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Changes in winter snow depth affects photosynthesis and physiological characteristics of biological soil crusts in the Tengger Desert

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Abstract

Water availability is a major limiting factor in desert ecosystems. However, a winter snowfall role in the growth of biological soil crusts is still less investigated. Here, four snow treatments were designed to evaluate the effects of snow depth on photosynthesis and physiological characteristics of biological soil crusts. Results showed that snow strongly affected the chlorophyll fluorescence properties. The increased snow depth led to increased contents of photosynthetic pigments and soluble proteins. However, all biological soil crusts also exhibited a decline in malondialdehyde and soluble sugar contents as snow increased. Results demonstrated that different biological soil crusts exhibited different responses to snow depth treatment due to differences in their morphological characteristics and microhabitat. In addition, interspecies differentiation in response to snow depth treatment might affect the survival of some biological soil crusts. Further, this influence might lead to changes in the structural composition and functional communities of biological soil crusts.

Additional key words: biological soil crusts; chlorophyll fluorescence; photosynthetic pigments; soluble sugar; water availability.

Introduction

Climate change impacts ecosystems worldwide, with semiarid and arid ecosystems particularly vulnerable because many fundamental aspects of their structure and function are closely connected with variations in temperature, CO_2, and precipitation (Salguero-Gómez *et al*. 2012). Water availability is a major limiting factor in desert ecosystems; even small changes in precipitation are expected to have a strong impact on species composition and biodiversity in the soil profile (Sala and Lauenroth 1982). Snow is an important source of precipitation, it influences soil temperature and moisture, insulates soil from severe freezing, and is a protective cover for many plants, since air temperatures in winter are often considerably lower than soil temperatures (Mondoni *et al*. 2012). In addition, as available stored water is released when snow melts, it can improve plant growth and development (Olsen *et al*. 2011). However, because of anthropogenic climate change, snow frequency, cover, depth, and cover duration can be changed considerably. Since global air temperatures are predicted to increase in winter (IPCC 2007), snow cover is expected to become thinner and melt earlier. As a result, a number of studies have focused on a decline in snow cover and advance in snow melt timing across a variety of arctic, subarctic, and alpine environments (Wipf and Rixen 2010). Evans and Fonda (1990), for example, examined community pattern expressed as a function of snow depth and snow cover duration, in order to look at their effect on soil moisture, soil temperature, and the growing season, while Tan *et al*. (2014) suggested that a decrease in snow cover can alter soil microbial activities, and hence element biogeochemical cycling in alpine forest ecosystems. However, changes in snow depth and cover duration are not consensus, as snow depth has increased in some areas (Callaghan *et al*. 2011). Indeed, an increase in snow depth can lead to enhanced ecosystem respiration during the late winter. Bosiö *et al*. (2014) analyzed the effect of increased snow cover on plant photosynthesis, showing higher absorption of photosynthetically active radiation on account of increased soil moisture and nutrients.

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Abbreviations: BSC – biological soil crusts; Car – carotenoid; Chl – chlorophyll; F_v/F_m – the maximum photochemical efficiency; MDA – malondialdehyde; Yield – the effective photochemical quantum yield of PSII.
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Biological soil crusts (BSC) are communities composed of cyanobacteria, green algae, lichens, and mosses that live on or within the uppermost millimeters of the soil (Eldridge *et al*. 2010). They are component of semiarid and arid ecosystems around the world (Bowker *et al*. 2016). BSC are important for soil stability and erosion prevention (Chaudhary *et al*. 2009), runoff and infiltration (Eldridge *et al*. 2010), nitrogen fixation and transformation (Castillo-Monroy *et al*. 2010), and C cycling (Thomas *et al*. 2008), have an influence on the establishment and development of vascular plants (Li *et al*. 2000), and serve as habitats for soil animals (Li 2012). However, differences in BSC types affect these functions. In BSC community successional pathways, cyanobacteria and green algae are pioneers in colonizing the soil surface, while when soil microhabitats improve, lichens and mosses gradually emerge (Lan *et al*. 2012). Although there has been concern about the effects of climate change on photosynthesis and the physiological characteristics of BSC, including moisture (Belnap *et al*. 2004), temperature (Grote *et al*. 2010), UV-B (Hui *et al*. 2015), light intensity (Lange *et al*. 1998), and wind (Jia *et al*. 2012), the effects of snow depth on BSC are poorly understood (Colesie *et al*. 2016, Zhao *et al*. 2016). Indeed, because snow is an important component of total precipitation in winter in semiarid and arid environments, and a considerable proportion of snow can thus be utilized by BSC, research on the influence of snow depth is both necessary and significant.

BSC are widely dispersed in the Tengger Desert, northern China. Actually, some research has been carried out on the distribution of BSC and their effects on hydrological process (Li 2012). Because the organisms, which make up BSC, are maintaining metabolically active states only when wet, a number of studies have demonstrated that BSC can be rehydrated and physiological activity recovered when moistened by dew, vapor, and rain (Zhao *et al*. 2014). However, because winter precipitation in the Tengger Desert is limited, the role of winter snow in establishment and development of BSC as a function of precipitation is unknown. In addition, the differences caused by varying depth of snow on photosynthesis and the physiological characteristics of BSC also remain unclear. Thus, a manipulative experiment using four snow depths was designed to evaluate the effects of snow depth on photosynthesis and the physiological characteristics of different BSC successional stages. In this study, chlorophyll (Chl) fluorescence, photosynthetic pigment contents, soluble protein contents, membrane lipid peroxidation, and the substances of osmotic adjustment were investigated with the aim to elucidate the role of snow on BSC in desert ecosystems in winter and evaluate how the effects on different BSC types vary. Specifically, based on previous visual observations, including increased soil moisture and the color of BSC, we hypothesized that photosynthesis and physiological characteristics of BSC were negatively affected by the removal of snow, as the removed snow caused a reduction in soil moisture. In contrast, increased snow depth has positive effects, and the degree of positive influence increases with volume of snow.

Materials and methods

Study site description: The study site for this research was in an artificial sand-fixing vegetation area on the southeast fringe of the Tengger Desert (37°28′N, 105°00′E, 1,339 m a. s. l.), in Shapotou district, China. In this region, the climate is temperate continental and summer air temperatures reach 38.1°C, while in the winter they fall to –25.1°C. Annual precipitation is 186 mm, of which 80% falls between May and September.

To protect 40 km of the Baotou-Lanzhou railway from sand burial, the artificial sand-fixing vegetation system was established in 1956 by planting xerophytic shrub seedlings, including *Artemisia ordosica*, *Caragana korshinskinn*, and *Calligonum arboresscens* Litv, and this system was further expanded in 1964, 1981, and 1987. Finally, dust deposition leads to the colonization and development of BSC on stabilized dunes (Li *et al*. 2011). All samples were collected from an area where BSC dominates, as reported in a previous study on the Tengger Desert (Li 2012).

BSC samples and snow depth manipulation: We selected three of the most frequent BSC types (*i.e*., moss, algae, and lichen) from the interspaces between shrubs in the artificial sand-fixing vegetation system. Of these types, *Bryum argenteum* Hedw., *Anabaena azotica* Ley., and *Collema tenax* (Sw.) Ach were the dominated types, respectively (Li *et al*. 2005). BSC was excavated by the cylindrical PVC containers (10 cm in diameter, 5 cm in height) following moistening with distilled water to collected intact samples. Subsequently, samples were air dried and stored in containers for 10 d until experiments began in February 2014.

Snow depth manipulation treatments were carried out outdoors. Treatments comprised snow removal (0S, control), snow depth reduction to half of that seen under ambient conditions (0.5S), ambient snow depth (S), and snow depth increased twice to that seen in ambient conditions (2S). During a snowfall event in February 2014 (snowfall reached 2.3 mm in 9 h, snow depth was 3.6 cm), the snow removal treatment was achieved by using euphotic plastic discs to block snowfall, while snow depth reduction was achieved by manually shoveling snow away. In contrast, the snow depth enhancement (2S) was achieved by artificial addition of natural snow using plastic discs (diameter of 10 cm). Overall, three replicates of each snow depth treatment were carried out for each BSC types. When the snow melted after 48 h, Chl fluorescence was determined in BSC, biological samples were immediately isolated, and stored at –80ºC for subsequent analyses.

Chl fluorescence of moss, algae, and lichen crusts was measured *in situ* using a pulse amplitude modulated – *2,000* fluorometer (*MFMS-2*, *Hansatech*, Kings Lynn, UK) at midday as described in Havaux *et al*. (2009). After 20 min of dark adaption, crusts were subjected to a weak modulated beam [<0.1 μmol(photon) m^{-2} s^{-1}] to obtain minimal fluorescence (F_0), followed by exposure to a saturation light pulse [8,000 μmol(photon) m^{-2} s^{-1}] in order to obtain maximal fluorescence (F_m). The maximum photochemical efficiency (F_v/F_m) of PSII was calculated using $(F_m - F_0)/F_m$, and the effective photochemical quantum yield of PSII (Yield) was determined by measuring instant maximal fluorescence (F_m') as well as steady state fluorescence (F_t). Yield was estimated using the formula: Yield = $(F_m' - F_t)/F_m'$.

Photosynthetic pigments: In order to determine contents of photosynthetic pigments, abrasive material from moss, algae, and lichen were extracted by soaking in 100% ice-cold ethanol for at least 30 min at 4°C, and then centrifuging twice for 30 min at 12,000 × *g*. The combined supernatant was used for both Chl and carotenoid (Car) contents estimation by reading absorbance at 649, 665, and 470 nm in a *752N* UV-Vis spectrophotometer (*Shanghai Precision and Scientific Instrument Company Ltd.*, Shanghai, China), using 100% ethanol as a blank (Lan *et al*. 2011).

Soluble protein: Fresh samples of moss, algae, and lichen were homogenized in 5 mL of a 50 mM phosphate buffer (1% polyvinylpyrrolidone, 1% phenylmethanesulfonyl fluoride, 1% ascorbic acid, and 1% *Triton-X100* at pH 7.8). The homogenate was centrifuged (15,000 × *g* at 4°C) for 20 min and the supernatant was then used to determine soluble protein contents. An aliquot of the extract was used following the method of Bradford (1976), based on a standard curve with bovine serum albumin.

Membrane lipid peroxidation determination was measured as the amount of thiobarbituric acid reactive substance assay (TBARS) determined by the thiobarbituric acid (TBA) reaction, as described by Lu *et al*. (2010). Fresh samples were homogenized in 10 mL of 10% trichloroacetic acid and 0.25% TBA. The mixture was then incubated in a water-bath (>95°C) for 30 min and then quickly cooled in an ice bath. After centrifugation at 5,000 × *g* for 10 min, the amount of TBARS in the supernatant was assayed spectrophotometrically (*752N UV, Shanghai Precision and Scientific Instrument Company, Ltd*, Shanghai, China) at 532 nm and then corrected for nonspecific absorption at 600 nm using the extinction coefficient 155 mmol L^{-1} cm^{-1}.

Osmotic adjustment substances: Soluble sugar content was determined using the anthrone-colorimetric method (Singh *et al*. 1987). Fresh samples were extracted twice using 80% ethanol at 80°C for 40 min and then immediately cooled, following centrifugation at 3,000 × *g* for 10 min; the supernatants were combined. Activated carbon was added to the supernatant for decolorization at 80°C for 30 min, and it was then diluted with 80% ethanol to 10 mL. Finally, 50 μL of the supernatant was added to a 10-mL test tube containing 5 mL of anthrone solution (*i.e*., 100 mg of anthrone in 100 mL of diluted sulfuric acid), andthe samples were then heated in boiling water for 10 min. Once cooled, soluble sugar quantifications were executed at 625 nm in a spectrophotometer and a standard curve was produced using sucrose.

Proline contents were measured following the method outlined by Bates *et al*. (1973). Fresh samples were ground in 5 mL of 3% sulfosalicylic acid and homogenized using vortex shaking, before being centrifuged at 12,000 × *g* for 10 min. The filtrate (2 mL) was then treated with 2 mL of sulfosalicylic acid, 2 mL of glacial acetic acid, and 4 mL of ninhydrin, before being subject to vortex shaking for 1 h in a boiling water bath, to initiate solution reaction. Then it was cooled immediately to terminate the reaction, 4 mL of toluene was added, and shaken for 20 s. The phase was then separated for 30 min, and the product extracted from the red toluene phase was evaluated at 520 nm.

Statistical analysis: The experiment contained three replications. Results are presented as mean ± standard deviation (SD) of three samples. Prior to analysis, original data were sin transformed to ensure compliance with a normal distribution, and differences between treatments were analyzed using one-way analysis of variance (*ANOVA*) and *Duncan*'s tests (p<0.05) in the package *SPSS 16.0* (*SPSS*, Chicago, IL, USA).

Results

Chl fluorescence: Results showed that snow strongly affected the Chl fluorescence properties of the three BSC types, compared with control treatment (Fig. 1). Indeed, values of F_v/F_m were higher for the ambient (S) and increased snow depth (2S) treatments than that of the control condition (0S). In the moss crust, F_v/F_m increased by 11.7, 113.1, and 194.2% in the 0.5S, S, and 2S treatments, respectively. However, the F_v/F_m of the algae and lichen crusts decreased in the 2S treatment, in contrast to 0.5S and S. When compared control conditions, F_v/F_m significantly increased by 149, 198, and 60% in the algae crust, respectively, and by 364.6, 221.9, and 233.3% in the lichen crust (Fig. 1*A*). Indeed, consistent with F_v/F_m results, the highest Yield values were recorded for the 2S treatment of the moss crust, the S treatment of the algae crust, and the 0.5S treatment of the lichen crust. Results showed significant increases of 257.9, 197.9, and 212.1%, respectively (Fig. 1*B*).

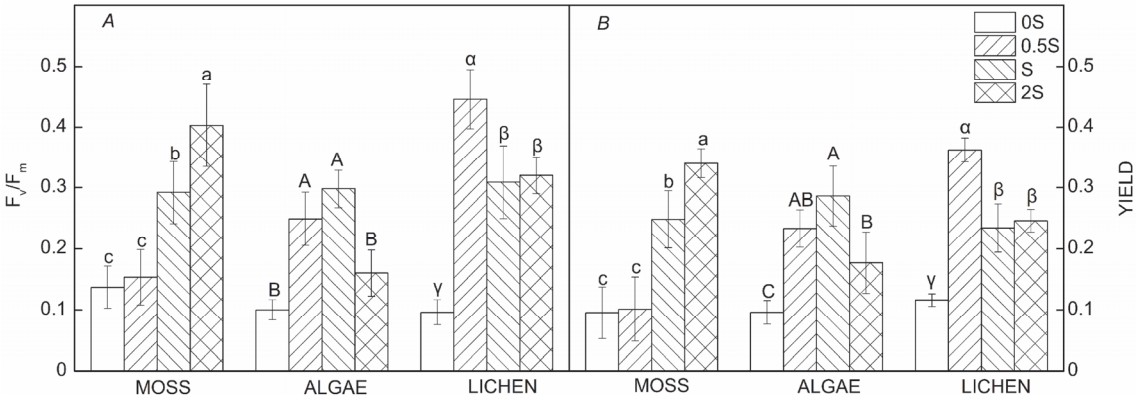

Fig. 1. Chl fluorescence measurements in three types of biological soil crusts (moss, algae, lichen) subject to four depths of snow treatment. Values are mean ± standard deviation (n = 3) and the *different letters* assign the values significantly different at P<0.05 according to *Duncan*'s tests.

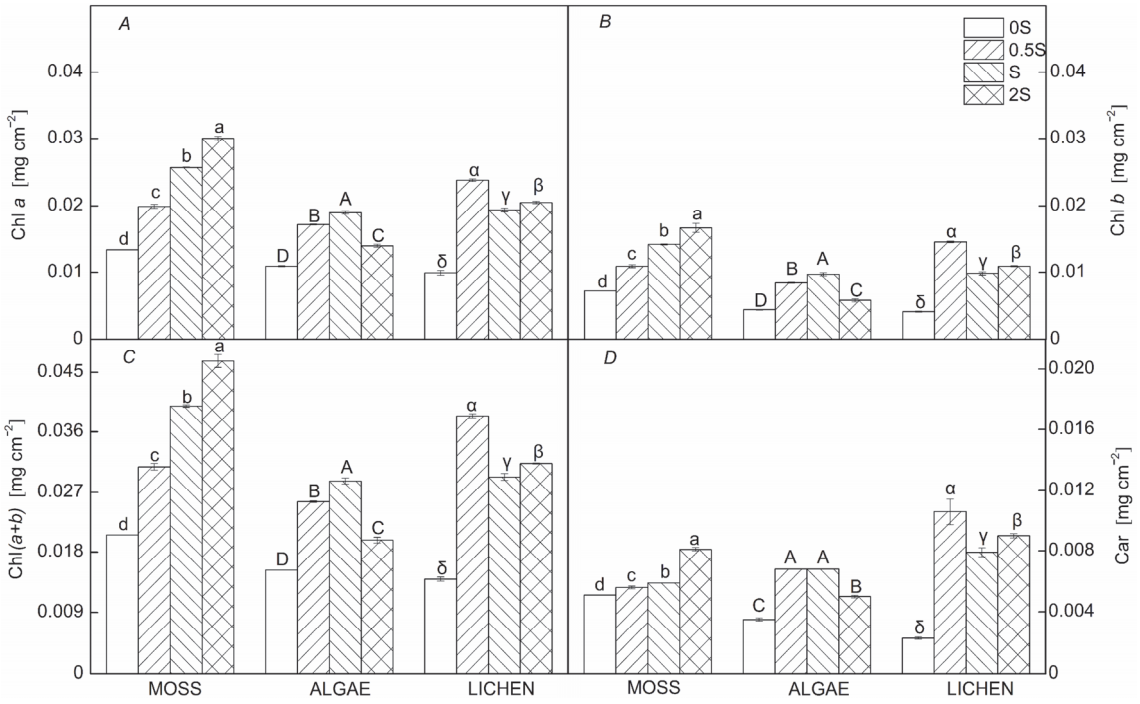

Fig. 2. Photosynthetic pigments contents in three types of biological soil crusts (moss, algae, lichen) subject to four depths of snow treatment.

Photosynthetic pigments content: Compared with those under the control conditions, increased snow levels caused increases in the contents of Chl *a*, Chl *b*, Chl (*a*+*b*), and Car (Fig. 2). When the moss crust was subjected to the 2S treatment, the contents of photosynthetic pigments reached maximum values, increases of 123.9% for Chl *a*, 131.9% for Chl *b*, 126.7% for Chl (*a*+*b*), and 58.8% for Car relative to the control. For the algae and lichen crusts, unlike the moss crust, photosynthetic pigments contents significantly increased and then decreased, but were still higher than those of the control (Fig. 2). Compared with control conditions, the Chl *a*, Chl *b*, Chl (*a*+*b*), and Car contents of the algae crust significantly increased by 74.3, 120.5, 87.6, and 94.3% in the S treatment, while they only increased by 28.4, 31.8, 29.4, and 42.9% in the 2S treatment. Similarly, the Chl *a*, Chl *b*, Chl (*a*+*b*), and Car contents of the lichen crust significantly increased by 140.4, 256.1, 174.3, and 360.8%, respectively, in the 0.5S treatment, but they increased by 96, 139, 109.3, and 243.5% in the S treatment, respectively (Fig. 2).

Soluble protein content was enhanced significantly in all three types when they were subjected to increased snow depth (Fig. 3). Compared with the control, the soluble protein content significantly increased by 6.6, 29.7, and 41.3% in the moss crust under the 0.5S, S, and 2S

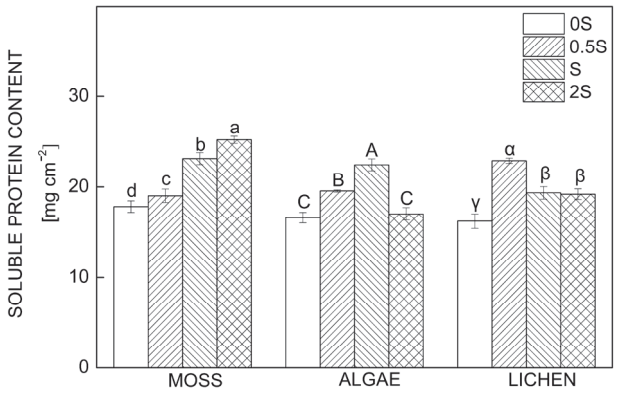

Fig. 3. Soluble protein contents in three types of biological soil crusts (moss, algae, lichen) subject to four depths of snow treatment.

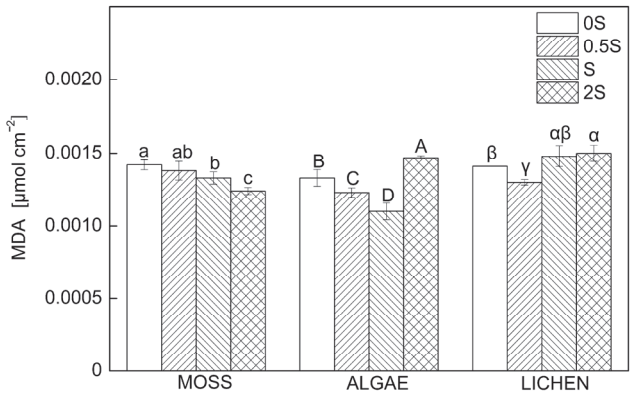

Fig. 4. Malondialdehyde (MDA) contents in three types of biological soil crusts (moss, algae, lichen) subject to four depths of snow treatment.

treatments, respectively. Soluble protein content reached maximum values under S and 0.5S treatments in the algae and lichen crusts, markedly increasing by 35.2 and 41.2%, respectively, compared with controls (Fig. 3).

Membrane lipid peroxidation: MDA contents were measured as a product of membrane lipid peroxidation. Results showed that MDA contents significantly changed in the three types of BSC when they were subjected to changes in snow depth (Fig. 4). In the moss crust, MDA contents decreased continuously, reaching 97.2, 93.7, and 87.3% of the initial control value under 0.5S, S, and 2S treatments, respectively. In the algae and lichen crusts, MDA contents significantly declined by 7.5 and 7.8%, respectively, under 0.5S treatment. However, compared with those under the control conditions, MDA contents significantly increased by 10.5% in the algae crust under the 2S treatment, and also significantly increased by 5 and 6.4% in the lichen crust under the S and 2S treatments, respectively (Fig. 4).

Osmotic adjustment substances: Results showed that the three types of BSC exhibited marked decreases in soluble sugar contents when subjected to increased snow depth treatments, and that this declines were sharper as snow levels increased (Fig. 5*A*). Compared with control conditions, soluble sugar contents were significantly reduced by 27.4, 24.8, and 18.5% under the 2S treatment for the moss, algae, and lichen crusts, respectively (Fig. 5*A*). Results also showed that the tendency of proline variation were similar to that of soluble sugar contents in crusts subjected to increased snow depth (Fig. 5*B*). An increase in snow depth significantly suppressed proline contents in

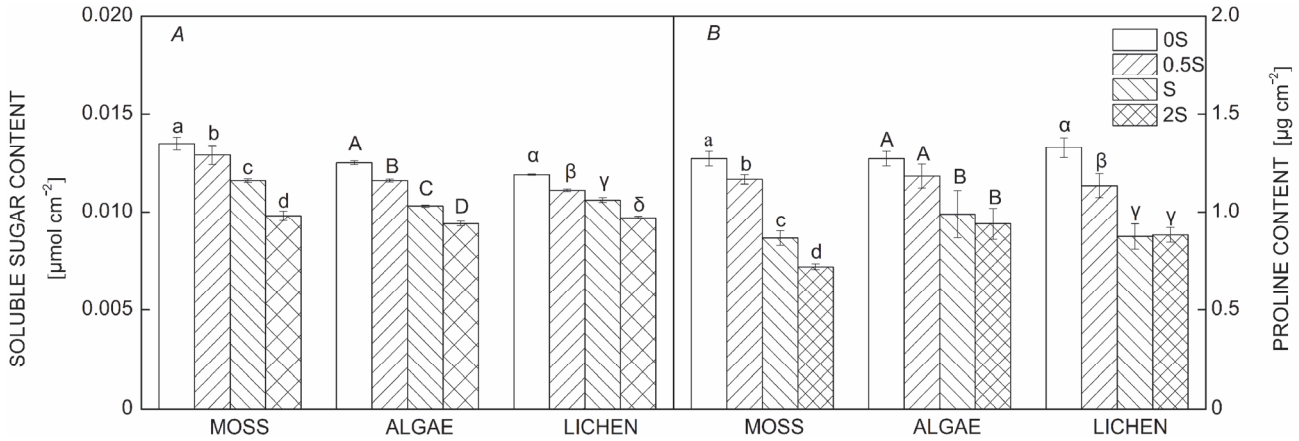

Fig. 5. Osmotic adjustment substances contents in three types of biological soil crusts (moss, algae, lichen) subject to four depths of snow treatment.

the three types of BSC, which continuously declined as snow levels increased. Indeed, when the snow level increased to twice of that under ambient conditions (2S), proline contents declined markedly, by 43.5% in the moss crust, 26.2% in the algae crust, and 33.6% in the lichen crust (Fig. 5*B*).

Discussion

Photosynthetic processes in various plants are known to be very sensitive to water stress (Ashraf and Harris 2013). Indeed, it is believed that primary producers within BSC (cyanobacteria, lichens, algae, and bryophytes) are all poikilohydric and return to photosynthetic activity soon after getting wet (Raggio *et al*. 2017). The results of this study showed that increased winter snow depth strongly affected the photosynthetic activity of moss, algae, and lichen, as demonstrated by both Chl fluorescence (Fig. 1) and contents of photosynthetic pigments (Fig. 2). Of these markers, Chl fluorescence is a widespread method used to assess the photosynthetic performance of plants, because it is both noninvasive and highly sensitive method. Thus, F_v/F_m denotes the maximum photochemical efficiency of PSII in the absence of a nonphotochemical quenching process (Karsten *et al*. 2007), and is widely applied for the assessment of the effects of environmental stress on plants (Kummerová *et al*. 2006). Yield is the proportion of absorbed light energy used for photochemical reactions (Wilson and Jacobs 2012). Moreover, photosynthetic pigmentation is one of the most obvious signs of photosynthesis, reflecting biomass change in the environment. Results showed clear differences between snow depth treatments in all three types of BSC. PSII photochemistry and photosynthetic pigmentation in moss crust were both positively affected by a moderate increase in snow depth, as there are dependent on water availability. Indeed, these results are in agreement with those reported by Bosiö *et al*. (2014), who showed that an increased snow depth prolonged the duration of snow cover, and favored plant photosynthesis in subarctic mires underlain by permafrost. However, results also showed that PSII photochemistry and photosynthetic pigmentation reached maximums levels under S and 0.5S treatments in the algae and lichen crusts (Figs. 1,2). Indeed, when the algae and lichen crusts were subjected to 2S treatment, both Chl fluorescence (Fig. 1) and photosynthetic pigments (Fig. 2) declined. Such a decrease in F_v/F_m could be a protective mechanism, or it could be due to sustained energy dissipation in PSII (Havaux and Kloppstech 2001). Similarly, a reduction in Yield likely corresponds to the efficiency of PSII associated with the induction of dormancy, while reductions in photosynthetic pigments were probably the result of the destruction of chloroplast structures, which suppressed the synthesis of new Chl and induced the degradation of the existing Chl (Peng and Zhou 2009).

We also found that Chl *a*, Chl *b*, and Chl (*a*+*b*) of BSC showed a high increase after 48 h when compared to the control conditions. This variation might be related to rapid recovery of cryptogam photosynthesis in crust base due to the change of their water environment with snow melting. Moisture is the most important abiotic factor for the growth of BSC in arid and semiarid lands, which can influences their photosynthetic and respiratory metabolism (Belnap *et al*. 2004, Sponseller 2007). Previous researches have indicated that most of organisms (algae, mosses, and lichens) in crusts have developed a variety of strategies (especially recovery of photosynthesis) to respond rapidly to water stress and rehydration during raining or snowing events (Li *et al*. 2014). The quick recovery and reassembly of pigments was a key response of organisms in crusts to changes in their water environment. This change in pigment contents can maintain their photosynthetic apparatus intact under dehydration and resume their photosynthetic activities within minutes after wetting (Abed *et al*. 2014). In addition, our results indicated that Car from three types of BSC highly increased during rehydration. Car are widely distributed in algaes, mosses, and lichens as a group of natural tetraterpenoid pigments (Domonkos *et al*. 2013), which play crucial roles in photosynthesis and photoprotection of photosynthetic organisms (Hashimoto *et al*. 2016). On the one hand, Car are essential pigments in photosynthesis of photosynthetic organisms in crust, which act as light harvesting antenna complexes in photosystems for photosynthesis (Cazzonelli and Pogson 2010b, Hashimoto *et al*. 2016). On the other hand, the quick massive accumulation of Car in BSC can protect photosynthetic organisms against radiation damage and stabilize structure of light-harvesting pigment–protein complexes (Wu *et al*. 2017). Thus, increased pigment contents during rehydration of BSCs is not only related to the recovery of photosynthesis, but is also related to protection mechanism by those pigments.

Soluble protein is an important indicator reflecting a plant ability to tolerate conditions of water stress. Indeed, results showed that the soluble protein contents of the three types considered here significantly increased when they were subjected to increased snow depth treatments (Fig. 3). In other words, improvements in soil moisture resulted in adjustments of the content of soluble proteins produced, which itself plays an important role in maintaining cellular osmotic pressure and the functional stability of intracellular macromolecules (Auton *et al*. 2011). Because the contents of soluble proteins varied in this study, which indicated that the different snow depths contribute to the variations of physiological response to snow among three BSCs. Low snowfall (translating into a shortage of water) during periods of snow cover may influence the production of soluble proteins that allow plants to adapt. Thus, we argue that when drought is the main limiting factor, these three kinds of BSCs are more likely to synthesize lower amounts of soluble proteins. At the same time, to a lesser extent, water stress causes a reduction in the synthesis of soluble proteins (Wei *et al*. 2014).

Malondialdehyde is the final product of lipid peroxidation, and thus an indirect reflection of the extent of cell damage. Previous work has shown that environmental factors can highly affect MDA accumulation in plants (Hui *et al*. 2013). Indeed, our experimental results revealed

remarkably lower MDA contents in moss, algae, and lichen crusts under 2S, S, and 0.5S treatments, respectively. In contrast, the significantly higher MDA contents in the algae and lichen crusts under the 2S treatment is reflection of increased lipid peroxidation and higher oxidative damage caused by water stress (Fig. 4). The remarkably higher MDA contents of algae and lichen crusts under high snow depth imply destruction of membrane function, in full agreement with correspondingly lower soluble protein and photosynthetic pigment contents. This conclusion, an accumulation of MDA, is similar to previous results from *Achillea* species and maize subjected to drought (Gharibi *et al*. 2015) or waterlogging stress (Tang *et al*. 2010).

Soluble sugar is an important constituent and source of energy for living organisms (Seyyednejad and Koochak 2011). Indeed, many poikilohydric organisms exhibit a decrease in soluble sugar after freeze–thaw cycles (Melick and Seppelt 1992). In terms of contents, proline is one of the most important cytosolutes, increasing in plants during adaptation to extreme environments, including in response to water stress, high temperatures, UV-B radiation, and exposure to heavy metals (Mafakheri *et al*. 2010). In our study, BSC exposed to increased snow depth treatments exhibited reduction in both soluble sugar and proline contents (Fig. 5), perhaps that is because the accumulation of both compounds can help cells to maintain the structural integrity of their cytoplasmic proteins after snow reduction (Sharmila and Pardha Saradhi 2010). A similar result was reported by Sara *et al*. (2012) who showed that water deficit caused an increase in the soluble sugars concentration and proline contents in the leaves of castor bean.

The water content of BSC is changing as snow depth increases/decreases; this variation either accelerates or inhibits photosynthesis and the growth of plants (Perata *et al*. 2011). Indeed, excess water can cause flood stress, and weaken photosynthesis (Kogawara *et al*. 2006). Our results demonstrate that the different types of BSC exhibited different responses to snow depth treatments because of their morphological characteristics and microhabitats, which influence their photosynthetic capacity and growth. The moss crust is usually located on the flat areas of windward slopes and inter-dune lowlands, while algae and lichen crusts are commonly distributed on the mounds of windward slopes. As a result, algae and lichen crusts are more sensitive to water stress, because they are mostly situated in high-light environments. These types can acquire water from BSC substrates, and maintain thallus water for longer periods. Therefore, algae and lichen crusts have high water-holding capacity, and can also attain maximum photosynthesis at lower water levels, compared to moss crust. This means that both photosynthesis and the physiological characteristics of algae and lichen were restrained in our experiments when snow depth treatments exceeded S and 0.5S, respectively. Our results, revealing interspecies differentiation in photosynthesis and physiological characteristics variations in response to snow depth treatments, may provide insights into the survival of BSC types in response to climate change. Indeed, these responses are likely to lead to changes in the structural composition and functional communities in BSC, as well as to variations in ecological function. Thus, our research results provide insights into the functional changes of BSC in desert ecosystems under different winter snow levels, and provide a theoretical foundation for ecosystem management.

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