Folia Geobot (2021) 56:205–213
https://doi.org/10.1007/s12224-021-09402-x

Contrasting seed germination response to moss and lichen crusts in Stipa caucasica, a key species of the Irano-Turanian steppe

Negar Ahmadian · Mehdi Abedi ·
Mohamad Sohrabi · Sergey Rosbakh

Received: 14 May 2021 / Revised: 11 November 2021 / Accepted: 8 December 2021 / Published online: 14 January 2022

Abstract Biological soil crusts (BSC) play a crucial role in arid ecosystem functioning, yet the effect of their properties (e.g. whether they are dominated by mosses and lichens) on the germination has rarely been investigated. Here, we analysed the effects of intact, dead and removed moss or lichen BSC on seed germination of *Stipa caucasica*, a key species in the Iranian *Artemisia* steppes. Our results revealed that both dead and intact moss BSC significantly and strongly reduced and delayed germination putatively due to the physical properties of the crust limiting water supply to the large seeds of the focal species. Further, we found out that intact lichen BSC had no significant effect on the germination traits studied whereas lichen BSC removal and heat treatment ('dead' BSC) reduced germination percentage. The reduction is most likely due to the allelopathy effects and surface properties of the lichen crust. The detected patterns suggest that moss and lichen BSC play different roles in *S. caucasica* seed regeneration in the steppe; however, the effect on the species population dynamics deserve further study including also later stages of seedling establishment.

Keywords Allelopathy · Biotic interactions · Caryopsis · Feather grass · Grassland · Regeneration

Introduction

Biological soil crusts (BSC), agglomerates of soil particles and cyanobacteria, algae, fungi, mosses and lichens (Belnap and Lange 2001), play a crucial role in arid ecosystem functioning (Briggs and Morgan 2011). They increase nitrogen fixation and soil carbon sequestration, increase soil organic matter and nutrients in their underneath soil (Barger et al. 2016) and alter soil surface texture and microclimate (Garcia-Pichel et al. 2016). Cumulatively, the BSC create a favourable environment for adult plant growth in the extremely resource-limited and semi-arid and arid deserts with scattered vegetation (Tongway and Ludwig 2001; Escudero et al. 2007; Langhans et al. 2009; Zhang et al. 2016). However, at the same time, the BSC may hinder plant

---

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s12224-021-09402-x.

N. Ahmadian · M. Abedi (✉)
Department of Range Management, Faculty of Natural Resources and Marine Sciences, Tarbiat Modares University, Noor, Mazandaran Province, Islamic Republic of Iran
e-mail: mehdi.abedi@modares.ac.ir; abedimail@gmail.com

M. Sohrabi
Department of Biotechnology, Iranian Research Organization for Science and Technology, Tehran, Iran

S. Rosbakh
Ecology and Nature Conservation Biology, University of Regensburg, Regensburg, Germany

establishment, and this fact probably depends on the composition of the soil crust, specifically whether moss or lichens are dominant.

In contrast to the performance of adult plants, the potential effects of BSC on seed germination and seedling growth, two key plant life stages (Poschlod et al. 2013), are poorly understood. The available literature on BSC effects on plant establishment is scattered and often reports controversial patterns. Previous research suggests that the BSC biological components affect plant regeneration and establishment differently. Specifically, the positive effects of relatively thin moss layer on seed germination and seedling establishment were associated with their accumulation of water and nutrients (Su et al. 2009) and with improved temperature conditions on their surface (Rasran et al. 2007). By contrast, a thick moss layer can negatively affect germination by creating a physical barrier that prevents water uptake (Gilbert and Corbin 2019) and light perception by the seeds (Donath and Eckstein 2010). Additionally, the allelopathic compounds released by mosses can inhibit germination of seeds on/in the BSC (van Tooren 1990).

Similarly to mosses, lichens present in the BSC can create favourable microsites for seed germination due to higher soil moisture contents (Ghiloufi et al. 2017). Contrastingly, the morphological characteristics of the lichen crust (e.g. homogeneous and flat surface), their allelopathic components (Escudero et al. 2007; Langhans et al. 2009) have been reported to have negative effects on seed germination.

Biological soil crusts in arid ecosystems are never homogeneous, their composition and thickness vary spatially, and they, moreover, may be disrupted or removed by biotic and abiotic factors (Tongway and Ludwig 2001). Grazing, being the most common type of disturbance, can contribute to small-scale soil heterogeneity (Golodets and Boeken, 2006; Concostrina-Zubiri et al., 2013), strongly break the soil crust (Liu et al., 2009) and may increase germination of exotic species (Hernandez and Sandquist 2011). Foliose lichens and mosses are more susceptible to grazing disturbances than other lichens (Rogers and Lange 1971; Muscha and Hild 2006). Despite the heterogeneity of the soil surface in arid ecosystems, the most evidence has been collected in experimental studies using complex BSC (i.e. consisting of both mosses and lichens) making it difficult to attribute the observed seed and seedling responses to the various BSC components (Serpe et al. 2006; Song et al. 2017; Havrilla et al. 2019; Song et al. 2020).

To disentangle effect of various BSC components we studied the germination response of *Stipa caucasica*, a key species in steppe flora (Wesche et al. 2016), to moss and lichens BSC that are common in the species habitat. From previous studies we know that the seed germination of some *Stipa* species is positively affected by the BSC, due to microhabitat and soil moisture improvement (e.g. *S. tenacissima*: Ghiloufi et al., 2017; *S. barbata*: Tavili et al., 2017), while other *Stipa* species respond negatively (*S. glareosa,* Song et al., 2020). We performed an indoor germination experiment combining soil without crust, with living crust and with dead crust (moss and lichen separately), to disentangle biological, chemical and physical effects of the BSC.

Materials and methods

Study area

The fieldwork was conducted at a site in the Almeh valley (37°21′8.42″ N and 56°12′48.60″ E) located in the southeastern part of Golestan National Park, Iran, influenced by mountain steppes climatic conditions (Bahalkeh et al. 2021a). The National Park was established in 1974 to protect the Irano-Turanian region, particularly *Artemisia* arid steppes and the Hyrcanian forest (Akhani, 1998). The climate of the study site is cold and arid with mean annual precipitation and temperature of 161.3 mm and 17°C, respectively (Golestan National Park report, 2016). The area has slopes no larger than 9°; the elevations ranges from 1,200 to 1,300 m a.s.l. The alluvial soils are with 80% sand, low organic matter and high stone cover up to 40%. Grazing by Persian gazelles (*Gazella subgutturosa subgutturosa*) in the main disturbance in the study site (Akhani 1998).

Artemisia steppes belong to typical vegetation of the Irano-Turanian region (Zohary 1973) and occupy larger territories in central and northeastern Iran (Zohary 1973). The plant communities are dominated by the dwarf shrub *Artemisia sieberi* Besser in association with several perennial (e.g. *S. caucasica* Schmalh) and annual grasses (*Avena barbata*, Pott ex Link, *Bromus tectorum* L and *Taeniatherum caput-medusae* (L) Nevski) and some shrubs (e.g. *Salsola* *arbusculiformis* Drobow). The plant cover is very sparse (less than 30%; Bahalkeh et al., 2021b) with bare soil usually covered by different BSC (Ahmadian et al. 2019). Typical BSC of the study region consists of mosses (average thickness 4 cm), lichens (average thickness 2 mm) and 'open soil' with physical crusts in the 1 cm of the topsoil.

Study species

As our model species to study the effects of SBC on seed germination, we selected perennial grass *Stipa caucasica* Schmalh, as it is one of the most common and typical species of the *Artemisia* steppes covering large territories from northern Iran to northern China (Wesche et al. 2016; Akhani 1998). In the study area, *S. caucasica* dominates in the vegetation with maximum cover up to 10% (*n*= 20 plots 4 m×4 m, unpublished results).

Stipa caucasica seeds mainly have non-deep physiological dormancy that is alleviated after a short period of after-ripening (Baskin and Baskin 2014). Several studies identified favourable conditions for germination and dormancy such as better germination in light (White and Van Auken 1996), a negative correlation between germination and precipitation (Hamasha and Hensen 2009), and high sensitivity to water stress and parent environment effects (Gilbert and Corbin 2019; Zaki et al., 2021). In addition, caryopses of *Stipa* have awns that help seeds to drill into the soil, which possibly promotes seed germination (Ghermandi 1995) or prevent it when placed on top of the moss (Morgan, 2006). *Stipa caucasica* has mean (*n* = 10) seed mass of 5.62 g and seed size of 11 mm length and 1 mm width (Seed Information Database; https://data.kew.org/sid) and our own measurements, respectively).

Seed and BSC sampling

Caryopses of *S. caucasica* (thereafter 'seeds') for the germination experiments were collected at maturity in June 2016 at the Almeh valley site from at least 20 plant individuals growing at least 2 m apart from each other. The collected, intact seeds were air-dried for several days at room temperature followed by cold temperature at 4°C for 60 days to preserve their viability (Baskin and Baskin 2014). Germination experiments were started in August 2016 and seeds without an awn were used.

Two types of BSC, one dominated by mosses and another by lichens, were also collected at same date of seed collection and from the same sites where seed were collected. The moss crust was composed of one species, *Circinaria hispida* (Mereschk.) A. Nordin, S.Savic, whereas the lichen crust were composed of nine species, including *Circinaria mansourii* (Sohrabi) Sohrabi, *Circinaria rostamii* Sohrabi, *Collema tenax* (Sw.) Ach, *Endocarpon pusillum* Hedw, *Gyalolechia fulgens* (Sw.) Søchting, Frödén & Arup, *Peccania terricola* H. Magn., *Psora decipiens* (Hedw.) Hoffm. *Toninia sedifolia* (Scop.) Timdal, *Tortella tortuosa* (Hedw.) Limpr). A crustose lichen *Circinaria mansourii* (Sohrabi) Sohrabi and two foliose species, including *Gyalolechia fulgens* (Sw.) Søchting, Frödén & Arup, and *Collema tenax* (Sw.) Ach were the dominant lichen species in the corresponding BSC.

To prevent the breakdown of lichen and moss samples, the soil surface was first irrigated by deionized water following by its removal together with a thin layer of underlying soil (10 mm) and transferred to the lab. The BSC were stored at room temperature for two months. Lichen and plant identification was confirmed by specialists of the Iranian Scientific and Industrial Research Organization (Cryptomorphous Iran, ICH) and Ferdowsi university of Mashhad, respectively.

BSC treatments

For each of the two BSC, four treatments were applied: 'intact', 'dead', 'removal' and 'open soil'. Open soil was considered as a control. In the 'open soil' treatment, seeds were germinated on the bare soil without BSC. Intact treatments included seed cultivation on either moss or lichens collected in the field in Petri dishes without any additional treatment. For the 'dead' treatment the BSC consisting of either mosses or lichens were heated first at 105°C for 72 hours and then at 121°C for 20 minutes (Zamfir 2000) followed by seed cultivation on the heated BSC surface. The main aim of this treatment was to evaluate the biotic role of crust. In the 'removal' treatment, *Stipa* seeds were germinated on the BSC, from which mosses and lichens were removed by scrapping

(Escudero et al. 2007). This treatment served to distinguish physical role of crust.

Seed germination tests

Stipa caucasica seeds were germinated in each of the treatments: two BSCs (moss and lichen) × four treatments as described above, in five replicates with 25 seeds each. The Petri dishes with the pre-treated BSC and seeds were incubated in climate chambers (Model TG, NoorSanaat, Iran) at 15/25°C (photoperiod 14/10 hours light/dark regime). These experimental conditions correspond to soil temperatures in early spring during natural germination of *S. caucasica* seeds (Ahmadian et al. 2018; Abdoli and Abedi 2019). The samples were sprayed daily with deionized water to maintain surface moisture. During the first two weeks, germination was scored every day and starting from day 14 every third day. Germination was scored over 30 days, a period during which the majority of viable seeds germinated. Seeds were regarded as germinated if the radicle had protruded at least 1 mm. The viability of the non-germinated seeds was tested by the 'cut' test: seeds with a white, firm embryo and endosperm were considered viable (Baskin and Baskin 2014). Only a low number of viable seeds were found, so viable seeds were excluded from the data analysis.

Data analysis

Seed germination in all treatments was characterized by three traits representing different aspects of the process: (1) final germination percentage (FGP), (2) germination speed and (3) germination synchrony. The FGP characterizes species' ability to complete the germination process in a given treatment. Mean germination time (MGT) was used as a proxy for seed germination speed; lower MGT values indicate faster seed germination in a particular treatment. Germination synchrony was estimated by calculating the *Z* synchronization index (Lozano-Isla et al. 2019), which varies from 0 (events of seed germination was evenly spread over the whole incubation period) to 1 (all seeds germinated at the same time). The three traits were calculated for each replicate (Petri dish) in each treatment.

Generalized linear models (GLMs) in combination with post-hoc Tukey test were employed to infer the statistically significant treatment effects on seed germination. The GLM for the FPG data included family 'binomial' (logistic regression) whereas the MGT and Z data were analysed using the family 'Gaussian' (linear regression). The 'open soil' treatment (control) was set as the reference group. Model assumptions were met in all cases. The analysis was conducted separately for moss and lichen BSC. All statistical tests were conducted using 95% CI, with significance determined by $P < 0.05$. Data are presented as mean ± standard error where possible. All statistical analyses were conducted in R 4.1.0 (R core development team, 2021). FGP, MGT and Z values for all species were calculated using the package 'GerminaR' (Lozano-Isla et al. 2019). The group comparison (post-hoc Tukey test) was done with the help of the package 'emmeans' (Lenth, 2018).

Results

The results of our experiment revealed different effects of the BSC treatments on the seed germination process in *S. caucasica*. Regarding the lichen crusts, we detected a significant decline in final germination percentage along the treatment row 'open soil' – 'intact' – 'removed' – 'dead' (Fig. 1, Table 1). The study species showed different responses to lichen treatments. Open soil had the highest germination percentage with no differences with 'intact' lichen. Removal treatment showed significant differences with 'open soil' for *S. caucasica*. Dead lichen had the lowest germination in comparison with other treatments. Seed germination speed and synchrony was not affected by any of the treatments (Fig. 1; Table 1).

As for the moss BSC, significantly higher seed germination percentages were recorded on the 'open soil' and the soil samples with the 'removed' BSC. Seed cultivation on 'intact' and 'dead' BSC resulted in comparatively lower germinations percentages. A similar pattern was also found for the seed germination speed; the mean germination time values were significantly lower in the 'open soil' and 'removed' treatments (Fig. 1 and Table 1). Germination synchrony did not differ significantly among the treatments (Fig. 1 and Table 1).

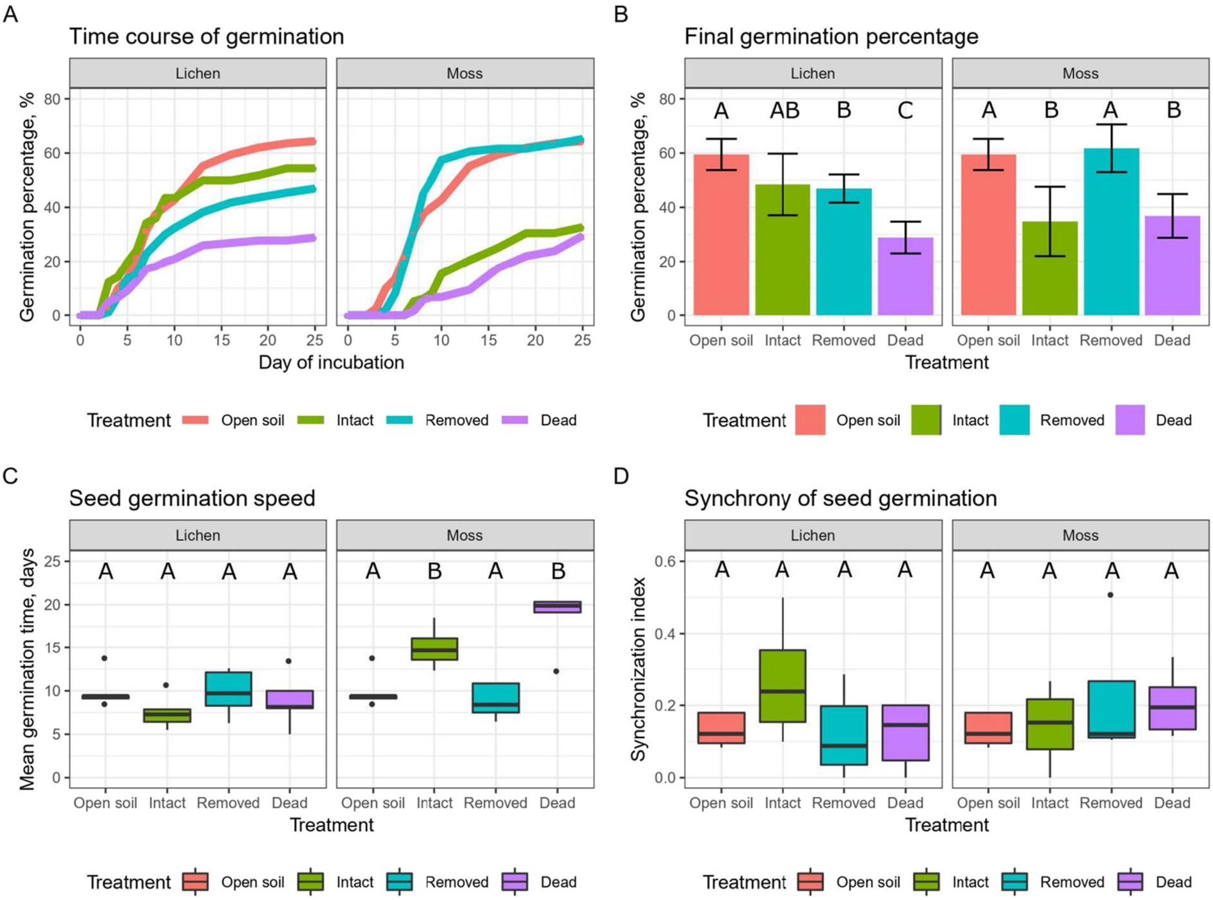

Fig. 1 Effects of different biological soil crusts on seed germination traits in *Stipa caucasica*: A – time course of germination, B – final germination percentage, C – seed germination rate, and D – synchrony of seed germination. Letters indicate statistical differences between groups (post-hoc Tukey test, $P < 0.05$).

Discussion

Effects of lichen crusts on *Stipa* germination

The lack of a significant effect of lichen crusts on FGP in our experiment contradicts the results of previous research mainly reporting inhibiting effects of lichens on seed germination (Escudero et al. 2007; Serpe et al. 2008; Havrilla et al. 2019). This result is not consistent for *S. glareosa* (Song et al. 2020), and also not consistent with positive effect on *S. tenacissima* and *S. barbata* germination, respectively (Ghiloufi et al. 2017; Tavili et al. 2017). There is only one study which, similarly to our experiment, found no significant effects of lichen crusts on seed germination (Slate et al. 2019). We speculate that the different species composition of lichen crusts used in the experimental studies could be a possible explanation for this controversy. For example, two studies by Ghiloufi et al. (2017) and Escudero et al. (2007) revealed that different proportions of crustose, squamulose and foliose lichens in a BSC had contrasting effects on seed germination, whereby the proportion of crustose lichens was found to be positively correlated with inhibitory effects of the BSC on germination percentage. In this context, the dominance of the crustose lichen *Circinaria mansourii* together with two folicose lichens *Gyalolechia fulgens* and *Collema tenax* in the ‘intact’ lichen BSC could explain their neutral effect on FGP in *S. caucasica*. In addition, seed germination behaviour on the BSC may differ under filed and experimental conditions: BSC with significant effects on germination in the field are known to have no effects on seed germination traits in

Table 1 Results of generalized linear models and post-hoc Tukey tests for the effects of lichen and moss treatments on seed germination parameters. The GLM for the final germination percentage (FGP) data included family 'binomial' (logistic regression) whereas the MGT and Z data were analysed using the family 'Gaussian' (linear regression). The 'Open soil' treatment (control) was set as the reference group. The model estimates for the FGP were back-transformed to proportions for the sake of clarity. The 'Test statistics' columns report z- and t-values for the binomial and Gaussian regressions, respectively. Bold values indicate significant effects of treatments ($P < 0.05$). Different letters indicate significant differences between the control ('Open soil') and other treatments as induced by the Tukey post-hoc test ($P < 0.05$).

Seed germination trait	Lichen				Moss						
	Treatment	Mean	*SE*	Test statistic	*P*	Group	Mean	*SE*	Test statistic	*P*	Group
Final germination percentage	Open soil	66	7.9	3.4	**< 0.001**	A	66	8.9	3.4	**< 0.001**	A
	Intact	55.3	11.1	−1.3	0.35	AB	34.8	13.4	−4.3	**0.035**	B
	Removed	46.9	11.1	−2.6	0.106	B	67.1	12.7	0.1	0.933	A
	Dead	28.9	11.1	−5.5	**0.004**	C	36.8	12.7	−4.3	**0.036**	B
Mean germination time	Open soil	10.1	1.1	9.0	**< 0.001**	A	10.07	1.17	8.6	**< 0.001**	A
	Intact	7.6	1.6	−1.6	0.135	A	15.05	1.75	2.8	**0.012**	B
	Removed	9.8	1.6	−0.2	0.87	A	8.83	1.65	−0.8	0.462	A
	Dead	8.9	1.6	−0.7	0.484	A	18.41	1.65	5.1	**< 0.001**	B
Synchronization index	Open soil	0.13	0.05	2.6	**0.018**	A	0.13	0.05	2.6	**0.022**	A
	Intact	0.27	0.07	1.9	0.072	A	0.14	0.08	0.1	0.893	A
	Removed	0.12	0.07	−0.2	0.881	A	0.22	0.07	1.2	0.238	A
	Dead	0.12	0.07	−0.2	0.85	A	0.2	0.07	1.0	0.335	A

the experiments, may not influence germination when a crust is used as the germination substrate (Su et al. 2009).

Lichen removal in our study showed negative effects on seed germinations as compared to ‘open soil’. Allelopathic compounds can be still available in the soil up to one year after removal (Bahalkeh et al., 2021b), therefore the soil in the ‘removed’ treatment most likely contained comparatively high allelopathic compounds since the lichen crust was removed right before the germination experiment. These compounds, similarly to previous findings (Escudero et al. 2007; Langhans et al. 2009), could thus have negative allelopathic effects on our study species germination. Furthermore, homogeneous and flat surface of lichens could also explain germination inhibition, as our lichen BSC were dominated by crustose lichens with relatively flat surface. Seed incubation on dead lichen BSC resulted in strong germination decrease, a finding consistent to Escudero et al. (2007). These differences could be related to lack or occurrence of some thermolabile compounds (Escudero et al. 2007).

Effects of moss crusts on *Stipa* germination

The negative effect of the ‘intact’ moss on final germination percentage of the study species is in line with previous research on BSC effects on *Stipa* seed germination (e.g. *S. glareosa*; Song et al. 2020), so this might be a widespread phenomenon. The most plausible explanation of these negative effects could be the physical properties of the moss crust, as significantly lower FGPs were recorded only in the ‘intact’ and ‘dead’ BSC treatments and not in the ‘removed’ one. In arid regions, moss crusts are known for their ability to absorb and retain water (Ahmadian et al. 2019), therefore the 4 cm-thick moss crust layer in our experiment most likely absorbed the available water and limited and the delayed germination of large-seeded drought-sensitive *Stipa* seeds on the crust surface (Daws et al. 2004; Serpe et al. 2006; Langhans et al. 2009; Briggs and Morgan 2011; Gilbert and Corbin 2019). The role of mosses as a physical barrier is consistent with Serpe et al. (2008), Song et al. (2017) and Huber and Kollmann (2020), and the positive effects on germination percentage on the moss removal treatment confirm this line of argument.

Conclusion

Overall, our results demonstrate that moss BSC in general reduced and delayed the germination of *S. caucasica*. Under natural conditions, these effects could negatively affect *S. caucasica* recruitment on the soils covered by the moss dominated BSC potentially leading to reduced population density of the species (e.g. Song et al. 2020). The results are derived from experimental study in well-watered conditions and real germination in the field would be probably much lower. It is also possible that further survival of germinating seeds will be affected differently in comparison with early stages of germination. For example, *Stipa* seeds usually bury themselves into the substrate and this might affect the survival of the seedlings especially in moss BSC where penetration into the crust with the aid of an awn would be easier than in the case of the lichen BSC. Alas, we were not able to mimic these processes in experimental conditions. The BSC in the study area, moreover, are not homogeneous. They may be dominated by moss, lichens or cyanobacteria or may be disturbed, for example, by wild undulates grazing and trampling; this heterogeneity provides enough opportunities for *S. caucasica* germination. To elucidate the effect of the biological soil crust on population dynamics of the species under study, we would need to know more about later phases of seedling establishment.

Acknowledgements We thank the Tarbiat Modares University for the financial support of the project. The staff at the Department of Environment in Golestan Province and security guards and experts in Golestan National Park made helpful contributions. The comments of two anonymous reviewers helped to improve the early version of the article.

References

Abdoli H, Abedi M (2019) Effect of temperature flactuation and cold stratification on germination of four dominant grass species (Case study: Golestan National Park). *J Seed Res* 29:56–66

Ahmadian N, Abedi M, Sohrabi M (2019) Comparison of Moss, Cyanobacteria and Artemisia shrub in soil moisture conservations and soil temperature modifications. *Iran J Range Desert Res* 26:451–460

Ahmadian N, Abedi M, Sohrabi M (2018) The protective effect of lichen in maintaining moisture and modulatingthe temperature fluctuations of soil susceptible to wind erosion. *Environ Erosion Res J* 31:71–86

Akhani H (1998) Plant biodiversity of Golestan National Park, Iran. *Stapfia*. 53:1–411

Bahalkeh K, Abedi M, Dianati Tilaki GA, Michalet R (2021a) Fire slightly decreases the competitive effects of a thorny cushion shrub in a semi-arid mountain steppe in the short term. *Appl Veg Sci* 24:e12575

Bahalkeh K, Abedi M, Dianati Tilaki GA, Michalet R (2021b) *Artemisia sieberi* shrubs have contrasting specific effects on understory species in Iranian steppes. *J Veg Sci* 32:e13067

Barger NN, Weber B, Garcia-Pichel F, Zaady E, Belnap J (2016) Patterns and controls on nitrogen cycling of biological soil crusts. In Weber B, Büdel B, Belnap J (eds) *Biological soil crusts: an organizing principle in drylands*. Springer, Cham, pp 257–285

Baskin CC, Baskin JM (2014) *Seeds: ecology, biogeography, and evolution of dormancy and germination.* 2 ed. Elsevier/Academic Press, San Diego

Belnap J, Lange OL (2001) *Biological soil crusts: structure, function and management, vol. 1.* Springer-Verlag, Berlin, pp 503

Briggs AL, Morgan JW (2011) Seed characteristics and soil surface patch type interact to affect germination of semi-arid woodland species. *Pl Ecol* 212:91–103

Concostrina-Zubiri L, Huber-Sannwald E, Martinez I, Flores Flores JL, Escudero A (2013) Biological soil crusts greatly contribute to small-scale soil heterogeneity along a grazing gradient. *Soil Biol Biochem* 64:28–36

Daws MI, Gamene CS, Glidewell SM, Pritchard HW (2004) Seed mass variation potentially masks a single critical water content in recalcitrant seeds. *Seed Sci Res* 14:185–195

Donath TW, Eckstein RL (2010) Effects of bryophytes and grass litter on seedling emergence vary by vertical seed position and seed size. *Pl Ecol* 207:257–268

Escudero A, Martínez I, De la Cruz A, Otálora MAG, Maestre FT (2007) Soil lichens have species-specific effects on the seedling emergence of three gypsophile plant species. *J Arid Environm* 70:18–28

Garcia-Pichel F, Felde VJMNL, Drahorad SL, Weber B (2016) Microstructure and weathering processes within biological soil crusts. In Weber B, Büdel B, Belnap J (eds) *Biological soil crusts: an organizing principle in drylands*. Springer, Cham, pp 237–255

Ghermandi L (1995) The effect of the awn on the burial and germination of *Stipa* speciosa (Poaceae). *Acta Oecol* 16:719–728

Ghiloufi W, Büdel B, Chaieb M (2017) Effects of biological soil crusts on a Mediterranean perennial grass (*Stipa tenacissima* L.). *Pl Biosyst* 151:158–167

Gilbert JA, Corbin JD (2019) Biological soil crusts inhibit seed germination in a temperate pine barren ecosystem. *PLOS One* 14:e0212466

Golodets C, Boeken B (2006) Moderate sheep grazing in semiarid shrubland alters small-scale soil surface structure and patch properties. *Catena* 65:285–291

Hamasha HR, Hensen I (2009) Seed germination of four Jordanian *Stipa* spp: differences in temperature regimes and seed provenances. *Pl Spec Biol* 24:127–132

Havrilla CA, Chaudhary VB, Ferrenberg S, Antoninka AJ, Belnap J, Bowker MA, Eldridge DJ, Faist AM, Huber-Sannwald E, Leslie AD and Rodriguez-Caballero E (2019) Towards a predictive framework for biocrust mediation of plant performance: a meta-analysis. *J Ecol* 107:2789–2807

Hawkes CV (2004) Effects of biological soil crusts on seed germination of four endangered herbs in a xeric Florida shrubland during drought. *Pl Ecol* 170:121–134

Hernandez RR, Sandquist DR (2011) Disturbance of biological soil crust increases emergence of exotic vascular plants in California sage scrub. *Pl Ecol* 212:1709–1721

Huber JK, Kollmann J (2020) Recruitment filtering by a moss layer disadvantages large-seeded grassland species. *Basic Appl Ecol* 42:27–34

Jensen K, Gutekunst K (2003) Effects of litter on establishment of grassland plant species: the role of seed size and successional status. *Basic Appl Ecol* 4:579–587

Jeschke, M. (2012) Cryptogams in calcareous grassland restoration: perspectives for artificial vs. natural colonization. *Tuexenia* 32:269–279

Langhans TM, Storm C, Schwabe A (2009) Biological soil crusts and their microenvironment: impact on emergence, survival and establishment of seedlings. *Flora* 204:157–168

Lenth R (2018) Package 'lsmeans'. *Amer Statistician* 34*:*216–221

Liu HSJ, Han XG, Li LH, Huang JH, Li X (2009) Grazing density effects on cover, species composition, and nitrogen fixation of biological soil crust in an Inner Mongolia steppe. *Rangel Ecol Managem* 62:321–327

Lozano-Isla F, Benites-Alfaro OE, Pompelli MF (2019) GerminaR: an R package for germination analysis with the interactive web application 'GerminaQuant for R'. *Ecol Res* 34:339–346

Morgan JW 2006 Bryophyte mats inhibit germination of non-native species in burnt temperate native grassland remnants. *Biol Invas* 8:159–168

Muscha JM, Hild AL (2006) Biological soil crusts in grazed and ungrazed Wyoming sagebrush steppe. *J Arid Environm* 67:195–207

Poschlod P, Abedi M, Bartelheimer M, Drobnik J, Rosbakh S, Saatkamp A (2013) Seed ecology and assembly rules in plant communities. In van der Maarel E, Franklin J (ed) *Vegetation ecology,* 2nd edition*.* John Wiley & Sons, Chichester, pp 164–202

Rasran L, Vogt K, Jensen K (2007) Effects of litter removal and mowing on germination and establishment of two fen-grassland species along a productivity gradient. *Folia Geobot* 42:271–288

Rogers RW, Lange RT (1971) Lichen populations on arid soil crusts around sheep watering places in South Australia. *Oikos* 22:93–100

Serpe MD, Orm JM, Barkes T, Rosentreter R (2006) Germination and seed water status of four grasses on moss-dominated biological soil crusts from arid lands. *Pl Ecol* 185:163–178

Serpe MD, Zimmerman SJ, Deines L, Rosentreter R (2008) Seed water status and root tip characteristics of two annual grasses on lichen-dominated biological soil crusts. *Pl & Soil* 303:191–205

Slate ML, Callaway RM, Pearson DE (2019) Life in interstitial space: Biocrusts inhibit exotic but not native plant establishment in semi-arid grasslands. *J Ecol* 107:1317–1327

Song G, Li X, Hui R (2017) Effect of biological soil crusts on seed germination and growth of an exotic and two native plant species in an arid ecosystem. *PLOS One* 12:e0185839

Song G, Li X, Hui R (2020) Biological soil crusts increase stability and invasion resistance of desert revegetation communities in northern China. *Ecosphere* 11:e03043

Su YG, Li SR, Zheng JG, Huang G (2009) The effect of biological soil crusts of different successional stages and conditions on the germination of seeds of three desert plants. *J Arid Environm* 73:931–936

Tavili A, Jafari M, Chahouki MAZ, Sohrabi M (2017). How do cryptogams affect vascular plant establishment? *Cryptog, Bryol* 38:313–323

Tobin PC, Berec L, Liebhold AM (2011) Exploiting Allee effects for managing biological invasions. *Ecol Letters* 14:615–624

Tongway DJ, Ludwig JA (2001) Theories on the origins, maintenance, dynamics, and functioning of banded landscapes. In Tongway DJ, Valentin C, Segheri J (Eds) *Banded vegetation patterning in arid and semiarid environments.* Springer, New York. pp 20–31

van Tooren BF (1990) Effects of a bryophyte layer on the emergence of seedlings of chalk grassland species. *Acta Oecol* 11:155–163

Wesche K, Ambarlı D, Kamp J, Török P, Treiber J, Dengler J (2016) The Palaearctic steppe biome: a new synthesis. *Biodivers & Conservation* 25:2197–2231

White JJ, Van Auken OW (1996) Germination, light requirements, and competitive interactions of *Stipa leucotricha* (Gramineae). *SW Naturalist* 41:27–34

Zaady E, Eldridge DJ, Bowker MA (2016) Effects of local-scale disturbance on biocrusts. In Weber B, Büdel B, Belnap J (eds) *Biological soil crusts: An organizing principle in drylands.* Springer, Cham, pp 429–449

Zaki E, Abedi M, Naqinezhad A (2021) How fire history affects germination cues of three perennial grasses from the mountain steppes of Golestan National Park. *Flora* 280:151835

Zamfir M (2000) Effects of bryophytes and lichens on seedling emergence of alvar plants: evidence from greenhouse experiments. *Oikos* 88:603–611

Zhang Y, Aradottir AL, Serpe M, Boeken B (2016) Interactions of Biological Soil Crusts with Vascular Plants. In Weber B, Büdel B, Belnap J (eds) *Biological soil crusts: An organizing principle in drylands.* Springer, Cham, pp 385–406

Zhang YM, Belnap J (2015) Growth responses of five desert plants as influenced by biological soil crusts from a temperate desert, China. *Ecol Res* 30:1037–1045

Zohary, M (1973) *Geobotanical foundations of the Middle East.* Stuttgart: Gustav Fischer-Verlag