Alterations to biological soil crusts with alpine meadow retrogressive succession affect seeds germination of three plant species

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Abstract: Biological soil crusts (BSCs) are the important components of alpine meadow ecosystems. The extent and morphology of BSCs vary greatly with alpine meadow retrogressive succession due to grazing pressure. There is significant interest in impacts of crust composition on plant seed germination, especially in (semi-) arid environments. However, little is known about the influences of BSCs, and their associations with alpine meadow succession, on germination of typical alpine meadow vascular plant species. In a full factorial common-garden experiment, we studied effects of: (1) crust type, (2) seed position, and (3) surface texture on seed germination. We chose three typical alpine meadow plant species (i.e. *Poa pratensis*, *Tibetia himalaica* and *Potentillen nivea*), which belonged to different functional groups (graminoids, legumes, and forbs) and play important roles in all alpine meadow succession stages. Crust type and seed position influenced seed germination, and the inhibitory effects of BSCs depended on the crust type and seed species tested. The major factors influencing seed germination were BSC type, seed position, soil texture, and the interactions between BSC type and seed position; species and seed position; species and

surface texture; and species, crust type, and surface texture. Cyanobacteria crust significantly inhibited germination of all seeds. Seed position also had a significant effect on seed germination ($p < 0.001$). Fewer seedlings germinated on the surface than below the surface, this was especially true for *P. nivea*. seeds within cyanobacteria and lichen crusts. Only germination rates of *T. himalaica* on the soil surface were significantly correlated with plant occurrence frequency within the alpine meadow community. The poor correlation for the other two species is possibly that they are perennials. Our results clearly demonstrated that BSCs can be biological filters during seed germination, depending on the BSC succession stage. Through their influences on seed germination, BSCs can strongly influence community assemblages throughout alpine meadow retrogressive succession.

Keywords: Crust type; Seed position; Microenvironment; Germination; Tibetan Plateau; Vascular plants

Introduction

Biological soil crusts (BSCs), which can consist of cyanobacteria, algae, microfungi, lichen and/or moss (Belnap and Gillette 1998; Ferrenberg et al. 2015), live within or on the soil surface (Eldridge and Greene 1994), and are critical structural and functional components of many ecosystems (Bowker 2007; Zhang and Belnap 2015). They can have important impacts on ecological function through physiological or physical processes. For example, BSCs can bind soil particles to protect the surface soil from wind and water erosion (Belnap and Gardner 1993; Eldridge and Leys 2002; Veluci et al. 2006; Mazor et al. 1996); fix nitrogen (N) and carbon (C) to increase soil nutrients and C storage (Austin et al. 2004; Hawkes 2003; Evans and Ehleringer 1993; Lange et al. 1994); modify the balance between water run-off and infiltration (Kidron and Yair 1997; Eldridge and Greene 1994); and influence soil roughness. These changes can create a suitable primitive habitat for vascular plant growth, which influence on seed germination and establishment.

The influences of BSCs on seed germination and establishment has become an important research topic because, through these influences, BSCs can impact ecosystem succession (Li et al.

2005; Hawkes 2004; Belnap et al. 2001). Studies have shown that BSCs can have facilitative (St Clair et al. 1984; Belnap and Harper 1995) and inhibitory (Hobs 1985; Eldridge et al. 2000) effects on seed germination. These contradictory findings may be due to differences in BSC composition (Su et al. 2009), plant traits (special chemical and structural characteristics) (Zaady et al. 1997; Langhans et al. 2009; Belnap 2006; Deines et al. 2007), or even BSC succession stage (Zellman. 2002) between studies.

The experiments described above mainly investigated BSCs in arid and semi-arid ecosystems, especially in desert ecosystems (Li et al. 2005; Rivera-Aguilar et al. 2005; Deines et al. 2007). Most of these studies were performed in relatively stable ecosystems, whereas BSCs proceed from early to late succession stages over long time periods. BSCs make up an important component of all alpine meadow ecosystems (Wang et al. 2014), but the BSC type and coverage changes with alpine meadow succession (Li et al. 2015). BSCs in alpine meadows are a special case, because they are the result of intensive land use, especially overgrazing, and alpine meadow is fine-textured. Extensive grazing pressure was shown to result in alpine meadow succession from Graminoid dominated zonal vegetation to *Kobresia humilis* meadow, and then to *K. pygmaea* meadow (Lin et al. 2015). These three meadow succession stages correspond with BSC succession from moss-dominated crust to cyanobacteria-dominated crust, and then lichen-dominated crust. Especially in *K. pygmaea* meadows, BSC, which mainly consist of cyanobacteria and lichen, grow aggressively, occupying large areas of the meadow. These cyanobacteria and lichen crusts, form a tight thin layer on the soil surface, and make profound changes to the soil microenvironment which is specific to the BSC components (Li et al.2015). An important question is how the changes to the alpine meadow microenvironment caused by the succession of BSCs affect germination of seeds banked in the soil and seeds dispersed to the soil surface. In alpine meadows, soil crack formations are very common, especially in the late succession stage, due to freezing and thawing and disturbance effects of rodents burrowing in the soil. These cracks result in meadow patchiness and landscape fragmentation (Li et al. 2010). BSCs may

contribute to the development of patchy vegetation patterns through effects on seed germination and establishment (Deines et al. 2007), which may play an important role in alpine meadow community succession. With alpine meadow retrogressive succession, the succession of BSCs follows plant community succession, but the roles of BSCs play in these succession stages are still not clearly understood. Therefore, we studied germination of three native vascular plant species (belonging to three functional groups) within four crust types, which represent the typical four degraded stages of alpine meadow BSC succession. We were interested in investigating whether seed position (surface vs sub-surface) or soil texture (cracks vs no-cracks) impacted seedling emergence within the different alpine meadow and BSC succession stages. Our goal was to determine whether different types of BSCs could act as natural barriers to germination in different vascular plant. Therefore, we aimed to test the following hypotheses:

(1) Seed position and crack formation have strong effects on germination success. Subsurface soil provides a more favorable environment for seed germination than the soil surface, and the effects of crack formation will vary with different BSC types.

(2) Cyanobacteria and lichen crusts will inhibit seed germination due to their barrier function (i.e. they form continuous layers over the soil).However, seed germination will increase with moss crusts because moss crusts provide more moisture retention.

1   Methods

1.1 Study area and collection of typical habitat species' seeds:

The study area was located in the town of Huangcheng at the northeast edge of the Qinghai-Tibetan Plateau (37°39.876′N，101°10.748′E, 3227 m, above sea level, Figure 1), within a typical

plateau continental climate. During the period from 1976 to 2001, the average annual air temperature was −1.7°C and the average annual precipitation was 500 mm, with 85% of the annual rainfall concentrated within the growing season from May to September. The soil type within the study area was alpine meadow soil.

The alpine meadows within the study area have been used as winter and spring pasture. Animals grazing cross the study area include yak and Tibetan sheep. Grazing intensity varied throughout the study area based on sheep stocking density. Meadows were stocked with four different densities of sheep: 3.65, 7.50, 8.25, and 11.25 sheep unit ha^{-1} (Lin et al. 2016; Figure 1). Different grazing intensities created alpine meadows that had been retrogressively degraded into 4 typical succession stages (Cao et al. 2007).The graminoid-dominated alpine meadow (zonal alpine meadow vegetation made up of two-layered communities with 90% vegetative cover, and grasses reaching up to 60 cm), graminoid+sedge-dominated succession stage, was approximately 80% vegetative cover, with *K. humilis* as the dominant sedge species. The *K. pygmaea* meadow succession stage had overall vegetative cover of 60% to 70%, and *K. pygmaea* was the dominant species, with an average height of 10cm. The cracked turf succession stage of *K. pygmaea* meadows was characterized with dense crack formation on the soil surface. The type and morphology of BSCs varied with the alpine
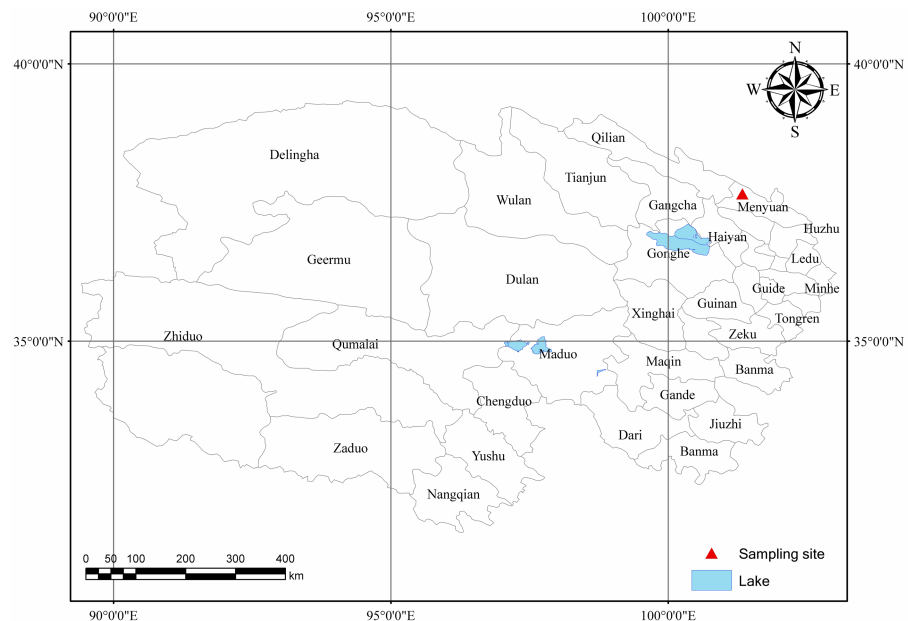

Figure 1 Location of experimental plot in Qinghai province of China.

meadow plant community succession types.

1.2 Investigated species

In this study, we chose three perennial habit-typical species, i.e. *Poa pratensis L.*, *Tibetia himalaica T.* and *Potentillen nivea L.* Plant seeds were collected from at least 10 plants per species within the study site from August to September 2013 according to their maturing timing of each species. Mature seeds were stored dry in a freezer below −20°C to simulate vernalization until spring 2014, when seeds were thawed, stored at 4°C for about 2 weeks until processing (May 2014).

1.3 BSCs collection

In the mid April, we carefully translocated soil monoliths, which measured 10 cm × 10 cm × 1-1.5 cm (length × width × height) and represented the typical BSCs within the sample site, from the 4 different alpine meadow succession stages (Figure 2). The four representative BSC succession stage types were moss crust, moss + cyanobacteria crust, cyanobacteria crust, and lichen crust, which corresponded with the graminoid-dominated alpine meadow, the graminoid+sedge-dominated succession stage, the *K. pygmaea* meadow succession stage, and the cracked turf succession stage of *K. pygmaea* meadows, respectively. First the ground was wetted to facilitate removal of intact BSCs, then the BSC sample was moved using a soil knife and shovel, and the bottom of the BSC was smoothed using a knife. The BSC samples were watered daily in order to encourage germination of

Figure 2 The four BSC succession stages and experiment design.

all seeds within samples. Once no seedlings sprouted from the sample for seven consecutive days, the sample was considered to be seed-free and ready for germination experiments (Su et al. 2007; Zhang and Belnap 2015).

1.4 Experiment 1

Experimental trays (12.0 cm × 12.0 cm × 3.0 cm) (length × width × height) were prepared with BSCs or sterilized sand. Autoclaved sand (3 cm) was used as the sterile control and a layer of BSC (1-1.5 cm, 10 cm × 10 cm) on the top of autoclaved sand (2 cm) was used as the experimental treatment for common garden experiments. Tray bottoms were lined with gauze to prevent seed loss. Each tray was planted with 25 seeds per species, which were either spread randomly on the surface of the crust (simulating natural seed dispersal) or inserted 1-1.5 cm deep into the crust or bare sand (mimicking emergence out of the seed bank). For each species and treatment, there were 6 replicates (Figure 2). Trays were placed outside to mimic field conditions, and all samples were kept moist with daily 300 ml watering. The common garden experiment started in May.

Within the moss crust samples at the beginning of the common garden experiment, mean moss cover was 79.3% ± 2.6% (mean ± SE), and moss normally grow to a height of 0.5-1.5 cm; For moss + cyanobacteria crust samples, the mean cover of moss and cyanobacteria, respectively was 46.7% ± 3.8% and 43.8% ± 2.2%. The moss height (0.5 cm) was lower than in the moss crusts samples.; In cyanobacteria crusts samples, the mean cyanobacteria cover was 81.0% ± 1.0%; that is the cyanobacteria covered nearly the entire space between vascular plants; In the lichen crust samples, the mean cover with lichen crust was of 55.8% ± 2.4%, and the main species of lichen were *Diploschistes diacapsis, Endocarpon spp.* and *Cladonia spp.*

1.5 Experiment 2

In the cracked turf succession stage of *K. pygmaea* meadows, the turf is often cracked from freezing and thawing or other disturbance (e.g., pika burrowing behavior or yak trampling). These cracks influence the BSCs of alpine meadows. In
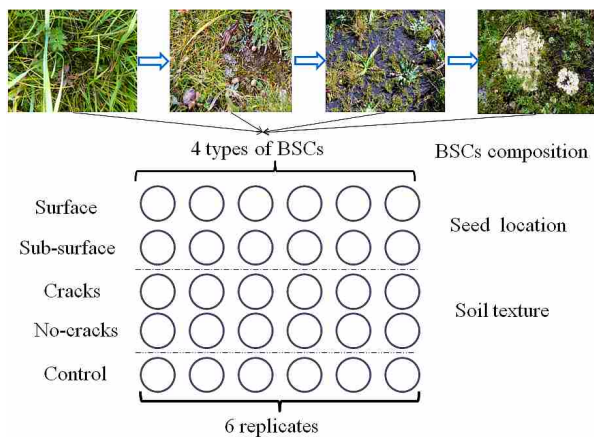
order to investigate seed emergence from this microhabitat, the same experimental procedure as for Experiment 1 was followed. The pots were concurrently placed in the same place as the Experiment 1 trays. Radical emergence from seeds was recorded daily and used to calculate percent germination (Zhang and Belnap 2015)

Experiment 1 and 2 were also devised to distinguish between effects of four crust types on seedling emergence due to (1) physical structure or (2) crust type. There were 120 trays we set in the experiment.

1.6 Germination experiment

Seeds were randomly placed on the soil surface or buried into the soil to mimic initial position of seeds after wind dispersal and germinated from the soil seed bank, respectively. For the cracked crust test, seeds were also randomly placed on the soil surface. Germination was recorded as radical emergence (approximately 2 mm) daily (Deines et al. 2007), and trials were terminated after no seed germinated occurred for seven consecutive days (Grime et al. 1981). Trials lasted for 26 days. At the end of trials, the seedlings were removed from the soil samples to examine root growth and confirm that the radical emerged from seeds, and not by propagation.

We also investigated the occurrence frequency of three plant species within alpine meadows to test for correlations between occurrence frequency and germination rate. Occurrence of the three plant species was estimated in August 2013 within six 0.25 m² quadrats selected randomly within the different grazing intensity areas. Soil water content is an important factor that influences seed germination, and BSCs may influence moisture status of seeds embedded in the crust (Belnap et al. 2001). Additionally, trampling by grazers can reduce moisture infiltration rates, surface sealing, and crust formation (Cerdà and Lavée 1999; Cao et al. 2007). Therefore, we measured soil water content for every succession stage and compared soil water content between cyanobacteria crust patches and adjacent plant patches. We used a Time-Domain Reflector (TDR) to measure soil water content at 0-10 cm depth and each plot was sampled 12 times. Significance was set at a level of $p < 0.05$.

1.7 Statistical analyses

Emergence data was analyzed using a Mixed Linear Model with seedling emergence as the response variable and species, seed position (surface vs subsurface), and soil texture (cracks vs no-cracks) as the dependent variables (SPSS 16, IBM, Chicago, USA). All differences were tested for at a significance level of $p < 0.05$. Effects of seed position and soil texture on germination in the three species were compared using independent samples T tests. Effects of crust types on seed germination were tested using a one-way ANOVA, followed by the least significant difference (LSD) post hoc test when significant differences between means were observed. Correlations between germination rates within typical alpine meadow BSCs and species occurrence within the alpine meadow were tested for the three vascular plant species using bivariate correlations.

2 Results

2.1 Influence of BSCs on seed germination

Germination varied significantly with species ($p<0.001$); BSCs strongly influenced species germination on the whole (Table 1; for Experiment

Table 1 Results of the mixed linear models predicting effects of species, BSC type, seed position, and soil texture on seedling emergence

Experimental 1	F	P	Experimental 2	F	P
Species	154.368	<0.000	Species	606.944	<0.000
Type	2.766	0.045	Type	6.851	<0.000
Position	92.403	<0.000	Texture	37.499	<0.000
Species ×Type	1.458	0.198	Species × Type	1.616	0.149
Type × Position	11.465	<0.000	Type × Texture	2.286	0.082
Species × Position	3.064	0.031	Species × Texture	7.967	0.001
Species ×Type ×Position	0.266	0.952	Species × Type × Texture	5.472	<0.000

Notes: Species = the three species studied in this experiment; Type = four types of BSC; Position = surface or subsurface; Texture = cracked or crack free.

1, p = 0.045; for Experiment 2, $p < 0.001$) in both experiments. Crust type did not significantly influence emergence for any of the three species in experiment 1 (Table 2, $p > 0.05$), but significantly affected emergence for all three species in experiment 2 (Table 2, $p < 0.05$). For *P. pratensis*, the germination rates in moss (40.0%) and cyanobacteria (46.1%) crusts were lower than in other crust types; however, the subsurface germination rates were nearly the same for all crust types (Table 3); BSC succession type had no significant effect on *T. himalaica* germination rates, which were very low within all crust types and locations. Cyanobacteria crusts significantly restrained surface *P. nivea* seed germination compared to germination on moss crusts ($p < 0.05$), but had no influence on subsurface germination (Table 3)

Experiment 2 showed crust type significantly influence germination rates of all three species (Table 2, $p<0.01$). Effects of crust surface texture on seed germination depended on BSC type (Table 4), however, crack-free cyanobacteria crust ($p < 0.01$) and, especially, crack-free lichen crust ($p <$ 0.01) drastically decreased germination rates of *P. pratensis* (Table 4). Crack formation significantly increased the germination rate of *P. pratensis* in three crust succession types, whereas it significantly affected *T. himalaica* only on the cyanobacteria crust ($p < 0.01$). On Cracked crusts, crust succession type had no significant effect on *T. himalaica* germination rate ($p > 0.01$). On crack-free crusts, however, cyanobacteria crust formation significantly suppressed *T. himalaica* germination, relative to germination of the same species on the other three crust succession types and controls.

2.2 Influence of the microenvironment on seed germination

The microenvironment influenced seed germination. Seed position significantly influenced germination rates (Table 1, $p < 0.001$) for all three studied plant species (Table 2, $p < 0.000$ for *P. pratensis* and *T. himalaica*, and $p < 0.030$ for *P. nivea*). The interactions between crust type and seed position and between species and seed position were significant (Table 1, $p < 0.05$). For all

Table 2 Results of the mixed linear models predicting effects of seed position and soil texture (cracked and crack-free) on seedling emergence

		Poa pratensis L.		Tibetia himalaica. T		Potentilla nivea L.	
		F	P	F	P	F	P
Experiment 1	Type	1.953	0.137	0.821	0.494	1.621	0.200
	Position	45.633	<0.000	32.609	<0.000	5.060	0.030
	Type ×Position	1.320	0.281	1.691	0.192	0.635	0.597
Experiment 2	Type	10.611	0.004	10.300	<0.000	8.321	0.002
	Texture	14.865	0.005	0.693	<0.000	88.094	<0.000
	Type × Texture	3.402	0.075	14.224	<0.000	11.796	<0.001

Table 3 Influence of seed position on vascular seed germination rate

Species	Position	Moss	Moss+cyanobacteria	Cyanobacteria	Lichen	Control
Poa pratensis L.	Surface	40.0±10.2b*B	68.3±10.0b*AB	46.1±13.3b*B*	70.6±13.9 b*AB	93.9±4.3aA
	Subsurface	100.0±0aAB	100.0±0aAB	92.8±6.6aB	100.0±0 aAB	100+0.0aA
Tibetia himalaica.T	Surface	2.7±0.8aAB	2.7±1.9bAB	1.3±0.8b*B	2.7±2.0bAB	6.7±1.7aA
	Subsurface	4.7±1.2aA	8.7±1.9aA	8.0±3.1aA	9.3±1.3aA	9.7±4.0aA
Potentillen nivea L.	Surface	18.0±5.7aA	14.0±4.6aAB	5.3±1.3bB	12.7±4.3aAB	8±3.6aAB
	Subsurface	30.7±12.1aA	20.7±4.6aAB	21.3±3.2aAB	14.0±3.8aAB	4.7±1.6aB

Notes: Different capital letters within the same row indicate significant differences at $p < 0.05$; different lowercase letters within the same column indicate significant differences between surface textures for the same species at $p < 0.05$. * indicates significance at $p<0.01$.The same statistical symbol protocol was applied to Table 4.

Table 4 Influence of soil texture on vascular seed germination rate

Species	Texture	Moss	Moss+cyanobacteria	Cyanobacteria	Lichen	Control
Poa pratensis L.	Cracks	100±0a A	94.5±3.6aA	100.0±0aA	92.8±5.0aA	100±0.0aA
	No-cracks	91.7±4.4b AB	93.3±2.6a AB	76.1±15.3b*BC	59.5±9.3b*C*	100±0.0aA
Tibetia himalaica.T	Cracks	4.0±1.8aB	7.3±1.9aAB	4.7±1.6aAB	6.0±1.7aAB	9.3±1.7aA
	No-cracks	6.0±2.7aAB	10.0±3.2aA	0±0b*C*	3.3±1.6aBC	8.7±1.6aA
Potentillen nivea L.	Cracks	25.3±3.2a B*C	47.3±4.4aA	33.3±7.9aAB	18.7±2.2aBC	14.7±6.1aC
	No-cracks	20.7±3.5aA	0±0bB	14.7±5.4bA	3.3±1.2b B*	16±3.7aA

BSC types, seed germination rate of *P. pratensis* in subsurface soil was significantly higher than on the surface soil, however, for the same seed position, germination rates of *P. pratensis* did not differ among crust succession types (Table 3). Seed germination rates on surface and subsurface did not differ for *T. himalaica* between moss crust and control treatments (Table 3, *p* > 0.05). However, within the three later BSCs succession stages, germination rates of *T. himalaica* significantly differed between surface and subsurface (Table 3, *p* < 0.05). For *P. nivea*, germination rates on both surface and subsurface only differed in cyanobacteria succession stage crust. These results indicate that seed location and BSC succession stage have different influences on seed germination rates for the three plant species studied.

Seed germination was significantly influenced by soil texture (Table 1 and 2), the interactions between species and texture, and the interaction among species, crust succession type, and texture. The interactions between crust type and texture had a significant effect on seed germination rates of *T. himalaica* and *P. nivea* (Table 2, *p* < 0.01). This suggests that soil texture strongly influences seed germination in a species-specific manner in alpine meadows.

Germination rates of *P. pratensis* on crack-free cyanobacteria crust and crack-free lichen crust were significant decreased (*p* < 0.01, No-cracks condition) compared with crack formation (Table 4). These results show that crack formation significantly increased seed germination rates for *P. pratensis* on three different crust types.

The germination rates of *T. himalaica* were very low (Table 4). Crack formation significantly influenced germination rates of this species only on the cyanobacteria crust (*p* < 0.01). Cracks-free cyanobacteria crust and Crack-free lichen crust significantly suppressed *T himalaica* germination relative to germination on cracked crust.

2.3 Correlations between seed germination and plant occurrence frequency

Historically, extensive and selective grazing have been regarded as the main factors causing degradation in alpine meadow, with alpine meadow retrogressive succession, growth and distribution of different plant functional groups changing according to their responses to grazing pressure and their reproductive strategies. Our experiments showed strong relationships between surface seed germination rates and species occurrence frequency within the alpine meadow only for *T. himalaica*. For the other two study species, there was no significant correlation between surface seed germination rate and their occurrence within the alpine meadow (Table 5). This poor correlation between occurrence and seed germination for the two perennial species may be explained by the importance of propagation through rhizomes for these two species.

Table 5 Correlation between plant seed emergence rate and plant occurrence frequency in an alpine meadow

	Poa pratensis L.	*Tibetia himalaica*. T	*Potentilla nivea* L.
Surface	0.841	<0.000	0.383
Sub-surface	0.454	0.771	0.118

3 Discussion

The traditional BSCs succession course in arid or semi-arid ecosystems proceeds from the early cyanobacteria crust successional stage into later-successional communities of lichen and moss crusts (Belnap and Elgredge 2003); however, in alpine meadows, BSC succession differs. BSC succession in arid and semiarid ecosystems occurs through natural processes and over long time periods. In contrast, BSC succession in alpine meadows is driven by plant community succession, which is highly influenced by extensive animal grazing, and proceeds relatively quickly.

3.1 The barrier effects of BSCs on seed germination

Our study showed that each of the four different types of BSCs had significant effects on the germination of three perennial grass species common to different alpine meadow succession stages; this is consistent with former studies (Zaady et al. 1997; Langhans et al. 2009). Crust type significantly influenced seed germination rates (Table 1) for all three plant species studied. Cyanobacteria crust significantly lowered surface seed germination rates relative to controls and all

other BSC types. This finding of cyanobacteria crust acting as a barrier to seed germination differs from findings of previous studies (Zaady et al. 1997). Cyanobacteria crust may impair seed germination through decreasing soil water content (Figure 3 and Figure 4). Under wet conditions a thick cyanobacteria crust develops, which limit rain water infiltration and, therefore, limit water availability for the perennial vegetation (Ram and Aaron 2007; Li et al. 2006). In contrast, the other crust types had variable influences on germination rates of subsurface seeds from the three plant species studied (Table 3). Intact BSCs can suppress germination of weedy forbs and enhance germination in native perennial grass (Eldridge and Simpson 2002). BSCs can also differently affect germination in native species (Hawkes 2004).The effects of BSCs on seed germination observed in these studies suggest that BSC
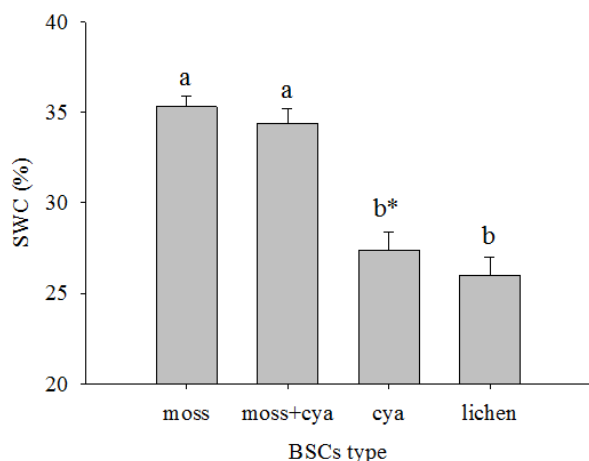

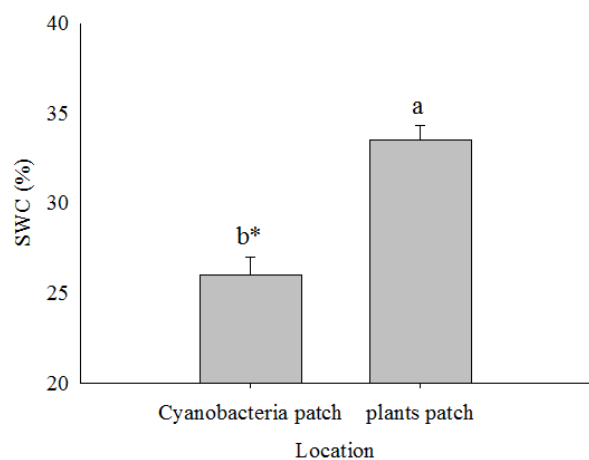**Figure 3** Soil water content changes with BSC succession (cya indicate cyanobacteria).

Figure 4 Soil water content of cyanobacteria patches and plant patches.

formation and succession can strongly influence the distribution of plant species, and eventually affect alpine meadow plant succession.

Seed position is important for seed germination. Influences of seed location differed among the three plant species tested. Germination rates of *P. pratensis* and *T. himalaica* seeds were significantly affected by location, but for *P. nivea*, seed location only affected germination rates within cyanobacteria crust succession type treatments. These results show cyanobacteria crust to be less favorable for perennial vascular plant seed germination than other crust types, which is consistent with the findings of Zaady et al. (1997) that reported cyanobacteria crusts to inhibit germination of the annual plants *Plantago* and *Reboudia* in Israel. The results of this study show that crust type, seed position, and their interaction strongly influence seed germination.

Li et al. (2005) found that seedling emergence was more successful in moss crusts than in algal crusts, but the present study demonstrated exceptions to these trends. Germination of some plant species was improved in moss crust, while other species had better germination rate in cyanobacteria crust. This variation may be related to moss height, because if the moss grows high, surface seeds will not make contact with the soil, and moisture levels will be insufficient for germination. However in another study, Serpe et al. (2006) observed that a biological soil crust dominated by short moss significantly inhibited germination of cheatgrass and three perennial grasses, while tall moss crust had little effect on germination, which is not in accordance with our results.

Previous studies on effects of BSCs on vascular plant germination have found varying results. Studies on a range of different crust types have found negligible effects of BSCs on seedling germination (Beyschlag et al. 2007; Eldridge et al. 2000; Keizer et al. 1985; Sedia and Ehrenfeld 2003; Li et al. 2005; Sylla 1987), while other studies have reported positive effects of crusts on seed germination (Belnap 2002; Kleiner and Harper 1977; Boeken et al. 2004;). Previous studies have primarily focused on testing how changes to BSC over time influence seed germination (Langhans et al. 2009; Su et al. 2007), and previous field studies investigating natural dispersal and emergence have

generally studied annual, not perennial plant species (Belnap and Harper 2001). However, in the harsh alpine meadow environment, perennial plants make up the most important component of the plant community. St. Clair et al. (1984) found that large increases in germination rates in two perennial grass species on crusted, relative to crust-free soils in the laboratory. Crisp (1975) in Australia found that establishment of the native perennial grass *Stipa* was not inhibited by crusts, whereas crusts did inhibit the annual grass *Schismus*. This study expanded on these previous findings to show that the positive or negative effects of BSCs on germination of alpine meadow perennial species can be influenced by the location of the seed within the soil.

Soil textures can influence seed germination. Previous studies have shown cracks in the soil surface to have positive effects on seed germination (Langhans et al. 2009). We found that crack formation tended to increase seed germination rates, especially in cyanobacteria and lichen crusts (Table 4). That is to say, cyanobacteria and lichen crusts without cracks decreased seed germination, and cracks in the same crust type improved seed germination. With alpine meadow degradation, the space separating plants increases; cyanobacteria and lichen form a thin layer on the soil surface, which unlike in arid and semi-arid ecosystems, is tightly bound with the soil, and is not easily be destroyed. That is, alpine meadow cyanobacteria and lichen crusts form a mechanical barrier over the soil surface. Our results showed crack-free cyanobacteria and lichen crusts inhibit *P. pratensis* seed germination. This inhibition may accelerate alpine meadow degradation. Indeed, the cyanobacteria crust succession stage is the ecosystem turning point from a degraded to a seriously and irreversible degraded alpine meadow. In the field we could observe more seedlings appeared in the cracked cyanobacteria and lichen crusts than in the place cyanobacteria and lichen crust occupied. When suitable micro-relief structures are not present on intact soil crusts to provide mechanical stability and sufficient moisture, seed germination is negatively impacted (Zaady et al. 1997; West 1990). Furthermore, interactions between BSC type and crust surface texture significantly influenced the three perennial vascular plant species examined in this study

(Table 1).This points towards an important role of BSCs in alpine meadow plant community succession, and loss or addition of BSCs may trigger transitions between steady ecosystem states. Our results also demonstrate that with alpine meadow degradation and BSC succession, BSCs impair seed germination of gramineous forage and other species, eventually resulting in the thorough degradation of the alpine meadow.

3.2 Impacts of soil moisture variation with BSC types on seed germination

BSCs affect the redistribution of runoff across the landscape and into soil (Eldridge et al. 2002). Our results show that soil water content to decrease with crust type succession, especially in meadows covered with cyanobacteria crust and lichen crust. A study performed in the Negev desert in Israel also found that removal of the thin cyanobacterial-dominant crust from a sandy dune and a well-developed lichen-dominant crust from a loess-covered hill slope resulted in a three to fivefold increased in sorptivity and steady-state infiltration under both ponding and tension (Eldridge et al. 2000), Deines et al (2007) regarded increases in seedling mortality on lichen crusts to be due to desiccation and inadequate water absorption. Spatial heterogeneity in landscapes is partly attributed to the presence of biological soil crusts; for example cyanobacteria crust patches can have lower water content than plant patches (Belnap et al. 2001). Through these influences on surface properties and water movement, BSCs play important roles in seedling emergence and establishment (Harper and Marble 1988; Zaady et al 1997) and eventually accelerate grassland retrogressive succession.

Alpine meadow retrogressive succession caused by extensive grazing is a growing concern. Succession of alpine meadow BSCs, which can influence seed germination, follow plant community succession (Bowker 2007). Therefore, it is crucial that ecosystem managers take measures to recover degraded alpine meadows with regard of BSCs conditions. One such effective measure is reseeding to recover specific degraded succession stages; therefore knowledge of the influences of BSCs on seed germination is crucial for effective restoration of degraded meadows.

4   Conclusions

BSC succession type significantly influenced seed germination rate, and this influence varied with BSC types. Effects of BSC on seed germination were influenced by seed position and soil surface structure. In some cases, BSCs became a barrier to plant seed germination. These results indicate that BSCs can serve as a biological filter during seed germination. Therefore, BSC succession may be an important trigger determining plant species diversity and community structure in alpine meadows. Future studies should make a full assessment of overall survival rates of vascular plant species and the influences of different BSC types on annual plant seed germination.

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