



Impacts of cyanobacteria-dominated biological soil crusts on seedling emergence and fate: an in situ experiment

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Abstract

Background and aims Biological soil crusts (BSCs) co-occur with vascular plants in many ecosystems. Nevertheless, little is known regarding the interaction among BSCs and vascular plants, and no standard methods exist aiming to evaluate BSC–plant interactions. While some reports emphasized the inhibition effect of BSCs on germination, others reported the opposite or did not find any differences between germination under crusted and non-crusted conditions. Contradictory findings were also reported regarding the BSC effects on vascular plants after germination,

with some reports claiming that BSCs promote growth, while others claim the opposite.

Methods By a seed addition experiment (using light and heavy seeds of three species belonging to the Fabaceae family) in an early-successional system in Germany, we tested in situ the emergence of seedlings under variable surface conditions (cyanobacterial crust, disturbed and removed crust), and quantified crust–plant interactions (survival, flowering) during and following seedling emergence.

Results In comparison to an average of 8% of the light *Lotus corniculatus* and 20% of the light *Ornithopus sativus* that emerged through the cyanobacterial BSC, 76% of the heavy *Glycine max* emerged. Once emerged, the crust did not significantly affect the survival, growth, biomass, or flowering of *G. max*, whereas many of the seedlings from lightweight seeds dried up soon after emergence. The thickness

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of the cyanobacterial biocrust had no influence on Fabaceae emergence.

Conclusion The cyanobacterial BSC acted as a filter that hindered the emergence of the lightweight seeds.

Keywords Biological filtering · Crust thickness · Eudicots · Phytometer · Seed mass · Soil ecology

Abbreviations

BSC	Biological soil crust
EPS	Exopolymeric substances
SWD	Surface wetness duration
Cyanocrust	Cyanobacterial biocrust

Introduction

Ecosystems develop after initiating situations, whether after severe natural and human-made disturbances such as volcanic eruptions, landslides, dune formation, or surface mining. These new surfaces have no or few biological legacies, and their colonization by plants and animals, and thus the formation of ecosystems starts all over again (Walker and del Moral 2011). The colonization of newly exposed substrates depends on landscape factors such as substrate conditions, as well as hydrometeorological and biotic factors. Among the biotic factors, the composition of the regional species pool and the dispersal abilities of those species (Eriksson 1993; Zaplata et al. 2011), as well as the presence of safe sites and facilitation, play an important role in plant establishment (e.g., Cutler et al. 2008; Fagundes et al. 2018).

In the early stages of primary succession, the growth conditions for plants are stressful and plant cover is low. At these initial stages, poikilohydric cryptogams and particularly autotrophic organisms such as cyanobacteria and green algae (accompanied by heterotrophs such as bacteria and fungi) can play a key role as first colonizers, forming so-called biological soil crusts (BSCs) (Belnap 2003; Bowker et al. 2018; Büdel and Veste 2008; Chamizo et al. 2015; Garcia-Pichel et al. 2013). As substantiated for the Negev desert following the examination of various abiotic conditions, surface wetness duration (SWD) primarily determines the crust properties, such as crust thickness, strength, the amount of exopolymeric substances (EPS), and the species composition of

the crust (Kidron et al. 2003, 2010). For instance, whereas newly established BSCs are less than 1 mm thick (e.g., Prasse and Bornkamm 2000), developed cyanobacterial/green-algae crusts vary between 1–5 mm (Büdel and Veste 2008; Chapin III et al. 1994; Rivera-Aguilar et al. 2005; Zaplata et al. 2021). Whereas cyanobacterial crusts may reflect specific abiotic conditions and can, therefore, be regarded as climax crusts under arid conditions (Kidron and Xiao 2024), they may be succeeded by later successional stages of more developed 5–20 mm-thick crusts, mosses, and lichens (Gypser et al. 2015; Xiao et al. 2016). Mosses and lichens may succeed the cyanobacterial crusts, being particularly predominant in semiarid and humid regions (Eldridge and Greene 1994; Gypser et al. 2015).

Species composition may largely determine the ecological functions of the BSCs (Porada et al. 2023; Verrechia et al. 1995; Weber et al. 2016). They play an important role in surface stabilization (Guida et al. 2023; Kidron et al. 2017), hydrological processes such as runoff generation (Kidron et al. 2003), infiltration (Fischer et al. 2010a; Gypser et al. 2016a; Sun et al. 2022; Xiao et al. 2019), or evaporation (Kidron and Tal 2012), but also by providing carbon and nitrogen to the ecosystem (Elbert et al. 2012; Fischer et al. 2023; Fischer and Veste 2018; Gypser et al. 2016b; Lange et al. 1992; Liao et al. 2024). By triggering runoff, BSCs assist in water redistribution, which in turn can lead to spatial vegetation patterns such as vegetation belts (Kidron 1999; Su et al. 2007; Veste et al. 2011). However, there are also reports that developed BSCs increased infiltration in comparison to early successional BSCs (Belnap et al. 2013), while on the other hand, there were also claims that since moss-dominated BSCs have high water-holding capacity, less water will reach the vascular plant roots in deeper soil layers (Xiao and Hu 2017; Yair et al. 2011).

The formation of BSCs can affect vascular plant growth. By fixing carbon and nitrogen, BSCs ameliorate the fertilization conditions of plants (Beyschlag et al. 2008; Xiao and Veste 2017). In arid regions, shrubs may provide shade and, subsequently, may facilitate longer SWD for crust growth (Kidron and Vonshak 2012). On the other hand, through leaf shading, plants may restrict BSC growth (Berkley et al. 2005). Moreover, in arid zones, the dark and, hence, low-albedo BSCs

may increase evaporation, decreasing, in turn, water availability. It was reported that BSCs impeded plant growth during drought years (Kidron 2014), but hastened plant flowering and decreased plant biomass even during 'normal' years (Kidron 2019).

However, BSC-plant interactions may already be present in the emergence phase. By establishing a firm layer, BSCs may hinder seedling emergence (Kaltenecker et al. 1999; Prasse and Bornkamm 2000), which may particularly affect small seeds (Huang and Gutterman 1998). Research on seedling emergence in an agricultural context shows that the strength of a physical soil crust is positively correlated with its thickness (Awadhwal and Thierstein 1985; Xie et al. 2007; Guo et al. 2008), and that emergence force and seed weight are positively correlated (Castro 1999; Rathore et al. 1981). Nevertheless, in contrast to physical crusts (Hillel 1998), BSCs may be elastic (Breen and Lévesque 2006). This may be especially the case in humid regions where the crust is commonly moist or wet. And yet, as observed in the Hühnerwasser catchment in Germany, field observations in the years prior to the current study year have revealed relatively poor growth over the biocrusts.

Most of the BSC effects on vascular plants were examined in arid regions. Little information exists from humid regions where water is commonly not limiting and, subsequently, the effects of the crusts on runoff or evaporation are subordinate. Also, one may speculate that under the moist conditions in the humid region, the physical barrier that the crust may exert on seedling emergence will be much less pronounced. Our field study was designed to answer the following questions:

(1) Do cyanobacterial biocrusts (cyanocrusts) hinder the emergence of vascular plants? Is it linked to seed size?

(2) Once emerged, do the BSCs affect the flowering and biomass of the vascular plants?

To this end, we placed variable-size seeds of three species in plots and measured their emergence and growth (time of flowering, plant height, and biomass), and we examined abiotic (precipitation, pH, soil water content) and biotic (crust thickness, penetration resistance) variables. Our phytometer study (Clements and Goldsmith 1924) took place over 55 days between 16 June and 11 August 2015.

Materials and methods

Study site

The study was conducted next to the Hühnerwasser catchment (Gerwin et al. 2009; Schaaf et al. 2013a, 2018), Lower Lusatia, Brandenburg, NE Germany. The area was established as part of the restoration program following the coal mining at this site. Soil is sandy to loamy-sandy (Fischer et al. 2010b), corresponding to the soil type of anthropic Regosols from anthropogenic deposits (FAO 1998).

The region is characterized by a humid continental climate (Köppen-Geiger classification Dfb) according to Peel et al. (2007). The nearest climate station Cottbus (Deutscher Wetterdienst – DWD, ID 880) shows a mean annual temperature of 10.0 °C (1991–2020) with the mean temperature during the coldest month (January) of 0.8 °C, and the mean temperature during the hottest month (July) of 19.8 °C. The mean annual precipitation is 566 mm (1991–2020), whereby the mean precipitation in January is 41.5 mm and the mean precipitation in July is 74.8 mm. The previously wet April is the month with the lowest precipitation at 30.6 mm.

A slightly sloping (~2%) area of 350 m² (latitude 51.60426–51.60457; longitude 14.26563–14.26601, WGS 84 coordinates; elevation 131–133 m a.s.l.) was chosen on the western edge of the Hühnerwasser catchment. The top substrate from the site in question was removed in late 2008 and was soon colonized by cyanocrusts, which formed a continuous horizontal layer. Unlike the 2–10 cm-tall lichens that characterize the open spaces in between the mature pine forests in the region, BSCs rapidly inhabited the artificial Hühnerwasser catchment as well as sand dunes in the region, with cyanobacteria accompanied with green algae forming in less than two years (Fischer et al. 2010b; Spröte et al. 2010).

Experimental design

Within the study site, 50 plots of approximately 35 cm×18 cm, covered with cyanocrusts were selected in the open spaces between the higher vegetation. The cyanocrusts in these plots corresponded to level 4 to 6 according to the classification by Belnap et al. (2008) and Zellman (2014). BSCs of class 4 level of development were

characterized by their pale colour and smooth surface, while class 6 crusts were darker and rougher. Mosses, which occurred only in the class 6 crusts, were tiny and just beginning to co-occur naturally with the cyanocrusts, and moss cover was always <10%. Crusts seemed to possess some tensile strength, since cracks were rare.

For the experiment, confamiliar species (related at the family level) were selected, having certain emergence traits in common, e.g., they possess two cotyledons of similar shape. We chose species from the Fabaceae family since this plant family can typically be found in nutrient-poor soils and early succession (Biber et al. 2013; Temperton et al. 2007) and also because it is the third largest terrestrial plant family, which therefore offers many alternatives for species selection on other test sites. The three species chosen were *Lotus corniculatus* L. (birdsfoot trefoil, with weight for a thousand seeds: 1.2 g as reported by Kirmer and Tischew (2006)), *Ornithopus sativus* Brot. (serradella, with weight for a thousand seeds: 3.7 g), and *Glycine max* (L.) Merr. (soybean, with weight for a thousand seeds: 189.4 g).

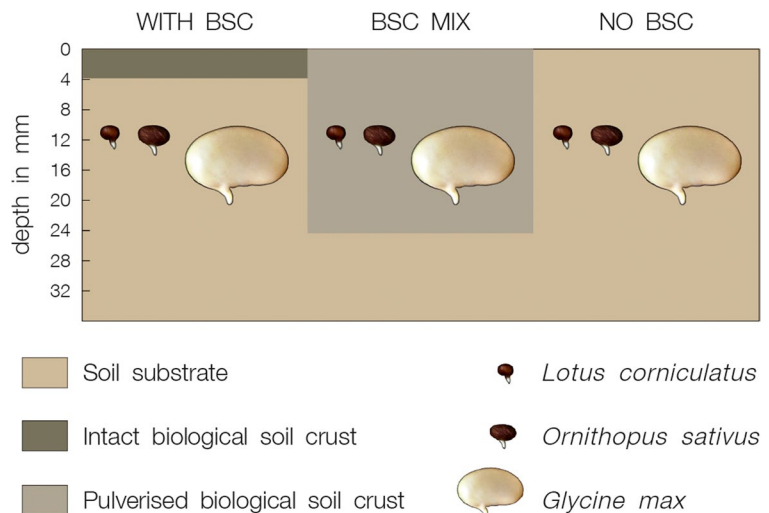
Within each plot, three subplots were created (Fig. 1): in the first, the BSCs remained intact (WITH BSC), in the second, the BSCs were mechanically disturbed (BSC MIX), and in the third, the BSCs were entirely removed (NO BSC), thus representing the within-site control group. As the subplots were immediately adjacent to each other, the experiment can be considered well positioned regarding

small-scale environmental heterogeneity in space (e.g., microtopography influencing runoff and infiltration; McGrath et al. 2012). We used soaked, pre-germinated seeds to focus on emergence (Pflugmacher et al. 2006). To avoid accidental breakage, we used seeds with completely protruded radicles of <1 mm in length.

One pre-germinated seed of each species was placed in each of the subplots. Following previous findings during which the location of the seeds (surface vs. sub-surface) was examined, and to avoid, as much as possible, an adverse effect of the abiotic conditions, we placed the seeds 1 cm under the crust (Fig. 2), or at 1 cm-depth in plots that lacked crust. A total of 150 seeds of each species were used (450 seeds in total). Each plot was watered at the start of the experiment.

In the WITH BSC subplot, we carefully removed substrate from below the crust until crust filaments hanging into the excavated space became visible (Fig. 2a) and a scratching sound was heard; these visual and acoustic cues indicated that the surface layer was ~1 cm. We placed the seeds on a plastic sheet that we held under the crust. Then, the substrate that had been excavated was mixed and replaced under the sheet. Once the space was filled firmly with substrate, the plastic sheet was pulled out. Each seed was at least 5 cm away from the edge of each subplot. We excluded plots where tension cracks in the BSC occurred, as cracks may have created pathways of least resistance for emergence.

Fig. 1 Schematic diagram of the experiment. Each plot possesses the three subplot types. Each experimental group possesses one pre-germinated seed of three vascular plant species of very different seed mass (smallest one: *L. corniculatus*, major: *G. max*, intermediate: *O. sativus*). The seeds were photographed, and their sizes are shown here in the correct relative dimensions. The length of a *G. max* seed was 1.34 cm on average



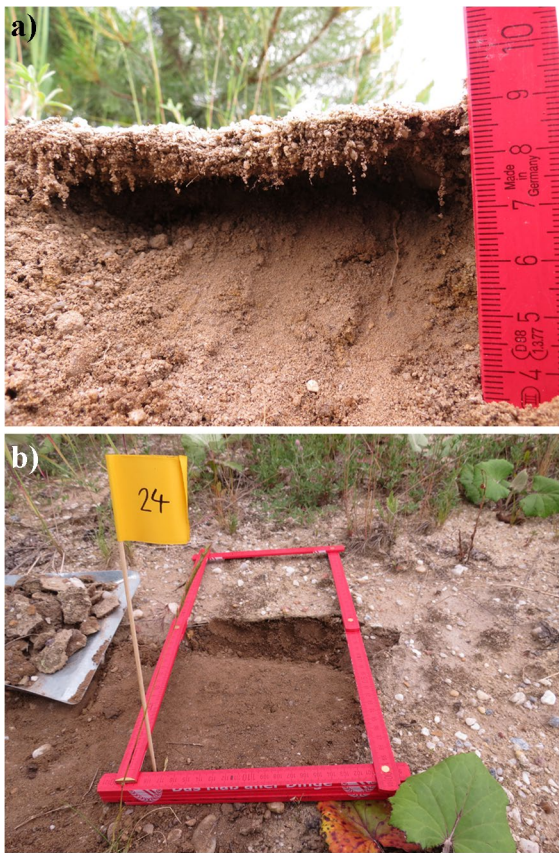


Fig. 2 Photographs showing plot preparation (16 June 2015). The dimensions of the field plots are always around 35 cm × 18 cm. **(a)** Lateral view at the intact crust subplot. **(b)** One plot with its subplots. The subplot types NO BSC (in the foreground) and WITH BSC (in the background) are ready-made. The middle subplot (BSC MIX) was filled with the crust pieces visible at the left after crushing them

To create a BSC MIX subplot in the centre of each plot, we collected BSC from this subplot and from the NO BSC subplot. We manually ground BSC pieces in a pan and applied a 2.5 cm thick layer to the BSC MIX subplot. Thus, the seeds inserted into the BSC MIX subplot were exposed to a substrate with the chemical and mineralogical composition of the crust, whilst their roots were able to reach the mineral soil below easily. The BSC MIX subplots simulated disturbed condition, which in a natural ecosystem, might be caused by trampling or small-scale digging by little animals, and corresponded roughly with the ‘weak disturbance’ regime achieved through raking by Langhans et al. (2010).

After removal of the BSC, some mineral substrate from the BSC MIX subplots was added to the NO BSC subplots by hand, so that the surface was level with the surface of the other subplots (Fig. 2b). NO BSC subplots corresponded to the ‘strong disturbance’ regime of Langhans et al. (2010), where BSCs were completely removed.

Within each plot, there were eight feasible combinations of emergence for each vascular plant species, derived from three subplot types and two possible outcomes (emergence, $\oplus$, and non-emergence, $\times$); yielding $2^3=8$. Both full emergence ($\oplus\oplus\oplus$) and the absence of emergence ($\times\times\times$) of a species in a plot would indicate that the subplots did not differ substantially for that species (no effect). If BSCs promote emergence, we expect the pattern $\oplus\times\times$, $\oplus\oplus\times$, or $\times\oplus\oplus$. If BSCs hinder emergence, seedlings will only appear at the two subplot types with the loosened substrate with or without BSC material ($\times\oplus\oplus$, $\times\oplus\times$, or $\times\times\oplus$). The $\times\oplus\oplus$ emergence pattern depicts the appearance of seedlings in both subplots with manipulated surfaces (BSC MIX and NO BSC), and may point more clearly towards mechanical hindrance rather than seedling emergence.

Data collection

Soil pH was determined from air-dried substrate samples taken from each plot, representing each subplot through composite samples (August 2015). The volumetric soil water content in the top 10 cm of soil in each subplot was measured on 23 July, 2015 with a mobile Time-Domain Reflectometry probe (EasyTest, Lublin, Poland). On the day the experiment ended, 11 August 2015, the cyanocrust thickness was measured in WITH BSC subplots with a vernier caliper immediately next to the base of each plant, or where the plant was expected to emerge if it did not. We collated weather station data (precipitation, as well as air temperature, relative humidity, global radiation, and wind speed to calculate the potential evapotranspiration) from the Hühnerwasser monitoring programme (Schaaf et al. 2013a), that are generally available (Moghadas et al. 2019). To prepare measurements of penetration resistance, pieces of BSC with their underlying sandy material were placed on sieves, saturated with

water from below, and air-dried to different levels of moisture content. The penetration resistances of the BSC pieces were then measured using a digital penetrometer (PCE-PTR 200, Taiwan) equipped with a round head adapter (area = 1 cm²). The gravimetric water content was then determined after oven-drying at 60 °C for 48 h. To identify the BSC organisms, samples were collected from each plot during dry surface conditions during August 2016 (and thus one year after the emergence experiment, which was justifiable according to the authors' field assessment, but admittedly represents a limitation), stored under dry conditions and partially rewetted for viewing (Nikon Eclipse inverted light microscope, Japan). Cyanobacteria were identified by epifluorescence microscopy with a Texas Red filter set, wavelength 542–644 nm, targeting the accessory pigment phycobilin. Digital photos were taken for image analysis (XC10, Olympus, Aartselaar, Belgium; cellID, Roquemaure, France). Identification was based on Ettl and Gärtner (1995) and Komárek (2016).

For each experimental plot, we recorded the number of seedlings that emerged during the period in which the seedlings were small (e.g., <4 cm, June 2015). If a certain species had more emergence in the presence of a cyanocrust than NO BSC, the plot effect was considered to promote seedling emergence. Alternatively, if the number of emerged seedlings was lower in the WITH BSC or MIX BSC areas, we regarded the BSC effect as hindering seed emergence. We also recorded whether emergence led to certain stages of establishment, i.e., the development of hypocotyl and leaves, and we registered the onset of the vegetative phase (growth) and the generative phase (flowering). We quantified the height, the aboveground biomass and the number of flowers for each plant on 5 dates during July and August 2015. After harvesting on 11 August 2015, the aboveground biomass (fresh and oven-dried) was measured, and the number of flowers on each plant was counted.

Statistical analysis

For each vascular plant species, differences in emergence between the three subplot types (WITH BSC, BSC MIX, NO BSC) were analysed by the χ^2 -independence test in the R statistical program (R Development Core Team 2016). A combined analysis of the subplot effects (no effect, promotion,

or hindrance) for the eight feasible combinations of emergence was performed. Since only *G. max* produced sufficient seedlings, we assessed whether the heights, aboveground biomass and number of flowers differed between the three subplot types by performing variance analyses (for normal distributed data: ANOVA, for non-normal distributed data: Kruskal–Wallis *H* test, SPSS (IBM 2016)). We compared BSC thickness and volumetric soil water content for WITH BSC subplots, where plants had emerged and where they had not emerged (for normal distributed data: *t*-tests, for non-normal distributed data: Mann–Whitney *U* tests, SPSS (IBM 2016)). Samples of WITH BSC and the experimentally created BSC MIX plus NO BSC were compared in their penetration resistances by *t*-tests (normal distributed data, SPSS (IBM 2016)). We performed correlation analysis to test for a dependence between BSC thickness and volumetric soil water content.

Results

Crust and plot properties

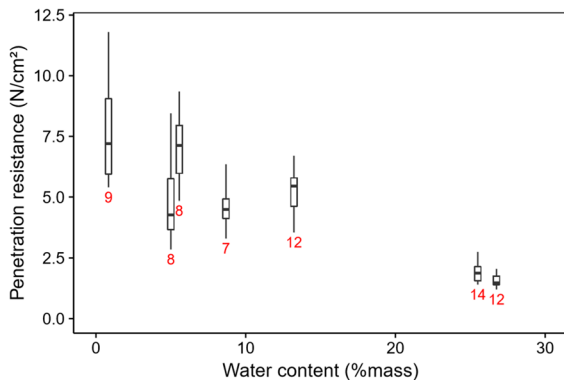
Various non-heterocystous cyanobacteria of the order Oscillatoriales, such as *Microcoleus* sp., *Phormidium* sp., and *Pseudanabaena* spp., and the two nitrogen-fixing cyanobacterial genera *Nostoc* and *Scytonema* of the order Nostocales were identified in the crusts. Filaments of the genus *Microcoleus* were observed on the top and underside of the crusts, composed of gelatinous, fine colorless sheaths in which several densely packed trichomes were present, as shown in Fig. S1e. Sheaths were sometimes simply branched. The end cells of the trichomes rarely had calyptra (Fig. S1f). High numbers of *Nostoc* sp. colonies in gelatinous spheres were found on the top of the crusts (Fig. S1i and j). The green algal species *Klebsormidium* cf. *crenulatum* was also observed at relatively low abundance (Fig. S1l).

The cyanocrusts were between 2.2 and 5.5 mm thick (3.8 ± 0.9 mm; Table S1). All the WITH BSC subplots, regardless of the plant species and whether plant emergence took place, did not show a significant difference in the BSC thickness (as validated by the Mann–Whitney *U* test) (Table 1). The crusts were hard when highly desiccated, while turning softer once wetted and moist. This observation was

Table 1 Mean BSC thickness on WITH BSC subplots where Fabaceae seedlings emerged and failed. The table shows the cyanocrust thickness at the exact locations of the plants or

where they were expected to emerge with standard deviations ($\pm$), sample sizes (n_1 , n_2), Mann–Whitney U (U), Wilcoxon-W (W), and significance indicated by p -value (p)

Plant species	BSC thickness [mm]		Mann–Whitney U test, two-sided			
	Seedlings emerged	Seedlings failed	n_1 , n_2	U	W	p
<i>L. corniculatus</i>	4.3 ± 1.0	3.7 ± 0.8	4, 46	63.5	1144.5	.29
<i>O. sativus</i>	3.6 ± 1.1	3.8 ± 0.8	6, 44	114	135.0	.58
<i>G. max</i>	3.9 ± 0.9	3.5 ± 0.9	38, 12	173.5	251.5	.20

**Fig. 3** Relationship between the crusted surface water content and the penetration resistance. All measurements (numbers given in red) were included in the boxplots. Due to a previous restriction on taking material, the cyanocrust pieces were brought to the laboratory in November 2017

confirmed by the penetrometer measurements, which showed substantially high penetration resistance when dry (Fig. 3).

The penetration resistance followed the order: WITH BSC > BSC MIX > NO BSC. WITH BSC always showed significantly higher values compared to BSC MIX (Table 2, with t -test for differences in the means), while the penetration

resistances of NO BSC were the lowest, 5.3 ± 0.7 N/cm² for more loamy and 4.3 ± 0.5 N/cm² for sandier samples.

Abiotic conditions during the experiment

During the experiment, the mean daily temperature was 19.5 °C and the potential evapotranspiration was, on average, 4 mm per day. In total, 158 mm of precipitation fell during the study period with daily rainfall amounts ≥ 2 mm on 17 days, ≥ 4 mm on 14 days, ≥ 8 mm on 4 days, and ≥ 16 mm on 1 day (Fig. 4).

No significant difference characterized the pH, as measured in August 2015, averaging 7.2 (± 0.23). Moisture measurements of WITH BSC were $12.7\% \pm 2.2$, $11.9\% \pm 2.1$ for BSC MIX, and $12.1\% \pm 2.1$ for NO BSC. When compared by two-sided paired t -tests, the WITH BSC subplot type had significantly different volumetric soil water content compared to the BSC MIX ($df=49$, $t=3.80$, $p=0.00$) and to the NO BSC ($df=49$, $t=2.70$, $p=0.01$). No significant difference was found between BSC MIX and NO BSC ($df=49$, $t=-0.82$, $p=0.42$). Similarly, there was no difference in the volumetric water content of the exact locations where *G. max* plants were

Table 2 Mean penetration resistance for samples regarding WITH BSC and BSC MIX. The table gives mean resistances to penetration [N/cm²] for cyanocrust pieces taken from the field site (WITH BSC) and their BSC MIX derivative. Stand-

ard deviations are indicated by $\pm$. Further, the degrees of freedom (df), the t -test statistics (t), and the significance indicated by p -value (p) are presented

Pieces	Penetration resistance [N/cm ²]		t -test, unpaired, two-sided			
	WITH BSC	BSC MIX	variance	df	t	p
P1	7.83 ± 1.33	4.85 ± 0.82	equal	10	4.82	<.01
P2	13.98 ± 2.19	5.83 ± 1.62	equal	11	7.56	.00
P3	15.45 ± 3.73	7.54 ± 1.15	unequal	4.4	4.62	<.01

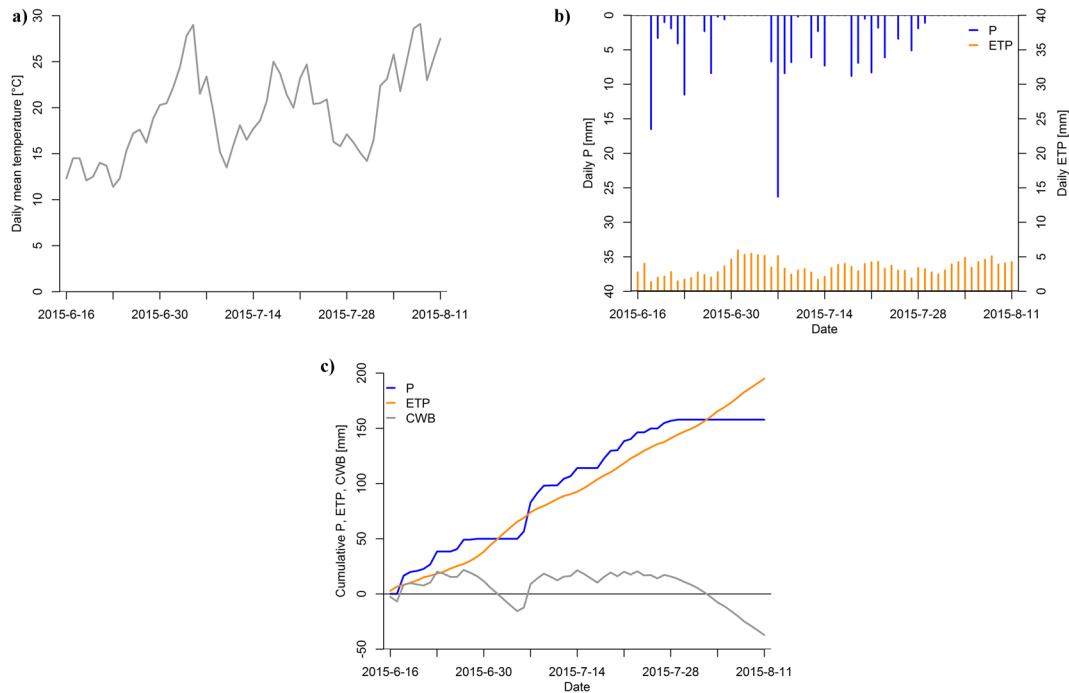


Fig. 4 Meteorological boundary conditions during the field experiment in summer 2015. **(a)** Daily mean temperature [°C], **(b)** Daily precipitation [mm] and daily potential evapotranspiration (Grass Reference ET according to Penman Monteith, [mm]), **(c)** Cumulative precipitation [mm], potential evapotran-

spiration [mm] and climatic water balance (CWB, [mm]) since the onset of the experiment. Data of the closest (~200 m) Hühnerwasser weather station was used; recording gaps were filled with data from a second Hühnerwasser weather station

Table 3 Mean volumetric water content of subplots where plant species were emerged and where emergence failed. For the locations where plants of the three test species were present (seedlings emerged) or absent (seedlings failed), the mean

water contents [%vol] with standard deviations ($\pm$), and details of the test method, such as the degrees of freedom (df), the t -test statistics (t), and the significance indicated by the p -value (p) are given

Plant species	Water content [%vol]		t -test, unpaired, two-sided			
	Seedlings emerged	Seedlings failed	variance	df	t	p
<i>L. corniculatus</i>	12.37 ± 2.24	12.16 ± 2.15	equal	148	0.51	.61
<i>O. sativus</i>	12.12 ± 2.21	12.26 ± 2.15	equal	148	-0.37	.71
<i>G. max</i>	12.26 ± 2.11	12.13 ± 2.27	equal	148	0.35	.73

present compared to those locations where the plants failed to emerge (Table 3, with t -test for differences in the means). However, there was a significant correlation (Spearman's $\rho=0.40$) between the cyanocrust thickness ($n=50$, not normally distributed) and soil moisture ($n=50$, normally distributed).

Seedling emergence and growth

The number of emerged seedlings differed according to subplot type. Whereas the emergence of *L. corniculatus* and *O. sativus* was significantly enhanced in subplots where the BSC had been destroyed or removed, no influence was registered for *G. max* (Table 4). Thus, hindrance by BSCs was observed most often for *L. corniculatus* (in 24 plots), slightly

Table 4 Absolute and relative emergence frequencies of three Fabaceae species as determined on 02 July 2015. The table shows the emergence frequency among the test species with different seed mass and the three subplot types, degrees of freedom (*df*), sample size which is the number of pre-germinated seeds placed in the ground on 16 and 17 June 2015

Plant species	Subplot type				Chi-square independence-test			
	WITH BSC	BSC MIX	NO BSC	Total	<i>df</i>	<i>n</i>	<i>Chisq</i>	<i>p</i>
<i>L. corniculatus</i>	4 (8%)	17 (34%)	14 (28%)	35 (23%)	2	150	10.36	< .01
<i>O. sativus</i>	10 (20%)	24 (48%)	21 (42%)	55 (37%)	2	150	9.36	< .01
<i>G. max</i>	38 (76%)	40 (80%)	38 (76%)	116 (77%)	2	150	0.30	.86

less often for *O. sativus* (22 plots), and least often for *G. max* (12 plots). As monitored on July 2, only 23% of *L. corniculatus* emerged. *L. corniculatus* appeared to be the most susceptible in the experiment, with many individuals turning discolored (cotyledons became yellow and whitish) and then dying. At the same time, 55 individuals of *O. sativus* were present (37%). This species appeared to be more robust than *L. corniculatus*, but some individuals also turned yellow (Fig. S2a, hardly recognisable due to the lack of color contrast with the substrate). In contrast, post-emergence mortality of *G. max* was the lowest, with 116 individuals (77%) being present on June 30 (Table 4, Table S2). The high resilience of this species was registered in subsequent observations (Table S2, Fig. S2b, Fig. S3a). No mortality was observed even following herbivory. A promoting effect was observed for *L. corniculatus* in 2 plots, for *O. sativus* in 4 plots, and for *G. max* in 13 plots (Table 5). In comparison to 2 cases for the particularly light seeds of *L. corniculatus* and 6 cases for the light seeds of *O. sativus*, in 20 cases the heavy seeds of *G. max* emerged from all subplots of each plot. Overall, and as seen in Table 5, the emergence of the vascular plant types is related to the three possible effects: no effect, promotion, and hindrance (χ^2 -independence-test; $df=4$, $n=150$, $\chi^2=15.15$, $p=0.00$).

The success of *G. max* was also observed in subsequent monitoring. *G. max* reached heights of about 10 cm at the end of the experiment. The height was similar in all subplot types at all times of measurement (Table 6). Similarly, the weight and dry matter content of all *G. max* (regardless of plot size) were not statistically different between the subplot types. In each subplot type, 12 of the 50 *G. max* plants flowered. The number of flowers per flowering plant

(*n*), chi-square statistics (*Chisq*) and significance indicated by *p*-value (*p*). Seedlings whose hypocotyl temporarily formed a loop due to (semi-physical or semi-biological) re-encrustation until full emergence were also considered (this only occurred in *G. max*)

(mean $\pm$ stdev; WITH BSC: 2.8 ± 1.4 ; BSC MIX: 2.3 ± 1.3 ; NO BSC: 2.3 ± 1.1) was statistically similar for each subplot type (ANOVA: $df_b, df_w=2, 33$, $F=0.75$, $p=0.48$). However, the total number of flowers was higher for the WITH BSC group (34; BSC MIX: 28; NO BSC: 27). For the other two species, the number of individuals was too small for further statistical analyses of plant height.

Discussion

Plant emergence

Biological soil crusts (BSCs) form at the surface of the soil, in the critical zone between above and below ground (Belnap et al. 2003). By forming a barrier, seedlings may be unable to reach the air (if the seeds are beneath the crust, as in our research) or the mineral soil (if the seeds are on top of the crust: Chapin III et al. 1994; McIlvanie 1942; Rivera-Aguilar et al. 2005). McIlvanie (1942) noted that seeds lying on the ground were not able to reach the subcrust, dried out, and died. Sylla (1987) expanded on the barrier effect exerted by the BSC. Similarly, and following field observations or experiments, Boudell et al. (2002), Danin (1978), Deines et al. (2007), Eckert et al. (1986), Langhans et al. (2009), Li et al. (2005), Prasse and Bornkamm (2000), and Zhang et al. (2016) reported on the impediment effect of BSCs on seedling emergence, which therefore exhibit higher emergence from cracks or non-crusted surfaces. Contrasting conclusions, however, were reported from greenhouse experiments. Crusted surfaces were repeatedly reported to have a higher germination rate,

Table 5 Number of plots showing effects of crusts as expressed by emergence pattern of three Fabaceae species in subplots; “” typify seedling emergence, whereas “×” indicate the plant did not emerge. Pre-germinated seeds of the

Fabaceae species *L. corniculatus*, *O. sativus* and *G. max* were placed in the ground on 16 and 17 June 2015, these emergence patterns were found on 02 July 2015

Effect of crust	Emergence pattern in subplots			Plant species		
	WITH BSC	BSC MIX	NO BSC	<i>L. corniculatus</i> 	<i>O. sativus</i> 	<i>G. max</i> 
	×			2	9	5
hindrance	×		×	13	8	4
	×	×		9	5	3
	Total			24	22	12
none	×	×	×	22	18	5
				2	6	20
	Total			24	24	25
promoting			×	0	1	8
		×		1	1	2
		×	×	1	2	3
	Total			2	4	13

Table 6 *G. max* heights and weights by subplot types. The table gives mean plant heights [cm] for specified dates, fresh and dry weights [g] after harvest of the aboveground biomass on 11 August 2015, standard deviations (after±), the test

method (Kruskal–Wallis H : abbreviated K-W H), degrees of freedom between groups (df_b) and within groups (df_w), the F test statistics (F), the chi-square statistics ($Chisq$). Significance is given by p -values (p)

Subplot type	Height [cm]		13 July	29 July	11 August	Weight [g]	
	02 July	07 July				fresh	dry
WITH BSC	4.4 ± 1.24	5.7 ± 1.25	7.2 ± 1.24	9.0 ± 1.47	10.4 ± 1.90	1.41 ± 0.46	0.54 ± 0.18
BSC MIX	4.1 ± 1.03	5.3 ± 1.06	6.8 ± 1.19	8.8 ± 1.31	10.4 ± 1.78	1.42 ± 0.55	0.58 ± 0.21
NO BSC	4.5 ± 0.95	5.6 ± 0.99	7.2 ± 0.84	9.0 ± 1.12	10.3 ± 1.53	1.51 ± 0.49	0.58 ± 0.19
Test method	ANOVA	ANOVA	ANOVA	ANOVA	K-W H	K-W H	ANOVA
df_b , df_w	2, 97	2, 91	2, 91	2, 91	2, 91	2, 90	2, 90
F	1.53	1.38	1.10	0.23			0.39
$Chisq$					0.62	1.25	
p	.22	.26	.34	.79	.73	.54	.68

especially if water was not limited (Hawkes 2004; St. Clair et al. 1984; Su et al. 2007). However, under limited water conditions, a lower percentage of seeds was reported even under lab conditions (Serpe et al. 2006). Some scholars emphasized the effect of seed size (Funk et al. 2014), with Li et al. (2005) reporting that small seeds had an advantage over large seeds.

All the above scholars regarded BSCs as a kind of barrier. BSCs, as observed in this study, indeed function as a mechanical growth barrier, facilitating higher emergence for heavier seeds but impeding the emergence of lightweight seeds. In this way, BSCs were certainly involved in the transient pattern formation in the initial plant colonization of the artificially created Hühnerwasser catchment area (Fig. S3b). The barrier imposed by the crust may resemble physical crusts (Awadhwai and Thierstein 1985; Rathore et al. 1981) when a BSC is dry.

The heavyweight seeds of *G. max* most frequently overcame the BSC obstacle, indicating that the force exerted by the crust was below the threshold required to impede *G. max* emergence. This was not the case for the lightweight seeds of the two other species. Having thinner radicles, they were unable to overcome the necessary strength imposed by the crust. This was supported by a parallel experiment in which seeds of *G. max* were sown in sandy but fertile garden soil at the first author's home address in 15299 Müllrose. While becoming much taller, their emergence corresponded to the highest emergence rate in our study (~80%). Interestingly, however, there was no correlation between crust thickness and seedling emergence (Table 1). This was somewhat different from the results of Huang and Gutterman (1998), in which emergence only occurred through cracks in thicker cyanocrusts. However, in the study by Huang and Gutterman (1998), the thicker BSCs were coated with a layer of approximately 0.5 cm of alluvial loess, which may have added additional strength to the crust due to its compactness.

Our data suggest that the presence of a thick cyanocrust may retain more water than a thin crust, an expected outcome given the higher water-holding capacity of biocrusts (Kidron et al. 2010). The crusts may also increase the water content of the soil immediately below the crust, as also reported by Li et al. (2006) and Li et al. (2013), who found lower wetting fronts on crusted surfaces. Rossi et al. (2012) explained that significantly increased hydraulic conductivity in BSCs may be due to the presence of extracellular polymeric substances (EPS), likely by

increasing the number of micropores or their stability within BSCs. Very close to our experimental site, within the fenced part of the Hühnerwasser catchment, a positive link between the presence of crust and soil moisture (Table S1) was already demonstrated by Schaaf et al. (2013a, b). Under the frequent rain events (and subsequent cloudiness) in our region, such findings are rather expected. Contrary to arid regions, where high evaporation leads to plants' rapid desiccation (Kidron 2014), frequent rainfall coupled with low evaporation implies a comparatively high surface moisture content (Kidron et al. 2022).

The negative correlation shown between the water content of the crust and penetration resistance (Fig. 3) implies that the force exerted by the dry crust is higher than the 3.9 N/cm² found to impede seedling emergence (Arndt 1965). Moreover, even under moderate water content, the crust may exert higher strength (Fig. 3). Thus, whereas a thickness-dependent crust strength may drastically affect seedling emergence (Prasse and Bornkamm 2000; Su et al. 2007), an apparent contradiction was noted: no correlation was found between crust thickness and seedling emergence, which are intuitively linked.

This discrepancy could be addressed if the clear dependence of crust strength and water content is considered. With thick crusts having high water-holding capacity (and therefore retaining their water for longer durations), water decreased the penetration resistance of the thick crusts. The water content of the crusts (which is higher in thick crusts) compensates for the higher strength of the thick crusts, leading to the current findings: while crust strength principally affects seedling germination, no link was found between crust thickness and seedling emergence. The higher water content of the thicker crust decreased the likely higher penetration resistance of the thicker crust. Interestingly, the penetration resistance of the crusts at our site was approximately twice as high as those measured in the Negev, being even higher under moderate moisture content than the dry crusts of the Negev (Kidron et al. 2010). While this can be explained by the difference in crust thickness (1–3 mm in the Negev versus 2–5.5 mm in Hühnerwasser), it may also stem from the presence of amorphous silica that acts as a cementing material (Felix-Henningsen 2000; Milnes and Twidale 1983). The high penetration resistance of the cyanocrusts at our site could possibly also anticipate the higher post-emergence mortality of seedlings from small-size

seeds. As commonly suggested (Gross 1984; Gross and Smith 1991), the size effect may be even more pronounced under adverse conditions.

Plant growth

BSCs could contribute to the vast changes in the plant species dominating the system, which are defining characteristics of early successional phases (Zaplata et al. 2013). This was found for the Arctic (Bliss and Gold 1999; Breen and Lévesque 2006) as well as for deserts (Kidron 2014, 2019). While some scholars maintain that the crusts decrease evaporation, resulting in higher water content available for plants (Breen and Lévesque 2006; Zellman 2014), others argue to the contrary (Kidron 2014, 2019). Similarly, while increasing surface temperatures and therefore improving the heat regime for plants in the Arctic (Gold 1998), increased surface temperatures in deserts increase evaporation, subsequently decreasing water availability for plants (Kidron and Tal 2012).

One of the possible effects mentioned frequently by various scholars is that by providing nutrients, BSCs increase plant biomass (Harper and Marble 1988). No such effect was observed during the current research. Plant growth and biomass were not significantly higher in biocrusted plots. This was in agreement with Kidron (2019), who compared plants of the same species that grew on crusted and non-crusted dunes. It was found that biomass and fecundity of those plants that grew on the non-crusted dune sections were significantly higher than those of the plants that grew on the BSCs, implying that despite the poor nutrient status of the mobile (non-crusted) dunes, no shortage of nutrients was evident, substantiating the cardinal effect of water on plant biomass. Yet, while the biocrusts were found to reduce the subsurface water content in the Negev, triggering in turn flowering (Kidron 2019), an increase in the subsurface temperatures may have triggered flowering in our catchment.

Conclusions

The effect of intact cyanobacterial and mechanically disturbed biocrusts, in comparison to bare sand, on the emergence and growth of three species of the Fabaceae family was investigated. We examined three species, two of which were characterized by lightweight seeds (*L. corniculatus*, *O. sativus*), and one

characterized by heavy seeds (*G. max*). By inserting the pre-germinated seeds under the crusts, we avoided the loss of seeds due to germination failure, herbivores, or episodic drying during warm weather spells. A clear difference in emergence success was noted, with the lightweight seedlings having a very low emergence success. Following further mortality of the lightweight seeds, statistical analysis of growth was therefore confined to the heavyweight species *G. max*. In comparison to bare soil, the cyanocrust did not have a significant effect on the height, biomass, or number of flowers of *G. max*. The crust effect is explained by the high penetration resistance of the crust. The lack of correlation between crust thickness and emergence is explained by the higher water content of the thick crust, which acted to compensate for the extra strength imposed by the thicker crust. This was possible given the frequent rain events at our site and therefore the relatively high water content of the crusts. It is suggested that, contrary to the rapid drying of crusts in arid regions, the prolonged wet conditions at our site and the subsequently the higher water content of the thick crust compensated for the expected high penetration resistance of the thick crust.

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Data availability All data are given in this article or its electronic supplementary material.

Declarations

Competing of interest The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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