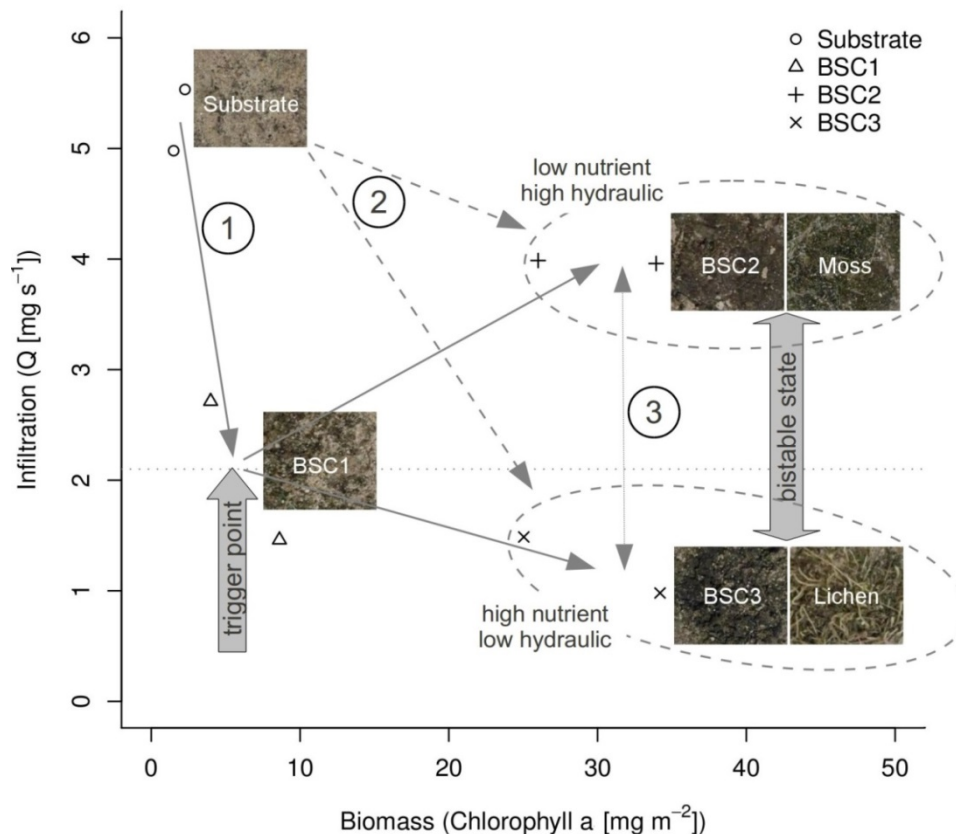


Fig. 6. Conceptual model for BSC development from non-crusted substrate to a synergic bimodal system state, based on a biomass vs. infiltration plot of the surface data. Each sample point represents the mean arithmetic value of 5 analytical replicates. Successional pathways (1) is depicted in solid, (2) in coarse dotted and (3) in fine dotted lines. Explanations see text.

surface roughness (Kidron, 2007; Kidron et al., 2003), they were able to store high amounts of moisture (Table 2) which facilitates longer hours of photosynthetic activity (Kidron et al., 2010). The low nutrient high hydraulic BSC2 patches receiving runoff water were floristically and chemically similar to the moss crust, whereas the high nutrient low hydraulic BSC3 patches generating runoff were dominated by green algae and floristically and chemically similar to lichens (Figure 3b and c). Hence, we attribute the distribution of mosses within our study plot to higher amounts of available moisture.

A conceptual model for BSC development under flat topographic conditions is shown in Figure 6. Three possible scenarios for BSC succession can be assumed.

(1) Succession through trigger point

Initial BSCs seal the surface, and infiltration becomes reduced to a given threshold value. Taking into consideration that the chlorophyll concentration reflects biomass accumulation, it can be assumed that BSC1 is at an earlier stage of crust growth, possibly due to shading. At the same time, it contained both mosses and lichens (Table 1), and it holds a highly variable, but intermediate position between BSC2 and BSC3 as related to hydraulic properties (repellency indices listed in Table 2, infiltration rates shown in Figure 4b and in Table 2). Hence, BSC1 possibly represents a successional stage from which the development into either of the feedback modes is triggered, where ponding precipitation will discharge through the weakest crust segments thus paving the way for vertical preferential flowpaths. Further development of the system occurs in a bimodal state, consisting of the two modes observed in this study.

(2) Crust type driven by initial surface heterogeneity

Variability of infiltration is highest on the uncrusted substrate, so homogeneous surface conditions cannot be assumed when biomass accumulation starts. Bypassing initial surface sealing, it is also well possible that the bimodal development of the system is controlled by initial heterogeneities, for example in microtopography or substrate texture, generated by the mining activities. While microclimate (such as shading) and hydrology determined micro-scale crust patchiness in Nizzana (Kidron and Vonshak, 2012), which is characterized by homogeneous parent material, these factors along with the properties of the parent material may control crust patchiness in Brandenburg, which is characterized by small scale heterogeneities of the parent material.

(3) Towards late BSC succession

Species inventory revealed that increasing coverage of the moss *Ceratodon purpureus*. The establishment of moss in late BSC succession can also be observed in other open landscapes, such as inland and coastal dunes (Daniëls et al., 1993; Fischer et al., 2010b; Haase, 2005). This is in conjunction with their broad ecological amplitude (Düll, 1993) and their preference to moist conditions (Kidron et al., 2010). In such moss plots a decreased coverage of the lichens *Placynthiella oligotropha* and *Cladonia subulata* could be found. Other open areas get filled up by soil crusts lichens *Placynthiella oligotropha* and the reindeer lichen *Cladonia subulata*. Differences in such a pattern and the development of the lichen thalli are connected to the water availability and the microclimatic conditions (Bültmann and Daniëls, 2001).

Irrespective of the successional pathway, the resulting two feedback mechanisms can be regarded as synergic, and such synergism could be hypothesized to contribute to self-organized surface structures, consisting of run-off generating and run-on receiving BSC patches, each of them associated with a respective regime of nutrients and of pyrite weathering products.

CONCLUSIONS

Two feedback mechanisms were identified for BSCs, mosses and lichens on tertiary substrate of a minesite recultivation area. Sealing of the surface by crust organisms resulted in accumulation of pyrite weathering products and of components of atmospheric deposition within the crust layer, promoting the development of a community adapted to high ionic strength in the soil solution and to low pH (high nutrient low hydraulic feedback). On the opposite, high infiltration caused leaching of these components into deeper soil where a low nutrient high hydraulic feedback mechanism has established. It was concluded that, irrespective of successional pathways, two synergic feedback mechanisms contributed to the generation of self-organized surface patchiness. Such small-scale microsite differentiation with different BSCs has important implications for the natural vegetation recovery in post-mining sites.

Acknowledgements. The authors are grateful to Hans-Georg Wagner (BTU Cottbus-Senftenberg) for his assistance with taxonomy and for providing literature, to Philipp Lange and to Wolfgang Wiehe (BTU Cottbus-Senftenberg) for technical assistance. The authors thank the Lausitzer und Mitteldeutsche Bergbau-Verwaltungsgesellschaft (LMBV) for assistance with necessary permissions. The authors further thank two anonymous reviewers for their truly helpful comments.

REFERENCES

- Arbeitsgemeinschaft Boden, 2005. Bodenkundliche Kartieranleitung. [Soil Mapping Guide]. 5th Edition. Schweizerbart'sche Verlagsbuchhandlung, Stuttgart, pp. 142–147. (In German.)
- Belnap, J., Lange, O.L. (Eds.), 2001. Biological Soil Crusts: Structure, Function and Management. Ecol. Studies 150, Springer, Heidelberg-Berlin-New York.
- Beyschlag, W., Wittland, M., Jentsch, A., Steinlein, T., 2008. Combined beneficial effects of cyanobacterial soil crusts and soil disturbance on germination, establishment and growth of higher plants on nutrient poor sand. *Basic Applied Ecology*, 9, 243–252.
- Bowker, M.A., 2007. Biological soil crusts rehabilitation in theory and practice: an underexploited opportunity. *Restoration Ecology*, 15, 13–23.
- Büdel, B., Veste, M., 2008. Biological soil crusts. In: Breckle, S.-W., Yair, A., Veste, M. (Eds.): *Arid Dune Ecosystems – The Nizzana Sands in the Negev Desert*. Ecological Studies 200, Springer, Berlin Heidelberg New York, pp. 149–155.
- Bültmann, H., Daniëls, F.J.A., 2001. Lichen richness-biomass relationship in terricolous lichen vegetation on non-calcareous substrates. *Phytocoenologia*, 31, 537–570.
- Cutler, N.A., Belyea, L.R., Dugmore, A.J., 2008. Spatial patterns of microsite colonisation on two young lava flows on Mount Hekla, Iceland. *Journal of Vegetation Science*, 19, 277–286.
- Daniëls, F.J.A., Biermann, R., Breder, C., 1993. Über Kryptogamen-Synusien in Vegetationskomplexen binnenländischer Heidelandschaften. [On cryptogamic synusias in vegetational complexes of inland heath landscapes]. *Berichte der Reinhold-Tüxen-Gesellschaft*, 5, 199–219. (In German.)
- Das, B.K., Roy, A., Koschorreck, M., Mandal, S.M., Wendt-Potthoff, K., Bhattacharya, J., 2009. Occurrence and role of algae and fungi in acid mine drainage environment with special reference to metals and sulfate immobilization. *Water Research*, 43, 883–894.
- Düll, R., 1993. *Exkursionstaschenbuch der Moose*. [Excursion Pocket Book of Mosses]. 4th Edition. IDH, Bad Münstereifel. (In German.)
- Elmarsdottir, A., Aradottir, A.L., Trlica, M.J., 2003. Microsite availability and establishment of native species on degraded and reclaimed sites. *Journal of Applied Ecology*, 40, 815–823.
- Eldridge, D.J., Greene, S.B., 1994. Microbiotic soil crusts: a review of the their roles in spoil and ecological processes in rangelands in Australia. *Australian Journal of Soil Research*, 32, 389–415.
- Ettl, H., Gärtner, G., 1995. *Syllabus der Boden-, Luft- und Flechtenalgen*. [Syllabus of soil, air and lichen algae]. Fischer, Stuttgart. (In German.)
- Felinks, B., 2000. Primärsukzession von Phytozoenosen in der Niederlausitzer Bergbaufolgelandschaft. [Primary succession of plant communities in the Lower Lusatian post mining landscape]. Dissertation. Brandenburgische Technische Universität, Cottbus. (In German.)
- Fischer, T., Veste, M., Schaaf, W., Bens, O., Dümig, A., Kögel-Knabner, I., Wiehe, W., Hüttl, R.F., 2010a. Pedogenesis in a topsoil crust three years after construction of an artificial water catchment in Brandenburg, NE Germany. *Biogeochemistry*, 101, 165–176.
- Fischer, T., Veste, M., Wiehe, W., Lange, P., 2010b. Water repellency and pore clogging at early successional stages of microbiotic crusts on inland dunes, Brandenburg, NE Germany. *Catena*, 80, 47–52.
- Fischer, T., Veste, M., Bens, O., Hüttl, R.F., 2012. Dew formation on the surface of biological soil crusts in central European sand ecosystems. *Biogeosciences*, 9, 4621–4628.
- Guiry, M.D., 2013. *AlgaeBase*. Retrieved from <http://algaebase.org/> on 24.06.2013.
- Hallett, P.D., Young, I.M., 1999. Changes to water repellence of soil aggregates caused by substrate-induced microbial activity. *European Journal of Soil Science*, 50, 35–40.
- Hasse, T., 2005. Charakterisierung der Sukzessionsstadien im *Spergulo-Corynephorum* (Silbergrasfluren) unter besonderer Berücksichtigung der Flechten. [Characterization of successional stages in *Spergulo-Corynephorum* (grey hair-grass meadows) under particular consideration of lichens]. *Tuexenia*, 25, 407–424. (In German.)
- Hoppert, M., Reimer, R., Kemmling, A., Schröder, A., Günzl, B., Heinken, T., 2004. Structure and reactivity of a biological soil crust from a Xeric sandy soil in Central Europe. *Geomicrobiology Journal*, 21, 183–191.
- Issa, O.M., Défarge, C., Trichet, J., Valentin, C., Rajot, J.L., 2009. Microbiotic soil crusts in the Sahel of Western Niger and their influence on soil porosity and water dynamics. *Catena*, 77, 48–55.
- Jahns, H.M., 1987. *Farne - Moose - Flechten Mittel-, Nord- und Westeuropas*. [Ferns - Mosses - Lichens of Central, North and Western Europe]. 3rd Edition. BLV, Munich, Vienna, Zurich. (In German.)
- Johnson, D.B., 1998. Biodiversity and ecology of acidophilic microorganisms. *FEMS Microbiology Ecology*, 27, 307–317.

- Kidron, G.J., 2007. Millimeter-scale microrelief affecting runoff yield over microbiotic crust in the Negev Desert. *Catena*, 17, 266–273.
- Kidron, G.J., Vonshak, A., 2012. The use of microbiotic crusts as biomarkers for ponding, subsurface flow and soil moisture content and duration. *Geoderma*, 181–182, 56–64.
- Kidron, G.J., Yaalon, D.H., Vonshak, A., 1999. Two causes for runoff initiation on microbiotic crusts: Hydrophobicity and pore clogging. *Soil Science*, 164, 18–27.
- Kidron, G.J., Yair, A., Vonshak, A., Abeliovich, A., 2003. Microbiotic crust control of runoff generation on sand dunes in the Negev Desert. *Water Resources Research*, 39, 1108–1112.
- Kidron, G.J., Vonshak, A., Dor, I., Barinova, S., Abeliovich, A., 2010. Properties and spatial distribution of microbiotic crusts in the Negev Desert, Israel. *Catena*, 82, 92–101.
- Kinross, J., 2012. The Algal Web, retrieved from <http://algalweb.net/algweb2.htm> 24.06.2013
- LMBV, 2012. Tagebau Schlabendorf-Süd. In: Lausitzer und Mitteldeutsche Bergbau-Verwaltungsgesellschaft mbH (Ed.): Wandlungen und Perspektiven. Lausitzer Braunkohlerevier, Schlabendorf. [Open-cast mining Schlabendorf-South. In: The Lusatian and Central German Mining Administration Company. (Ed.): Changes and Perspectives. Lusatian Mining District, Schlabendorf]. Band 20, Senftenberg. (In German.)
- Linne van Berg, K.-H., Hoef-Emden, K., Marin, B., Melkonian, M., 2012. Der Kosmos-Algenführer. Die wichtigsten Süßwasseralgen im Mikroskop. [The Kosmos-Guide of Algae. Most important freshwater algae under the microscope]. 2nd Edition. Franckh-Kosmos, Stuttgart. 266 pp. (In German.)
- Lukešová, A., 2001. Soil algae in brown coal and lignite post-mining areas in Central Europe (Czech Republic and Germany). *Restoration Ecology*, 9, 341–350.
- Mager, D.M., Thomas, A.D., 2011. Extracellular polysaccharides from cyanobacterial soil crusts: A review of their role in dryland soil processes. *Journal of Arid Environments*, 75, 91–97.
- Menon, M., Yuan, Q., Jia, X., Dougill, A.J., Hoon, S.R., Thomas, A.D., Williams, R.A., 2011. Assessment of physical and hydrological properties of biological soil crusts using X-ray microtomography and modeling. *Journal of Hydrology*, 397, 47–54.
- Meyer, G., Waschkies, C., Hüttel, R.F., 1999. Investigations on pyrite oxidation in mine spoils of the Lusatian lignite mining district. *Plant and Soil*, 213, 137–147.
- Minchin, P.R., 1987. An evaluation of relative robustness of techniques for ecological ordinations. *Vegetatio*, 69, 89–107.
- Moberg, R., Holmasen, I., 1992. Flechten von Nord- und Mitteleuropa. [Lichens of North and Central Europe]. Fischer, Stuttgart, Jena, New York. (In German.)
- Orandi, S., Yaghubpur, A., Sahraei, H., 2007. Influence of AMD on aquatic life at Sar Cheshmeh copper mine. Abstract. In: Goldschmidt Conference, Cologne, Germany, August 2007.
- Rietkerk, M., Dekker, S.C., de Ruiter, P.C., van de Koppel, J., 2004. Self-organized patchiness and catastrophic shifts in ecosystems. *Science*, 305, 1926–1929.
- Rossi, F., Potrafka, R.M., Pichel, F.G., De Philippis, R., 2012. The role of the exopolysaccharides in enhancing hydraulic conductivity of biological soil crusts. *Soil Biology and Biochemistry*, 46, 33–40.
- Schaaf, W., Hüttel, R.F., 2005. Soil chemistry and tree nutrition of post-lignite-mining sites. *Z. Pflanzenernähr. Bodenk.*, 168, 483–488.
- Schaaf, W., Bens, B., Fischer, A., Gerke, H.H., Gerwin, W., Grünwald, U., Holländer, H.M., Kögel-Knabner, I., Mutz, M., Schloter, M., Schulin, R., Veste, M., Winter, S., Hüttel, R.F., 2011. Patterns and processes of initial terrestrial-ecosystem development. *Journal of Plant Nutrition and Soil Sciences*, 174, 229–239.
- Scheffer, M., Carpenter, S., Foley, J.A., Folke, C., Walker, B., 2001. Catastrophic shifts in ecosystems. *Nature*, 413, 591–596.
- Scheffer, M., Carpenter, S.R., 2003. Catastrophic regime shifts in ecosystems: linking theory to observation. *TRENDS in Ecology and Evolution*, 18, 648–656.
- Spröte, R., Fischer, T., Veste, M., Raab, T., Wiehe, W., Lange, P., Bens, O., Hüttel, R.F., 2010. Biological topsoil crusts at early successional stages on Quaternary substrates dumped by mining in Brandenburg, NE Germany. *Géomorphologie: relief, processus, environnement*, 4, 359–370.
- Veste, M., 2005. The importance of biological soil crusts for rehabilitation of degraded arid and semi-arid ecosystems. *Science of Soil and Water Conservation*, 3, 42–47.
- Veste, M., Littmann, T., 2006. Dewfall and its geo-ecological implication for biological surface crusts in desert sand dunes (north-western Negev, Israel). *Journal of Arid Land Studies*, 16, 139–147.
- Veste, M., Breckle, S.-W., Eggert, K., Littmann, T., 2011. Vegetation pattern in arid sand dunes controlled by biological soil crusts along a climatic gradient in the Northern Negev desert. *Basic and Applied Dryland Research*, 5, 1–16.
- Viles, H.A., 2008. Understanding dryland landscape dynamics: do biological crusts hold the key? *Geography Compass*, 2/3, 899–919.
- Wiegand, G., Felinks, B., 2001. Primary succession in post-mining landscapes of Lower Lusatia - chance or necessity. *Ecological Engineering*, 17, 199–217.
- Williams, J.D., Dobrowolski, J.P., West, N.E., 1999. Microbiotic crust influence on unsaturated hydraulic conductivity. *Arid Soil Research and Rehabilitation*, 13, 145–154.
- Wirth, V., 1995. Flechtenflora. Bestimmung und ökologische Kennzeichnung der Flechten Südwestdeutschlands und angrenzender Gebiete. [Lichen Flora. Determination and Ecological Characterization of Lichens in South-West Germany and Adjacent Territories]. 2nd Edition. Ulmer, Stuttgart.
- Wirth, V., Düll, R., 2000. Farbatlas Flechten und Moose. [Color Atlas of Lichens and Mosses]. Ulmer, Stuttgart. (In German.)
- Worldclim, 2014. <http://www.worldclim.org/>, retrieved on 15.03.2014.

Received 30 May 2014

Accepted 16 September 2014

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