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The contribution of the phototrophic fraction in the fertility of different successional stages of induced biological soil crusts

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Abstract

Inoculation of cyanobacteria has been studied as a valuable approach to promote soil stabilization and fertilization and counteract the erosion of marginal soils. One of the results of the inoculation of cyanobacteria is the formation of biological soil crusts, or biocrusts, which are complex soil communities playing a pivotal role in providing essential ecosystem services in drylands. While numerous studies have addressed the effects of different biocrust attributes on ecosystem functions, few studies have focused on the distribution of biocrust successional stages in the soil and their link with soil fertility properties. In this work, we investigated how the distribution of biocrust types (cyano-crust; cyano/moss crust, and moss crust) is related to soil nutrient status. We evaluated phototrophic abundance, exopolysaccharide production, and nutrient content in distinct biocrust types in an experimental area in the Hopq Desert, China, where their occurrence had been induced by cyanobacteria inoculation. In addition, we investigated the correlation between these variables. Photosynthetic pigment content, total carbohydrates, exopolysaccharides, organic C, and total N increased during the biocrust maturation stages. We found significant correlations between the levels of organic C, total carbohydrates, and total N with the abundance of diazotrophic cyanobacteria. Organic N was greater in the cyano/moss crust, while available P accumulated mainly in the cyano-crust. The three biocrust types are essential to each other as each represents a stage in which distinct nutrients are stored. This study complements previous studies by offering a more comprehensive view of how phototrophic variability in the distribution of biocrusts dominated by cyanobacteria or by mosses is closely interconnected with nutrient content and biocrust development.

Keywords Dryland soils · Scytonemin · Exopolysaccharides · Nitrogen · Phosphorus · Cyanobacteria/Mosses

Introduction

Cyanobacteria are photoautotrophic prokaryotes able to colonize very diverse habitats across the world and act as important primary producers and N_2 fixers in many terrestrial environments (Rikkinen 2017). Some species of cyanobacteria are encompassed between the ecosystem engineers as a result of their ability to form biological soil crusts, or biocrusts (Gilad et al. 2004), complex communities naturally occurring at the soil surface in many low-productivity terrestrial ecosystems. Biocrusts are composed of varying proportions of phototrophs (cyanobacteria, microalgae, bryophytes, lichens), heterotrophic organisms (bacteria, fungi, archaea), and viruses (Mugnai et al. 2021; Weber et al. 2022). They contribute to important ecological functions, intervening in carbon (C) and nitrogen (N) fixation (Belnap 2006), nutrient cycling (Elbert et al. 2012; Strauss et al. 2012), soil stabilization (Rossi et al. 2018), and surface hydrological cycles (Adessi et al. 2018; Cantón et al. 2020; Eldridge et al.

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2020). Due to their contribution to ecosystem functions and their global relevance for terrestrial ecosystems (Rodriguez-Caballero et al. 2018), they are receiving scientific attention as valuable biotechnological tools for land rehabilitation and restoration (Rossi et al. 2017; Antoninka et al. 2020; Chamizo et al. 2020).

On loose substrates, pioneer cyanobacterial species can promote the development of cyanobacterial biocrusts (hereafter cyano-crust), an incipient stage of biocrusts in which cyanobacterial filaments and cyanobacteria-secreted extracellular polymeric substances (EPSs) produce stable soil aggregates (Mugnai et al. 2018a). To date, cyanobacteria are the only microbial group that has been used for large-scale inoculation experiments to promote biocrust development (Zhou et al. 2020a) and the only type of microbial inoculant for which long-term effects of inoculation have been evaluated through follow-up studies (Wang et al. 2009; Lan et al. 2014). Cyanobacterial inoculation trials conducted in the field at experimental sites in Qubqi (Hobq) Desert, Inner Mongolia, began in 2001 (Hu et al. 2012). These inoculation treatments concretely resulted in the development of biocrusts that reached different stages of development, characterized by the dominance of phototrophs (mainly cyanobacteria and microalgae) or the dominance of mosses and/or lichens in the crust biome (Lan et al. 2013). Progression towards "more mature" biocrust stages that include mosses or lichens is not a given, and is strictly dependent on the balance with environmental stresses, even at the microscale. Biocrust development is affected by climate, topography, vegetation (and plant litter), disturbance, and rainfall (Ju et al. 2021). It has been observed how "immature" biocrusts lacking mosses or lichens and rich in cyanobacteria can persist for years at that stage (Li et al. 2013, 2016) representing stable climax communities (Kidron and Xiao 2024). The result of this uneven development is the "patchy" biocrust spatial arrangement of the biocrust mat at the topsoil, where biocrusts densely colonized by mosses or lichens are interspersed with less-developed biocrusts dominated by cyanobacteria in a continuous mosaic pattern (Li et al. 2016). This pattern is a common feature in natural environments (Bowker and Maestre 2012) while it has never been observed on a laboratory scale for controlled studies, probably due to the extent to which natural environmental conditions can be reproduced. Biocrust induction in the Hobq desert field has resulted in the fixation of sand dunes, a progression from "sand" to "soil" owing to the increase in silt and clay particles, and a significant fertilizing effect (Wang et al. 2009; Lan et al. 2014).

The photoautotrophic fraction of the biocrust community is responsible for about 50% of the C fixed as EPS or extracellular C (Rogers and Burns 1994) and of the release of N in organic and inorganic forms (Barger et al. 2016). In this context, diazotrophic cyanobacteria, such as *Nostoc* spp. and *Scytonema* spp., are very important for nutrient availability. This group of cyanobacteria colonizes biocrusts spontaneously following the establishment of the non-heterocystous pioneer species (Becerra-Absalón et al. 2019), often recognized in members of the genera *Microcoleus* (Couradeau et al. 2016) and recently also in members of the genera *Trichocoleus* and *Leptolyngbya* (Roncero-Ramos et al. 2020). Heterocystous cyanobacteria have a higher ability to fix atmospheric N than non-heterocystous ones, thanks to the physical separation between nitrogenase activity (taking place in the heterocysts) and oxygenic photosynthesis (Issa et al. 2014). By providing available N, the phototrophic biocrust fraction exerts a great influence on the coexisting heterotrophic species, promoting synergical interactions between species and/or promoting the activity of soil organic matter (SOM) decomposers (Maier et al. 2018). When colonization of mosses or lichens occurs, biocrusts acquire greater capacity to contribute to ecosystem functions, playing central roles in soil fertilization, N fixation, particle aggregation, carbon storage, water regulation, and soil stabilization (Rodriguez-Caballero et al. 2018).

In recent years, significant progress has been made on cyanobacteria inoculation technology at laboratory scale. Heterocystous and non-heterocystous strains have been employed to assess their potential contributions to soil fertility and biocrust formation (Rossi et al. 2022). In parallel, several field studies have investigated the various factors influencing biocrust succession (Zhou et al. 2020b; de-Bashan et al. 2022; Mugnai et al. 2024) or new biomarkers to identify the successional trajectory in biocrusts (Zhao et al. 2023). Biocrust succession depends on multiple factors, including time scale, geographical area, and other deterministic variables, such as climate and soil properties. The strong interaction of these factors at the macroscale contributes to defining the trajectory of biocrust succession and the presence of different biocrust morphotypes. However, the investigation of spatial patterns influencing biocrust succession at the micro-landscape scale (ranging from centimeter to meter) remains largely to be conducted.

Despite several researches demonstrating that biocrusts dominated by mosses (henceforth moss crust) represent the climax of biological soil crust succession in dryland ecosystems (Lan et al. 2015; Deng et al. 2020), a recent study evidenced that under conditions of low water availability, cyano-crust is both the initial and final (climax) stage, resulting in a stable community with no further biological changes (Kidron and Xiao 2024).

In this context, our study aims to answer the following questions: **i**) What is the contribution of different induced biocrust successional stages to soil fertility? **ii**) What are the connections between soil nutrients, EPS secretions, and phototrophic abundance that potentially characterize induced biocrust succession? The answer to these questions would

provide a key clue to understanding the micro-scale colonization dynamics associated with phototrophic components and their role in the areal distribution related to soil chemical composition. In addition, this study may provide important information to improve inoculation biotechnology, optimizing its effect to increase soil fertility.

Material and methods

Description of the experimental site

The "Working Station for Desertification Control" is located in Dalate County (40°24′09″N, 109°59′52″E), on the eastern edge of the Hobq Desert, Inner Mongolia, on a plateau with an elevation of 1040 m. The climate of this area is classified as semiarid and continental monsoon, with temperatures ranging between 40.2 °C and -34.5 °C and between 66 °C and -39 °C on the ground. Windy days (>5 ms^{-1}) per year are more than 180, while the mean annual precipitation is 293 mm, with a mean annual evaporation of 2448 mm (Rao et al. 2009; Zheng et al. 2018). Fog and dew are abundant occurring for more than 40% in the mornings (Zheng et al. 2018). The experimental area is sparsely colonized by *Elymus dahuricus, Artemisia desertorum, Sophora alopecuroides, Medicago sativa*, and *Cassia tora* (Zheng et al. 2018). Before inoculation, the sandy substrate was characterized by shifting dunes with an average height of 5 m (Li et al. 2014). It had a pH of 8.6, and average contents of total N, organic C, and $CaCO_3$ of 0.19, 0.41, and 4.48 g kg^{-1}, respectively (Wang et al. 2009). The site was inoculated in 2003 with a liquid suspension of a mixed inoculum of autochthonous *Microcoleus vaginatus* (Gom.) and *Scytonema javanicum* (Born et Flah.) in a 10:1 ratio, that was sprayed from a tanker truck equipped with a mounted sprinkler. The detailed inoculation procedure is reported, among others, in Li et al. (2013), Colica et al. (2014), and Rossi et al. (2017). From 2001 to 2005 the cyanobacterial inoculation involved an area of approximately 3.3 ha and the coverage of biological soil crusts was over 70% (Hu et al. 2012).

Sample collection

Biocrust sampling was conducted in July 2016. Samples were collected according to the stage of biocrust development as in Lan et al. (2013), who distinguished biocrusts based on the dominant organisms in the biocrusts and the degree of moss colonization. Based on this assumption, we collected three types of samples: one biocrust type dominated by cyanobacteria and devoid of moss colonization ("cyano-crust"); a second type representative of the most developed biocrusts, *i.e.*, colonized by moss species such as *Synthrichia caninervis*, *Bryum argenteum* and *Didymodon vinealis* (Zhou et al. 2020b) for at least 75% of the surface ("moss crust"); and a third intermediate type, collected at the confluence between the other two biocrust types and having moss colonization for 25–75% of the surface ("cyano/moss crust"). Uninoculated sand samples collected outside the fenced experimental area were assumed to be the situation prior to cyanobacterial inoculation and thus used as a control.

Three 40×40 cm square frames delineating sampling points within the site were randomly placed at three different locations (experimental replicates, $N=3$), in spaces devoid of small plants or shrubs (Table S1). The sampling points were separated by roughly 40 m from each other, with vegetation interposing them, thus reducing any possible mutual interference. Three pseudo-replicates ($n=3$) per biocrust type (cyano-crust, cyano/moss crust, and moss crust) were sampled within each square frame using a 75 mm clean circular knife which was pressed approximately 5 cm into the soil. Plastic bags were used for sample collection and transport; once in the laboratory, the samples were air-dried and homogenized with mortar and pestle before analysis. Soil moisture (water content by volume) of each biocrust type was measured with a soil moisture meter (TZS-II. HEB Biotechnology; Fig. S1).

Morphological characterization of biocrust cyanobacteria

Preliminary inspection of the biocrust samples for cyanobacterial morphotypes present was conducted under an optical microscope (Zeiss Axioskop microscope, Carl Zeiss, Jena, Germany), after removing possible colonizing mosses, wetting, and slightly sectioning the samples to allow light penetration and observation in bright field. At least three biocrust samples for each biocrust type were inspected at the sub-sample level. To obtain more detailed images of the most recurrent morphology of cyanobacteria and for more accurate morphological identification of them, we proceeded with isolation. Briefly, crust fragments were immersed in BG11 and $BG11_0$ sterile liquid media to isolate heterocystous and non-heterocystous strains, respectively (Rippka et al. 1979), and incubated under the illumination of 20 µmol photons m^{-2} s^{-1} and at 25 °C, until green coloration was visible in suspension. Next, the culture suspension was concentrated by centrifugation $9500\times g$ at 8 °C for 5 min and repeatedly spread onto BG11 and $BG11_0$ agar plates maintained in the conditions described above. Single colonies were finally withdrawn with a sterile loop from the agar and re-suspended in liquid BG11 and $BG11_0$ media, in Pyrex flasks incubated in an orbital shaker (Innova 44B, New Brunswick, USA) under continuous illumination (light intensity = 20 µmol photons m^{-2} s^{-1}). To further purify the

cultures, the strains were transferred to BG11 and $BG11_0$ liquid media supplemented with 100 µg mL^{-1} cycloheximide (Sigma Chemical Co.) to remove eukaryotic contamination. The culture was then incubated for 22 h in the dark with three other antibiotics (ampicillin, rifampicin, and ciprofloxacin) to selectively kill heterotrophic bacteria (Ferris and Hirsch 1991). Morphological identification of isolates was carried out by using appropriate taxonomic keys (Komárek and Anagnostidis 1999, 2005). Morphological traits such as the presence of heterocysts and sheats, trichome characteristics, or cell and colony morphology were used for genus identification.

Total carbohydrate content

Total carbohydrates of the biocrust samples were quantified according to Mugnai et al. (2018b). A 30-mg aliquot of homogenized biocrust sample was suspended in 1 mL of distilled water and mixed with 1 mL 5% phenol and 5 mL H_2SO_4 in screw-cap glass vials (Dubois et al. 1956). The mixture was shaken vigorously, lifting the cap briefly to allow degassing. Subsequently, the mixes were allowed to stand for 10 min. The vials were then cooled in water for 15 min. The total carbohydrate concentration was finally measured with a UV–VIS spectrophotometer (Varian Cary 50, Varian Inc., Palo Alto, CA, USA) by reading the absorbance of the reaction mixture at 488 nm. The calibration curve was performed using D-glucose at different concentrations as the standard. At least three determinations were carried out for each biocrust sample.

Fractionated extraction and quantification of EPSs in biocrusts

EPSs were extracted from biocrust samples as two operationally defined fractions: one water-soluble (henceforth loosely bound EPSs, LB-EPSs) and one more tightly bound to cells and sediments (henceforth tightly bound EPSs, TB-EPSs). We applied the method described in Swenson et al. (2018). Briefly, 3 g of each biocrust sample, previously homogenized with mortar and pestle, was suspended in 10 mL of distilled water for 15 min and shaken vigorously at fixed intervals. Then, the samples were centrifuged at 4,000 × *g* at 8 °C for 30 min to recover the supernatants containing LB-EPSs. Water extraction was repeated three times on each sample to significantly recover all soluble EPSs. For recovery of TB-EPSs, the pellets resulting from the previous extractions were suspended in 10 mL of distilled water and incubated at 80 °C for 1 h. Next, the samples were centrifuged at 4,000 × *g* at 8 °C for 30 min to recover supernatants containing TB-EPSs. Cellular integrity, and thus the absence of intracellular material owing to leakage, was checked by the quantification of chlorophyll *a* in the extracts (see below). Quantification of LB-EPSs and TB-EPSs after extraction was conducted by the phenol–sulfuric acid assay (Dubois et al. 1956).

Quantification of pigments in biocrusts

Chlorophyll *a* was determined as a proxy of phototropic abundance in the different biocrust types. Scytonemin was determined as an index of the abundance of heterocystous cyanobacteria. Pigments were extracted from biocrusts and quantified according to Couradeau et al. (2016). After the homogenization process, 1 g of biocrust sample was treated with 90% acetone at 4 °C for 24 h. Extracts were then cleared by centrifugation at 3500 × *g* for 20 min and the supernatants were analyzed by UV–Visible Spectrophotometer (Varian Cary 50, Varian Inc., Palo Alto, CA, USA) recording absorbance at 663 nm, 490 nm, and 384 nm. These wavelengths correspond to the absorbance of chlorophyll *a* (Chl-*a*), carotenoids, and scytonemin, respectively. Pigment concentration was finally calculated by applying the trichromatic equation established by Garcia-Pichel and Castenholz (1991):

$$A_{384corr} = 1.04A_{384} - 0.79A_{663} - 0.27A_{490}$$

$$A_{663\,corr} = 1.02A_{663} - 0.027A_{384} + 0.01A_{490}$$

$$A_{490\,corr} = 1.02A_{490} - 0.08A_{384} - 0.026A_{663},$$

and using the specific extinction coefficients (ε) of 89.7 L g^{-1} cm^{-1} for chlorophyll *a* (Couradeau et al. 2016), 112.6 L g^{-1} cm^{-1} for scytonemin, and 200 L g^{-1} cm^{-1} for carotenoids (Brenowitz and Castenholz 1997).

Carbon, Nitrogen, and Phosphorus in biocrusts

Organic carbon (OC) and total N (t-N) were determined by dry combustion with an elemental analyzer Perkin Elmer 2400 Elemental Analyzer, Series 2, on moisture-free (105 °C overnight) and pulverized aliquots treated with excess HCl to selectively remove carbonates, according to Santi et al. (2006).

Inorganic N was extracted by 2 M KCl with a soil-to-solution ratio of 1:10, according to Bremner and Keeney (1966). Ammonia (NH_4^+) in the extract was measured by a colorimetric method with Na-salicylate in place of phenol in Berthelot's reagent, according to Rhine et al. (1998). Nitrate (NO_3^-) in the same extract was measured by the colorimetric method based on the nitration of salicylic acid, according to Cataldo et al. (1975).

Available phosphorus (P-*av*) was determined by extraction with sodium bicarbonate and quantification by spectrophotometry using the ascorbic acid method (Olsen et al. 1954).

Statistical analysis

All the analyses were performed in experimental triplicate ($N=3$) with a minimum number of three instrumental replicates for each measurement. Analysis of variance (ANOVA) was applied to statistically evaluate any significant differences among different crust types. The ANOVA analysis was carried out after verifying whether the data satisfied the assumptions of normally distributed data and homogeneity of variances. Tukey's honest significant difference test (HSD) was used for pairwise multiple comparisons among treatments. Results were considered significant at $P \leq 0.05$. The Pearson test was used to assess the degree of correlation between the different biocrust types. Linear regression equations were calculated to establish eventual relationships between data sets using pigment content or EPS amounts as predictors. The statistical analysis was performed using GraphPad Prism version 9 (GraphPad Software, San Diego, CA, USA).

Results

Microscopical observation of cyanobacterial morphotypes

Microscopical observations of biocrust samples collected at the experimental site (Fig. 1A), consisting of cyano-crust, cyano/moss crust, and moss crust (Fig. 1B-D) showed the presence of several prominent cyanobacteria morphotypes that we identified morphologically at least at the genus level. In cyano-crust, we observed with a high frequency the presence of morphotypes that can be associated with members of the genera *Microcoleus* (Fig. 1E-F) and *Phormidium* (Fig. 1G). The most frequently observed morphotype in cyano-crust was that of *Microcoleus*, characterized by a high number of bundles enclosed in thin transparent sheath (Fig. 1F). The filaments ranged from 5 to 10 µm with ends sometimes forming calyptra (Fig. 1E). Although the presence of *Microcoleus* sp. was observed in all biocrust types, we detected it with decreasing frequency from cyano-crust to moss crust. The genus *Phormidium* was also predominant in cyano-crust. *Phormidium* cells were arranged in unbranched filaments with clearly defined sheaths (Fig. 1G). A more pronounced presence of heterocystous morphotypes was observed in the cyano/moss crust samples (Fig. 1H-J) where, from preliminary observations, we identified many spherical colonies of cell filaments enveloped by a mucopolysaccharidic sheath between the soil particles (Fig. 1H). These spherical colonies are typical of *Nostoc*, where the mucilaginous extracellular matrix composed mainly of polysaccharides provides protection against adverse abiotic conditions. Spherical colonies were also observed in moss crust (Fig. 1K). The genus *Scytonema* was the second more recurrent heterocystous genus observed in cyano/moss crust. It is characterized by filaments growing upright, isopolar, branching, and

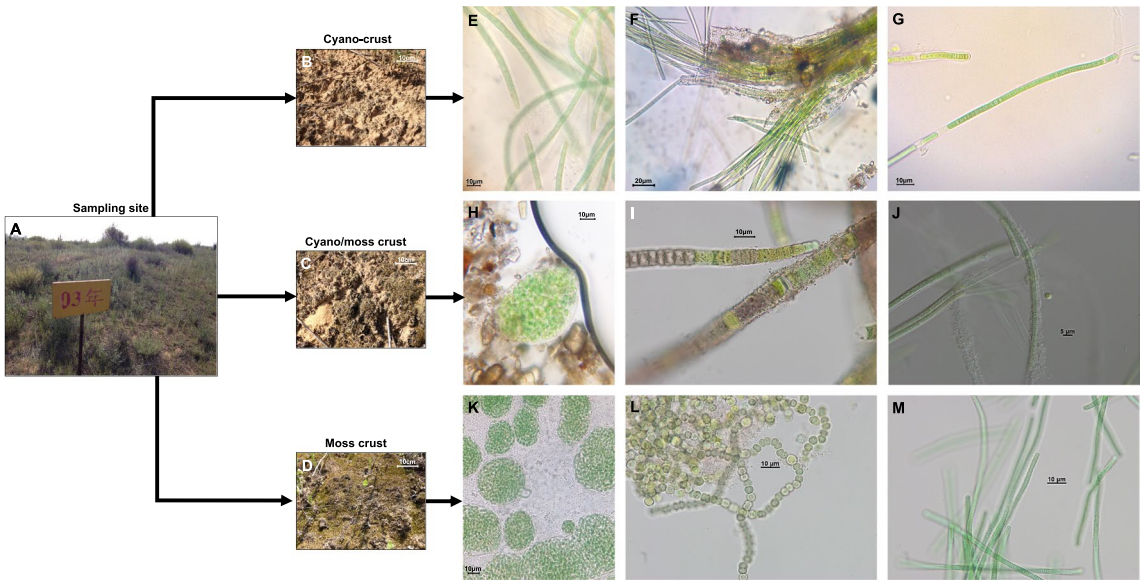

Fig. 1 Sampling site inoculated in 2003 (**A**) characterized by the presence of biocrusts classifiable as cyano-crust (**B**), cyano/moss crust (**C**), and moss crust (**D**). (**E-G**) Microphotograph of cyanobacterial strains isolated from cyano-crust fragments: *Microcoleus vaginatus* (**E**), *Microcoleus* sp. (**F**), and *Phormidium* sp. (**G**). (**H-J**) Microphotographs obtained from cyano/moss crust showing spherical colonies typical of the genus *Nostoc* (**H**) and morphologies ascribable to *Scytonema javanicum* (**I**) and *Schizothrix* sp. (**J**). (**K-M**) Microphotograph of cyanobacterial strains observed in moss crust fragments: *Nostoc* sp. (**K**), *Nostoc commune* (**L**), and *Leptolyngbya* sp. (**M**)

with individual trichomes in each sheath envelope. The sheath appeared thin, unlamellated, and colorless to dark yellow (Fig. 1I). These morphological traits are consistent with the description of *Scytonema javanicum* provided by Alwathnani and Johansen (2011). Morphotypes with features typical of *Schizothrix* sp. were found, albeit rarely, in samples of cyano/moss crust. This is a non-heterocystous genus characterized by solitary trichomes, sometimes pseudobranched (5–7 µm thin), surrounded by a thick smooth sheath containing 1–2 trichomes (Fig. 1J). Moss crust appeared to be dominated mostly by diazotrophic *Nostoc* species (Fig. 1K and 1L), visible as spherical green ovoid colonies (Fig. 1K). After the isolation procedure, microscopical observations of *Nostoc* revealed a filamentous morphology, with cells 4–5 µm wide and 4–5 µm long and well-differentiated heterocysts (Fig. 1L). This morphological characterization is consistent with the morphological traits of *Nostoc commune* noted by Alwathnani and Johansen (2011). Morphotypes that can be associated with *Leptolyngbya* were widely observed in the different biocrust types, although they were more frequently found in moss crust. *Leptolyngbya* sp. presented bright blue-green trichomes, with cells 2–3 µm wide, with or without sheath materials around the cells (Fig. 1M).

Pigment content of biocrusts

The pigment contents of the biocrusts are reported in Fig. 2. As expected, all samples showed higher contents of Chl-*a* compared to the control ($P < 0.01$). Chl-*a* concentration was significantly higher in moss and cyano/moss crust than in cyano-crust ($P < 0.01$; Fig. 2A). Scytonemin content was highest in cyano/moss crust. Moss crust and cyano/moss crust showed comparable scytonemin contents, while cyano/moss crust exhibited significantly higher content than cyano-crust (Fig. 2B). The abundance of carotenoids in the three biocrust types followed the trend of Chl-*a* (Fig. 2A and 2C), while the scytonemin/Chl-a ratio was highest in the cyano-crust, showing an opposite trend from previous pigment quantifications (Fig. 2D).

Organic C, total carbohydrate, and EPS contents of biocrusts

All biocrust samples showed a significantly higher OC content than the control (Fig. 3A). The OC content resulted in the order cyano-crust < cyano/moss crust < moss crust. However, when expressed according to the Chl-*a* content, OC showed no significant differences between the three biocrust types (Fig. 3B).

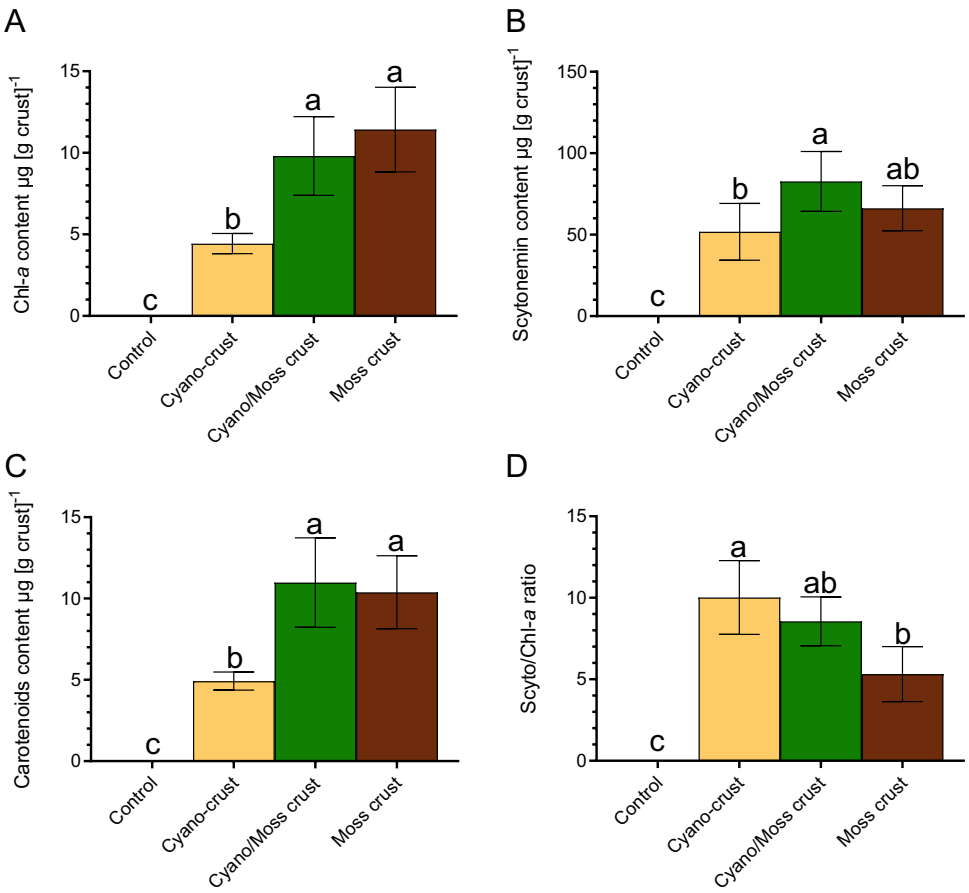

Fig. 2 Bar plot reporting the content of chlorophyll-*a* (Chl-*a*) (**A**), scytonemin (**B**), carotenoid content (**C**), and scytonemin /Chl-*a* ratio (**D**) in different biocrust successional stages: cyano-crust, cyano/moss crust and moss crust. Different lowercase letters indicate significant differences ($P < 0.05$)

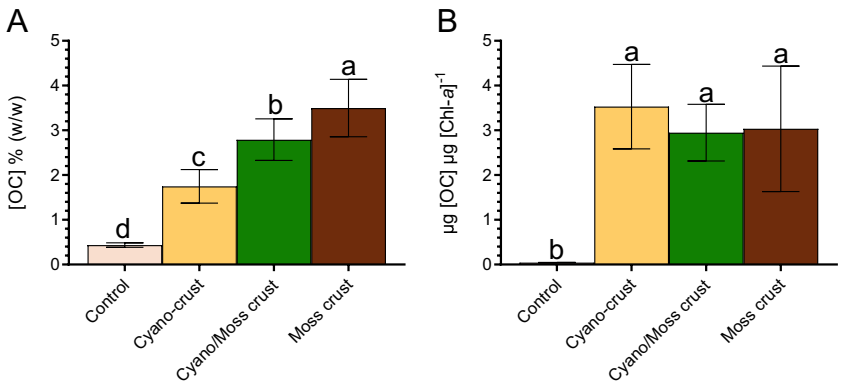

Fig. 3 Bar plot reporting the organic C (OC) content of the different biocrust successional stages: cyano-crust, cyano/moss crust, and moss crust, expressed on soil weight (**A**) and chlorophyll-*a* (Chl-*a*) content (**B**) bases. Different lowercase letters indicate significant differences ($P < 0.05$)

Total carbohydrate content showed a significant increase from cyano-crust to cyano/moss crust (53%) and from cyano/moss crust to moss crust (97%). The content of LB-EPSs and TB-EPSs was the highest in the moss crust (Fig. 4A and 4B). However, while LB-EPSs had similar contents in cyano-crust and cyano/moss crust, TB-EPS content increased almost linearly with biocrust development, that is, in the order cyano-crust < cyano/moss crust < moss crust (Fig. 4B). A linear correlation was observed between the contents of TB-EPSs and Chl-*a* (Fig. S2), as well as a significant positive correlation between the contents of LB-EPSs and scytonemin (Fig. S3).

On a Chl-*a* content basis, we observed an increase in LB-EPSs and TB-EPSs from cyano-crust to moss crust (Fig. 4C and 4D). However, normalizing on a Chl-*a* basis, there is no difference in LB-EPS contents between cyano/moss crust and moss crust. We also found no significant differences between the TB-EPS contents of cyano-crust and cyano/moss crust. Based on scytonemin content, LB-EPSs and TB-EPSs were more abundant in moss crust than in cyano/moss crust and cyano-crust (Fig. 4E and 4F).

Nitrogen, carbon, and phosphorous in biocrusts

We found higher amounts of total nitrogen (t-N), ammonium (NH_4^+), and nitrate (NO_3^-) in biocrusts than in the control (Fig. 5A-C). Higher N contents were detected in cyano/moss crust and moss crust compared to cyano-crust ($P = 0.01$ and $P < 0.01$, respectively). The highest contents of NO_3^- and NH_4^+ were found in moss crust, while no statistical difference was found between cyano/moss crust and cyano-crust (Fig. 5B, C).

The three biocrust types showed no significant difference in terms of N expressed on a Chl-*a* basis (Fig. 5D). Conversely, a similar content pattern was observed for NH_4^+ and NO_3^- when expressing the values on a dry weight or Chl-*a* basis (Fig. 5D, E, F). On a scytonemin basis, N was higher in moss crust than in the cyano/moss crust and cyano-crust, the latter two biocrust types showing no statistically different contents (Fig. 5G). On a scytonemin basis, a similar content pattern was found for both NH_4^+ and NO_3^- (Fig. 5H, I).

As expected, available phosphorous (P-*av*) contents were higher in the biocrusts compared to the control ($P < 0.05$) (Fig. 6A). P-*av* contents expressed on a dry weight basis were similar and not statistically different among biocrust types. However, when expressed on a Chl-*a* basis, cyano-crust showed a significantly higher P-*av* content than the other two biocrust types (Fig. 6B), whereas, on a scytonemin basis, the amount of P-*av* showed no statistical difference between the biocrust types (Fig. 6C).

A significant ($P < 0.05$) correlation between the amounts of Chl-*a* and scytonemin was revealed by the Pearson test in cyano-crust ($r = 0.92$; $P < 0.01$) and cyano/moss crust ($r = 0.77$; $P < 0.05$). In all three biocrust types, a strong correlation was found between scytonemin and carotenoid contents (Fig. 7; Table S2).

In cyano-crust, Chl-*a* showed a moderate correlation with TB-EPSs ($r = 0.52$, $P < 0.05$), and a stronger correlation with P-*av* ($r = 0.88$; $P < 0.01$). In addition, Chl-*a* exhibited a moderate correlation with OC ($r = 0.54$ $P < 0.05$). Scytonemin content showed correlations with total carbohydrates ($r = 0.73$; $P \leq 0.05$), OC ($r = 0.66$; $P < 0.05$), t-N ($r = 0.60$; $P < 0.05$) and P-*av* ($r = 0.76$; $P < 0.01$); (Fig. 6A). Conversely, in cyano/moss crust we found no correlation between pigment content and total carbohydrates or EPSs (Fig. 6B). However, scytonemin content showed a correlation with NH_4^+ content ($r = 0.60$; $P < 0.05$) (Fig. 7B; Table S3). Chl-*a* showed a moderate correlation with t-N content ($r = 0.55$; $P < 0.05$). We also found a significant correlation between the contents of scytonemin and Chl-*a* ($r = 0.77$; $P < 0.01$), and a significant correlation between the contents of scytonemin and carotenoids ($r = 0.90$; $P < 0.01$).

Unlike the other two biocrust types, in moss crust we did not find significant correlations between Chl-*a* and soil nutrient contents (Fig. 7C; Table S4).

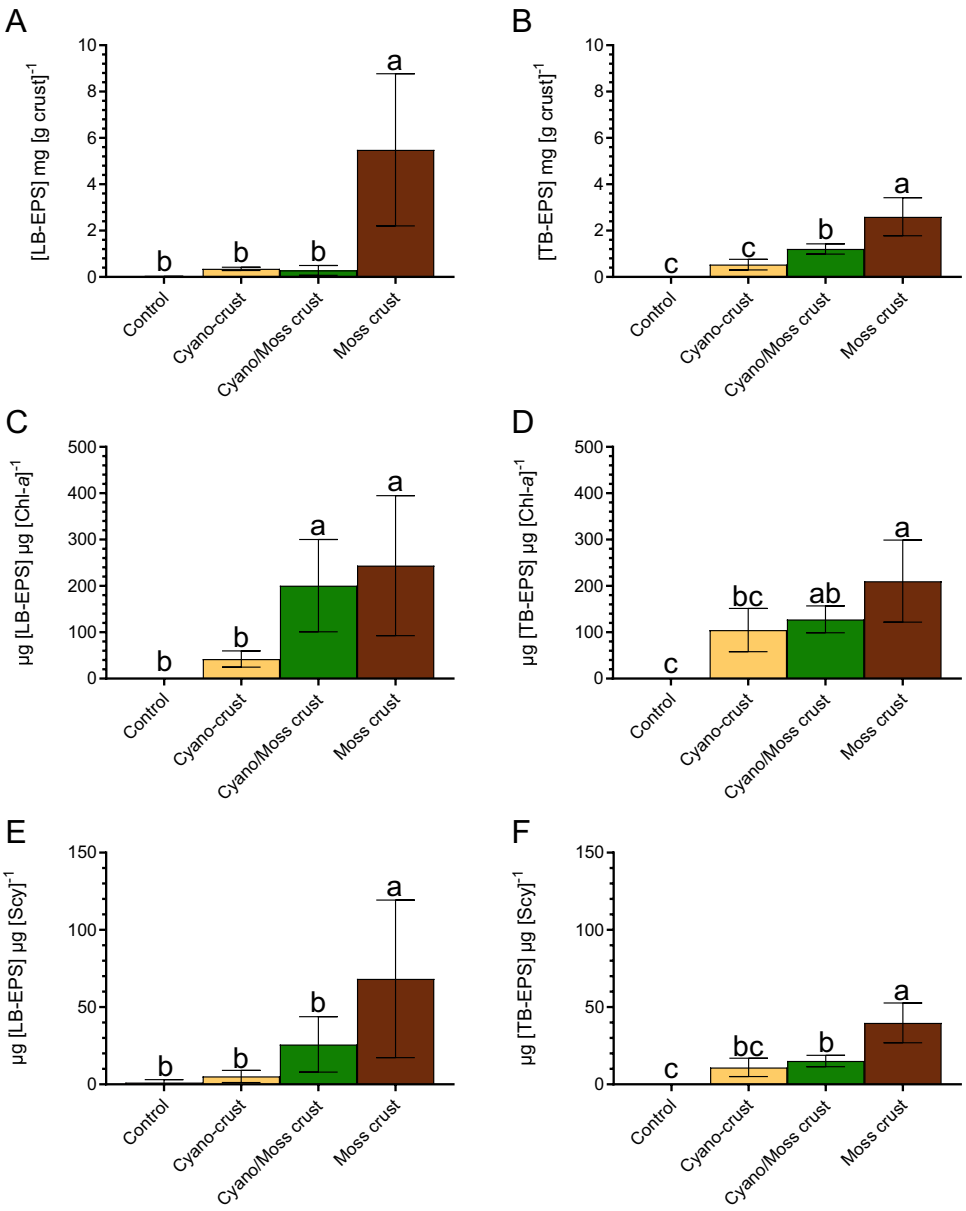

Fig. 4 Bar plot reporting the LB-EPS (**A**) and TB-EPS (**B**) contents, as mg per g of biocrust, in the different biocrust successional stages: cyano-crust, cyano/moss crust and moss crust, expressed on the contents of chlorophyll *a* (Chl-*a*) (**C**, **D**) and scytonemin (**E**, **F**). Different lowercase letters indicate significant differences ($P < 0.05$)

Discussion

The induction of biocrusts through cyanobacteria inoculation led to significant chemical changes in the substrate and significant nutrient enrichment. Specifically, the onset of biocrusts produced an accumulation of OC, total carbohydrates, specific biogenic pigments strongly involved in light energy storage (chlorophyll *a,* scytonemin, carotenoids), and EPSs in the topsoil. We used Chl-*a* as an index of phototrophic abundance and hypothesized the possible use of this variable to assess the degree of biocrust development (Castle et al. 2011). Our results confirmed an increase in phototrophic abundance from cyano-crust to cyano/moss crust. In addition, we determined scytonemin content to indirectly assess the variation in the abundance of heterocystous cyanobacteria (Couradeau et al. 2016), whose onset is considered an important driver for the further maturation of early-stage biocrusts (Bowker et al. 2002). Scytonemin is a pigment that accumulates in the outer EPS envelopes of heterocystous cyanobacteria (especially in the sheaths and capsules) and shields cells against the harmful effects of UV radiation (Garcia-Pichel et al. 1992). The contents of scytonemin measured in the present study are comparable to those reported for natural (i.e., non artificially induced) mature biocrusts of other biomes (Couradeau et al. 2016; Swenson et al. 2018). We also observed a higher abundance of scytonemin than Chl-*a* or carotenoids in the biocrusts, which is in line with what Wu et al. (2013) observed for induced biocrusts in the same experimental area. Scytonemin increased significantly from cyano-crust to cyano/

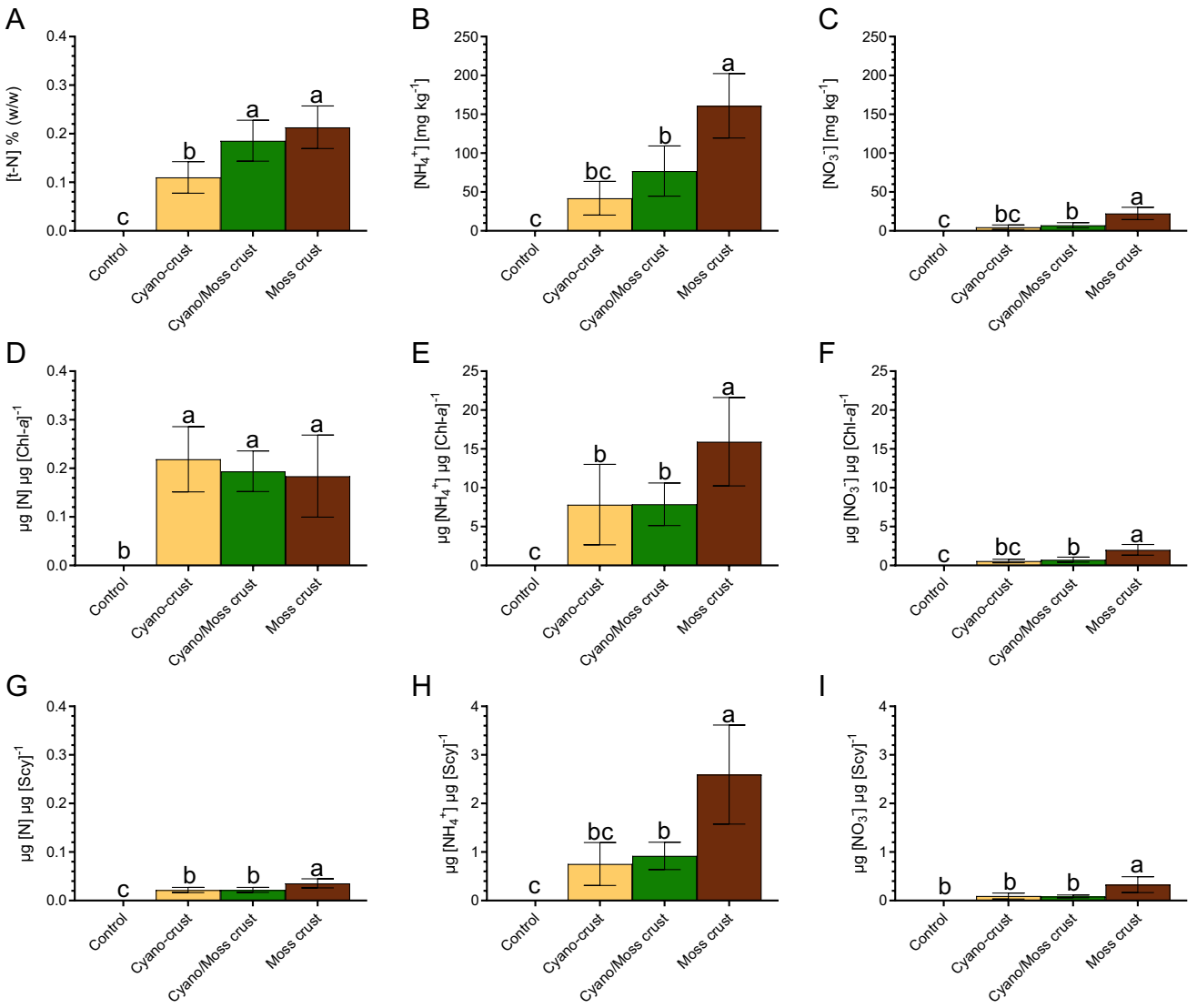

Fig. 5 Bar plot reporting total nitrogen (t-N) (**A**), ammonium (NH_4^+) (**B**) and nitrate (NO_3^-) (**C**) contents of the different biocrust successional stages: cyano-crust, cyano/moss crust, and moss crust, expressed on biocrust weight, chlorophyll-*a* (Chl-*a*) content (**D**, **E**, **F**) and scytonemin content (**G**, **H**, **I**) bases. Different lowercase indicate significant differences ($P < 0.05$)

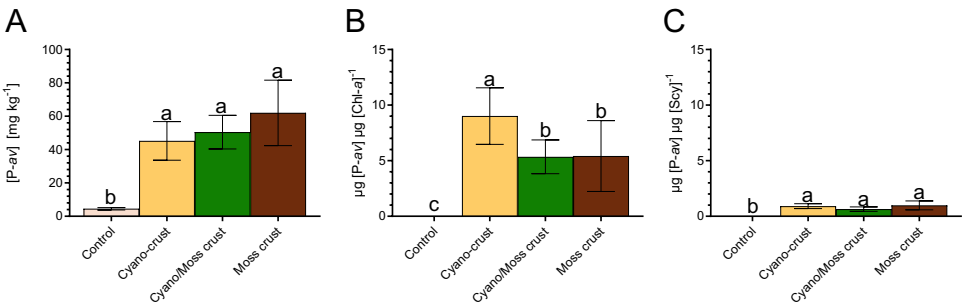

Fig. 6 Bar plot reporting available P (P-*av*) content of the different biocrust successional stages: cyano-crust, cyano/moss crust, and moss crust (**A**), expressed on the basis of chlorophyll-*a* (Chl-*a*) (**B**) and scytonemin contents (**C**). Different lowercase letters indicate significant differences ($P < 0.05$)

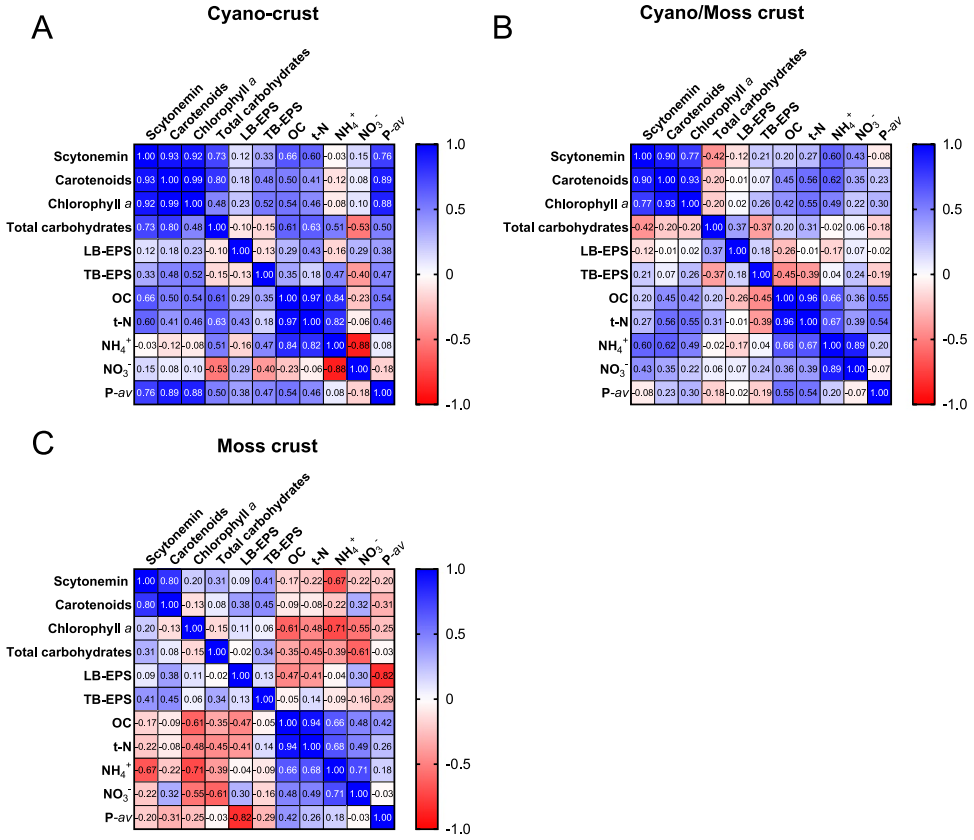

Fig. 7 Heat map based on Pearson correlation between the main variables investigated in the three biocrust types: cyano crust (**A**), cyano/moss crust (**B**), and moss crust (**C**). Red and blue colours indicate positive and negative correlations between the variables, respectively

moss crust, suggesting an enrichment in the heterocystous cyanobacterial population at this stage. The accumulation of scytonemin underlies a progressive adaptation of the cyanobacterial community to the strong solar irradiation in the environmental setting (Balskus and Walsh 2008; Orellana et al. 2020). In moss crust, both cyanobacteria and mosses are sources of Chl-*a*, with mosses known to provide the vast majority (90%) of the photosynthetic activity at that stage (Lan et al. 2017). We did not find a significant difference in Chl-*a* content between cyano/moss crust and moss crust. This supports the hypothesis of a decline in cyanobacteria abundance alongside the establishment of mosses in the biocrust community. Such a hypothesis is plausible, considering that Lan et al. (2012) documented a decline in cyanobacteria abundance associated with the colonization of moss genera such as *Bryum*, *Didymodon,* or *Tortula*. Moreover, since scytonemin content showed no decline from cyano/moss crust to moss crust, we can assume that the cyanobacterial population at these stages to be largely represented by heterocystous members. In contrast, carotenoids, synthesized by both cyanobacteria and mosses, plausibly doubled their concentrations in the transition from cyano-crust to moss crust.

Considering the variation in pigment contents and the microscopical observations of cyanobacteria in the three biocrust types, two main phases in biocrust development can be recognized: a first phase represented by cyano-crust, characterized by the dominance of non-heterocystous cyanobacteria, consisting mainly of *Microcoleus* sp. and *Phormidium* sp., and a second phase, represented by the cyano/moss crust and moss crust, characterized by the progressive spread of mosses and a more pronounced abundance of heterocystous cyanobacteria in the biocrust population. The diazotrophic cyanobacterial morphotypes predominantly present in cyano/moss crusts and moss crusts were *Scytonema javanicum* and *Nostoc* sp. (particularly *Nostoc commune*), respectively. Our observations are supported by a recent survey of biocrusts collected in the southern margin of the Gurbantunggut Desert (Lan et al. 2021), which demonstrated a greater abundance of heterocystous and unicellular cyanobacterial species in biocrusts colonized by mosses and lichens, compared to less "mature" biocrusts dominated by cyanobacteria. Molecular analyses conducted at the same site and examining two biocrust types, the supposed initial successional stage (cyano-crust) and the more mature biocrust stage (moss crust), revealed a cyanobacterial distribution consistent with our observations using light microscopy (Fig. S4; Li and Hu 2021; Li et al. 2023). Thus, it is possible to associate the increase in scytonemin content with a shift in the cyanobacterial community. The more solar radiation energy is absorbed, the more the albedo decreases and the more the temperature of the biocrusts increases. This

may be unfavorable especially to some non-heterocystous pioneering species such as *Microcoleus vaginatus* (Garcia-Pichel et al. 2013), hence explaining the decline of their relative abundance.

The onset of mosses and heterocystous cyanobacteria in the more advanced stages of biocrusts may explain the observed increase in OC, total carbohydrates, and EPSs. Total carbohydrate content, including intra- and extracellular carbohydrates, is an index of soil C-pool (Mager 2010) and biocrust development in relation to soil stability (Mazor et al. 1996; Belnap et al. 2008). Indeed, we observed the accumulation of total carbohydrates increasingly moving from cyano-crust to moss crust, as also happens for OC. No significant differences were found between the three biocrust types in terms of OC content when this is expressed on a Chl-*a* basis, confirming a likely relationship between phototrophic abundance and OC content. The latter is a key factor that determines soil quality and fertility, and is related to the ability of biocrust organisms to fix CO_2 photosynthetically (Kumar et al. 2022).

While total carbohydrates encompass both intracellular and extracellular glucides, EPSs contain only extracellular polysaccharides. Both LB-EPSs, the soluble fraction of EPSs, and TB-EPSs, the fraction of EPSs bound to biotic surfaces and sediments, play important functional roles in the development and maturation of biocrusts. LB-EPSs are readily released as slime into the surrounding soil sphere and have low levels of adhesion to biotic and abiotic surfaces. Owing to their physicochemical nature, LB-EPSs are an easily accessible source of C for the heterotrophic fraction of the community (Chen et al. 2014; Chamizo et al. 2019). On the other hand, TB-EPSs are relatively insoluble and organized into condensed, gel-like structures that stably adhere to microbial cells and substrate particles (Rossi et al. 2018). For this reason, TB-EPSs have been attributed to the role of biocrust structure stabilizers (Chen et al. 2014). We observed an increase in LB-EPSs and TB-EPSs from cyano-crust to moss crust, which is consistent with increased stability along the biocrust development gradient (Rossi et al. 2018); in particular, TB-EPS content increased almost linearly (Fig. 4B). During biocrust development, stability is also increased by moss colonization due to the action of rhizoids engulfing soil particles (Antoninka et al. 2016). There were no significant differences in TB-EPS contents when expressed on a Chl-*a* basis (Fig. 4D), indicating that TB-EPSs are intimately linked to the presence of phototrophs. This assumption is further supported by the observed correlation between Chl-*a* concentration and the amount of TB-EPSs (Fig. S2). In this study, the amount of Chl-*a* can definitely be considered a better predictor of TB-EPS content than scytonemin. This means that it is not possible to isolate the sole contribution of the heterocystous cyanobacterial community in the synthesis of EPSs. However, a connection between the heterocystous cyanobacterial community and the production of LB-EPSs is suggested by the significant correlation found between the content of LB-EPSs and the content of scytonemin ($r = 0.64$; $P = 0.001$; Fig. S3).

We observed a significant increase in t-N from cyano-crust to moss crust. NH_4^+ and NO_3^- contents in moss crust were more than three times higher than in cyano-crust (Fig. 5B, C). This result is in line with studies conducted by Xu et al. (2021) in China and Maier et al. (2018) in South Africa, both showing a higher N content in biocrusts with mosses. N dynamics are intimately dependent on the biocrust biome but are also closely dependent on soil type, environmental conditions, and any disturbances (Hu et al. 2019). In addition to obtaining N through fixation and mineralization, the moss crust has a high ability to accumulate N through dust trapping (Li and Xiao 2022) and, owing to the higher water-holding capacity than cyano-crust, limits N loss by leaching (Sun et al. 2021).

Phosphorus is another important, often limiting, factor in drylands (Belnap 2011; de-Bashan et al. 2022). Due to its central role in energy transfer (e.g., ATP), cell structure (phospholipids), metabolism, and signaling, P is a fundamental nutrient whose abundance has been studied in natural biocrusts from hot and cold environments (Craigie 2011; Baumann et al. 2019; Pushkareva et al. 2021). We found P-*av* contents in the three biocrust types (45.22 ± 4.34; 50.44 ± 4.03; 62 ± 16.86 mg P kg^{-1} cyano-crust, cyano/moss crust and moss crust, respectively) much higher than those found by Wu et al. (2013) in a 7-year-old induced biocrust, i.e., about 6 mg P kg^{-1}. However, soil P content is strongly influenced by structural and environmental biogeochemical factors (Zhang et al. 2014), which must be taken into account when comparing different data sets. In contrast to OC and t-N, we did not find significant differences in the contents of P-*av* between biocrust types, all of which were, however, significantly higher than in the control. Cyanobacteria and P-solubilizing heterotrophic bacteria are known to mobilize bound phosphates (Healey 1982; Mandal et al. 1999). The presence of biocrusts is known to significantly impact on soil P status. The activities of phosphatase secreted by soil microorganisms or released from dead cells were reported by Tabatabai (1994) to be even 3000 times higher in biocrusts compared to bare mobile dunes. Meanwhile, induced biocrusts have been shown to promote the hydrolysis of organophosphorus compounds into P-*av* (Tang et al. 2013) and the circulation of P in the soil (Wu et al. 2013).

The correlation analysis (Fig. 7A; Table S2) showed that in cyano-crust, extensively colonized by cyanobacteria and devoid of mosses, the contents of t-N, C, and P-*av* correlated with the contents of Chl-*a*, carotenoids, and scytonemin. This is indicative of the fact that, at this stage, the distribution of the abundance of nutrients depends closely on the metabolic activities of cyanobacteria. Total N showed a

significant correlation with scytonemin ($r = 0.60$, $P < 0.05$), which in turn is representative of the abundance of heterocystous cyanobacteria. The increase in N levels due to the presence of cyanobacteria was also observed in an inoculation experiment conducted on a pot scale by Taira et al. (2021). Cyanobacteria also contain N in their EPSs, which are abundantly released during soil colonization (Togashi et al. 2013). As for t-N abundance, P-*av* showed a strong correlation with Chl-*a* content ($r = 0.88$, $P < 0.05$), which is an indicator of phototrophic abundance, and consequently, with the overall abundance of cyanobacteria. Most of the cyanobacteria involved in P mobilization appeared to be heterocystous cyanobacteria, based on the significant correlation between P-*av* and scytonemin content ($r = 0.76$, $P < 0.05$). We also observed a moderate correlation of P-*av* with TB-EPSs ($r = 0.52$, $P < 0.05$). A link between EPSs and P solubility in soils was demonstrated by De Caire et al. (2000) and by Yi et al. (2008). The latter authors showed that EPSs are involved in the dissolution and release of tricalcium phosphate. Therefore, it is not unexpected that EPS production has been seen as a physiological response to P and N depletion in past studies (De Philippis et al. 1991, 1993; Xiao and Zheng 2016). Furthermore, not only do cyanobacteria participate in the P cycle through the release of EPSs, but they also secrete other substances, such as peptide N, riboflavin, and glycolate, that form chelation complexes with tricalcium phosphate, Cu, Zn, Ni, and ferric iron, thus contributing to the availability of these nutrients to plants (Belnap 2011).

When analyzing the cyano/moss crust, we did not find a set of correlations between values comparable to those found for cyano-crust (Fig. 7B; Table S3). This suggests that the change in community composition associated with biocrust maturation and moss emergence is consistent with appreciable changes in the entire set of metabolic pathways in biocrusts. Whereas in the cyano-crust the content of the three investigated pigments was only correlated to t-N, in cyano/moss crust we found significant correlations with the NH_4^+ contents as well. This could mean that at the cyano/moss stage, there is a concrete increase in the levels of NH_4^+ owing to the greater abundance of heterocystous cyanobacteria and, possibly, of microbial species involved in N-transformation processes (Maier et al. 2022).

In the moss crust, which is colonized by mosses for almost the entire crust surface, correlation analysis showed a different scenario than in the other two crust morphotypes (Fig. 7C; Table S4). No consistent correlations were found between pigment and EPS contents or nutrient status. N availability should reasonably depend on the nitrogenase activity of biocrust organisms. However, a study conducted on biocrusts from the Gurbantunggut Desert, China, assigned the lowest nitrogenase activity to moss crusts (Wu et al. 2009). Moreover, a literature review by Barger et al. (2016) based on the survey of 21 publications confirmed the lower nitrogenase activity associated with moss-dominated biocrusts and, thus, an inconsistency between N levels in biocrusts and potential nitrogenase activity.

Similar to what we postulated in the case of P-*av*, a large fraction of available N may be inherited from earlier maturation stages where N is fixed and accumulated ("inheritance hypothesis") (Wu et al. 2023). At the same time, the stability of the N stock in the moss crust could also be due to wind-borne N inputs on the one hand, and lower N emissions (as NO and HONO) (Weber et al. 2015), N losses via leaching (Young et al. 2022) and erosion (Gao et al. 2020), on the other hand. It is also plausible that the organic matter derived from plant litter may contribute to the nutrient pool in the soil, thereby influencing biocrust formation and development.

Conclusion

Our investigation analyzed the differences in main characteristics and nutrient status of the three main types of biocrusts spatial-closely arranged in the topsoil of an experimental area inoculated with cyanobacteria 13 years before. Overall, this study confirmed that the outcome of cyanobacterial inoculation in terms of soil fertility depends mainly on cyanobacterial ability to work as nutrient accumulators from the early stages of colonization. In particular, we highlighted the key role of heterocystous cyanobacteria in determining the nutrient status of biocrusts. We found a significant relationship between scytonemin, a proxy for heterocystous cyanobacteria, and NH_4^+. Although the cyano-crust can be classified as an earlier stage than the cyano/moss and moss crust within the patchy spatial configuration of the biocrust mat, they are responsible for the first and more important accumulation of P, which is essential for the progression of the biocrusts to more "mature" stages. Analyzing the cyano-crust, we found robust correlations between chlorophyll-*a*, scytonemin, and several key variables such as P, t-N, and OC, suggesting a central role of cyanobacteria in this primary successional stage. In addition, the significant correlation between TB-EPSs and chlorophyll-*a* suggests the involvement of cyanobacteria in the synthesis and accumulation of this more condensed EPS fraction involved in biocrust stability. In this context, the results on scytonemin content and its correlation with NH_4^+ suggest that the main actors promoting the shift from cyano-crust to cyano/moss crust are diazotrophic cyanobacteria. In addition, N accumulation in the form of NH_4^+ seems to occur mainly at the cyano/moss stage, working as a driver to moss establishment. From what we have observed, we believe that the more "mature" moss crust benefits greatly from the inheritance

of N and P accumulated during the earlier biocrust stages. From this perspective, all stages of biocrust development seem crucial to contribute to the final nutrient reservoir in moss crusts. To improve the odds of a successful inoculation treatment, further research is warranted on the role of climatic conditions of the inoculation area, particularly precipitation pattern and abundance, and the contribution of non-rainfall water as a key water source for biocrust activity, thus influencing soil nutrient cycling and biocrust formation. For future studies, it will be important to elaborate inoculation procedures that promote a more even progression of cyanocrust to moss crust, considering inoculation-side interventions aimed at improving microenvironmental conditions to favor biocrust succession. Screening and testing of novel cyanobacterial strains with pronounced N-fixing abilities should be also considered to obtain inoculant formulations more suitable to promote N accumulation.

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Author contributions AA, HL, SC, FR and GM Conceptualization; FR, GM and HL Sampling; GM and GC Formal analysis and Methodology; all authors Data curation; GM, FR and AA Writing—original draft; all authors Writing—Review&editing.

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Data availability Data related to this paper may be requested directly from the corresponding author (FR; federico.rossi@unipi.it).

Declarations

Conflict of interest All the authors declare that they have no financial or non-financial conflict of interest.

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