

Diversity of Algae in Terrestrial Ecosystems of Northeastern Iran: A Focus on Agricultural and Horticultural Soil Crusts

Zahra Bagheri-Bafian¹, Parisa Khaksarmoghadam¹, Maryam Dehghan¹, Soghra mohajer¹, Zeinab Shariatmadari^{1*} 

Received: 2025-06-22 Accepted: 2025-08-05

Abstract

Biological soil crusts (BSCs) are communities formed by a consortium of microorganisms, including green microalgae, cyanobacteria, fungi, and bacteria. They act as ecosystem engineers across all terrestrial environments, especially in drylands. However, their resilience in intensively managed, saline-alkaline agricultural and horticultural soils remains unexplored. This study characterized the algal diversity of BSCs in relation to key soil biochemical properties across nine agricultural and horticultural sites in Northeast Iran. For this purpose, soil pH, electrical conductivity (EC), and chlorophyll content were analyzed using established methods. Chemical analysis revealed high pH and EC in certain BSC samples from the studied sites. According to the results, Cyanophyta and Chlorophyta were the dominant algal groups in all collected BSC samples in Northeastern Iran. Although both soil pH and EC showed significant negative correlations with chlorophyll a content, the algal community consisted of extremophile taxa adapted to such stressful conditions. Furthermore, the number of identified algal taxa correlated negatively with soil pH and EC, and positively with chlorophyll content. The most dominant genera were *Chlorococcum* (Chlorophyta) and *Phormidium* (Cyanophyta), whose prevalence aligns with their documented salinity tolerance. Other identified taxa, such as *Pseudanabaena*, *Nostoc*, *Calothrix*, and several diatoms, further support the presence of a stress-adapted algal community. This study demonstrates that elevated soil pH and EC are key environmental filters that shape biological soil crusts' algal communities, selecting for a specialized, tolerant consortium.

Keywords: Biological soil crusts, Soil pH, EC, Soil chlorophyll content, Khorasan

Introduction

Biological soil crusts (BSCs) are complex communities composed of microorganisms

such as cyanobacteria, green microalgae, lichens, fungi, and bacteria that inhabit the upper layers of the soil (Belnap, 2003; Weber et al.,

¹-Faculty of Life Sciences and Biotechnology, Shahid Beheshti University, G.C., Tehran, Iran

*Corresponding email address: z_shariat@sbu.ac.ir

Doi: [10.48308/pae.2026.243007.1135](https://doi.org/10.48308/pae.2026.243007.1135)



Copyright: © 2025 by the authors. Submitted for possible open access publication under the terms and conditions of the Creative Commons Attribution (CC BY) license (<https://creativecommons.org/licenses/by/4.0/>).

2022). These living organisms significantly influence soil conditions by enhancing soil stability through the binding of soil particles (Bethany et al., 2019), improving rainwater absorption and increasing soil permeability (Kakeh et al., 2020), and reducing salinity and environmental pollutants through microbial activity (Kakeh et al., 2020; Li et al., 2021).

As pioneer colonizers of terrestrial ecosystems, cyanobacteria and green microalgae contribute to photosynthesis, organic matter production, water conservation, soil stabilization, and the gradual preparation of habitats for mosses and vascular plants (Belnap and Lange, 2001). Soil serves as the most crucial non-aqueous habitat for cyanobacteria, where they are particularly vital in arid and semi-arid environments (Etemadi-Khah et al., 2017). Cyanobacteria play a crucial role in the formation and functioning of BSCs (Patova et al., 2023). They facilitate the establishment of other microorganisms by binding soil particles, engaging in photosynthesis (Cruz et al., 2023; Karimi et al., 2023), and fixing nitrogen (Roncero-Ramos et al., 2022). Consequently, the extracellular polymeric substances (EPS) produced by cyanobacteria possess adhesive properties that help bind soil particles and mitigate the adverse effects of wind and water erosion (Sepehr et al., 2019).

Soil microalgae have garnered increasing interest as bioindicators due to their acute sensitivity to ecological changes and pollution, offering a powerful tool for assessing soil quality and health (Muñoz-Martín et al., 2019; Minaoui et al., 2021; Roy et al., 2022; Rotondo et al., 2023). Their presence, abundance, and community structure are shaped by key environmental factors such as pH, moisture, nutrient availability, and contaminant levels (Garcia-Pichel et

al., 2013; Xu et al., 2021; Jassey et al., 2022). Among these microorganisms, cyanobacteria and eukaryotic green microalgae are particularly fundamental, driving essential ecological processes and overall ecosystem function (Cano-Díaz et al., 2020; Oliverio et al., 2020; Jassey et al., 2022).

Over the years, from the 1950s to the present, numerous researchers have studied soil biological communities (Harper and Marble, 1988), and extensive studies have identified various algal species and their ecological roles. For instance, Shaaban (2017) documented 34 algal species in soil samples collected from the Western Desert of Egypt. Similarly, Samolov et al. (2020) identified green algae and cyanobacteria as dominant microorganisms in desert soil crusts. Additionally, Jusko and Johansen (2023) identified several new cyanobacterial species from soil BSCs on San Nicolas Island, California. The aforementioned research employed a multi-faceted approach to classify cyanobacteria based on morphological, molecular, ecological, and biogeographic factors. Furthermore, Samolov et al. (2022) provided comprehensive insights into the biodiversity of microalgae and cyanobacteria isolated from soil BSCs across a climatic gradient in Chile.

Research on BSCs and their microalgal components has also gained momentum in Iran. In the Kalat Naderi region of Khorasan Razavi, for example, researchers identified nitrogen-fixing cyanobacterial species such as *Calothrix*, *Nostoc*, and *Anabaena* (Aslani et al., 2014). Other studies have reported genera like *Phormidium*, *Leptolyngbya*, *Trichocoleus*, and *Microcoleus* in the desert soils of Kavir National Park (Etemadi-Khah et al., 2017). Moreover, Hassanzadeh et al. (2018) identified various green algae

and cyanobacteria, including *Chlorococcum*, *Lyngbya*, and *Phormidium*, in semi-arid regions of southern Khorasan Razavi. Their study explored the relationship between biocrust distribution and the physicochemical properties of soil, noting that at higher altitudes and in older structures with lighter soil textures and higher pH, initial sequences of cyanobacteria and green algae dominated. Furthermore, Sepehr et al. (2019) demonstrated that cyanobacteria could colonize stable soils in arid environments while enhancing nitrogen and organic carbon content in the soil.

Although BSCs have been studied in Khorasan Razavi Province, no comparative analysis exists of their microalgal flora across different regions of this province and North Khorasan Province. This study examines the hypothesis that soil chemical properties, specifically pH and EC, influence the cyanobacterial and algal composition of BSCs. Accordingly, soil chlorophyll content was used as a key indicator to assess the associated algal microflora. We conducted a comprehensive survey of BSC algal communities across diverse soil types, including agricultural, horticultural, and degraded agricultural fields, in northeastern Iran.

Material and methods

Study area and sampling sites description

The study areas

North Khorasan and Razavi Khorasan provinces, are situated in northeastern Iran (Fig. 1), a country known for its remarkable geomorphological diversity. Iran features a range of geological formations, including high mountain ranges, broad plains, and extensive coastlines. This varied topography significantly influences climatic conditions across the nation, resulting in multi-

ple climatic zones that range from arid to humid (Ahmadi & Kamangar, 2025; Ghorbani, 2021). North Khorasan Province covers an area of approximately 28,434 km² (Sadooghi et al., 2025). Its capital, Bojnourd, lies at an altitude of about 1,070 m above sea level (Shafiei et al., 2024). Despite its relatively small size, the province exhibits considerable climatic diversity: its western parts experience a cold semiarid climate, the eastern areas have a cold dry climate, and the northern regions feature a cold semihumid climate (HashemiDevin, 2013).

Khorasan Razavi Province, with an area of approximately 117,769 km², is also situated in northeastern Iran and is centered on Mashhad. Topographically, 49.2 % of the province is mountainous, while the remaining 50.8 % comprises plains and lowlands (Mostafavi et al., 2023). Climatically, the province is divided into two main zones: arid and semiarid. A large portion of its southern, eastern, and western areas experiences an arid climate, whereas semiarid conditions prevail in the northern and higher-altitude regions. In other words, the climate shifts from semiarid in the north to arid in the south (Mostafavi et al., 2023).

A total of nine study stations were selected from these two provinces, with three located in North Khorasan Province and six in Razavi Khorasan Province. The selected stations primarily focused on areas under cultivation of agricultural and horticultural crops (Table 1). Additionally, some stations were chosen from agricultural lands that have become inactive and barren in recent years.

Soil sampling and preparation

Field methods and laboratory analysis

Soil sampling was conducted in March 2025, following the methodology outlined by Anders-



Fig.1. Geographical location of the study area: North Khorasan and Razavi Khorasan provinces in northeastern Iran

Table 1. Geographic details and land-use descriptions of the studied sites

No.	Location	Latitude	Elevation	Description/Products
		Longitude		
1	North Khorasan Province; Honameh	37°30'56.7"N 58°01'15.4"E	1354.9 m	Active farmland/Apple, Peach and Apricot
2	North Khorasan Province; Ghale-cheh	37°29'18.6"N 58°00'28.1"E	1275.0 m	Inactive farmland/Grapes
3	North Khorasan Province; Mohammad abad	37°28'48.7"N 57°58'16.0"E	1194.4 m	Active farmland/Wheat
4	Khorasan Razavi Province; Avandar	36°30'34.0"N 58°24'10.2"E	1677.1 m	Inactive farmland/Wheat and Barley
5	Khorasan Razavi Province; between Avandar and Ghosun	35°37'02.8"N 58°18'16.1"E	1673.6 m	Active farmland/Wheat
6	Khorasan Razavi Province; Kharasf	35°39'48.6"N 58°11'24.2"E	1517.5 m	Inactive farmland/Wheat and Barley
7	Khorasan Razavi Province; Ghaleh-Agha-Hasan, Sar-e- chah	35°11'34.1"N 59°54'41.0"E	1736.2 m	Active farmland/Saffron
8	Khorasan Razavi Province; Ghaleh-Agha-Hasan, Sang lakha	35°09'47.9"N 59°56'43.1"E	1736.2 m	Active farmland/Wheat and Barley
9	Khorasan Razavi Province; Ghaleh-Agha-Hasan,Boland asnabad	35°07'28.9"N 59°54'01.1"E	1679.4 m	Active farmland/Wheat and Barley

en (2005). In brief, crust sampling was conducted by collecting soil samples, up to maximum depth of 5 cm, randomly from different parts of each site. After air-drying the crust samples for 48 hours in a location away from direct sunlight, plant residues were removed from the soil samples. The soil was then gently pounded and sieved.

In order to identify the microflora of BSCs, 10 grams of each biocrust were cultivated in sterile petri dishes containing sterile BG-11 medium (Table 2). The BG-11 culture medium was used as a standard culture medium, promoting the growth of a diverse group of algal species and cyanobacteria. Subsequently, petri dishes were placed under controlled conditions: a 16-hour light and 8-hour dark photoperiod at a temperature of $25 \pm 5^\circ\text{C}$. The growth of the algal colonies was continuously monitored over three

weeks, and afterward, individual algal colonies were observed using a light microscope (Olympus BH-2). For this purpose, semi-permanent slides of each colony were prepared to identify algal taxa. Different key references such as Komárek and Anagnostidis (1986 and 2005), John et al. (2002) and Komárek (2014) was applies to identify cyanobacteria; Prescott (1970) was used for identification of green algal species and Cox (1996) for identification of diatom species.

Soil bio-chemical properties

Soil pH and EC measurements

The pH and EC levels in the collected BSCs were measured according to Pauwels et al. (1992) methodology. To measure pH, a dry and sieved soil sample was suspended in distilled water and then stirred. After sedimentation, the pH of the supernatant was measured. Addi-

Table 2. BG-11 medium culture (Stanier et al, 1971)

Ingredient	Quantity (g/L)
NaNO ₃	1.5 gr
K ₂ HPO ₄	0.04 gr
MgSO ₄ .7H ₂ O	0.075 gr
CaCl ₂ .2H ₂ O	0.036 gr
Citric Acid	0.006 gr
Ferric ammonium citrate	0.006 gr
EDTA (disodium magnesium salt)	0.001 gr
NaCO ₃	0.02 gr
Trace metal mix	1 ml / 1lit
H ₃ BO ₃	2.86 gr
MnCl.4H ₂ O	1.81 gr
ZnSO ₄ .7H ₂ O	0.222 gr
Na ₂ MoO ₄ .2H ₂ O	0.390 gr
CuSO ₄ .5H ₂ O	0.079 gr
Co(NO ₃) ₂ .6H ₂ O	0.0494 gr

tionally, the saturated extract method was employed to determine EC. In this method, a dry and sieved soil sample was placed in a container, and distilled water was gradually added while stirring the mixture. The mixture was left to sit for 4 hours following all the soil samples were moistened. The saturated mud was then filtered under suction using a Buchner funnel, and subsequently, the EC of the solution was measured with an EC meter.

Soil chlorophyll content

The measurement of the chlorophyll content in the BSCs was conducted based on the method described by Caesar et al. (2018). In this method, the soil sample was moistened 24 hours before measurement to activate chlorophyll. After adding 0.05 g of magnesium carbonate to prevent acidification and chlorophyll degradation, 6 ml of ethanol (99%) was added. The test tubes were then placed in hot water at 80 °C for approximately 10 minutes, after which they were transferred to an ice bath for about 20 minutes. Subsequently, the test tubes were centrifuged at 3000 rpm for 10 minutes, and the supernatant was used to measure chlorophyll content using a spectrophotometer (Unico, Italy) at three wavelengths: 665, 649, and 750 nm. Finally, the pigment content was calculated using the following

formulas:

$$Chl\ a\ [\mu g] = [13.5275 \times (A_{665} - A_{750}) - 5.201 \times (A_{649} - A_{750})] \times DF \times S$$

$$Chl\ b\ [\mu g] = [22.4327 \times (A_{649} - A_{750}) - 7.0741 \times (A_{665} - A_{750})] \times DF \times S$$

$$Chl\ a + b\ [\mu g] = Chl\ a + Chl\ b$$

DF = dilution factor, and S= amount of solvent [ml]

Data analyses

To study the linear relationship between variables such as pH, EC, Chlorophyll content and the number of algal taxa, Pearson's correlation coefficient was calculated using IBM SPSS Statistics (version 26). Additionally, Microsoft Excel 2024 was used for graph drawing. Also, R (version 4.4.3) was used to create a correlation heatmap of the variables.

Results

Soil chemical properties

The measurements indicate that the pH value of the soil samples in the study stations reflects the alkaline nature of the soil in the studied areas (Fig. 2). Among these, the lowest pH value was recorded at station 1 (8.14). At the same time, the highest was noted at station 5 (9.2). Additionally, the EC measurements in the biocrust samples revealed significant variability (Fig. 3).

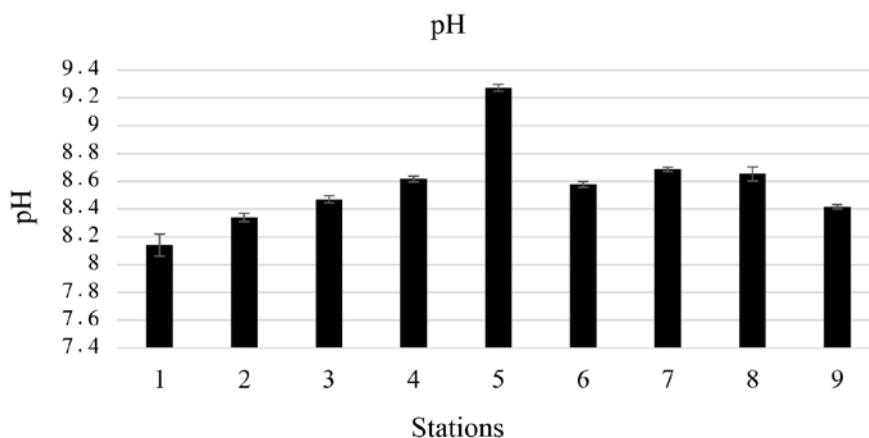


Fig. 2. Comparison of pH value in soil samples of different sites

The EC levels ranged from 87.6 to 501 $\mu\text{S/m}$, with these values observed at stations 8 and 4, respectively.

Soil Chlorophyll Content

Soil chlorophyll content was measured in order to determine the algal activity of collected BSC samples; according to the measurements, the highest chlorophyll content was calculated in stations 2, 7, 1, and 6 with the content of 1.02, 0.63, 0.61, and 0.58 ($\mu\text{g/g}$), respectively. The lowest chlorophyll content was calculated in site 5-0.20 ($\mu\text{g/g}$). As it can be seen in Fig. 3, the chlorophyll a content of the second site is significantly higher than sites 5 and 8. Although, total chlorophyll content of sites 2 is significantly

higher than sites 5 and 7, chlorophyll b content does not show significant difference in any sites (Fig. 4).

Algal diversity

In the present study, a total of 21 cyanobacterial and microalgal taxa were identified, with Cyanophyta representing the highest diversity, comprising 17 taxa. This was followed by two taxa from Chlorophyta and two species from Bacillariophyta.

Notably, *Phormidium* was the most frequently observed cyanobacterium within the algal flora of the biocrust samples, exhibiting a presence rate of 26%. Following this genus, *Pseudanabaena*, with four species identified. Additionally,

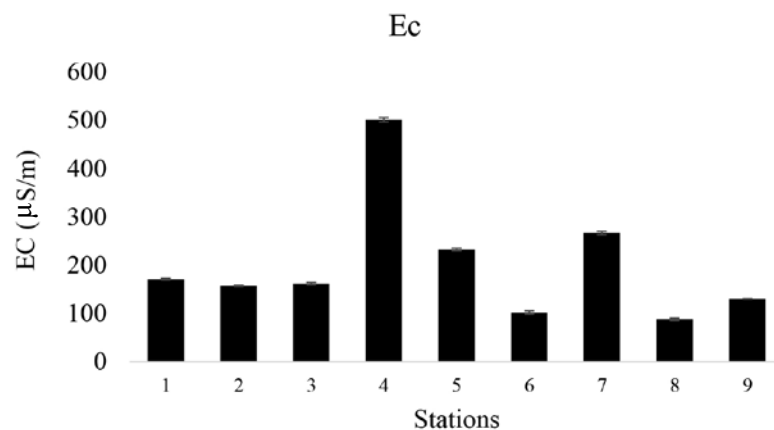


Fig. 3. Comparison of EC level in soil samples of different sites

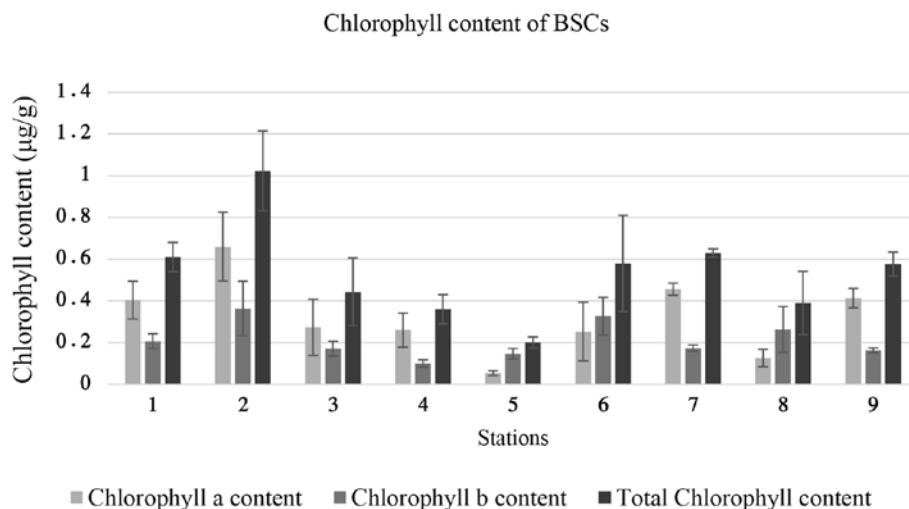


Fig. 4. Analysis of chlorophyll levels in soil samples from various locations

Table 3. Microalgal and cyanobacterial diversity in biological soil crusts across agricultural and natural sites in Khorasan provinces, Iran

No	Taxon	Family	Site no.
Bacillariophyta			
1	<i>Nitzschia</i> sp.	<i>Bacillariaceae</i>	2,8
2	<i>Pinnularia</i> sp.	<i>Pinnulariaceae</i>	9
Chlorophyta			
3	<i>Oedocladium</i> sp.	<i>Oedogoniaceae</i>	2
4	<i>Chlorococcum</i> spp.	<i>Chlorococcaceae</i>	1,2,3,4,5,6, 7,8,9
Cyanophyta			
5	<i>Anagnostidinium amphibium</i>	<i>Wilmottiaceae</i>	3
6	<i>Calothrix marchica</i>	<i>Rivulariaceae</i>	2
7	<i>Nostoc</i> sp.	<i>Nostocaceae</i>	2
8	<i>Oscillatoria simplicissima</i>	<i>Oscillatoriaceae</i>	6
9	<i>Oxynema lloydianum</i>	<i>Oscillatoriaceae</i>	1
10	<i>Phormidium janthiphorum</i>	<i>Oscillatoriaceae</i>	1
11	<i>Phormidium karakalpakense</i>	<i>Oscillatoriaceae</i>	8
12	<i>Phormidium pachydermaticum</i>	<i>Oscillatoriaceae</i>	1
13	<i>Phormidium terebriform</i>	<i>Oscillatoriaceae</i>	6
14	<i>Phormidium</i> sp.	<i>Oscillatoriaceae</i>	5,7
15	<i>Phormidium willei</i>	<i>Oscillatoriaceae</i>	8
16	<i>Planktolyngbya brevicellularis</i>	<i>Pseudanabaenaceae</i>	3
17	<i>Pseudanabaena frigida</i>	<i>Pseudanabaenaceae</i>	9
18	<i>Pseudanabaena balatonica</i>	<i>Pseudanabaenaceae</i>	1
19	<i>Pseudanabaena minima</i>	<i>Pseudanabaenaceae</i>	1,2,4,8
20	<i>Pseudanabaena</i> sp.	<i>Pseudanabaenaceae</i>	7
21	<i>Trichormus variabilis</i>	<i>Aphanizomenonaceae</i>	6

several cyanobacterial genera were represented by only one species, including *Trichormus variabilis* (Kützing ex Bornet & Flahault) Komárek & Amernann, *Planktolyngbya brevicellularis* G. Cronberg & Komárek, and *Anagnostidinium amphibium* (Gomont) Strunecký, Bohunická, J.R. Johansen & Komárek. Among the different study stations, site 1 had the highest number of identified species, with more than half belonging to the genus *Phormidium*.

Discussion

In this study, we investigated the BSCs of nine agricultural and horticultural lands in Northeast Iran, measuring various biochemical properties of the soil and the associated algal diversity at each site. The results indicated that Cyanophyta and Chlorophyta are the predominant groups of microorganisms forming the BSCs, both of which were present in all collected soil samples (Fig. 5).

Our findings revealed that soil chlorophyll content is inhibited at high pH levels, consistent with the research by Liu et al. (2014), which identified a negative correlation between soil pH and chlorophyll a content. Although it has been reported that cyanobacteria generally prefer neutral to slightly alkaline pH for optimal growth (Alghanmi and Jawad, 2019), our results indicated that higher pH levels in the sampled soils were associated with lower chlorophyll content, particularly for chlorophyll a (Fig. 6). Furthermore, the EC values of some soil sam-

ples were significantly higher than others. While the EC level exhibited a negative correlation with chlorophyll content, this correlation was not statistically significant. It is evident that the algal flora in these soil samples consists of extremophile microorganisms capable of surviving in stressful conditions characterized by high EC and pH values.

The number of identified taxa at the study stations indicates that soil pH and EC values can significantly impact algal communities (Fig. 6). Specifically, stations 4 and 5 exhibited the

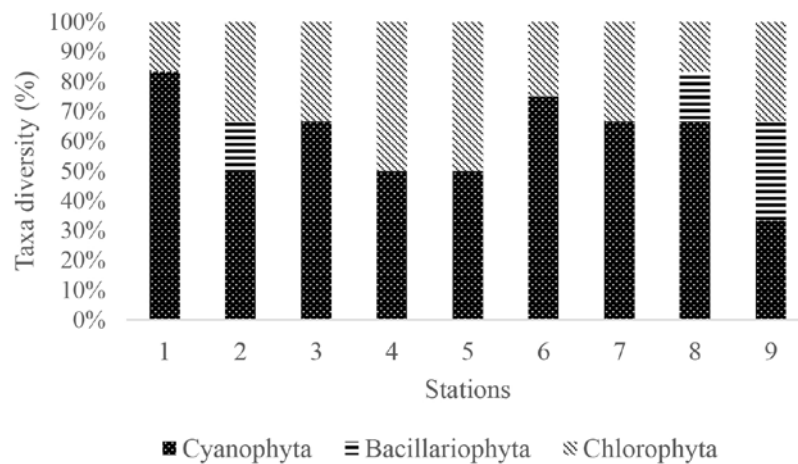


Fig. 5. Diversity of algal taxa at the phylum level in study stations

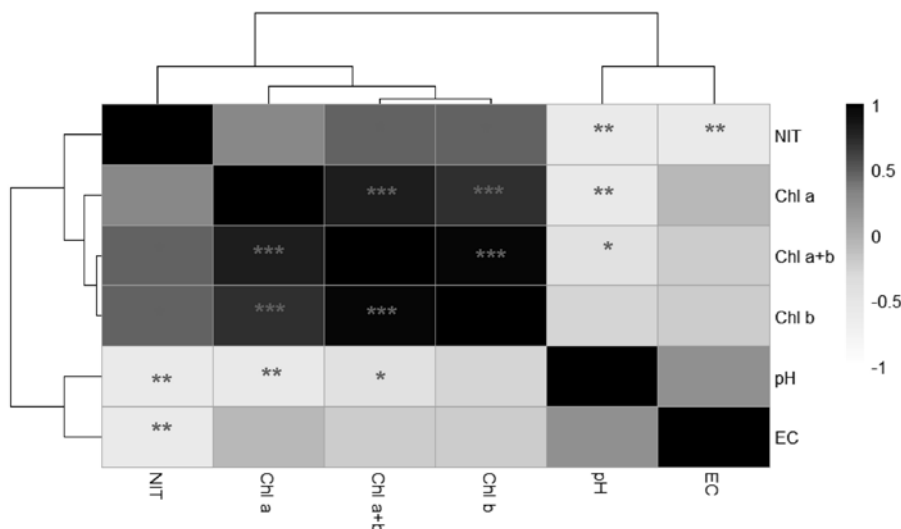


Fig. 6. Heatmap of Pearson correlation coefficients among the number of identified taxa (NIT), chlorophyll a (Chl a), chlorophyll b (Chl b), total chlorophyll (Chl a+b), electrical conductivity (EC), and pH across the studied sites. (sig< 0.001= ***, sig< 0.01= ** and sig<0.05= *)

lowest numbers of taxa and chlorophyll content. Notably, the number of identified taxa demonstrated a negative correlation with both soil pH and EC, while showing a positive correlation with chlorophyll b and total chlorophyll content. Analysis of the algal flora identified *Chlorococcum* (Chlorophyta) and *Phormidium* (Cyanophyta) as the dominant genera. The prevalence of *Chlorococcum* aligns with its documented role as a primary component of BSC communities (Belnap et al., 2003). Similarly, the genus *Phormidium* is not only recognized as a key cyanobacterium in the BSCs of arid and semi-arid regions (Büdel et al., 2009), but also as a dominant species in agricultural soils, particularly in slightly saline and alkaline environments (Alghanmi & Jawad, 2018). Moreover, its presence in soils is associated with several agronomic benefits, including improved soil fertility, enhanced plant growth, and potential utility in disease control (Rezaee et al., 2019; Younesi et al., 2019; Ghotbi-Ravandi et al., 2021; Righini et al., 2022).

As previously indicated, the chemical analysis revealed high salinity across all soil samples. The widespread presence of *Phormidium* in these conditions highlights its tolerance to salinity stress. This is supported by numerous studies confirming the resistance of *Phormidium* species to saline environments (Etemadi-Khah et al., 2017; Tashlykova & Afonina, 2022; Zafar et al., 2022). Additionally, members of this genus have been reported to play an efficient role in desalination processes (Zafar et al., 2022). Moreover, a study by Singh et al. (2022) identified several *Phormidium* species, including *Phormidium karakalpakense* (Muzafarov) Anagnostidis & Komárek, *Phor-*

midium janthiphorum (Gomont) Elenkin, and *Phormidium terebriforme* (C. Agardh ex Gomont) Anagnostidis & Komárek, from terrestrial habitats, further corroborating our findings. It is also noteworthy to mention that *Oxynema*, a genus recently separated from *Phormidium*, comprises halophilic species. Specifically, *Oxynema* sp., identified in our high-EC soils, is recognized as a typical halophile (Chatchawan et al., 2012). In the present study, only two genera belonging to the Chlorophyta were observed. The relative scarcity of green algae compared to cyanobacteria across samples may reflect a high tolerance of the present taxa to environmental salinity stress. The genus *Chlorococcum*, identified in the soils, is an important component of BSC (Belnap et al., 2001). While species-level classification based on morphology is difficult and requires molecular confirmation, the widespread presence of *Chlorococcum* species in soils with high EC, exceeding permissible salinity limits, demonstrates the genus's salinity tolerance (Asulabh et al., 2012; Assobhi et al., 2014). Furthermore, Putri et al. (2021) showed that some *Chlorococcum* species grew better in saline culture medium (20 ppm NaCl).

The other chlorophyte genus was *Oedocladium* sp., the notably high chlorophyll a, chlorophyll b, and total chlorophyll content at the second station may be attributed to its presence. Terrestrial species of this genus are known; for instance, *Oedocladium carolinianum* Beaney & Hoffman isolated from soil (Wang et al., 2022).

Among non-heterocystous cyanobacteria, *Pseudanabaena* was the most diverse genus following *Phormidium*, with four identified species. This genus is a key microorganism in BSC formation and one of the most abundant cyano-

bacteria in arid and semi-arid regions of North Africa (Büdel et al., 2009). *Pseudanabaena minima* (G.S.An) Anagnostidis was widespread in several stations, and its growth at the station with the highest soil EC suggests its potential as a salinity-tolerant species, a finding consistent with reports of its presence across a wide EC range in agricultural soils (Ahlesaadat et al., 2017). *Anagnostidinium amphibium* (Gomont) Strunecký, Bohunická, J.R.Johansen & Komárek (recently renamed from *Geitlerinema amphibium*) is a species found in both aquatic and terrestrial habitats, including soil and freshwater (Johansen et al., 2017; Pradhan et al., 2020).

Among heterocystous cyanobacteria, one species each from the genera *Calothrix marchica* and *Nostoc* sp. were identified in BSC samples of the second station. *Calothrix marchica* was also reported from crust samples of tropical dry forests in Baja California Peninsula (Kumar et al., 2016). *Calothrix* species have been reported from agricultural soils in various Iranian regions, including Gilan, Qazvin, Tehran (Irankhahi et al., 2022), and Kermanshah (Nowruzi et al., 2017).

Additionally, *Nostoc* is recognized as a prevalent heterocystous cyanobacterium in Iranian soils, known for its capability to endure high radiation level (Irankhahi et al., 2022). In addition, *Trichormus variabilis* was observed at Site 6. This species has previously been reported in Iranian soils (Irankhahi et al., 2022), as have other species of the genus *Trichormus* (Ahlesaadat et al., 2017).

The presence of the two diatom species, *Nitzschia* sp., and *Pinnularia* sp., in slightly alkaline soils indicates their tolerance for high pH. Species of *Nitzschia* can tolerate high pH in alkaline saline lakes (Hecky & Kilham, 1973). This

species is considered as pollution-tolerant species (Minaoui et al., 2021). Similarly, *Pinnularia* species, identified from both freshwater and terrestrial ecosystems, tolerate a broad pH range from acidic to alkaline conditions (Fazlutdinova et al., 2023).

In conclusion, this study elucidates the impact of high soil pH and EC on algal communities in BSCs and identifies species tolerant to such conditions. Further research is required to determine the influence of other environmental factors on BSC-forming microorganisms and BSC characteristics.

Acknowledgments

The authors are grateful to Shahid Beheshti University's Departments of Biological Science and Biotechnology for providing such a valuable opportunity to do this scientific work.

References

- Ahlesaadat M, Riahi H, Shariatmadari Z, Hakimi Meybodi MH. (2017). A taxonomic study of cyanobacteria in wheat fields adjacent to industrial areas in Yazd province (Iran). *Rostaniha*. 18 (2): 107-121. <http://DOI.org/10.22092/BOTANY.2018.115930>.
- Ahmad MN, Anuar MI, Abd Aziz N, & Murdi AA. (2025). Function and application of Soil Electrical Conductivity (EC) sensor in agriculture: A Review. *Advances in Agricultural and Food Research Journal*, 6(1). <https://DOI.org/10.36877/aafjr.a0000552>.
- Ahmad, M. N., Anuar, M. I., Abd Aziz, N., & Murdi, A. A. (2025). Function and application of Soil Electrical Conductivity (EC) sensor in agriculture: A Review. *Advances in Agricultural and Food Research Journal*, 6(1).

- Ahmadi M, & Kamangar M. (2025). Classification of the new raster-based method for Iranian regional climate. *Researches in Earth Sciences*, 16(3), 71-90. <https://doi.org/10.48308/esrj.2025.238444.1253>.
- Alghanmi HA, & Jawad HM. (2018). Effect of Environmental Factors on Cyanobacteria Richness in Some Agricultural Soils. *Geomicrobiology Journal*, 36(1), 75–84. <https://doi.org/10.1080/01490451.2018.1517196>.
- Alghanmi HA, & Jawad HM. (2019). Effect of environmental factors on cyanobacteria richness in some agricultural soils. *Geomicrobiology Journal*, 36(1), 75-84. <https://doi.org/10.1080/01490451.2018.1517196>.
- Alghanmi, H. A., & Jawad, H. M. (2019). Effect of environmental factors on cyanobacteria richness in some agricultural soils. *Geomicrobiology Journal*, 36(1), 75-84.
- Andersen RA. (2005). Algal culturing techniques. Elsevier Academic Press. 578 pp. ISBN: 0080456502, 9780080456508.
- Andersen, R. A. 2005. Algal culturing techniques. Elsevier academic Press. 578 pp.
- Aslani E, Riahi H, Shariatmadari Z, & Bazzi F. (2014). The study of heterocystous cyanobacteria from paddy fields in Kalat Naderi district in north-east of Iran. *The Iranian Journal of Botany*, 20(2), 257-264. <https://doi.org/10.22092/ijb.2014.101684>.
- Assobhi B, Ennasry H, Latique S, Kara M, Alaoui Mhamdi M, & Bahhou J. (2024). Influence of salinity, nitrogen and phosphorus concentrations on the physiological and biochemical characteristics of two Chlorophyceae isolated from Fez freshwater, Morocco. *Scientific Reports*, 14(1), 8259. <https://doi.org/10.1038/s41598-024-58864-4>.
- Asulabh KS, Supriya G, & Ramachandra TV. (2012). Effect of salinity concentrations on growth rate and lipid concentration in *Microcystis* sp., *Chlorococcum* sp., and *Chaetoceros* sp. In the *National Conference on Conservation and Management of Wetland Ecosystems. School of Environmental Sciences, Mahatma Gandhi University, Kottayam, Kerala*.
- Belnap J, & Lange OL. (Eds.). (2001). Biological soil crusts: Structure, function, and management. Springer. <https://doi.org/10.1007/978-3-642-56475-8>.
- Belnap J, Büdel B, & Lange OL. (2001). Biological soil crusts: characteristics and distribution. *Biological Soil Crusts: Structure, Function, and Management*. Springer International Publishing. 150: 3-30. https://doi.org/10.1007/978-3-642-56475-8_1.
- Belnap J, Büdel B, & Lange OL. (2001). Biological soil crusts: characteristics and distribution. In *Biological soil crusts: structure, function, and management* (pp. 3-30). Berlin, Heidelberg: Springer Berlin Heidelberg. <https://doi.org/10.1007/978-3-642-56475-8>.
- Belnap J, Büdel B, & Lange OL. (2003). Biological soil crusts: characteristics and distribution. *Biological Soil Crusts: Structure, Function, and Management*, 3-30. https://doi.org/10.1007/978-3-642-56475-8_1.
- Bethany J, Giraldo-Silva A, Nelson C, Barger NN, Garcia-Pichel F. (2019). Optimizing the production of nursery-based biological soil crusts for restoration of arid land soils. *Appl Environ Microbiol*. 2019 Jul 18;85(15): e00735-19. <https://doi.org/10.1128/AEM.00735-19>.
- Büdel, B., Darienko, T., Deutschewitz, K., Dojani, S., Friedl, T., Mohr, K.I., Salisch, M., Reisser, W. and Weber, B., 2009. Southern

- African biological soil crusts are ubiquitous and highly diverse in drylands, being restricted by rainfall frequency. *Microbial Ecology*, 57(2), pp.229-247. <https://DOI.org/10.1007/s00248-008-9449-9>.
- Caesar J, Tamm A, Ruckteschler N, Leifke AL, & Weber B. (2018). Revisiting chlorophyll extraction methods in biological soil crusts—methodology for determination of chlorophyll a and chlorophyll a+b as compared to previous methods. *Biogeosciences*, 15(5), 1415-1424. <https://DOI.org/10.5194/bg-15-1415-2018>.
- Chatchawan T, Komárek J, Strunecký O, Šmarda J, & Peerapornpisal Y. (2012). Oxynema, a new genus separated from the genus Phormidium (Cyanophyta). *Cryptogamie, Algologie*, 33(1), 41-59. <https://DOI.org/10.7872/crya.v33.iss1.2011.041>.
- Cox EJ. (1996). Identification of Freshwater Diatoms from Live Material First Chapman and Hall. edition. London, Melbourne, Madras. ISBN: 0412493802.
- Cruz JD, Delattre C, Felpeto AB, Pereira H, Pierre G, Morais J, & Vasconcelos V. (2023). Bioprospecting for industrially relevant exopolysaccharide-producing cyanobacteria under Portuguese simulated climate. *Scientific Reports*, 13(1), 13561. <https://DOI.org/10.1038/s41598-023-40542-6>
- Etemadi-Khah A, Pourbabaee AA, Alikhani HA, Noroozi M, & Bruno L. (2017). Biodiversity of isolated cyanobacteria from desert soils in Iran. *Geomicrobiology Journal*, 34(9), 784-794. <https://DOI.org/10.1080/01490451.2016.1271064>.
- Fazludtinova AI, Allaguvatova RZ, & Gaysina LA. (2023). Ecotonic Communities of Diatoms in the Southeastern Part of the Kamchatka Peninsula. *Earth*, 4(2), 209-222. <https://DOI.org/10.3390/earth4020011>.
- Garcia-Pichel F, Loza V, Marusenko Y, Mateo P, Potrafka RM. (2013). Temperature drives the continental-scale distribution of key microbes in topsoil communities. *Science* 340, 1574-1577. <https://DOI.org/10.1126/science.1236404>.
- Ghorbani M. (2021). Geological setting and crustal structure of Iran. In *The Geology of Iran: Tectonic, Magmatism and Metamorphism* (pp. 1-22). Cham: Springer International Publishing. https://DOI.org/10.1007/978-3-030-71109-2_1.
- Ghotbi-Ravandi AA, Neyshabouri FA, Aghashariatmadri Z, & Farahabadi SM. (2021). Phormidium sp. improves growth, auxin content and nutritional status of wild barley (*Hordeum spontaneum* L.). *Plant, Algae, and Environment*, 5(1), 616-623. <https://DOI.org/10.48308/jpr.2021.222483.1007>.
- Hakkoum Z, Minaoui F, Douma M, Mouhri K, & Loudiki M. (2020). DIVERSITY AND SPATIAL DISTRIBUTION OF SOIL CYANOBACTERIA ALONG AN ALTITUDINAL GRADIENT IN MARRAKESH AREA (MOROCCO). *Applied Ecology & Environmental Research*, 18(4). http://dx.DOI.org/10.15666/aeer/1804_55275545.
- Harper K T, & Marble J R. (1988). A role for nonvascular plants in management of arid and semiarid rangelands. In *Vegetation science applications for rangeland analysis and management* (pp. 135-169). Dordrecht: Springer Netherlands. https://doi.org/10.1007/978-94-009-3085-8_7.
- Hashemi Devin M. (2013). Evaluate the MEI Effect on Winter Precipitation in Northern Khorasan. *Journal of Climate Research*,

- 1392(13), 31-44.
- Hassanzadeh M, Sepehr A, Farzam M, & Bahreini M. (2018). Distribution of biological soil crust along surface evolution of an arid alluvial fan. *Research in Earth Science*, 9 (1), pages 1-13. <https://DOI.org/10.29252/esrj.9.1.1>.
- Hecky RE, & Kilham P. (1973). Diatoms in alkaline, saline lakes: ecology and geochemical implications 1. *Limnology and Oceanography*, 18(1), 53-71. <https://DOI.org/10.4319/lo.1973.18.1.0053>.
- Irankhahi P, Riahi H, Shariatmadari Z, & Aghashariatmadari Z. (2022). Diversity and distribution of heterocystous cyanobacteria across solar radiation gradient in terrestrial habitats of Iran. *Rostaniha*, 23(2): 264–281. <https://DOI.org/10.22092/BOT.J.IRAN.2023.360711.1336>.
- Jassey VEJ, Walcker R, Kanlol P, Gelsen S, Heger T, Lamentowicz M, Hamard S, & Lara E. (2022). Contribution of soil algae to the global carbon cycle. *New Phytologist*, 234(1), 64-76. <https://DOI.org/10.1111/nph.17950>.
- Johansen JR, Strunecký O, Bohunická M, Čapková KČ, Raabová L, Dvořák P, & Komárek J. (2017). A revision of the genus *Geitlerinema* and a description of the genus *Anagnostidinema* gen. nov. (Oscillatoriophycidae, Cyanobacteria). *Fottea*, 17(1): 114–126. <https://DOI.org/10.5507/fot.2016.025>.
- John DM, Whitton BA, & Brook AJ. (Eds.). (2002). The freshwater algal flora of the British Isles: An identification guide to freshwater and terrestrial algae. Cambridge University Press. ISBN 0521 77051 3 hardback.
- John, D. M., Whitton, B. A., & Brook, A. J. (Eds.). (2002). The freshwater algal flora of the British Isles: An identification guide to freshwater and terrestrial algae. Cambridge University Press.
- Jusko BM, & Johansen JR. (2023). Description of six new cyanobacterial species from soil biocrusts on San Nicolas Island, California, in three genera previously restricted to Brazil. *Journal of Phycology*. <https://DOI.org/10.1111/jpy.13332>.
- Kakeh J, Gorji M, Mohammadi MH, Asadi H, Khormali F, & Sohrabi M. (2020). Studying the Effects of Biocrusts on Soil Water Dynamic and Evaporation. *Iranian Journal of Soil and Water Research*, 51(5), 1255-1264. <https://DOI.org/10.22059/ijswr.2020.292760.668400>.
- Kakeh J, Gorji M, Mohammadi MH, Asadi H, Khormali F, Sohrabi M, & Cerdà A. (2020). Biological soil crusts determine soil properties and salt dynamics under arid climatic condition in Qara Qir, Iran. *Science of the Total Environment*, 732, 139168. <https://DOI.org/10.1016/j.scitotenv.2020.139168>.
- Kakeh J, Gorji M, Sohrabi M, Tavili A, Pourbabaee AA. (2018). Effects of biological soil crusts on some physicochemical characteristics of rangeland soils of Alagol, Turkmen Sahra, NE Iran. *Soil and Tillage Research*. 181: 152-159. <https://DOI.org/10.1016/j.still.2018.04.007>.
- Karimi A, Tahmourespour A, & Hoodaji M. (2023). The formation of biocrust and improvement of soil properties by the exopolysaccharide-producing cyanobacterium: a biogeotechnological study. *Biomass Conversion and Biorefinery*, 13(17), 15489-15499. <https://DOI.org/10.1007/s13399-022-02336-0>.
- Komárek J, & Anagnostidis K. (2005). Cyano-

- prokaryota: Oscillatoriales. Tl. 2 / 2nd Part. In J. Komárek & K. Anagnostidis (Eds.), *Süßwasserflora von Mitteleuropa* (Vol. 19/2, illustrated ed., 759 pp.). Elsevier Spektrum Akademischer Verlag.
- Komárek J, Kaštovský J, Mareš J, & Johansen JR. (2014). Taxonomic classification of cyanoprokaryotes (cyanobacterial genera) using a polyphasic approach. *Preslia*, 86, 295-335. <https://DOI.org/10.23855/preslia.2014.295>.
- Kumar D, Kaštánek P, & Adhikary S P. (2016). Diversity of cyanobacteria in biological crusts on arid soils in the Eastern region of India and their molecular phylogeny. *Current Science*, 1999-2004. <https://DOI.org/10.18520/cs/v110/i10/1994-1999>.
- Liu R, Li K, Zhang H, Zhu J, & Joshi D. (2014). Spatial distribution of microbial communities associated with dune landform in the Gurbantunggut Desert, China. *Journal of Microbiology*, 52(11), 898-907. <https://DOI.org/10.1007/s12275-014-4075-3>.
- Liu, R., Li, K., Zhang, H., Zhu, J., & Joshi, D. (2014). Spatial distribution of microbial communities associated with dune landform in the Gurbantunggut Desert, China. *Journal of Microbiology*, 52(11), 898-907.
- Minaoui F, Hakkoum Z, Douma M, Mouhri K, & Loudiki M. (2021). Diatom communities as bioindicators of human disturbances on suburban soil quality in arid Marrakesh area (Morocco). *Water, Air, & Soil Pollution*, 232(4), 146. <https://DOI.org/10.1007/s11270-021-05094-3>.
- Mostafavi, J., Fallah-Ghalhari, G., & Baaghdeh, M. (2023). Evaluation of the consequences of climate change on the drought of Khorasan Razavi province using the SPEI index. *Mostafavi, J., Fallah-Ghalhari, G., & Baaghdeh, M. (2023). Evaluation of the consequences of climate change on the drought of Khorasan Razavi province using the SPEI index.*
- Muñoz-Martín MÁ, Becerra-Absalón L, Perona E, Fernández-Valbuena L, García-Pichel F, Mateo P. (2019). Cyanobacterial biocrust diversity in Mediterranean ecosystems along a latitudinal and climatic gradient. *New Phytol.* 221, 123-141. <https://DOI.org/10.1111/nph.15355>.
- Novakovskaya IV, Patova EN, Dubrovskiy YA, & Novakovskiy AB. (2022). Soil algae in pine forests of the middle taiga (Komi Republic, Russia). *Diversity*, 14(2), 136. <https://DOI.org/10.3390/d14020136>.
- Nowruzi B, Fahimi H, & Ordodari, N. (2017). Molecular phylogenetic and morphometric evaluation of *Calothrix* sp. N42 and *Scytonema* sp. N11. *Rostaniha*, 18(2), 210-221. <https://DOI.org/10.22092/ros.2017.113708>.
- Oliverio AM, Geisen S, Delgado-Baquerizo M, Maestre FT, Turner BL, & Fierer N. (2020). The global-scale distributions of soil protists and their contributions to belowground systems. *Science Advances*, 6(4), eaax8787. <https://DOI.org/10.1126/sciadv.aax8787>.
- Patova E, Novakovskaya I, Gusev E, & Martynenko N. (2023). Diversity of cyanobacteria and algae in biological soil crusts of the Northern Ural mountain region assessed through morphological and metabarcoding approaches. *Diversity*, 15(10), 1080.
- Pauwels JM, Van Ranst E, Verloo M, Mvondo Z.A., (1992). *Soil Science Laboratory Manual. Methods of Soil and Plant Analysis, Equipment, Management of Glassware and Chemicals. Agricultural Publications*, No. 28, 180 p.

- Pradhan B, Patra S, Dash SR, Maharana S, Behera C, & Jena M. (2020). Antioxidant responses against aluminum metal stress in *Geitlerinema amphibium*. *SN Applied Sciences*, 2(5), 800
- Prescott GW. (1962). *Algae of the Western Great Lakes area*. With an illustrated key to the genera of desmids and freshwater diatoms. Revised [Second] edition. pp. [i]-xiii, 1-977. Dubuque, Iowa: Wm. C. Brown Company Publishers 135 South Locust Street.
- Rezaee M, Ghotbi-Ravandi AA, Hassani SB, & Soltani N. (2019). *Phormidium* improves seed germination and growth parameters of *Trifolium alexandrinum* in hexadecane-contaminated soil. *Journal of Phycological Research*, 3(1), 312-325. <https://DOI.org/10.29252/JPR.3.1.312>
- Righini H, Francioso O, Martel Quintana A, & Roberti R. (2022). Cyanobacteria: a natural source for controlling agricultural plant diseases caused by fungi and oomycetes and improving plant growth. *Horticulturae*, 8(1), 58. <https://DOI.org/10.3390/horticulturae8010058>.
- Rindi F, & López-Bautista JM. (2008). Diversity and ecology of Trentepohliales (Ulvophyceae, Chlorophyta) in French Guiana. *Cryptogamie, Algologie*, 29(1), 13-43.
- Rotondo L, Mora VTe, mporette PBea, mud SPedro, zo F. (2023). The use of an algal bioindicator in the assessment of different chemical remediation strategies for PAH-contaminated soils and sediments. *J. Environ. Chem. Eng.* 11, 110098. <https://DOI.org/10.1016/j.jece.2023.110098>
- Roy AG, ogoiN, YasminF, Farooq M. (2022). The use of algae for environmental sustainability: trends and future prospects. *Environ. Sci. Pollut. Res.* 29, 40373-40383. <https://DOI.org/10.1007/s11356-022-19636-7>.
- Sadooghi N, Panahi Y, Delshad A, Maurin M, & Dadar M. (2025). Epidemiological analysis of human brucellosis in North Khorasan province, Iran (2018–2023): a six-year multicenter retrospective study. *BMC Infectious Diseases*, 25(1), 1083. <https://DOI.org/10.1186/s12879-025-11516-y>.
- Samolov E, Baumann K, Büdel B, Jung P, Leinweber P, Mikhailyuk T, & Glaser K. (2020). Biodiversity of algae and cyanobacteria in biological soil crusts collected along a climatic gradient in Chile using an integrative approach. *Microorganisms*, 8(7), 1047. <https://DOI.org/10.3390/microorganisms8071047>.
- Samolov E, Baumann K, Büdel B, Jung, PLeinweber P, Mikhailyuk T, & Glaser K. (2020). Biodiversity of algae and cyanobacteria in biological soil crusts collected along a climatic gradient in Chile using an integrative approach. *Microorganisms*, 8(7), 1047. <https://DOI.org/10.3390/microorganisms8071047>.
- Sepehr A, Hassanzadeh M, RodriguezCaballero E. (2019). The protective role of cyanobacteria on soil stability in two Aridisols in northeastern Iran. *Geoderma Regional*. 16: e00201. <https://DOI.org/10.1016/j.geodrs.2018.e00201>.
- Shaaban AES M, Mansour H, & Saber A A. (2017). Soil Algae of El-Farafra Oasis (The Western Desert, Egypt) and N₂-fixation Efficiency of Five Heterocytous Cyanophytes. *Egyptian Journal of Botany*, 57(3), 517-524. <https://DOI.org/10.21608/ejbo.2017.858.1063>.
- Shafiei R, Firouzeh N, & Rahimi MT. (2024). Serological and molecular survey of *Toxoplasma gondii* in aborted livestock fetuses from

- Northeast Iran. *BMC Research Notes*, 17(1), 290. Belnap, J. (2003). The world at your feet: Desert soil crusts. *Frontiers in Ecology and the Environment*, 1, 181-189. <https://DOI.org/10.1186/s13104-024-06915-4>.
- Singh Y, Singh G, Singh DP, & Khattar JIS. (2022). A checklist of blue-green algae (Cyanobacteria) from Punjab, India. *Journal of threatened Taxa*, 14(3), 20758-20772. <https://DOI.org/10.11609/jott.6754.14.3.20758-20772>.
- Stanier RY, Kunisawa R, Mandel, M. (1971). Purification and properties of unicellular blue- green algae (order Chroococcales). *Bacteriology Review*, 35: 171-205.
- Tashlykova NA and Afonina EY. (2022). Diversity of plankton communities of chloride lakes of Southeastern Transbaikalia. In IOP Conference Series: Earth and Environmental Science. 1112 (1): 012108. IOP Publishing. [http:// DOI:10.1088/1755-1315/1112/1/012108](http://DOI:10.1088/1755-1315/1112/1/012108).
- Thomas AD, Bhagya S, & Thomas SC. (2017). Soil algae in the southern Kalahari are edaphic specialists and indicate soil properties. *Journal of Arid Environments*, 144, 114-121. <https://DOI.org/10.1016/j.jaridenv.2017.04.012>.
- Varshney P, Mikulic P, Vonshak A, Beardall J, & Wangikar PP. (2015). Extremophilic micro-algae and their potential contribution in biotechnology. *Bioresource technology*, 184, 363-372. <https://DOI.org/10.1016/j.biortech.2014.11.040>.
- Wang Y, Jia J, Chi Q, Li Y, Wang H, Gong Y., ... & Hu Q. (2022). Critical assessment of the filamentous green microalga *Oedocladium carolinianum* for astaxanthin and oil production. *Algal Research*, 61, 102599. DOI: <https://DOI.org/10.1016/j.algal.2021.102599>.
- Weber B, Belnap J, Büdel B, Antoninka AJ, Barger NN, Chaudhary VB, Darrouzet-Nardi A, Eldridge DJ, Faist AM, Ferrenberg S, Havrilla CA, Huber-Sannwald E, Issa OM, Maestre FT, Reed SC, Rodriguez-Caballero E, Tucker C, Young KE, Zhang Y., ... Bowker MA. (2022). What is a biocrust? A refined, contemporary definition for a broadening research community. *Biological Reviews*, 97, 1768-1785. <https://DOI.org/10.1111/brv.12862>.
- Williams A, Buck B, Soukup D and Merkle D. (2010). Geomorphic controls of biological soil crust distribution, Mojave Desert (USA), Paper presented at the 19th World Congress of Soil Science.
- Xu HF, Raanan H, Dai GZ, Oren N, Berkowicz S, Murik O, Kaplan A, Qiu BS. (2021). Reading and surviving the harsh conditions in desert biological soil crust: the cyanobacterial viewpoint. *FEMS Microbiol. Rev.* 45, fuab036. <https://DOI.org/10.1093/femsre/fuab036>
- Younesi H, Hassani SB, Ghotbi Ravandi AA, & Soltani N. (2019). Plant growth promoting potential of *Phormidium* sp. ISC108 on seed germination, growth indices and photosynthetic efficiency of maize (*Zea mays* L.). *Journal of Phycological Research*, 3(2), 375-385. <https://DOI.org/10.29252/JPR.3.2.375>
- Zafar AM, Javed MA, Hassan AA, Sahle-De-messie E, & Harmon S. (2022). Biodesalination using halophytic cyanobacterium *Phormidium keutzingianum* from brackish to the hypersaline water. *Chemosphere*, 307, 136082. <https://DOI.org/10.1016/j.chemosphere.2022.136082>

Zahra Z, Choo DH, Lee H, & Parveen A. (2020).
Cyanobacteria: review of current potentials and
applications. *Environments*, 7(2), 13. [https://
DOI.org/10.3390/environments7020013](https://DOI.org/10.3390/environments7020013).

Zancan S, Trevisan R, & Paoletti MG. (2006).
Soil algae composition under different agro-eco-
systems in North-Eastern Italy. *Agriculture, Eco-
systems & Environment*, 112(1), 1-12. [https://
DOI.org/10.1016/j.agee.2005.07.002](https://DOI.org/10.1016/j.agee.2005.07.002).