



Enzymatic activity of different sequence of biocrusts and loess soils in Incheh Borun region

Farhad Khormali^{1*}, Behnaz Atashpaz¹, Sara Marinari², Rosita Marabottini²

¹ Department of Soil Science, Gorgan University of Agricultural Sciences and Natural Resources, Gorgan, Golestan, Iran. E-mail: fkhormali@gau.ac.ir

² Department of Biological Agro-Food and Forestry Systems (DIBAF), University of Tuscia, Viterbo, Italy.

Article Info.

ABSTRACT

Article type:

Research Article

Article history:

Received: 04 Mar. 2025

Received in revised from: 27 Apr. 2025

Accepted: 28 Apr. 2025

Published online: 18 Jun. 2025

Keywords:

Dry region,
Soil organism's activity,
Organic carbon,
Stability.

Soil enzyme activity is an indicator of microbial community and functions that reflects changes in soil biological properties, soil organic matter dynamic and nutrient cycling. Therefore, this study was conducted to investigate the enzyme activity in different sequences of biocrusts and loess soils in the semi-arid region of Incheh Borun, Golestan province, Iran. The Incheh Borun region has the highest abundance of biological crusts on loess plateau. Biocrusts were identified based on morphological characteristics. Enzyme activity was measured (cellulase, chitinase, α -glucosidase, β -glucosidase, acid phosphomonoesterase, arylsulfatase, β -xylosidase, butyrate esterase and leucine aminopeptidase) in the presence of cyanobacteria, lichen and moss crusts and their absence (i.e., the physical crust) as affected by three treatments (crust, soil and soil + crust) and three replications at a depth of 0- 2 cm. The results showed that the presence of biocrusts compared to physical crust in the surface parts (0 to 2 cm depth) improved the activity of enzymes in all three treatments. The highest enzyme content was related to the β -glucosidase enzyme in the lichen biocrust, and the lowest content was observed in the β -xylosidase enzyme in the physical crust. The lichen crust (*Diploschistes diacapsis* (Ach.) Lumbsch) had the greatest enzyme activity compared to other crusts. This species can fix the carbon of atmosphere by photosynthesis and increasing soil stability better than the other biocrusts. The most enzyme activity in the presence of biological crusts indicates a more active biological diversity or microbial population compared to the physical crusts. This can improve soil quality.

Cite this article: Atashpaz, B., Khormali, F., Marinari, S., Marabottini, R. (2025). Enzymatic activity of different sequence of biocrusts and loess soils in Incheh Borun region. DESERT, 30 (1), DOI: 10.22059/jdesert.2025.102040



1. Introduction

Biological soil crusts constitute more than 70% live coverage in plant communities (Weber *et al.* 2016). In many regions, even in dry and cold ones with poor soils, biological crusts are formed as living crusts on top of the soils (Bowker *et al.*, 2018). They are inclusive with different kinds of biological crusts as well as a group of decomposers such as bacteria and fungi (Bowker *et al.*, 2018). With the activity of these bacteria and fungi on the soil surface, the conditions for the formation of different sequences of biological crusts are provided. (Feng *et al.*, 2024).

Biological crusts improve soil properties in dry lands, and this effect is different according to the presence of various biological crusts (Su *et al.*, 2009). This useful function includes water storage, atmospheric carbon and nitrogen fixation, preventing soil erosion and providing an environment for the accommodation and activity of other living organisms (Reeve *et al.*, 2023).

Also, biocrusts distributed to several orders based on the predominant creatures ((Reeve *et al.*, 2023). On the other hand, numerous elements like territory type and structure, severity of solar radiation and topography are effective in the order way. Therefore, biocrusts have different biological features during the various steps of sequence (Budel *et al.*, 2009). In addition, these creatures start from physical crusts (the soil is free of microorganisms' activity) and terminates with sphagnum at the ending of the series (Bowker *et al.*, 2023).

Loess soils are strongly affected by erosion. Therefore, biological shells play a significant role in stabilizing this sensitive area, and investigations the role of biocrusts in environments are increasingly deemed. Investigations were carried out on loess soils include: the broadcast of biological soil crusts and their influencing elements (Lü *et al.*, 2011), the potential of these crusts in contacting with soil compression (Warren *et al.*, 2019a), efficacy of biocrusts on soil microbial crowd as well as enzymatic acting (Jungblut *et al.*, 2012), moreover soil physicochemical attributes (Sethi *et al.*, 2012).

Soil enzymes are considered an indicator of the health of the soil environment. That is important catalysts in soil function and is necessary for microorganism's life in soil as well as plant growth (Gao *et al.*, 2017). In recent decades, investigation the association between soil biocrusts and enzyme activity has gained much interest. It is reported the existence of bio-filaments can enhance the Soil enzyme activity (Zhang *et al.*, 2012, Zhang *et al.*, 2015), however that depends on various types of shells (García-Velázquez *et al.*, 2022). Also, Drahorad *et al.* (2021) expressed that enzymatic activity has been affected with the stage of the biocrust sequence. Ghiloufi *et al.* (2019) showed that the content of enzymatic activities was higher in bio crusts compared with the bare crust-free soil. Allison and Martiny (2008) studied the relationship between the activity of microbial function and biological soil crusts with global warming and high precipitation and suggested while elevated temperature alone had no significant effect on biocrusts, changes in the rainfall time during summers greatly affected them.

The connection between enzymatic activity of soil and biocrusts has been studied previously, but there is not accurate information on the effects of different series of biological shells have been developed about enzyme activity in loess soils. Therefore, this research was done to investigate the enzymatic activity of different sequences of biocrusts and loess soils in the semi-arid region of Incheh Borun.

2. Material and Methods

2.1. The characteristics of study region

The Incheh Borun region is situated at the northeast of Iran. This area has the most plenty of biological crusts on loess plateau. Biocrusts in the study region were identified based on

morphological characteristics. The reports of the meteorological station have showed the annual average of mean temperature and precipitation is about 19.2 °C and 253 mm, respectively. Also, this range has a soil with aridic and thermic regime. According to soil taxonomy, it had typic haplocalcids classification (Staff Survey Soil, 2010). After conducting numerous field visits, based on morphological characteristics and based on previous studies, the dominant lichen species in the study area was *Diploschistes diacapsis* (Ach.) Lumbsch (Soleimanzadeh *et al.*, 2019). This species had whitish to grey thallus, consisting of irregularly angular, 0.5-2.5 mm wide and 1-3 mm thick, flat to convex, dull, usually pruinose areoles that found in dry areas with calcareous and gypseous soils (De Armas *et al.*, 2022).

2.2. Study design

To investigate the enzymatic activity, we designed three treatments in order: A plot with dimensions of 25 × 25 meters was prepared in a place with the most dispersion of biological crusts (Fig. 1). In this area, three samples were randomly collected from each crust (crust treatment). For each treatment, the three samples were taken from 0-2 cm depths and were mixed (soil treatment). The boundary between the soil and biological crusts, in which the roots of biocrusts are attached to the subsurface of soil was separated and considered as a soil + crust treatment. Also, a sample of soil with no crust was taken to be used as a control in the same way as explained above.

At first, one sample was selected from the biological crusts (cyanobacteria, lichen, and moss) and the physical crust (Physical (as opposed to biological) soil crusts results from raindrop or trampling impacts. They are often hardened relative to uncrusted soil due to the accumulation of salts and silica), then, each crust isolated of soil below that and passed through a 1 mm sieve. Some crusts are mixed with the sub soil, and we named these samples soil + crust treatment. Therefore, the test was done in three factors of soil, crust and soil + crust for each crust with three repetitions.

2.3. Enzymatic activity

Potential enzyme activities in crust, soil + crust and soil treatments evaluated by the fluorogenic methylumbelliferyl (MUF)-substrates (Yang *et al.*, 2023). The samples were kept in dark conditions for 3 days at 25 °C, then 2 grams of each treatment (crust, soil + crust, soil) were blended by 50 milliliters of distilled aqua and centrifuged at 9600 rpm on three minutes. 50 microliters of each suspension was taken and placed in 96- black microplates (with three repetitions in each row). 50 µl of 0.5 M sodium acetate buffer and 100 µl of 1 mM substrate compound were increased. They were remained at 30°C for 30 minutes moreover, assessed with an automated fluorometric plate reader (Marinari *et al.*, 2020).

SEI (Synthetic Enzyme indicator demonstrated as the total of enzyme functions, with three biological and physical crust treatments (Moscatelli *et al.*, 2018). Shannon's indicator was calculated for study samples. (Zak *et al.*, 1994).

2.4. Statistical analysis

A mixed analysis of variance in location based on completely randomized design with three replicates was conducted to determine the significant difference between the averages of the three groups (soil, crust and soil + crust). The crusts were assigned to locations. The homogeneity of variances for different crusts was checked with Bartlett's test as a prerequisite for the mixed analysis of variance. Significant differences were reported at $p < 0.05$ based on the Least Significant Difference (LSD) method.

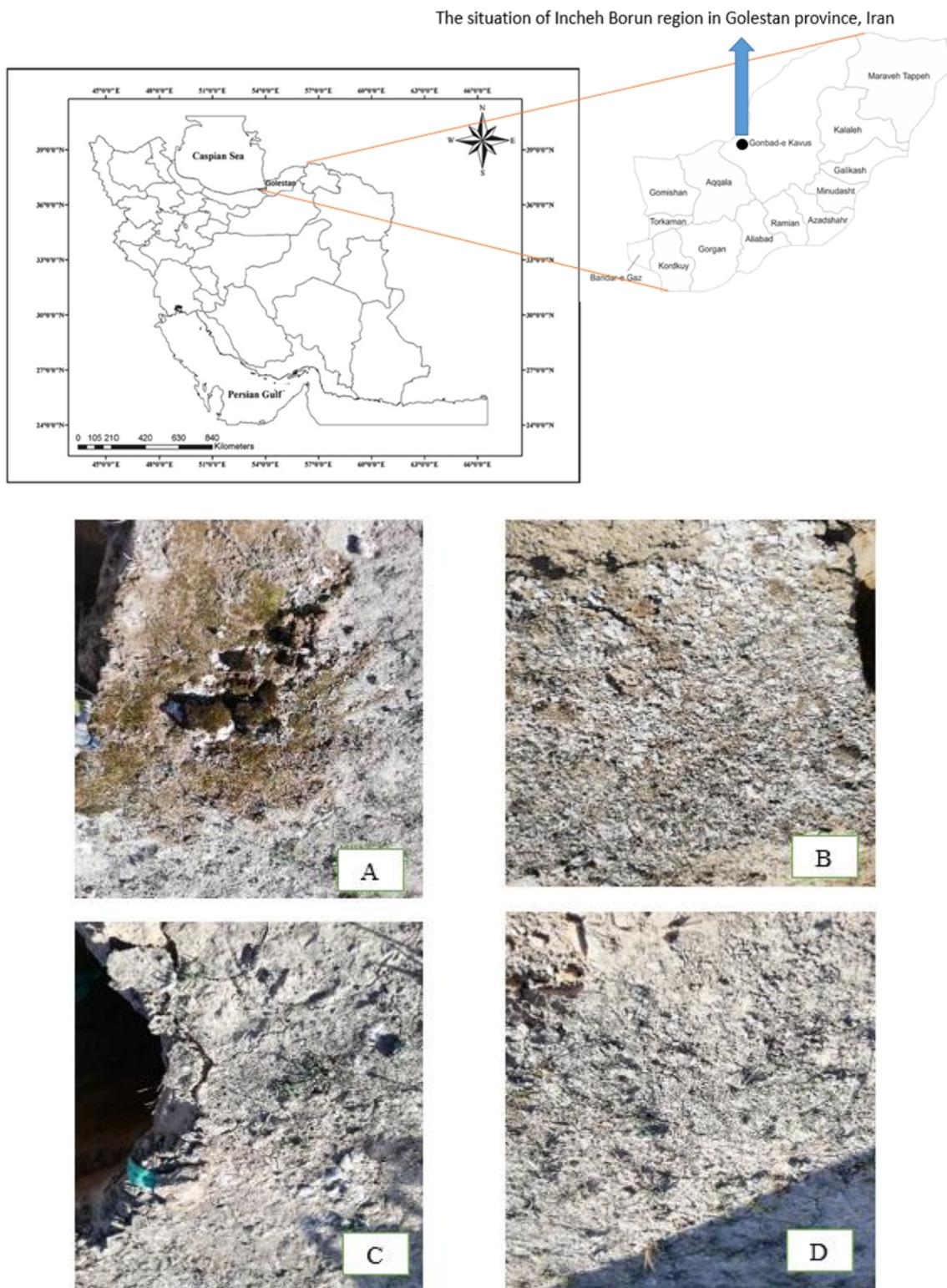


Fig. 1. Location of Golestan province in Iran and the Incheh Borun region in Golestan province, Biological and physical crusts: A) Moss, B) Lichen (*Diploschistes diacapsis* (Ach.) Lumbsch) C) Cyanobacteria D) Physical crust

3. Results

Analysis of the variance for the effect of different sequences of biocrusts (physical crust, cyanobacteria, lichen, and moss) on enzymatic activity in three treatments (crust, soil + crust and soil) is shown in Table 1. According to the chi-square values in Bartlett's test, the variance across the crusts was equal (data not shown).

3.1. Cellulase

The cellulase content in the crust treatment was in order: cyanobacteria > lichen > moss > physical crust (Fig. 2A). There was no notable variation between cyanobacteria and lichen however they had a significant difference with moss and physical crusts at $p < 0.05$. The most cellulase in soil + crust treatment was observed in lichen crust (998.6 nmol MUF/g⁻¹ h⁻¹) and the lowest ones was detected in physical crust (16.6 nmol MUF/g⁻¹ h⁻¹). Lichen had a meaningful variation at $p < 0.05$ with cyanobacteria, moss and physical crusts. This enzyme in soil treatment followed by cyanobacteria > lichen > moss > physical crust respectively and significant difference was observed among them.

Table 1. ANOVA for the effect of different sequences of biocrusts on enzymatic activity

S.O.V	DF	Mean Square (MS)								
		Cellulase	Chitinase	β -glucosidase	α -glucosidase	Acid phospho-monoesterase	Arylsulfatase	β -xylosidase	Butyrate esterase	Leucine aminopeptidase
Crust	3	506094.8**	15319143.4**	3749410.7**	39730.7**	2437143.4**	47144.7**	52665.6**	926758.6**	2077867.2**
Error I	8	12922.1	23318.2	8092.8	1030.0	29375.7	294.9	1456.2	9787.7	27406.8
Treatment	2	344734.1**	1992586.2**	392410.7**	36763.3**	1649856.9**	15894.1**	16808.7**	1142130.7**	2186095.6**
Crust* Treatment	6	251798.1**	1394565.9**	346724.7**	9078.4**	434268.1**	9656.7**	7637.9*	152397.8**	371489.1**
Error II	16	12286.8	32051.3	14309.4	616.2	24173.4	502.0	1911.7	14828.8	40799.2
CV (%)	-	45.1	21.8	18.8	27.6	26.8	39.2	47.8	15.4	27.6

S.O.V: Sources of variations, DF: Degrees of freedom, CV: Coefficient of variation, ** Significant at $p < 0.01$, * Significant at $p < 0.05$

3.2. Chitinase

The highest content of chitinase enzyme was observed in lichen crust (4280.9) and the lowest ones was affiliated to physical crust (5.9) (crust treatment), in addition lichen had a significant difference with other crusts (Fig. 2B). This enzyme in soil + crust treatment was in order: lichen > moss > cyanobacteria > physical crust and also there was a significant difference among them. As similar soil + crust treatment, the content of chitinase in soil treatment was lichen > moss > cyanobacteria > physical crust respectively.

3.3. β -glucosidase

As shown in Fig. 2C, the β -glucosidase content in crust treatment was in order: lichen > cyanobacteria > moss > physical crust and there was a substantial contrast among them at $p < 0.05$. The maximum and the minimum amount of this enzyme in soil + crust treatment were observed in lichen (1895.2 nmol MUF /g⁻¹ h⁻¹) and physical crust (79.1 nmol MUF /g⁻¹ h⁻¹) respectively as well as a considerable distinction among them at $p < 0.05$. The value of β -glucosidase in soil treatment was lichen > cyanobacteria > moss > physical crust and lichen biocrust had a significant difference with other crusts at $p < 0.05$.

3.4. α -glucosidase

The content of α -glucosidase enzyme in crust treatment was in order: lichen> moss> cyanobacteria> physical crust and had a meaningful contrast at $p<0.05$ (Fig. 2D). About soil + crust treatment, the maximum amount of α -glucosidase was apperceived in the lichen and the lowest content of that was observed in physical crust and there was a notable variation among them at $p<0.05$. This enzyme in soil treatment was moss> lichen> cyanobacteria> physical crust and moss crust had a significant with other biological and physical crusts.

3.5. Acid phosphomonoestrerase

Acid phosphomonoestrerase enzyme in crust treatment was in order: lichen> moss> cyanobacteria> physical crust. In soil + crust treatment, the highest content of this enzyme was related to lichen and the lowermost was determind in the physical crust and they had a meaningful contrast at $p<0.05$ (Fig. 2E). The most value for acid phosphomonoestrerase content in soil treatment was associated with 386.7 in lichen crust and the minimum ones with 57.5 nmol MUF /g⁻¹ h⁻¹ was related to physical crust and a significant difference among biological and physical crust.

3.6. Arylsulfatase

Arylsulfatase enzyme in crust treatment was in order: lichen> moss> cyanobacteria> physical crust and lichen had a significant difference with other crusts. In soil + crust treatment, the highest content of this enzyme was related to lichen crust (225 nmol MUF /g⁻¹ h⁻¹) and the lowest ones was observed in physical crust (3.4 nmol MUF /g⁻¹ h⁻¹) About soil treatment, the value of arylsulfatase enzyme followed by lichen> moss> cyanobacteria> physical crust and similar to soil + crust treatment, there was no significant difference among moss, cyanobacteria and physical crust (Fig. 2F).

3.7. β -xylosidase

The maximum amount of β -xylosidase in crust treatment was observed in lichen crust. The value of β -xylosidase enzyme in soil + crust treatment was in order lichen> cyanobacteria> moss> physical crust in case of soil treatment, the content of β -xylosidase enzyme followed by lichen> cyanobacteria> moss> physical crust (Fig. 2G).

3.8. Butyrate esterase

About the crust treatment, there were no remarkable distinctions among the butyrate esterase amount of biological soil crusts and the highest value of that was related to lichen. In soil + crust treatment, the value of butyrate esterase was in order: lichen> moss> Cyanobacteria> physical crust (Fig. 2H). In case of soil treatment, the highest of butyrate esterase was related to lichen and the least ones was observed in the physical crust.

3.9. Leucine aminopeptidase

Leucine aminopeptidase enzyme in crust treatment was lichen> moss> cyanobacteria> physical. The most content of this enzyme in soil + crust treatment was observed in lichen and had a significant difference with physical crust (Fig. 2I). Although there was no meaningful variation among the value of leucine aminopeptidase in this treatment. About soil treatment, the amount of this enzyme was lichen> cyanobacteria> moss> physical crust.

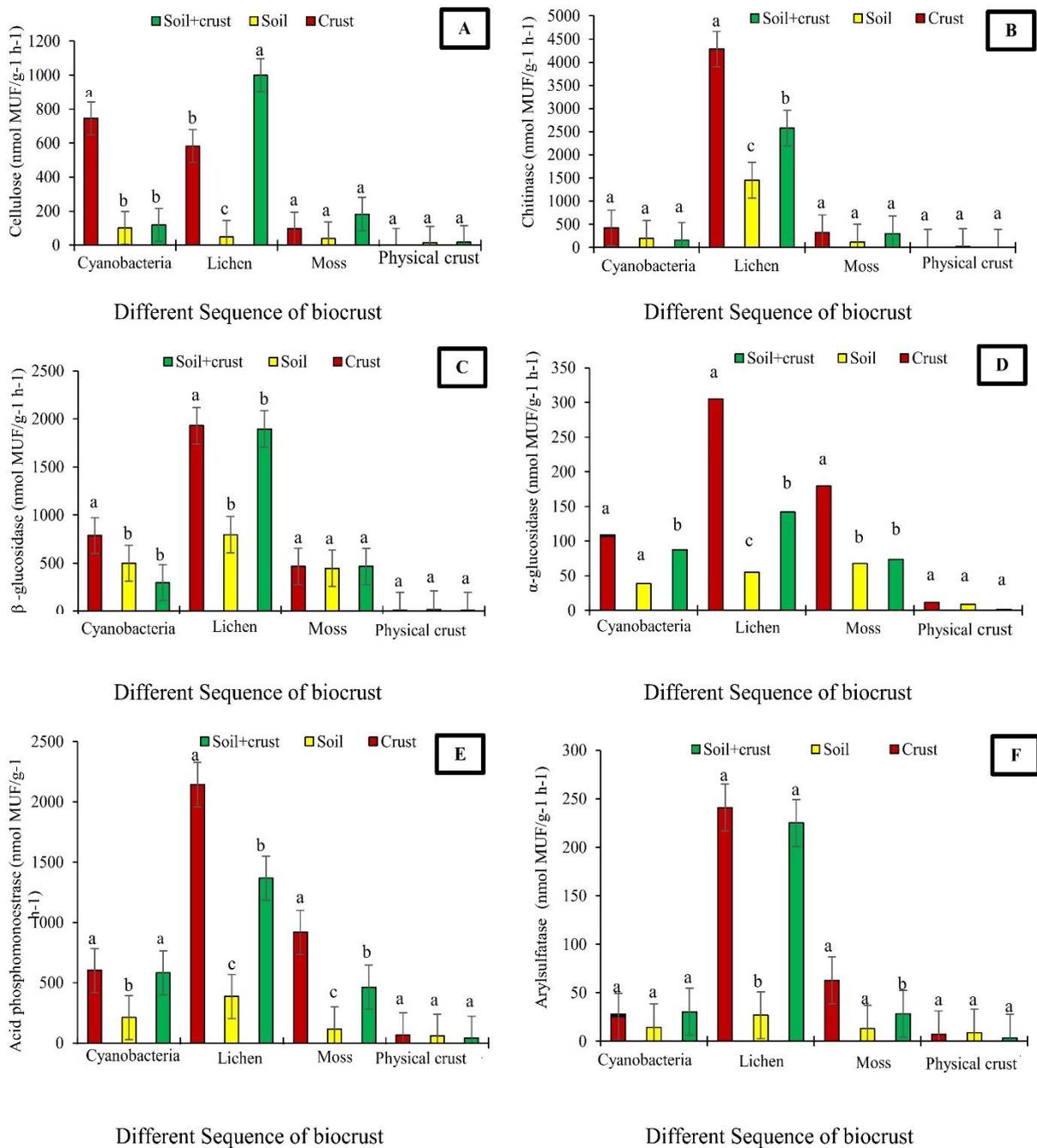
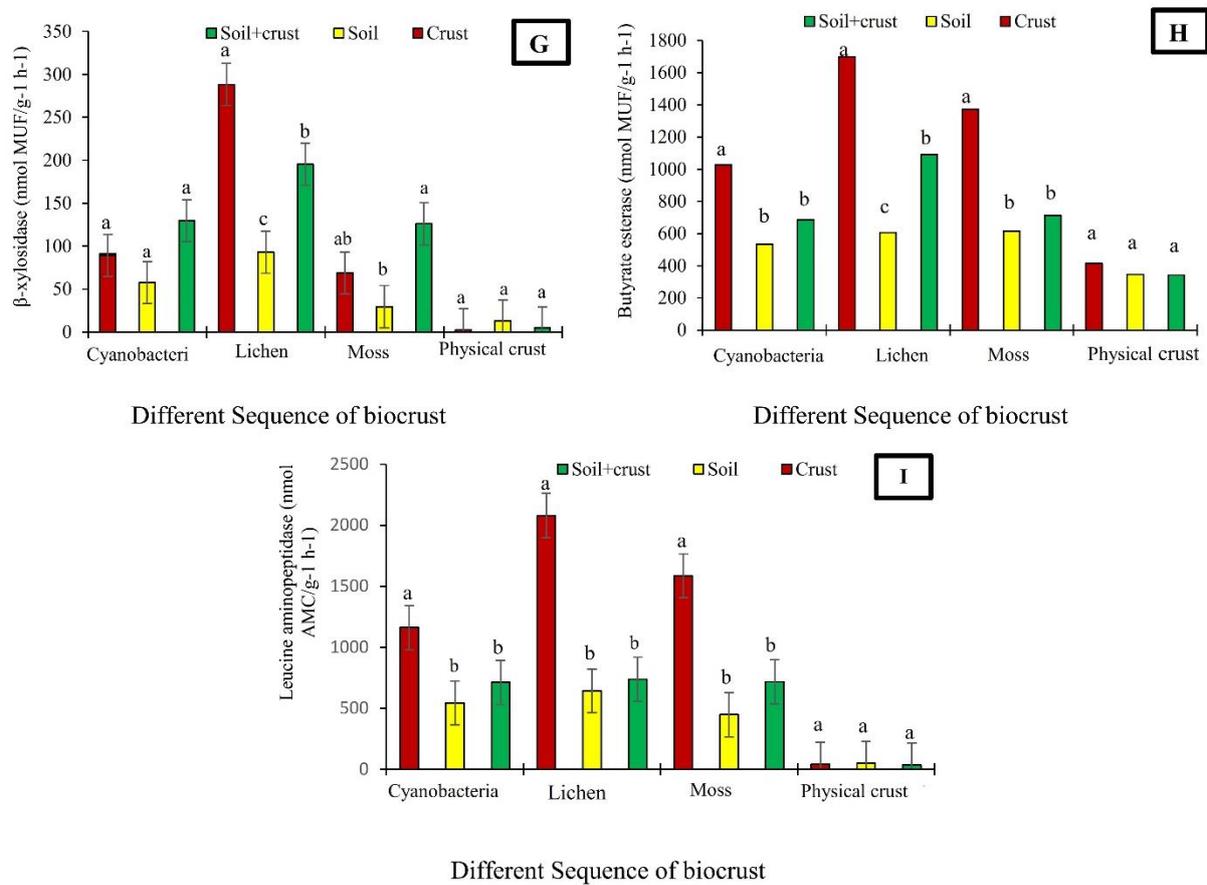


Fig. 2. Enzymatic activity in three different treatments (crust, soil and soil + crust) in different sequences of biological and physical crusts (different letters indicate significant differences at $p < 0.05$ and bars denote standard errors of the means). A: Cellulase, B: Chitinase, C: β -glucosidase, D: α -glucosidase, E: Acid phosphomonoesterase, F: Arylsulfatase, G: β -xylosidase, H: Butyrate esterase and I: Leucine aminopeptidase

**Fig. 2.** Continued

3.10. Synthetic enzymatic index (SEI)

Figure 3 shows the activity of the enzyme expressed as a synthetic enzyme indicator (SEI) according to three treatments i.e. crust, soil + crust and soil respectively. The content of SEI index in crust treatment was lichen > cyanobacteria > moss > physical crust and lichen had a significant difference with biological and physical crusts. Although there was no significant difference among cyanobacteria, moss as well as physical crust at $p < 0.05$. In soil + crust and also in soil treatments, the highest content of SEI index was related to lichen biocrust and the lowest ones was observed in physical crust.

3.11. Microbial functional diversity (Shannon Index)

The results of Shannon index were observed in Fig. 4. Microbial functional diversity as expressed by Shannon Index in

Crust and soil treatments were in order: cyanobacteria > lichen > moss > physical crust. In soil + crust treatment, the maximum value of Shannon Index was mentioned in lichen and moss biocrusts and the minimum ones as similar to crust and soil + crust treatments were related to physical crust. Although there was no significant difference between them as well as among the different sequence of biological soil crusts at $p < 0.05$.

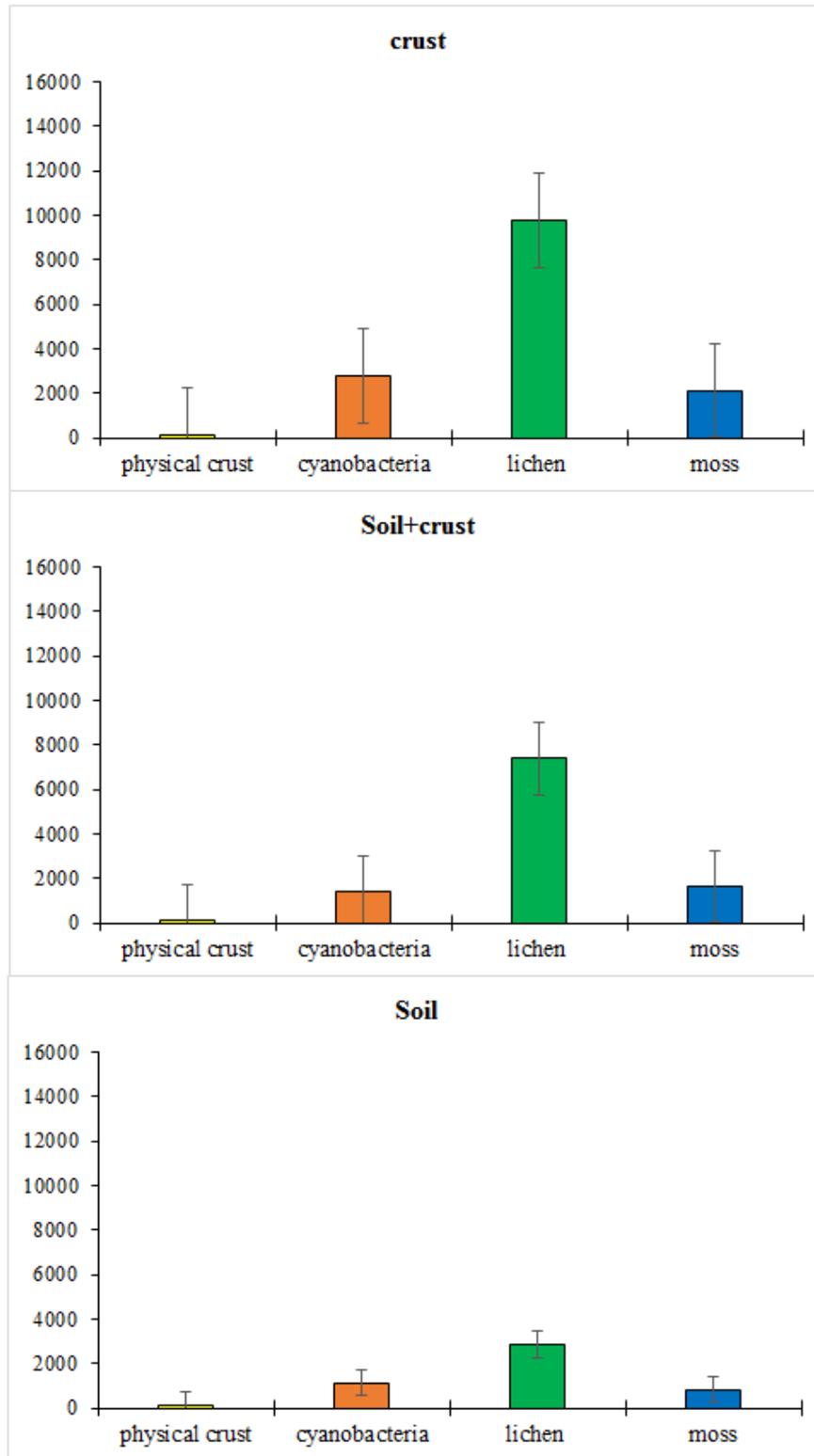


Fig. 3. Synthetic enzymatic index (SEI) at three sampling levels (crust, soil + crust and soil).

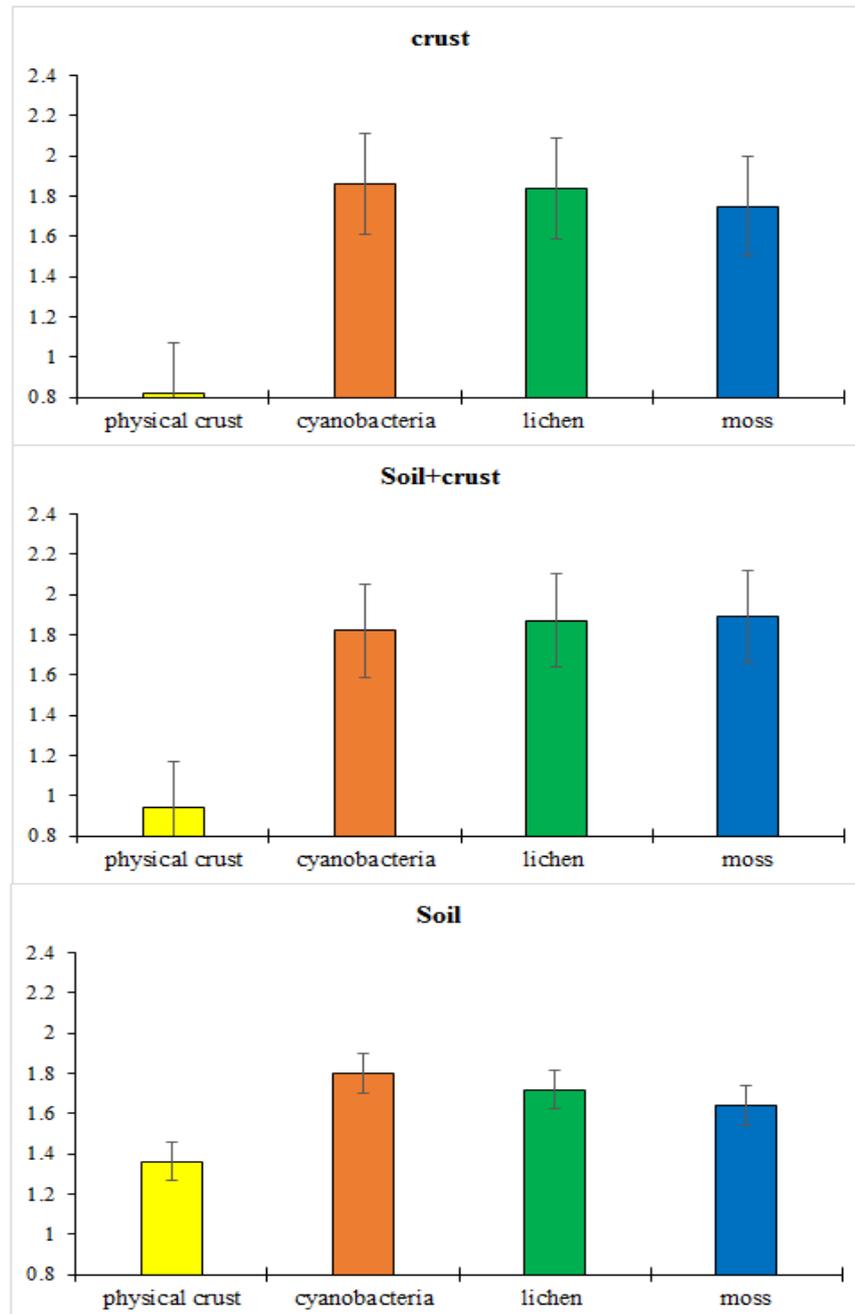


Fig. 4. Microbial functional diversity (Shannon Index)

4. Discussion

In order to investigate soil changes in natural and agricultural environments, the use of enzyme activity factor is effective (Jat *et al.*, 2021). A biological soil crust may create more desirable surroundings, i.e. suitable soil with high levels of soil nutrients and organic matter, which can lead to increased soil enzymes activity (Mangalassery *et al.*, 2015) that is confirmed by our prior result (Atashpaz *et al.* 2023). This is supported with the outcome of Li *et al.* (2009) who stated that soil biological crusts are the dominant factors affecting C and N input and exchange in arid ecosystems.

Cellulase is the superlative organic composition at the ecosystem, accounting for approximately half of the biomass synthesized by photosynthetic CO fixation. Cellulase is mainly obtained from plant residues and a slight content is produced by bacteria and fungi in the soil. Also, cellulase activity in forest soils is much higher than that in dry lands because of lignocellulosic materials and high relative abundance of fungi in these soils. Besides, the low value of cellulase in arid and semi-arid lands depends on their low organic carbon.

The results showed that cellulase content in crust treatment was in this order: cyanobacteria> lichen> moss> physical crust. This order in soil + crust treatment was lichen> moss> cyanobacteria> physical crust, in soil treatment was cyanobacteria> lichen> moss> physical crust. Therefore, this enzyme was more abundant in the different series of biocrusts than the physical crust, which was true to the consequences of Miralles *et al.* (2012) carried out in the Tabernas Desert. This is especially the case with cyanobacteria, which have a significant character in carbon and nitrogen stabilization as well as the add on organic matter to soils.

The content of chitinase decreased in the crust, soil + crust, and soil treatments, respectively, which could be related to the presence of lichens and their effect on increasing the amount of chitinase in the subsoil. Also, the content of chitinase in three treatments was higher in biocrusts than the physical crust. Brankatschk *et al.* (2013) supported with the chitinase enzyme had a more function in biocrust.

α - and β -glucosidase are the main members of the glucosidase enzyme family. The function of β -glucosidase in the carbon sequence is significantly important in soil quality. Lichen had more α -glucosidase and β -glucosidase and β -xylosidase value in all three treatments (crust, soil, soil + crust) compared to the two other biocrusts of cyanobacteria and moss as well as Physical crust. However, the amount of these two enzymes in different sequences of biocrusts were greater than the physical one. This indicates that biological crusts, due to having more enzyme activity and also with the increase of soil carbon compared with the physical crust, can better protect the soil surface against water and wind erosion.

Acid phosphomonoestrerase enzyme hydrolyses the P esters (Sarapatka, 2003). The content of organic matter in soil regulates the activity of acid phosphomonoestrerase enzyme (Sarapatka, 2003).

Results show that the content of acid phosphomonoestrerase in all treatments of this study in biocrusts was greater than the physical crust that explained due to the high biological activity in biological crusts. Also, the content of acid phosphomonoestrerase enzyme in crust, soil and soil + crust treatments in the lichen crust was greater than the cyanobacteria and moss crusts. Considering that the lichen species identified in this study was *Diploschistes diacapsis* (Ach.) *Lumbsch* which consists of two parts: algae and fungus and they fix carbon by performing photosynthesis. Increasing soil organic carbon improves soil aggregation and, therefore, it can be said that the lichen crust effectively increases soil stability and quality index compared to other biocrusts (Mager, 2010).

The results showed the highest content of arylsulfatase activity in three treatments was related to lichen biocrust. Also, the arylsulfatase activity in all three treatments in biocrusts was greater than the physical crust that had no biological activity. This matter is due to the greater biological activity in biological soil crusts.

Esterase is generally demonstrated using α -naphthyl acetate or butyrate as substrates.

According to the results, biological soil crusts had a higher butyrate esterase activity compared with the physical crust in all treatments. The content of butyrate esterase activity in the three studied treatments was in this order: lichen> moss> cyanobacteria> physical crust. Also, leucine aminopeptidase enzyme in biological soil crusts was greater than the physical

one. This enzyme in study treatments (crust, soil + crust and soil) in lichen biocrust was the greatest. This issue is due to the higher enzymatic activity in lichen crust compared with other biological and physical crusts (Liu *et al.*, 2014). The Shannon diversity and synthetic enzymatic indexes in the biological soil crusts were higher than the physical crusts, which improves soil characteristics, erosion resistance and increases soil stability. (Grzyb *et al.*, 2022).

5. Conclusion

Biological soil crusts increased significantly soil cellulase, chitinase, α -glucosidase, β -glucosidase, acid phosphomonoesterase, arylsulfatase, β -xylosidase, butyrate esterase and leucine aminopeptidase activities in Incheh Borun area, Golestan province, Iran. Generally, the amount of these enzymes in biocrusts was more than the physical crust. In fact, biocrusts had a higher enzyme content due to their higher activity and among them, lichen (*Diploschistes diacapsis* (Ach.) Lumbsch) had a higher enzymatic activity than the others. Since the increase of enzyme activity -especially β -glucosidase that plays an important role in carbon and nitrogen, health, quality and stability of soil. At this end, the biological soil crusts have increased the soil quality.

Author Contributions

Conceptualization, B.A., F.Kh., S. M., and R.M.; methodology, B.A.; software, F.Kh.; validation, F.Kh and S.M.; formal analysis, B.A.; investigation, F.Kh and S.M; resources, B.A.; data curation, R.M.; writing—original draft preparation, B.A.; writing—review and editing, B.A.; visualization, F.Kh and S.M.; supervision, F.Kh and S.M.; project administration, F.Kh and S.M. funding acquisition, B.A. All authors have read and agreed to the published version of the manuscript.

All authors contributed equally to the conceptualization of the article and writing of the original and subsequent drafts.

Data Availability Statement

Data available on request from the authors.

Acknowledgements

The authors would like to thank all participants of the present study.

Ethical considerations

The authors avoided from data fabrication and falsification.

Funding

The study was funded by the University of GUASNR, Country IRI, and Grant No. 2020-1-IT02-KA107-078816.

Conflict of interest

The authors declare no conflict of interest.

References

Allison, S.D., Martiny, J.B. (2008). Colloquium paper: Resistance, resilience, and redundancy in microbial communities. *Proceedings of the National Academy of Sciences of the United States of America*, 105(Suppl 1), 11512–11519. <https://doi.org/10.1073/pnas.0801925105>.

- Atashpaz, B., Khormali, F., Malekzadeh, E., Soleymanzadeh, M. (2023). Evaluating the Effect of Different Sequences of Biological Crusts on Loess Derived Soil Biophysiological Properties in the Semi-arid Regions of Northern Iran. *Journal of Soil Science and Plant Nutrition*, 23, 6777–6787. <https://doi.org/10.1007/s42729-023-01535-6>.
- Bian, D.D., Liao, C.Y., Sun, C.Z., *et al.* (2011). Effect of soil biological crust on the distribution of soil microorganisms in the loess hilly region. *Agricultural Research in the Arid Areas*, 229, 109–114.
- Bowker, M.A., Anenberg, J., Kebede, H.Y., Antoninka, A., Bailey, L. (2023). Biocrusts, *Encyclopedia of Soils in the Environment (Second Edition)* 1, 127-138.
- Bowker, M.A., Reed, S.C., Maestre, F.T, Eldridge, D.J. 2018. Biocrusts: The living skin of the Earth. *Plant and Soil*. 429, 1-2. <https://doi.org/10.1007/s11104-018-3735-1>.
- Brankatschk, R., Fischer, T., Veste, M., Zeyer, J. (2013). Succession of N cycling processes in biological soil crusts on a Central European inland dune. *FEMS Microbiology Ecology*, 83, 149–160. <https://doi.org/10.1111/j.1574-6941.2012.01459.x>.
- Büdel, B., Darienko, T., Deutschewitz, K., Dojani, S., Friedl, T., Mohr, K.I., Salisch, M., Reisser, W., Weber, B. (2009). Southern African biological soil crusts are ubiquitous and highly diverse in drylands, being restricted by rainfall frequency. *Microbial Ecology*, 57, 229-247. <https://doi.org/10.1007/s00248-008-9449-9>.
- Cui, Y., Lü, Y.Z., Li, B.G. (2004). Physico-chemical properties of soil microbiotic crusts on Erdos Plateau. *Soils* 36, 197–202.
- Darby, B.J., Neher, D.A., Belnap, J. (2010). Impact of biological soil crusts and desert plants on soil microfaunal community composition. *Plant and Soil*, 328, 421–431. <http://dx.doi.org/10.1007/s11104-009-0122-y>.
- De Armas, I.S., Bergeron, A., Bhardwaj, A., Patarroyo, M., Akay, M.H., Al Rameni, D., Nascimbene, A., Patel, M.K., Patel, J., Marcano, J. and Kar, B. (2022). Surgically implanted Impella device for patients on Impella CP support experiencing refractory hemolysis. *American Society for Artificial Internal Organs Journal*, 68(12), 251-e255. <https://doi.org/10.1097/mat.0000000000001712>.
- Deng, S., Zhang, D., Wang, G., Zhou, X., Ye, C.H., Fu, T., Ke, T., Zhang, Y., Liu, Y., Chen, L. (2020). Biological soil crust succession in deserts through a 59-year-long case study in China: How induced biological soil crust strategy accelerates desertification reversal from decades to years, *Soil Biology and Biochemistry*, 141, 107665. <http://dx.doi.org/10.1016/j.soilbio.2019.107665>.
- Drahorad, S., Felix-Henningsen, P., Siemens, J., Marschner, B., Heinze, S. (2021). Patterns of enzyme activities and nutrient availability within biocrusts under increasing aridity in Negev desert. *Ecosphere*, 13: e4051. <http://dx.doi.org/10.1002/ecs2.4051>.
- Feng, Z., Wang, G., Jiang, Y., Chen, C., Chen, D., Li, M., Morel, J.L., Yu, H., Chao, Y., Tang, Y., Qiu, R., Wang, S.H. (2024). Microbial survival strategies in biological soil crusts of polymetallic tailing wetlands. *Geoderma*, 443, 116852. <https://doi.org/10.1016/j.geoderma.2024.116852>.

- Frechen, M., Kehl, M., Rolf, C., Sarvati, R., Skowronek, A. (2009). Loess chronology of the Caspian Lowland in Northern Iran. *Quaternary International*, 128, 220-233. <https://doi.org/10.1016/j.quaint.2008.12.012>.
- García-Velázquez L, Gallardo A, Ochoa V, Gozalo B, Lázaro R, Maestre FT. (2022). Biocrusts increase the resistance to warming-induced increases in topsoil P pools. *Journal of ecology*, 110(9):2074-2087. <https://doi.org/10.1111/1365-2745.13930>.
- Ghiloufi, W., J. Seo, J. Kim, M. Chaieb, and H. Kang. (2019). "Effects of Biological Soil Crusts on Enzyme Activities and Microbial Community in Soils of an Arid Ecosystem. *Microbial Ecology*, 77: 201–16. <https://doi.org/10.1007/s00248-018-1219-8>.
- Grzyb, A., Agnieszka, W.M., Remigiusz, Ł., Jakub, C. (2022). Spatial and Temporal Variability of the Microbiological and Chemical Properties of Soils under Wheat and Oilseed Rape Cultivation. *Agronomy*, 10, 2259. <https://doi.org/10.3390/agronomy12102259>.
- Jat, H.S., Datta, A., Choudhary, M., Sharma, P.C., Dixit, B., Jat, M.L. (2021). Soil enzymes activity: Effect of climate smart agriculture on rhizosphere and bulk soil under cereal based systems of north-west India, *European Journal of Soil Biology*, 103: 103292. <https://doi.org/10.1016/j.ejsobi.2021.103292>.
- Jungblut, A.D.; Vincent, W.F.; Lovejoy, C. (2012). Eukaryotes in Arctic and Antarctic cyanobacterial mats. *FEMS Microbial Ecology*, 82: 416–428. <https://doi.org/10.1111/j.1574-6941.2012.01418.x>.
- Li, X.R., Zhang, Y.M., Zhao, Y.G. (2009). A study of biological soil crusts: recent development, trend and prospect. *Advances in Earth Science*, 24,11–24. <https://doi.org/10.11867/j.issn.1001-8166.2009.01.0011>.
- Lu, M., Zhou, X., Luo, Y., Yang, Y., Fang, C., Chen, J., Li, B. (2011). Minor stimulation of soil carbon storage by nitrogen addition: A meta-analysis. *Agriculture, Ecosystems and Environment*, 140, 234-244. <http://dx.doi.org/10.1016/j.agee.2010.12.010>.
- Mager, D.M. (2010). Carbohydrates in cyanobacterial soil crusts as a source of carbon in the southwest Kalahari, Botswana. *Soil Biology and Biochemistry*, 42(2): 313-318. <http://dx.doi.org/10.1016/j.soilbio.2009.11.009>.
- Mangalassery, S., Mooney, S.J., Sparkes, D.L., Fraser, W.T., Sjögersten, S. (2015). Impacts of zero tillage on soil enzyme activities, microbial characteristics and organic matter functional chemistry in temperate soils. *European Journal of Soil Biology*, 68:9–17. <https://doi.org/10.1016/j.ejsobi.2015.03.001>.
- Marinari, S., Moscatelli, M.C., Marabottina, R., Moretti, P., Vingianib, S. (2020). Enzyme activities as affected by mineral properties in buried volcanic soils of southern Italy. *Geoderma* 362, 114123. <http://dx.doi.org/10.1016/j.geoderma.2019.114123>.
- Meng, J., Bu, C.F., Zhao, Y.J. (2010). Effects of BSC on soil enzymeactivities and nutrients content in wind-water erosion crisscross region, Northern Shaanxi Province, China. *Journal of Natural Resources*, 25, 1864–1874.
- Moscatelli, M.C., Secondi, L., Marabottini, R., Papp, R., Stazi, S.R., Mania, E., Marinari, S. (2018). Assessment of soil microbial functional diversity: land use and soil properties affect CLPP-MicroResp and enzymes responses. *Pedobiologia*, 66, 36-42. <https://doi.org/10.1016/j.pedobi.2018.01.001>.

- Rahimzadeh, N., Gribenski, N., Tsukamoto, S., Kehl, M., Pint, A., Kiani, F., Frechen, M. (2019). Timing and development of sand dunes in the Golestan Province, Northern Iran—implications for the Late-Pleistocene history of the Caspian Sea. *Aeolian Research*, 41, 100538. <http://dx.doi.org/10.1016/j.aeolia.2019.07.004>.
- Reeve, S., Palmer, B., Cobb, P., Pietrasiak, N., Lipson, D.A. (2023). Facilitating restoration of degraded biological soil crusts using mixed culture inoculation, *Journal of Arid Environments*, 208, 104876. <https://doi.org/10.1016/j.jaridenv.2022.104876>.
- Rohman, A., Dijkstra, B.W., Puspaningsih, N.N.T. (2019). β -Xylosidases: Structural diversity, catalytic mechanism, and inhibition by monosaccharides. *International Journal of Molecular Sciences*, 20, 5524. <https://doi.org/10.3390/ijms20225524>.
- Sarapatka, B. (2003). Phosphatase activities (ACP, ALP) in agroecosystem soils. Doctoral thesis Swedish University of Agricultural Sciences, Uppsala, 1-113.
- Sethi, S.K.; Samad, L.K.; Adhikary, S.P. (2012). Cyanobacteria and micro-algae in biological crusts on soil and sub-aerial habitats of eastern and northeastern region of India. *Phycos*, 42: 1–9.
- Soil Survey Staff. (2010). Keys to Soil Taxonomy. 11th Edition, USDA-Natural Resources Conservation Service, Washington DC.
- Soleimanzadeh, M., Khormali, F., Sohrabi, M., Ghorbani Nasrabadi, N., Kehl, M. (2019). Evaluating biological attributes of soil quality in loessial soils under lichen biological soil crusts in northern Golestan province. *Agricultural Engineering Journal*, 42(3) 1-17. <https://doi.org/10.22055/agen.2019.26696.1445>.
- van Dyk, J.S., Pletschke, B.I. (2011). A review of lignocellulose bioconversion using enzymatic hydrolysis and synergistic cooperation between enzymes—Factors affecting enzymes, conversion and synergy. *Biotechnology Advances*, 30, 1458–80. <https://doi.org/10.1016/j.biotechadv.2012.03.002>.
- Wang, R., Zhu, Q.K., Bu, N., *et al.* (2010). Study on physicochemical properties of BSCs in the hilly-gully regions of the Loess Plateau. *Arid Zone Research*, 27, 401–408.
- Wang, D., Fonte, S.J., Parikh, S.J., Six, J., Scow, K.M. (2017). Biochar additions can enhance soil structure and the physical stabilization of C in aggregates. *Geoderma*, 303, 110-117. <http://dx.doi.org/10.1016/j.geoderma.2017.05.027>.
- Warren, S.D.; St. Clair, L.L.; Leavitt, S.D. (2019a). Aerobiology and passive restoration of biological soil crusts. *Aerobiologia*, 35: 45–56. <https://link.springer.com/article/10.1007/s10453-018-9539-1>.
- Weber, B., Budel, B., Benlap, J. (2016). Biological soil crust: An organizing principal in dry lands. *Ecological studies*, 226, 2196 – 971x.
- Yang Y, Chen Y, Li Z, Zhang Y, Lu L. (2023). Microbial community and soil enzyme activities driving microbial metabolic efficiency patterns in riparian soils of the Three Gorges Reservoir. *Frontiers in Microbiology*, 21; 14:1108025. <https://doi.org/10.3389/fmicb.2023.1108025>.

- Zak, J.C., Willig, M.R., Moorhead, D.L., Wildman, H.G. (1994). Functional diversity of microbial communities a quantitative approach. *Soil Biology and Biochemistry*, 26, 1101–1108. [http://dx.doi.org/10.1016/0038-0717\(94\)90131-7](http://dx.doi.org/10.1016/0038-0717(94)90131-7).
- Zelikova, T.J., Housman, D.C., Grote, E.E., Neher, D.A., Belnap, J. (2012). Warming and increased precipitation frequency on the Colorado Plateau: implications for biological soil crusts and soil processes. *Plant and Soil*, 355, 265–282. <https://doi.10.1007/s11104-011-1097-z>.
- Zhang, Y., Yang, W.K., Wang, X.Q., Zhang, D.Y. (2005). Influence of cryptogamic soil crusts on accumulation of soil organic matter in Gurbantunggut Desert, northern Xinjiang China. *Acta Ecologica Sinica*, 25, 3420-3425.
- Zhang, W., Zhang, G.S., Liu, G.X., Dong, Z.B., Chen, T., Zhang, M.X., Dyson, P.J., An, L.Z. (2012). Bacterial diversity and distribution in the southeast edge of the Tengger Desert and their correlation with soil enzyme activities. *Journal of Environmental Sciences*, 24, 2004–2011. [https://doi.org/10.1016/s1001-0742\(11\)61037-1](https://doi.org/10.1016/s1001-0742(11)61037-1).
- Zhao, H.L., Guo, Y.R., Zhou, R.L., Drake, S. (2010). Biological soil crust and surface soil properties in different vegetation types of Horqin Sand Land, China. *Catena*, 82, 70-76. <http://dx.doi.org/10.1016/j.catena.2010.05.002>.
- Zhao, H.L., Guo, Y.R., Zhou, R.L., Drake, S. (2011). The effects of plantation development on biological soil crust and topsoil properties in a desert in northern China. *Geoderma*, 160, 367–372. <http://dx.doi.org/10.1016/j.geoderma.2010.10.005>.