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Effect of snow cover on water content, carbon and nutrient availability, and microbial biomass in complexes of biological soil crusts and subcrust soil in the desert

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ABSTRACT

Winter snowfall is an important water resource for organisms in desert ecosystems. Changing snow depth is expected to exert a potential influence on growth and ecological functions of biological soil crusts (BSCs), which are known as a dominant functional vegetation unit of desert ecosystems. However, limited attention has been paid to this potential effect on BSCs. A field simulation experiment was conducted to measure the water content, nutrient concentrations (organic carbon; total nitrogen; available nitrogen; available phosphorus; available potassium; ammonium nitrate; and nitrate nitrogen), and microbial biomass (carbon, nitrogen, and phosphorus) in samples (cyanobacterial and lichen crusts and subcrust soil) under snow cover of different depths after a four year experiment (from October 2013 to April 2017) in the Gurbantunggut Desert. The results showed that water content increased with increasing snow depth ($P < 0.05$). Snow removal and snow cover reduction decreased nutrient and microbial biomass concentrations in both biocrust types ($P < 0.05$). The concentrations of most measured nutrients and microbial biomass decreased significantly when snow depth was increased to twice ambient conditions ($P < 0.05$). Moreover, the concentrations of nutrients and microbial biomass were significantly influenced by snow depth ($P < 0.05$), crust type ($P < 0.001$), and their interaction ($P < 0.05$). The results demonstrated that variation in snow depth adversely affect the carbon and nutrient availability and microbial biomass in BSCs. Such changes might lead to a cascading effect in species composition and function of BSC communities in arid regions.

1. Introduction

Biological soil crusts (BSCs) are widespread communities that display patchy distributions surrounding vascular plants in arid and semiarid regions (Eldridge and Greene, 1994). Biological soil crusts are known to be a dominant functional vegetation unit of desert ecosystems. They result from an intimate association between soil particles and cyanobacteria, algae, microfungi, lichens, and bryophytes (in different proportions), which live within the uppermost millimeters of the soil surface (Belnap et al., 2001; Maestre et al., 2013; Colesie et al., 2014). Their presence can change soil physical and chemical characteristics (Chartres, 1992), facilitate colonization and growth of vascular plants (Mendoza-Aguilar et al., 2014), supply a microhabitat for soil animals and microorganisms (Li et al., 2010), impact soil hydrological processes (Kidron et al., 2009), influence nutrient cycling by fixing carbon (C) and nitrogen (N) (Maestre et al., 2013), and improve soil stability with fungal filaments or moss rhizoids (Lan et al., 2015). Water (rain, snow, dew, etc.) is an important driver of the C and N exchange rate in BSCs in deserts because most organisms (cyanobacteria, lichen, moss, etc.) present in BSCs are poikilohydric and therefore only exhibit physiological activity in wet conditions (Lindo et al., 2013; Grote et al., 2010). The structure and composition of BSCs are determined to a large extent by precipitation patterns (e.g., frequency, amount and time of precipitation), which in turn influence their physical and chemical properties (Sponseller, 2007; Belnap et al., 2004).

Snow is one of the most important water resources controlling BSC development and ecological functions in desert regions (Zhao et al., 2016). Changes in snow depth in desert ecosystems can influence soil nutrient cycling (Ball et al., 2011; Tan et al., 2014; Hui et al., 2019) and thus affect soil properties. Generally, soil moisture and soil temperature

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are closely associated with snow cover depth (Groffman et al., 2011). Soil temperatures are often higher than air temperatures in winter because of the insulating effect of snow cover on the soil (Bokhorst et al., 2013). Snow cover can also temporarily store water and nutrients (Clark et al., 2011), releasing them after it melts in spring. Snow water may be utilized by organisms directly from soil. Hence, snow cover directly and indirectly influences arid ecosystems in various ways.

Decreasing snow cover may cause greater damage than ambient snow depth to soil organisms (including cryptogams, microbes, and fauna) in the BSC by water constraints and by intensifying freezing and thawing cycles (Comerford et al., 2013; Tan et al., 2014). Increasing snow cover could prevent BSCs from permanently freezing, impede frequent BSC thawing and freezing events, and provide higher soil moisture availability during winter (Groffman et al., 2011; Hardy et al., 2001; Steinweg et al., 2008). Variations in the soil environment caused by snow cover may also affect the activity of soil microorganisms, which in turn affects soil nutrient dynamics (Yang et al., 2010). Soil microbial biomass, which indicates the level of soil fertility, plays a critical role in nutrient transformation in desert ecosystems (Jia et al., 2017). Sufficient nutrient availability can improve the formation of microbial biomass, and therefore measuring the proportions of C, N, and P in the microbial biomass may represent another useful tool for assessing the nutrient limitations of ecosystem processes in terrestrial ecosystems (Cleveland and Liptzin, 2007; Khan et al., 2016). Numerous studies have focused on the responses of microbial biomass to environmental changes, disturbances, and ecological restoration processes in dryland ecosystems (Johnson et al., 2012; Zhou et al., 2013; Tan et al., 2014). For this reason, microbial biomass has increasingly been used as a sensitive indicator of ecosystem function to assess soil biological properties (Wieder et al., 2013).

However, previous studies have mainly focused on the effects of changes in summer precipitation on the properties of BSCs in arid regions (Angel and Conrad, 2013; Miralles et al., 2013; Zelikova et al., 2012; Zhao and Zhang, 2021), with little attention given to the effect of snow cover on water content, nutrient concentration, and microbial biomass in the complexes of biological soil crusts and subcrust soil. In fact, variations in nutrient concentration may be particularly important because the soil of most desert ecosystems is poor in available carbon and nitrogen (Gallardo and Schlesinger, 1992; He et al., 2014). Kidron et al. (2015) showed that N and C fixation by BSCs plays a crucial role in adjusting N and C inputs and losses in nutrient-poor habitats of desert ecosystems. BSCs can modulate nutrient cycling by increasing cover, diversity, and biotic interactions, which promote an increase in the activity of enzymes (such as β-glucosidase and urease enzymes) (Maestre et al., 2013). This effect of BSCs on nutrients is mainly modulated by water availability in arid and semiarid lands, where water has been observed as a primary limiting factor to development and succession of BSCs (Zhang et al., 2013). Moreover, chlorophyll and carbohydrate contents, species composition, and BSC biomass are influenced by water availability (Kidron et al., 2012), for which winter snowfall is an important source of available water that may influence the growth and development of BSCs (Zhao et al., 2018). Ultimately, the dynamics of soil nutrients in BSCs may be affected by changes in snow cover (Chen and Duan, 2015; Zhao et al., 2018).

Cyanobacterial and lichen crusts are widely distributed in the Gurbantunggut Desert. Among BSC species, cyanobacteria often occur in the earlier BSC successional stages, with lichen crusts appearing later (Bowker, 2007). The water retention ability and available water content of soils are higher in lichen crusts than in cyanobacterial crusts (Li et al. 2017). Therefore, cyanobacterial and lichen crusts may have different responses to variation in snow cover. The Gurbantunggut Desert receives significant amounts of snow in winter, leading to the formation of snow cover on the ground that ranges from 20 to 30 cm in depth and lasts for 100–150 days (Yin and Zhang, 2016). Therefore, the effects of snowfall depth on key physical and chemical properties must be evaluated in addition to the microbial biomass of BSCs and soil, which is also important to fully understand the influence of global climate change on arid and semi-arid regions. The objectives of the study were to explore how snow depth modulates physical and chemical properties (water content, nutrient concentration, and microbial biomass) in cyanobacterial and lichen crusts and the subcrust soil, where the formation, development, and succession of BSCs rely heavily on these physical and chemical properties. Given the obvious importance of available water in the soil of this arid desert region, it was hypothesized that increased or decreased snow depth would cause adverse effects on carbon and nutrient availability, and microbial biomass in complexes of biological soil crusts and subcrust soil after a four year experiment.

2. Materials and methods

2.1. Study site description

The study was conducted from October 2013 to April 2017 in the Gurbantunggut Desert (44°11′–46°20′N, 84°31′–90°00′E) in the Xinjiang Uygur Autonomous Region, Northwest China (Fig. 1a), which has the largest fixed and semifixed desert dunes in China, occupying an area of 4.88×10^4 km^2. The desert is characterized by a typical temperate continental climate. The average air temperature is 7.26 °C and ranges from an average minimum of −41.6 °C in January to an average maximum of over 40 °C in July. The long-term mean annual precipitation is approximately 79.5 mm, which falls mainly during spring, whereas the mean evaporation exceeds 2000 mm (Zhang et al., 2007). It begins to snow in November, and the snow ends in March. There is a long period of steady snow cover during winter, after which the accumulated snow starts to thaw as the temperature rises in spring, providing appropriate growth conditions for vascular plants and BSCs (Zhao et al., 2016). Subshrubs and small trees such as *Haloxylon persicum* and *H. ammodendron* are widespread, with a cover of<30%. In the Gurbantunggut Desert, cyanobacterial, lichen, and moss-dominated BSCs are abundantly distributed. The cyanobacterial crusts are composed of *Microcoleus vaginatus*, *M. paludosus*, and *Lyngbya martensiana*; the lichen crusts are dominated by *Collema tenax*, *Xanthoparmelia desertorum*, *Psora decipiens*, and *Diploschistes muscorum*; and the moss crusts are made up mainly of *Tortula desertorum* and *Bryum argenteum* (Zhang et al., 2007; Zhou et al., 2016).

The study area is situated in the northwest part of the natural vegetation area in the Gurbantunggut Desert, which contains representative cyanobacterial and lichen crusts that are found throughout the desert. Samples of cyanobacterial and lichen crust have the same texture of the subcrust soil and are situated in interdunal depressions between fixed desert dunes, where the soils are sandy, contain little organic matter, have negligible total N, and have a pH in the neutral to slightly alkaline range (7.51 ± 0.14 to 8.05 ± 0.25) (Zhang et al., 2011).

2.2. BSC collection and manipulation of snow cover

In the cyanobacterial crusts dominated by *M. vaginatus* and in the lichen crusts dominated by *C. tenax*, 75 samples of each crust type were taken. The samples were 15 cm deep, 10 cm in diameter, and included the crust layer and the underlying soil. All BSCs were excavated in the intervening spaces between shrubs where their coverage exceeded 95% following a rainfall event (Jia et al., 2012). The samples were stored in cylindrical plastic pipes; after sampling, they were air-dried in shaded conditions and then placed at the study site (Fig. 1b and 1c) until the experiments began.

The experiment was conducted near the cyanobacteria and lichen crust collection site. The experiment included the following five treatments: ambient snow depth (1.0S, control), snow removal (0S), decrease of snow depth to half the ambient depth (0.5S), 1.5-fold increase of ambient snow depth (1.5S), and twofold increase of ambient snow depth (2.0S). Each treatment was performed on three plots (2 m × 2 m) located at least 2 m apart from each other (Fig. 1a–1d). The treatment locations

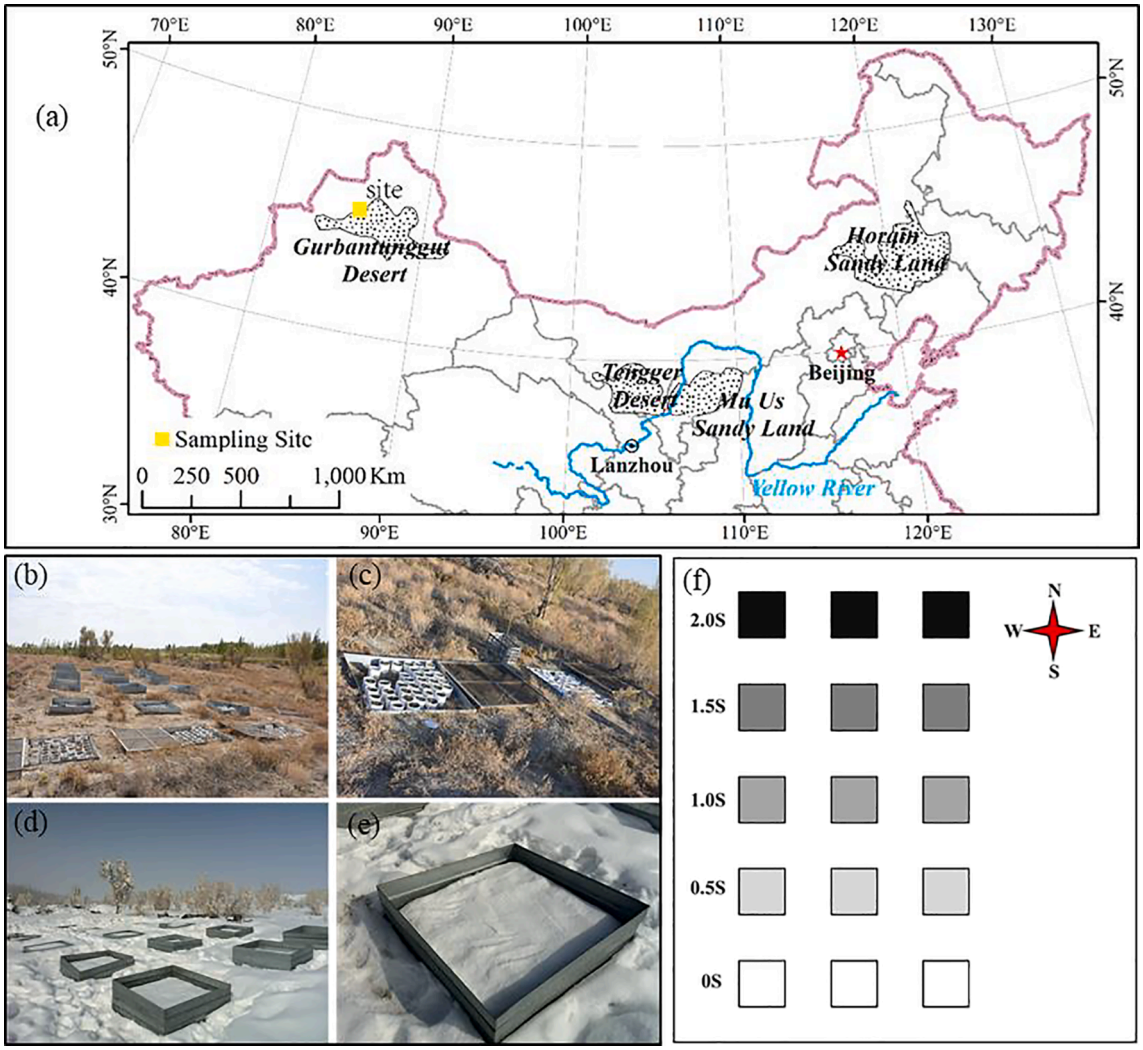

Fig 1. Location of the site (a), five snow-depth treatments: without snow cover (b, c) and with snow cover of different depths (d, e), and experimental site layout (f).

were arranged in the order 0S—0.5S—1.0S—1.5S—2.0S from south to north in the study site (Fig. 1f). This arrangement considered wind direction and avoided impacts on downwind plots. Climatological data from the study site (2008–2012) indicated that west-northwest and west were the main wind directions (including gales) in winter (https://www.doc88.com/p-6763811716759.html). Therefore, the direction of the treatments was arranged to go from south to north, nearly perpendicular to the wind direction, to avoid three plots of each treatment located in the upwind or downwind direction. Snow treatments were conducted by building snow fences in each plot (Fig. 1d and 1e). Each fence was designed as a square enclosure (2 m length, 2 m width and 10 cm height), where the upper and lower margins were folded slightly inward (up margin > down margin) so that one could be easily placed on top of the other. After snow fell, the fences were directly piled one on top of the other in each plot. The number of fences was dictated by snow depth, where the height and number of the fences increased with snow depth from 0S to 2.0S. To avoid the impact of wind decreasing or increasing snow cover depth, snow fences were vertically erected in the soil before the snow season and removed at the end of the snow season. Five samples of each crust type were placed in each plot (Fig. 1c). The snow treatments lasted from October 2013 to April 2017, starting in early October of each year and finishing in late March of the next year when the snow cover melted. Snow removal was achieved by a mesh screen (1 mm aperture) that prevented BSCs from being covered by snowfall, but maintained adequate ventilation and photosynthetically active radiation (the mesh screen was present only during snowfall events, including the start of snowfall events, and was removed when snowfall was over). The snow depths in different treatments were measured using a ruler at three places in all plots (Bokhorst et al., 2013). The snow depth reduction and increase treatments were accomplished by manually shoveling snow away from or into a plot following every major snowfall event (>5 cm snowfall). There were 10 major snow events during the period from October 2013 to April 2017 (Table 1).

Table 1
Snow manipulations during the study period.

Manipulation date	Ambient snow depth (cm)
2014.02.01	10
2014.02.25	6
2014.03.12	8
2015.01.27	9
2015.02.13	8
2015.12.12	13
2016.01.22	16
2016.02.26	6
2016.12.25	11
2017.02.24	6

2.3. Sampling

A composite sample was created from the five samples collected in each crust type in each sample plot. Samples (mixed crusts and subcrust soil) for further analyses were collected from a depth of 0–5 cm in April 2017 after four years of snow manipulation. Each sample contained<0.5 cm of crust (usually cyanobacterial crust < lichen crust) and the underlying soil. Three composite samples from the cyanobacterial and lichen-dominated crusts were prepared from each plot. All samples were kept in airtight plastic bags and immediately used for further analysis. Each composite sample (0–5 cm) was divided into three portions. The first portion was used to measure water content; the second portion was air-dried and passed through a 2-mm sieve to determine the concentrations of organic carbon, total nitrogen, available nitrogen, available phosphorus, and available potassium. The third portion was passed through a 2-mm sieve and kept in a refrigerator at 4 °C to measure the concentrations of ammonium-N (NH_4^+-N), nitrate-N (NO_3^--N), and microbial biomass (carbon, nitrogen, and phosphorus).

2.4. Chemical analyses

Water content was determined gravimetrically after drying the soil samples in an oven at 105 °C for 24 h (Wu et al., 2013). Organic carbon was determined by wet oxidation with dichromate oxidation and titration with ferrous ammonium sulfate (Nelson and Sommers, 1982). Total nitrogen was analyzed by semimicro Kjeldahl digestion (Gallaher et al., 1976). The available nitrogen concentration was estimated by the alkaline $KMnO_4$ method (Liu et al., 2015). Available phosphorus was determined by Mo-Sb colorimetry after $NaHCO_3$ extraction, and available potassium was measured with the flame photometer method after ammonium acetate extraction (Li et al., 2013). The NH_4^+-N and NO_3^--N in the filtered 2 M KCl extracts of fresh soil were analyzed using a continuous-flow ion autoanalyzer in which NO_3^- was decreased with cadmium and the resulting NO_2^- was determined by the colorimetric method (Edwards and Jefferies, 2013).

Microbial biomass carbon and nitrogen were determined by the chloroform fumigation extraction method as described by Vance et al. (1987). The $K_2Cr_2O_7$ wet-oxidation method was used to determine microbial biomass carbon in the filtrates, where it was assayed using the difference in organic carbon between the fumigated and non-fumigated samples and applying a conversion factor of 0.38 (Yang et al., 2010). The microbial biomass nitrogen in the filtrates was estimated by the semimicro Kjeldahl method and was calculated from the difference between organic N extracted from the fumigated and non-fumigated samples using a conversion factor of 0.54 (Yang et al., 2010). Microbial biomass phosphorus was extracted by modified fumigation and $NaHCO_3$ extraction and was determined colorimetrically with a modified Mo-Sb colorimetric method (Xue et al., 2014). One part of the fresh soil was fumigated with free-ethanol chloroform in vacuum desiccators for 24 h, and another part was kept at room temperature. Subsequently, the fumigated and unfumigated soil samples were treated by 0.5 M $NaHCO_3$ at a pH of 8.5 for 30 min by mixing in an oscillator and filtering. The microbial biomass phosphorus concentration in the extracted solutions was determined by recording their absorbance at 700 nm after adding Mo-Sb chromatography solution for 30 min. Finally, the phosphorus concentration was calculated as the difference in organophosphorus between the fumigated and unfumigated soil samples, which was adjusted using an experimentally derived conversion factor of 0.40 (Brookes et al., 1982).

2.5. Statistical analyses

All parameters were measured in triplicate (three composite samples from the replicate plots), and the results are presented as the mean ± standard deviation (SD). Statistical analyses were performed using SPSS 16.0 for data processing (Chicago, USA). Two-way ANOVA was conducted to analyze the effects of biocrust type and snow depth on soil water content, soil nutrients, and SMB (each variable was separately analyzed). All variables were tested for data normality and homogeneity of variance before the analysis was performed. Significance was identified at the $P < 0.05$ level with Tukey's test.

3. Results

3.1. Water content

Biocrust type and snow depth had significant effects on water content separately, but not in interaction (Table 2). Reductions in snow depth decreased the water content both in the cyanobacteria and the lichen crusts (Fig. 2). In contrast, the deep snow treatment increased the water content in the 0–5 cm layer of both crust types. The highest value in the 2.0S treatment was the highest overall (Fig. 2). The water content was decreased by 71.5% (0S in cyanobacterial crust), 10.8% (0.5S in cyanobacterial crust), 67.1% (0.5S in lichen crust), and 4.9% (0.5S in lichen crust) compared with the 1.0S treatment. However, water content increased by 52.97% (2.0S in cyanobacterial crust), 33.1% (1.5S in cyanobacterial crust), 33.9% (2.0S in lichen crust), and 14.8% (1.5S in lichen crust) compared with the 1.0S treatment.

3.2. Nutrient concentration

Snow depth and crust type, both separately and in combination, significantly influenced nutrient concentrations (Table 2). Variations in snow depth led to considerable variations in nutrient concentrations (Fig. 3, $P < 0.05$). The snow removal treatment decreased the nutrient concentrations of organic carbon, total nitrogen, available nitrogen, available phosphorus, available potassium, NH_4^+-N, and NO_3^--N in the cyanobacterial and lichen crusts and the underlying soil compared to those under ambient snow cover. Moreover, the nutrient concentrations in complexes of cyanobacterial crust and subcrust soil samples increased under higher snow depths. There were sharp increases of approximately 18.30%, 24.34%, 19.56%, 12.91%, 19.51%, and 18.74% for organic carbon, total nitrogen, available phosphorus, available potassium, NH_4^+-N, and NO_3^--N respectively in the 1.5S treatment (Fig. 3, $P < 0.05$) compared with the 1.0S treatment. The nutrient concentrations in complexes of cyanobacterial and subcrust soil samples decreased significantly in the 2.0S treatment compared to those in the 1.5S treatment, but the concentrations of available potassium, NH_4^+-N, and NO_3^--N were higher than those after snow removal. In the lichen crusts,

Table 2
Results of two-way analysis of variance (ANOVA) of the effect of crust type, snow depth, and the interaction between them on water content, nutrient concentration, and microbial biomass.

Property	Crust type	Snow depth	Crust type × Snow depth
	F-values	F-values	F-values
Water content	47.77***	30.84***	0.98
Organic carbon	4029.66***	19.27***	23.83***
Total nitrogen	243.22***	16.72***	6.37**
Available nitrogen	84.97***	19.50***	7.06**
Available phosphorus	2952.97***	37.84***	16.37***
Available potassium	631.14***	70.11***	23.11***
NH_4^+-N	9.36**	23.10***	3.92*
NO_3^--N	16.35***	145.37***	50.09***
Microbial biomass carbon	7.36*	26.83***	6.79**
Microbial biomass nitrogen	49.64***	445.20***	122.96***
Microbial biomass phosphorus	270.90***	251.94***	70.53***

Note: ***, **, and * show significant influence at 0.001, 0.01, and 0.05 levels respectively.

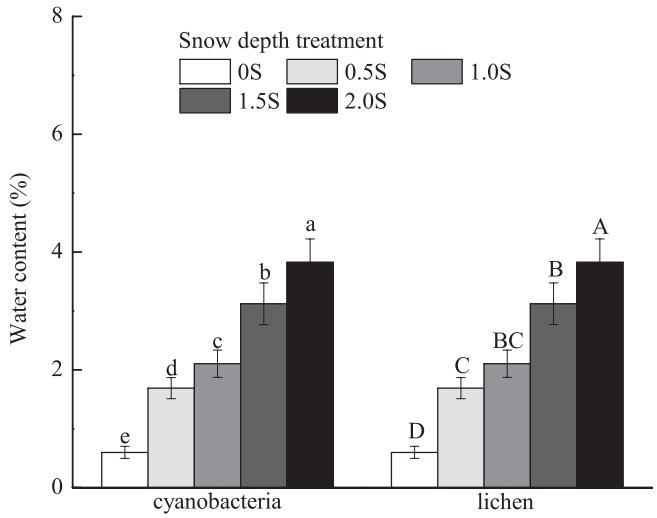

Fig 2. Effects of snow depth on water content in cyanobacteria and lichen crusts and underlying soil in the 0–5 cm layer. Each bar and vertical line indicates the mean value and SD respectively ($n = 3$). Different letters indicate significant differences (at $P < 0.05$) among the five snow depth treatments in complexes of cyanobacteria crust and subcrust soil (lowercase letters) and complexes of lichen crust and subcrust soil (capital letters) respectively.

nutrient concentrations declined with increasing snow-cover depth (Fig. 3, $P < 0.05$). Fig. 3 also indicates that the lichen crusts had higher nutrient concentrations, except for NH_4^+-N and NO_3^--N, after four years of snow depth manipulations.

3.3. Microbial biomass

Crust type, snow depth, and their combination had a significant effect on microbial biomass (Table 2). Snow removal or snow-cover reduction resulted in significant decreases in the concentrations of microbial biomass carbon, nitrogen, and phosphorus (Fig. 4, $P < 0.05$). Microbial biomass carbon, nitrogen, and phosphorus reached their maximum values in the 1.5S treatment and then decreased in the 2.0S treatment (Fig. 4a). In the cyanobacterial crusts, decreased snow depth and the 2.0S treatment induced significant decreases in the concentrations of microbial biomass carbon, nitrogen, and phosphorus compared to the 1.0S treatment. In the lichen crusts, the microbial biomass carbon, nitrogen, and phosphorus concentrations reached their maximal values under the 1.0S treatment, being significantly higher than under lower and higher snow depths (Fig. 4b and 4c, $P < 0.05$).

4. Discussion

Snow depth alters the soil microenvironment, influencing water content and soil temperature (Tan et al., 2014). The results of this study suggest that the water content in the cyanobacteria and lichen crusts and the subcrust soil sharply increases with snow depth (Fig. 2). As a scarce resource in desert regions, water availability during the snow melting season may be a main determining factor influencing cryptogam growth and microbial activity (Benassi et al., 2011), which ultimately affects crust properties (Wu et al., 2015). Previous research has shown that water and nutrient contents in BSCs become higher with increasing

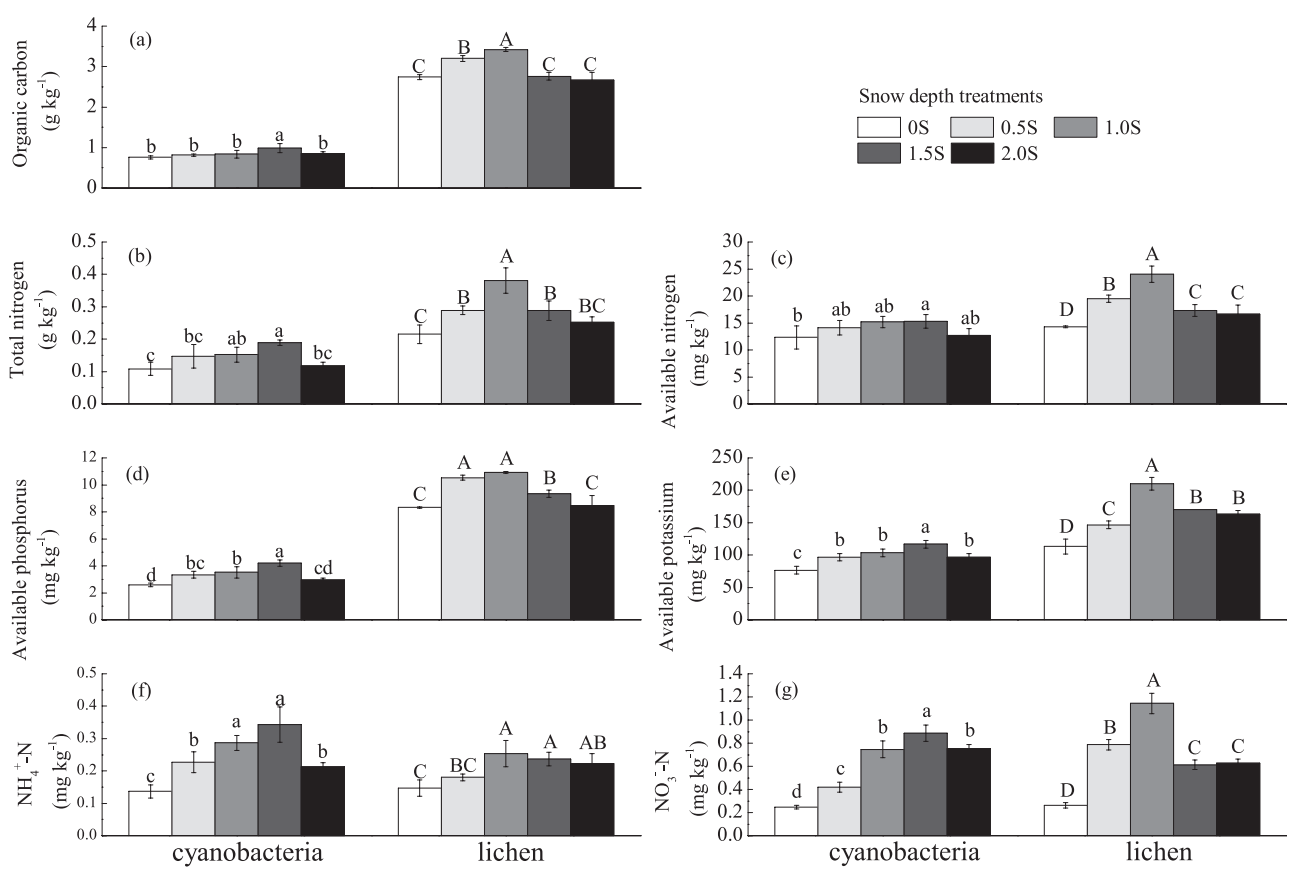

Fig 3. Effects of snow depth on concentrations of organic carbon (a), total nitrogen (b), available nitrogen (c), available phosphorus (d), available potassium (e), NH_4^+-N (f), and NO_3^--N (g) in cyanobacteria and lichen crusts and underlying soil in the 0–5 cm layer. Each bar and vertical line indicates the mean value and SD respectively ($n = 3$). Different letters indicate significant differences (at $P < 0.05$) among the five snow depth treatments in complexes of cyanobacteria and subcrust soil (lowercase letters) and complexes of lichen and subcrust soil (capital letters) respectively.

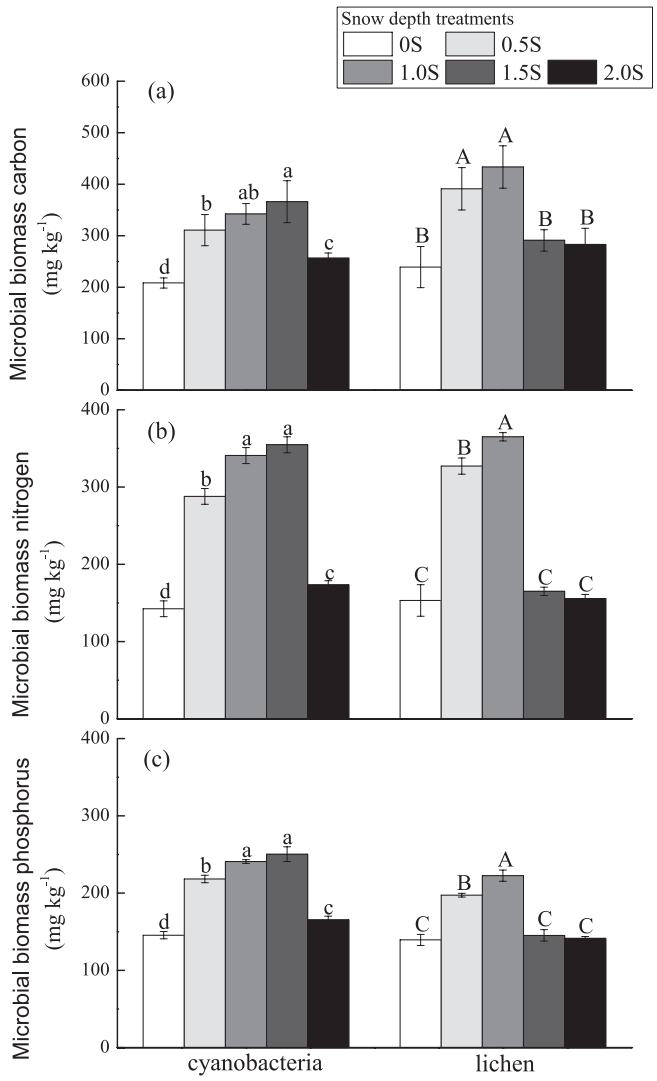

Fig 4. Effects of snow depth on microbial biomass carbon (a), nitrogen (b), and biomass phosphorus (c) in cyanobacteria and lichen crusts and underlying soil in the 0–5 cm layer. Each bar and vertical line indicates the mean value and SD respectively ($n = 3$). Different letters indicate significant differences (at $P < 0.05$) among the five snow depth treatments in complexes of cyanobacteria and subcrust soil (lowercase letters) and complexes of lichen and subcrust soil (capital letters) respectively.

precipitation (Chen and Duan, 2015). Furthermore, deep snow cover may lead to an increase in soil temperature, preventing BSCs from repetitive freezing and thawing due to fluctuating temperatures close to 0 °C (Steinweg et al., 2008) and positively affecting plants, microbial activity, and soil nutrients in winter (Groffman et al., 2011). The soil temperature was higher under increasing snow cover than under snow removal treatments (maximum snow depth from 63.4 cm to 18.2 cm, corresponding minimum temperature decreased from 0.01 °C to –4.54 °C), which showed the insulating effect of snow cover (Sorensen et al., 2018). The soil surface could easily freeze under the snow removal treatments, and the events occurring in soil freeze–thaw cycles might have impacted aboveground and belowground ecosystem processes in different ways (Bombonato and Gerdol, 2012). Comerford et al. (2013) observed that freeze–thaw events could induce variation in microbial diversity by exacerbating soil cation imbalances. They may also influence the growth and development of organisms in BSCs by environmental filtering because crust organisms have different tolerances to freeze–thaw events (Schmidt and Vimercati, 2019).

Snow depth influenced nutrient concentrations in cyanobacterial and lichen crusts and the subcrust soil after four years of snow-cover manipulation. The removal or reduction of snow cover resulted in lower nutrient concentrations (Fig. 3). This may have occurred because cyanobacterial and lichen layers that were not covered with snow froze easily, contained little available water, and possessed very low microbial activity (Zhao et al., 2018; Hui et al., 2019). The results of our study also indicate that the concentrations of available forms of N were significantly lower under snow removal and decreased snow depth after four years of snow-cover manipulation (Fig. 3). This likely occurred because water deficit and lower temperatures under snow removal resulted in a decrease in microbial metabolism. The soil microenvironment under snow cover might be beneficial for microbial growth and activity during the winter (Schadt et al., 2003). Suitable water and temperature conditions accelerate soil aerobic microbial growth, and the metabolic products of soil microbes can improve soil nutrient content (Li et al., 2010). The results of this study indicate that the concentrations of microbial biomass carbon, nitrogen, and phosphorus in cyanobacteria and lichen crusts and the subcrust soil declined under snow removal and snow-cover reduction andsignificantly decreased also under snow addition treatments (except for treatment 1.5S in cyanobacterial crusts) compared to control (Fig. 4). Changes in snow depth have been reported to be the influencing environmental factor for the dynamics of microbial biomass (Zhao et al., 2018; Hui et al., 2019). One possible reason for the decrease in microbial biomass with decreasing snow depth was that snow removal and snow-cover reduction increased the frequency and duration of soil freeze–thaw cycles, which had a negative influence on microbial biomass (Tan et al., 2014). Another possible reason is low soil water availability under snow removal and snow-cover reduction may have resulted in increased oxidation potential (e.g., more rapid oxygen diffusion may cause high aerobic bacterial activity and low anaerobic bacterial activity) in the soil surface and may have greatly influenced microbial communities during the whole winter (Blodau et al., 2004).

The results of this study indicate that soil nutrients and microbial biomass also decreased under high snow depths after four years of treatment. This reduction likely occurred because of inhibition of organism activity and loss of soil nutrients. In fact, excessive snow depths probably suppressed microbial metabolism and reduced organic matter decomposition and nutrient cycling (Webber et al., 1976), mainly due to a lack of oxygen because of the high density of the snow cover, the overly wet conditions, and the loss of soil nutrients by leaching during the period of snow melting (Edwards and Jefferies, 2013; Zhao et al., 2018). After four years of treatment, the NH_4^+-N and NO_3^--N concentrations in cyanobacteria and lichen crusts had significantly declined under the 1.5S and 2.0S treatments in the present study, probably because massive amounts of NH_4^+-N and NO_3^--N ran off with the snow melt water (Xu et al., 2018). Moreover, the concentrations of soil nutrients and microbial biomass in cyanobacteria and lichen crusts reached peak values under the 1.0S or 1.5S treatments, possibly because the moderate snow-depth was favorable for photosynthesis and growth of BSC organisms (Yin and Zhang, 2016; Zhao et al., 2016).

The effects of snow depth varied in different crust types after four years of snow depth manipulations. Specifically, lichen crusts had higher nutrient concentrations, except for NH_4^+-N and NO_3^--N. This likely occurred because of differences in organism composition and community structure between BSCs (Liu et al., 2017a,b). Among BSC species, cyanobacteria often occur in the earlier BSC successional stages, whereas lichen crusts appear later (Bowker, 2007). Differences in organism composition and community structure between cyanobacterial and lichen crusts may affect photosynthesis, nutrient cycling, nitrogenase activity, and exopolysaccharides (Housman et al., 2006; Lan et al., 2012), ultimately causing variations in soil nutrients and microbial biomass. Along with differences in organism composition and community structure, differences in soil physical structure under cyanobacterial and lichen crusts may also cause different responses of the crust and soil layers to variations in snow cover (Hui et al., 2019; Zhang et al., 2021). Moreover, variations in water retention ability and available soil water

content (lichen crusts > cyanobacterial crusts) in the two types of BSC may contribute to this difference (Li et al., 2017).

5. Conclusions

Snow depth change will significantly alter the carbon and nutrient availability and microbial biomass in BSC and subcrust soil in the Gurbantunggut Desert. The results of this study have demonstrated that both snow reduction (especially snow removal) and substantial increase (2.0S) in this region seemed to negatively influence carbon and nutrient availability and microbial biomass after four years of snow manipulation. If the patterns of snow-depth change arranged in our experiments hold true in the future, the results from this study indicate that development of BSCs will be suppressed because crusts and subcrust soil will become nutrient-deficient, leading to fertility declines in arid regions, which are already inherently low in soil nutrients and fertility. Moreover, the combination of crust type with snow depth can influence carbon and nutrient availability and microbial biomass. These results imply that crust type may regulate the effect of change in snow depth on complexes of biological soil crusts and subcrust soil. Our results provide an accurate prediction of how water content, carbon and nutrient availability, and microbial biomass in the crust and the subcrust soil respond to changes in snow depth. Further assessments of the development of BSCs and their ecological function responses to the negative influence of snow depth variations are required in arid and semiarid areas of China, where global climate change is expected to alter snow depths.

CRediT authorship contribution statement

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Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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