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## Winter snowfall can have a positive effect on photosynthetic carbon fixation and biomass accumulation of biological soil crusts from the Gurbantunggut Desert, China

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**Abstract** Winter snowfall is an important factor in the growth and development of biological soil crusts (BSCs) in temperate desert regions of China. In this study, intact algae, lichen, and moss crusts from the Gurbantunggut Desert were collected and exposed to five experimental treatments—snow removal (0S), snow decrease to half that of ambient conditions (1/2S), ambient snow (S), snow increase to 1.5 times that of ambient conditions (3/2S), and snow increase to twice that of ambient conditions (2S)—to evaluate the effect of snowfall on the ecophysiological parameters of the BSCs during the melt and at the end of the growing period. The results clearly identified differences in physiological and ecological indexes between snowfall manipulation treatments in March, and further found that the values of most of the ecophysiological indexes were influenced by snow removal/reduction treatments, the type of BSC and their

interaction effect. The chlorophyll fluorescence parameters, chlorophyll content, and the rates of photosynthesis and respiration of all three types of crust declined because of decreased soil water content with decreased snow cover, and this effect would likely be even greater under conditions of decreased precipitation. The rates of photosynthesis and respiration of the main types of BSC were changed by variations in the winter snowfall, and confirmed the existence of long-term snowfall impacts on photosynthetic carbon fixation and biomass accumulation. These results provide a foundation for future studies to assess the potential effects of snowfall on the carbon sequestration of BSCs from arid and semi-arid regions.

**Keywords** Algal crusts · Lichen crusts · Moss crusts · Biomass · Net photosynthetic rate

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### Introduction

Desert ecosystems are important locations for carbon (C) storage and play a key role in the C cycle in the terrestrial biosphere, although they are generally assumed to be relatively minor participants in the global C cycle because of their low productivity (Asner et al. 2003; Finch 2012). Overall, nearly 22 % of the Earth's land surface is covered by deserts and semi-deserts, which account for about 8 % of terrestrial C stocks (Janzen 2004). These regions are generally about a third as effective as the average biome at storing C on a per area basis (Janzen 2004). Standing biomass and soil organic carbon (SOC) are potential locations of stored C. The standing biomass C in deserts is estimated to account for only 1.7 % of the global total, although desert SOC is estimated to account for 9.5 % (Jobbagy and Jackson 2000; Janzen 2004). Desert areas have sparse vegetation cover and low productivity depending on climatic features, such as the lack of rain during

much of the year. At the same time, this feature limits the rate of microbial respiration in soil, leading to the effective accumulation and persistence of SOC (Finch 2012; Jobbagy and Jackson 2000). In desert regions, the residence time of soil carbon is approximately 200 years, which far exceeds that of other ecosystems (Jarvis et al. 2007).

Biological soil crusts (BSCs) are the dominant functional vegetation unit in arid and semi-arid regions (Rajeev et al. 2013). BSCs are not only an important participant in C cycling in desert ecosystems, but also an important source of SOC in desert regions (Housman et al. 2006; Mager 2010). There are large differences in the geographical locations and climate features along the distribution range of BSCs, but they all have a similar appearance and constitution, and fulfill a wide range of ecological functions, including soil stabilization (Bowker et al. 2010), control of runoff or infiltration processes (Kidron et al. 2003; Belnap and Troxler 2006), C and nitrogen (N) fixation, and nutrient cycling (Belnap and Troxler 2006). Additionally, BSCs can be considered “ecosystem engineers” that interface between soil and atmosphere (West 1990; Bowker et al. 2008a). BSCs usually comprise a thin mantle of the soil, and are the dominant biotic component (Evans and Lange 2003), being composed mainly of mosses, lichens, fungi, and cyanobacteria (Pointing and Belnap 2012), which play an important role in arid and semi-arid ecosystems. They affect many significant ecological processes in desert ecosystems, such as soil ecological processes (Fearnehough et al. 1998; Bowker et al. 2005; Chen et al. 2009), hydrological processes (Maestre et al. 2002; Liu et al. 2006; Wang et al. 2009), biogeochemical cycles (Harper and Belnap 2001; Evans and Lange 2003; Viles 2008), and biological processes (Liu et al. 2013). Colonization by BSCs might facilitate the subsequent survival and reproduction of vascular plants and soil animals by providing and recycling critical nutrients (Mayland and McIntosh 1966; Li et al. 2010, 2011).

One of the major ecological roles of BSCs is their contribution to C storage and the C cycle, which results from the balance between photosynthesis and C mineralization by heterotrophic respiration. The photosynthetic C fixation capacity of BSCs is an important factor for C fixation in desert regions, and provides the material and energy basis for other ecological functions. In general, well-developed BSCs have a larger photosynthetic C fixation capacity than vascular plants in the same desert ecosystem because of their higher coverage (BSCs can account for 70 % of the live surface cover), and their high light use efficiency (e.g., light use efficiency of lichen can reach 0.5–2 %) (Palmqvist 2000). In some desert ecosystems, the cyanobacterial crust contributes more than 75 % of the SOC (Mager 2010). Regions covered with a BSC might have SOC reserves more than ten times higher than non-covered regions, even when they are located in the same area (Evans and Belnap 1999; Li et al. 2002). It is generally acknowledged that there is a linear relationship between the

photosynthetic rate and chlorophyll content of BSCs; therefore, the chlorophyll content can strongly indicate the C content and photosynthetic C fixation capacity of BSCs (Bowker et al. 2002; Serpe et al. 2013). Moisture is an important abiotic driver of the C and N exchange rate in BSCs, because most plants present in BSCs (cyanobacteria, moss, lichen, etc.) are poikilohydric and therefore only undertake physiological activity in wet conditions (Grote et al. 2010; Lindo et al. 2013). The structure and composition of BSCs are determined to a large extent by precipitation patterns, which then influence their photosynthetic C sequestration rate (Belnap et al. 2004; Sponseller 2007). Temperature is another important factor influencing the C exchange rate of BSCs. Because the rates of C fixation and release are sensitive to temperature variations, the relationship between the sources and sinks in the C exchange processes of BSCs are likely to change when the temperature changes (Colesie et al. 2014). As significant abiotic drivers of the C exchange rate of BSCs, moisture and temperature have been explicitly considered in climate models (Elbert et al. 2012). It has been reported that an increase in precipitation causes significant changes in plant community structure and composition at functional levels under harsh environmental conditions (Stevens et al. 2010).

Previous investigations have mainly focused on the effects of a change in summer precipitation on BSC C exchange processes in arid regions (Johnson et al. 2012; Zelikova et al. 2012; Angel and Conrad 2013; Drahorad et al. 2013; Miralles et al. 2013), with little attention given to the influence of winter snowfall. Snow cover directly and indirectly affects ecosystems, especially in arid and semi-arid regions, and its influence is not only limited to the winter. As a special form of precipitation, snowfall and cover is a pre-condition for survival during the harsh environmental conditions experienced in arid and semi-arid ecosystems. During winter, snow cover can lead to a higher CO<sub>2</sub> flux, provide suitable conditions for physiological activity, and sustain microbial activities and mineralization processes by increasing soil temperature (Rogers et al. 2011). A deep snowpack has been reported to induce high photosynthetic rates in plants (Leffler and Welker 2013), as well as increasing N mineralization and altering the amount of plant-available N in ecosystems (Schimel et al. 2004). On the one hand, plants can benefit from a deep snowpack that insulates plants and soil from freezing stress (Elise et al. 2015). Generally speaking, plant recovery from photo-inhibition is strongly temperature dependent (Gombos et al. 1994; Murata et al. 2007). Thus, thylakoid membranes in chloroplasts will be damaged during cold stress, and chlorophyll content and fluorescence will reflect this damage (Theocharis et al. 2012; Kolaksazov et al. 2014). On the other hand, deep snow might also contribute to increased available water supplies from more shallow soils for plant growth (Dawson et al. 2002). Once plants have recovered from drought stress, photosynthetic performance and N availability could be enhanced (Schimel et al. 2004;

Leffler and Welker 2013). When snow melts it also can change the soil water content and help plant growth and development (Wang et al. 2006). The impact of snow cover on photosynthetic C fixation in BSCs remains poorly understood, particularly in the Gurbantunggut Desert, which is the biggest fixed and semi-fixed desert in China (Zhang et al. 2009). In winter, the Gurbantunggut Desert experiences 95–110 days of stable snow cover, with snow accumulating to 10–30 cm. Germination and development of plants in this region is dependent on snowmelt water in the early spring.

Timely winter snowfall is an important factor in the growth and development of plants in the following year. This is also true for BSCs in the temperate desert in China. In this study, intact BSCs (algae, lichen, and moss crusts) from the Gurbantunggut Desert were collected as experimental material (Zhang et al. 2009). Five experimental treatments were applied: snow removal (0S), snow decrease to half that of ambient conditions (1/2S), ambient snow (S), snow increase to 1.5 times that of ambient conditions (3/2S), and snow increase to twice that of ambient conditions (2S). Snow removal began in October 2013 and ended in March 2014 when the snow cover in the treatments had melted. We measured chlorophyll fluorescence, chlorophyll content, moisture contents, biomass, and the rates of photosynthesis and respiration after snowmelt (March 2014) in three typical BSCs from the Gurbantunggut Desert, and a similar test was then conducted at the end of the growing period (October 2014) to evaluate the long-term impact of the snowfall treatments. By combining the responses of all of these factors, we were able to extract information regarding the life traits of these three types of BSC, such as whether a decrease or increase in snow depth affected photosynthetic C fixation and biomass accumulation in BSCs. We hypothesized that declining winter snowfall will affect the ecophysiological parameters of the main BSCs in the Gurbantunggut Desert, and that long-term impacts exist with regard to snowfall and photosynthetic C fixation and biomass accumulation in the BSCs. Therefore, photosynthetic C fixation and biomass accumulation in BSCs might be altered by changes to the snowfall in the melt and in the following growth period.

## Methods

### Site description and snow manipulation

The study site was situated in the Gurbantunggut Desert, which is located in the center of the Jungger Basin (44°11′–46°20′N, 84°31′–90°00′E) in the Xinjiang Uygur Autonomous Region of China. At the study site, the mean annual air temperature ranges from 6 to 10 °C, with extreme minimum and maximum temperatures of –40 and 40 °C, respectively. Precipitation falls primarily in the spring, with an annual mean of approximately 79.5 mm, while the mean annual evaporation is 2606.6 mm (Zhang et al. 2007). Snow accumulates to

10–30 cm in the winter. *Haloxylon ammodendron* and *H. persicum* are the dominant natural vegetation in this area, although their surface cover is less than 30 %. The most common landscape feature is an abundance of BSCs on the sandy soil surface of the desert. BSCs grow primarily during cool, wet periods when dew, fog, snowmelt, and temporary rainfall are available. There are three main types of BSCs—algae, lichen, and moss crusts. The cyanobacterial/lichen crusts are mainly composed of *Microcoleus vaginatus*, *M. paludosus*, *Anabaena azotica*, *Porphyrosiphon martensianus*, *Collema tenax*, *Psora decipiens*, *Xanthoparmelia desertorum*, and *Diploschistes muscorum*, and the moss crusts are predominantly comprised of *Syntrichia caninervis*, *Bryum argenteum*, and *Tortula muralis* (Zhang et al. 2009; Su et al. 2013).

We randomly collected intact algal, lichen, and moss crusts from areas with 100 % coverage from the Gurbantunggut Desert in cylindrical PVC containers (10 cm in diameter and 5 cm in height) in early September 2013. Samples were air-dried and stored until the experiments began in October 2013. Five experimental treatments were applied: snow removal (0S), snow decrease to half that of ambient conditions (1/2S), ambient snow (S), snow increase to 1.5 times that of ambient conditions (3/2S), and snow increase to twice that of ambient conditions (2S). Each treatment had three replicates. Snow removal/increase began in October 2013 and ended in March 2014 when the snow cover had melted. The rates of photosynthesis, respiration, and other indices were measured in March 2014 (after snow) and October 2014 (growing period). The snow decreases/increases were achieved by manually shoveling snow away/in following each major (> 5 cm snow deposition) precipitation event. Snow decrease/increase treatments were performed by constructing a snow fence that was erected perpendicular to the earth to increase the depth and duration of snow cover. The depth of snow was measured using a ruler (Bokhorst et al. 2013).

### Measurement of the moisture content of crusts and sand

The moisture content of crusts and sand was determined gravimetrically (Liu et al. 2006). Three samples were collected per treatment from soil depths of 0–2 and 2–5 cm, weighed with an electronic balance, and then weighed again after being oven-dried at 105 °C for 24 h. At the same time, crust and sand moisture were determined as the difference between the weights of the wet and oven-dry samples, and the moisture content was expressed in grams of water per gram of oven-dried soil ( $\text{g g}^{-1}$ ).

### Measurement of chlorophyll content and biomass

Chlorophyll was extracted from the cyanobacteria, lichen, and moss with 100 % ethanol at 4 °C (Lan et al. 2011). Abrasive materials were placed in centrifuge tubes and extracted in 25 mL of ice cold ethanol for 30 min at

4 °C. The tubes were centrifuged for 30 min twice at 12,000g after the extraction. A UV–Vis spectrophotometer (model 752N; Shanghai Precision and Scientific Instrument Company Ltd., Shanghai, China) was used to analyze the absorbance of the extracts at 470, 649, and 665 nm. Chlorophyll data were obtained from independent triplicate samples. According to the methods of Belnap and Gardner (1993) and Bowker et al. (2008b), the data for chlorophyll *a* (Chl *a*) were used as the total biomass proxy for algal, lichen, and moss crusts, i.e., Chl *a* content was used to estimate the biomass of crusts. Biomass accumulation was determined by the difference between Chl *a* in October and March. Chl *a*, chlorophyll *b* (Chl *b*) and carotenoid (Car) contents were calculated using the following formulas:

$$\begin{aligned} \text{Chl } a &= 13.95A_{665} - 6.88A_{649}, \\ \text{Chl } b &= 24.96A_{649} - 7.32A_{665}, \\ \text{Car} &= (1000A_{470} - 2.05\text{Chl } a - 114\text{Chl } b)/245, \\ x &= CVn/S, \end{aligned}$$

where *x* is the pigment content (mg/g fr. wt.), *C* is the pigment concentration (mg/L), *V* is the extract volume (L), *n* is the dilution factor and *S* is the sample area (cm<sup>-2</sup>).

#### Determination of chlorophyll fluorescence

Chlorophyll fluorescence from the cyanobacteria, lichen, and moss crusts were measured using pulse amplitude modulated (PAM) fluorometry (MFMS-2, Hansatech, Kings Lynn, UK) as described by Havaux et al. (2009). Three samples from each treatment for each crust were induced in a photon flux density equal to 400 μmol m<sup>-2</sup> s<sup>-2</sup> for 5 s, and then dark-induced for 20 min. The initial fluorescence (*F*<sub>0</sub>) was determined by modulated light (<0.1 μmol m<sup>-2</sup> s<sup>-2</sup>), and the maximum fluorescence (*F*<sub>*m*</sub>) was measured with a 0.8 s saturating pulse at 8000 μmol m<sup>-2</sup> s<sup>-2</sup>. The maximum photochemical efficiency (*F*<sub>*v*</sub>/*F*<sub>*m*</sub>) of photosystem II (PSII), fluorescence yield (*Y*), and the rates of electron transport (ETR) were estimated using the following formula:

$$\begin{aligned} F_v/F_m &= (F_m - F_0)/F_m \\ Y &= (F'_m - F_t)/F'_m \\ \text{ETR} &= Y \times 0.84 \times 0.5 \times \text{PPFD} \end{aligned}$$

where

$$F'_m$$

is the maximal fluorescence level after the application of a saturating light pulse and *F*<sub>*t*</sub> represents the fluorescence in the steady state of photosynthesis.

#### Estimation of photosynthetic C fixation

A CO<sub>2</sub>/H<sub>2</sub>O analyzer (LI-840A; LI-COR, Inc., Lincoln, NE, USA) was used to measure the CO<sub>2</sub> concentration

(Chen et al. 2009). A circular cubic chamber (3.14 × 20<sup>3</sup> cm<sup>3</sup>) was used to measure the net photosynthetic (*P*<sub>*n*</sub>) and respiratory (*R*<sub>*d*</sub>) rate. The CO<sub>2</sub> concentrations inside the chamber were collected every second for 2 min after the chamber was placed on the base rim when measuring *P*<sub>*n*</sub>. The chamber was lifted, vented and placed on the base rim. It was then covered by a lightproof cloth mantle and CO<sub>2</sub> fluxes were recorded again after measuring *P*<sub>*n*</sub>. Power for the LI-840 was provided by a battery (12 V, 20 Ah). Data acquisition software provided with the LI-840 was used to record data.

#### Statistical analysis

All experimental results were presented as the mean ± standard deviation (SD) of three replicates. Statistical analyses were performed using the SPSS 16.0 statistical package (SPSS, Chicago, IL, USA) using one- and two-way analyses of variance (ANOVA). A two-way ANOVA was used to evaluate the type of BSCs, decrease and increase in snow depth, and their combined effect on biomass, moisture content, chlorophyll fluorescence, and CO<sub>2</sub> exchange. For each type of BSC, a one-way ANOVA was used to determine the effects of a decrease and increase in snow depth. In all cases, Duncan's test was used at a significance level of *P* < 0.05.

## Results

#### Sand moisture content

Sand moisture content of BSCs was significantly affected by snow manipulations (*P* < 0.001), type of BSCs (*P* < 0.001), and the interaction between snow manipulations and type of BSCs (*P* < 0.001; Table 1) in March. There was a highly significant positive correlation between sand moisture content and addition of snow, and a significant positive correlation between sand moisture content and type of BSCs. Similar two-way ANOVA results were observed in October (Table 2). In March, moisture content of the sand at a depth of 0–2 cm beneath the lichen crusts have 52.1 % (0S), 21.1 % (1/2S) negative change, and 320.0 % (2S) positive change compared with the control (S) (Fig. 1a). Moisture content beneath the algae crusts at the depth of 0–2 cm have 32.1 % (0S), 21.7 % (1/2S) negative change, and 107.6 % (3/2S), 349.9 % (2S) positive change compared with S (Fig. 1b). Moisture content beneath the moss crusts at the depth of 0–2 cm have 73.5 % (0S) negative change, and 4.3 % (1/2S), 46.9 % (2S) positive change compared with S (Fig. 1c). Moisture content of sand beneath the algal crusts at a depth of 2–5 cm have 78.7 % (0S) negative change, and 3.3 % (1/2S), 50.7 % (3/2S), 68.8 % (2S) positive change; beneath the lichen crusts have 81.1 % (0S), 26.1 % (1/2S) negative change, and 49.4 % (2S) positive change; and beneath the moss crusts have -36.1 % (0S), -18.0 % (1/2S) negative

**Table 1** Results of two-way ANOVA of effects of snow manipulation treatments and different kinds of BSCs on soil moisture contents, chlorophyll fluorescence, chlorophyll content, and the rates of photosynthesis and respiration in March 2014 (after snow)

BSC parameters	F-ratios		
	BSCs	Snow	Snow × BSC
Moisture content (0–2 cm)	118.2***	161.4***	26.3***
Moisture content (2–5 cm)	73.0***	92.4***	5.5***
$F_v/F_m$	0.1	16.5***	4.5***
Y	11.4***	17.4***	5.9***
ETR	11.6***	21.8***	5.3***
Chlorophyll <i>a</i>	891.6***	1466.0***	402.2***
Chlorophyll <i>b</i>	1615.0***	1139.0***	363.8***
Carotenoid	129.4***	1554.0***	299.2***
Net photosynthetic rate ( $P_n$ )	0.4	15.7***	0.3
Respiration ( $R_d$ )	57.8***	6.2***	1.3

F-ratios from two-way ANOVA are given. Degrees of freedom (*df*) were mostly the same for all parameters (BSCs: 2; Snow: 4; Snow × BSC: 8) except for moisture content (BSCs: 2; Snow: 3; Snow × BSC: 6)

BSCs biological soil crusts,  $F_v/F_m$  the maximum photochemical efficiency of PSII, Y fluorescence yield, ETR the rates of electron transport

\*\*\*  $P < 0.001$ , \*\*  $P < 0.01$

**Table 2** Results of two-way ANOVA of effects of snow manipulation treatments and different kinds of BSCs on soil moisture contents, chlorophyll fluorescence, chlorophyll content, and the rates of photosynthesis and respiration in October 2014 (the end of the growing period)

BSC parameters	F-ratios		
	BSCs	Snow	Snow × BSC
Moisture content (0–2 cm)	111.1***	21.1***	2.3**
Moisture content (2–5 cm)	32.9***	26.2***	0.9
$F_v/F_m$	31.5***	107.5***	7.9***
Y	63.7***	171.5***	13.9***
ETR	99.1***	104.1***	9.4***
Chlorophyll <i>a</i>	314.4***	1297.0***	25.7***
Chlorophyll <i>b</i>	1000.0***	350.1***	22.2***
Carotenoid	279.4***	280.8***	31.2***
Net photosynthetic rate ( $P_n$ )	1.6	32.0***	0.2
Respiration ( $P_d$ )	13.9***	3.7**	0.2

F-ratios from two-way ANOVA are given. Degrees of freedom (*df*) were the same for all parameters (BSCs: 2; Snow: 4; Snow × BSC: 8)

BSCs biological soil crusts,  $F_v/F_m$  the maximum photochemical efficiency of PSII, Y fluorescence yield, ETR the rates of electron transport

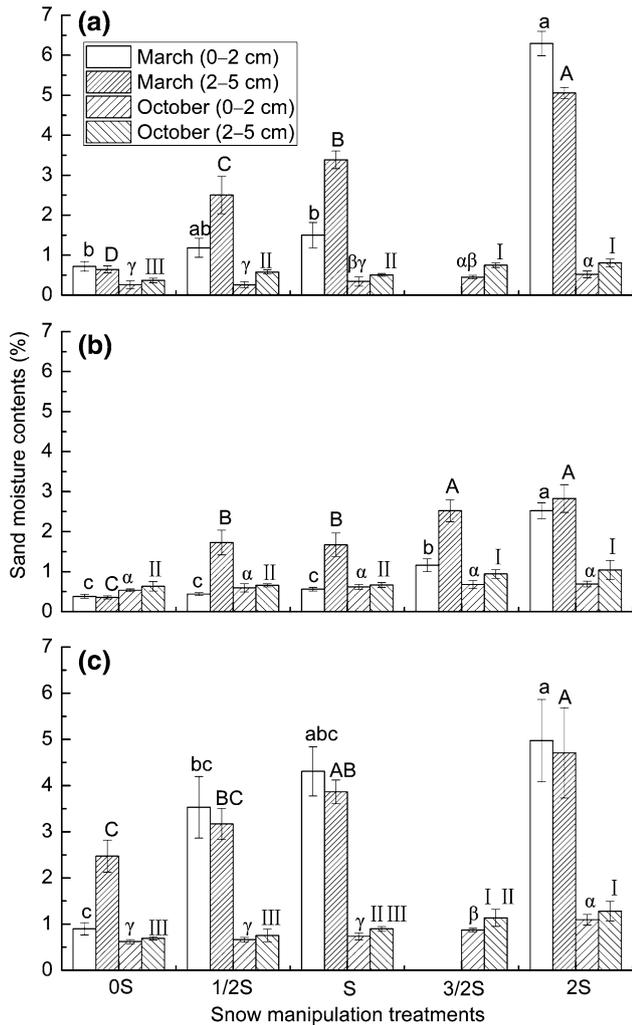
\*\*\*  $P < 0.001$ , \*\*  $P < 0.01$

change, and 21.8 % (2S) positive change compared with S (Fig. 1). However, after one growing season there was a decrease in the soil moisture content beneath the three BSCs when compared with the moisture content in March. For each BSC, no obvious changes in soil moisture were found for the five treatments in October.

#### Chlorophyll fluorescence

Y and ETR of BSCs were significantly affected by snow manipulations ( $P < 0.001$ ), type of BSCs ( $P < 0.001$ ), and the interaction between snow manipulations and type of BSCs ( $P < 0.001$ ; Table 1) in March.  $F_v/F_m$  was not significantly affected by type of BSCs ( $P = 0.925$ ), but was significantly affected by snow manipulations ( $P < 0.001$ ) and the interaction between snow manipu-

lations and type of BSCs ( $P < 0.001$ ; Table 1). In addition, similar two-way ANOVA results were obtained in October (Table 2). When compared with the control (S),  $F_v/F_m$  changed by 24.3 %, –13.1, 26.2 and 41.9 % for the lichen crust (Fig. 2a); 70.8, 10.4, 51.2 and 84.3 % for the algae crust (Fig. 2b); and 56.7 %, 24, 0 %, –0.01 % and 24.0 % for the moss crust (Fig. 2c) in March. Over the whole summer period, the chlorophyll fluorescence parameters were higher for all snow treatments than in March for all three BSCs. An increase in the value of  $F_v/F_m$ , Y, and ETR was observed with an increase in snow depth. The highest values of the chlorophyll fluorescence parameters for lichen, algae, and moss crusts were observed with the S, 1/2S, and 3/2S treatments, respectively. When compared with snow removal (0S), the highest values of  $F_v/F_m$ , Y, and ETR increased by 132.8, 86.2, and 58.1 %, for the algae crust (Fig. 2b, e, h); by 49.5,



**Fig. 1** Variation in moisture content in sand beneath the lichen (a), algae (b) and moss (c) crusts in March 2014 (after snow) and October 2014 (after the growing period). The snow manipulation treatments were snow removal (0S), snow decrease to half that of ambient conditions (1/2S), ambient snow (S), snow increase to 1.5 times that of ambient conditions (3/2S), and snow increase to twice that of ambient conditions (2S). Data for 3/2S for lichen (a) and moss (c) are missing

56.1 and 62.8 %, for the lichen crust (Fig. 2a, d, g); and by 242.0, 130.1 and 114.8 %, for the moss crust (Fig. 2c, f, i) for S, 1/2S and 3/2S treatments, respectively. Slightly different results were obtained for the lichen crust. The values of the chlorophyll fluorescence parameters decreased as the snow depth increased, with  $F_v/F_m$ ,  $Y$ , and ETR significantly decreased by 2.5 % and 23.3, 12.2 and 8.8 %, and 10.0 and 5.6 %, in 3/2S and 2S, respectively, compared with 0S (Fig. 2a, d, g).

#### Photosynthetic pigment content

During March, the Chl *a*, Chl *b*, and Car contents were increased and then decreased with the increase of snow

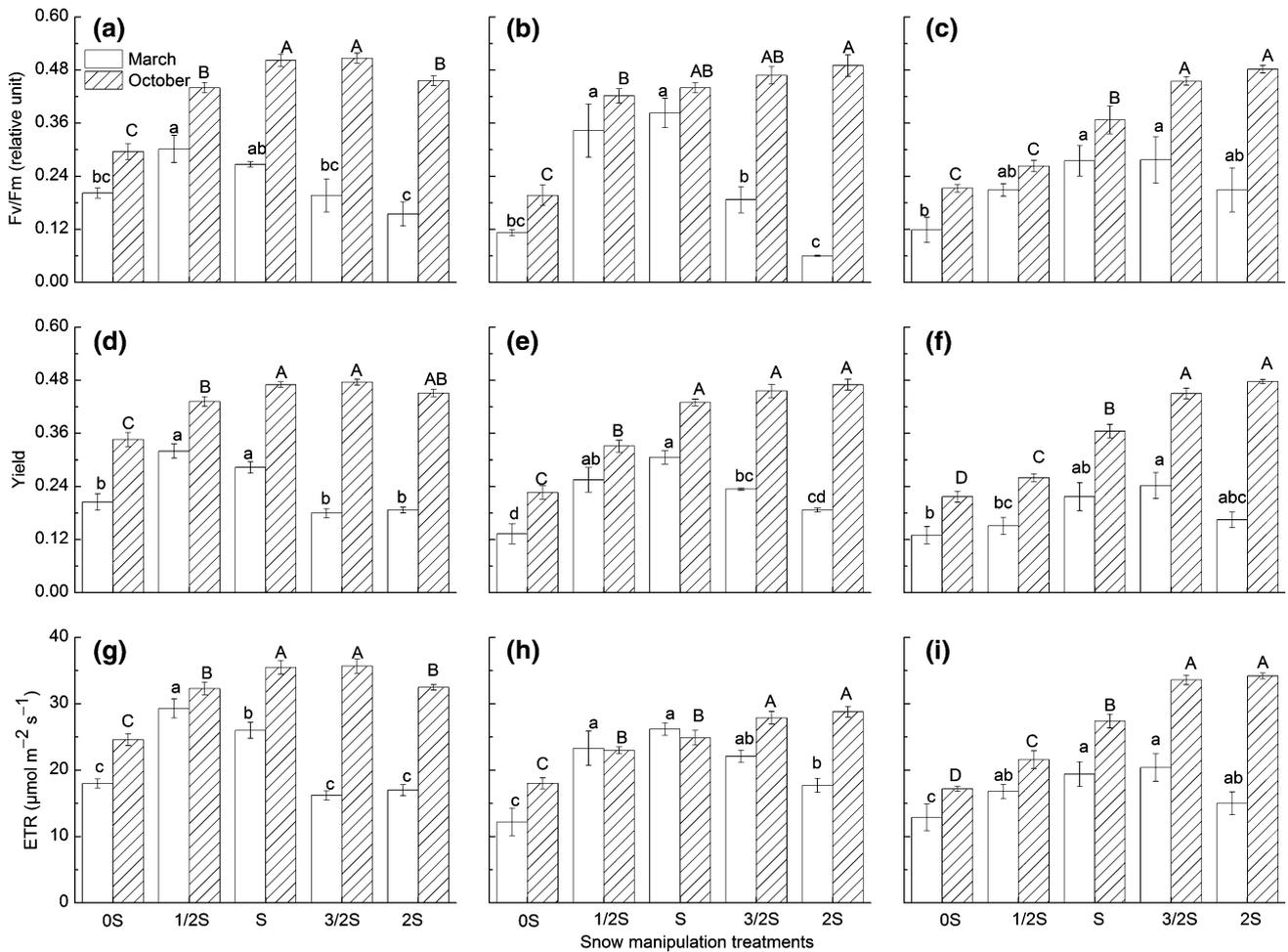
depth during the snow manipulation treatments. A two-way ANOVA showed that the photosynthetic pigment content was significantly affected by snow manipulations ( $P < 0.001$ ), type of BSCs ( $P < 0.001$ ), and the interaction between snow manipulations and type of BSCs ( $P < 0.001$ ) in March. Additionally, similar two-way ANOVA results were shown in October (Table 2). In March, compared with the control condition (S), the Chl *a* content changed in the 0S, 1/2S, 3/2S and 2S treatments by 30.8 %, -10.5, 41.7, and 88.9 %, respectively, in the lichen crust (Fig. 3a); 72.6, 9.6, -2.0, and 14.0 %, respectively, in the algae crust (Fig. 3b); and 146.2, 23.1, 52.4, and 255.6 %, respectively, in the moss crust (Fig. 3c). The photosynthetic pigment content was higher for all snow treatments over the whole summer period than in March for all three BSCs. The Chl *a*, Chl *b*, and Car contents were increased with increased snow depth. The highest values of the photosynthetic pigment contents were obtained in the 2S treatment, except Chl *b* in the moss crust where the highest values of Chl *b* were obtained in 3/2S. When compared with the 0S treatment, the Chl *a*, Chl *b*, and Car contents significantly increased ( $P < 0.05$ ) by 16.4, 14.0, and 17.8 % in the algae crust (Fig. 3b, e, h); 25.0, 18.8, and 6.6 % in the lichen crust (Fig. 3a, d, g); and 12.5, 1.2, and 18.9 % in the moss crust (Fig. 3c, f, i) in 1/2S, 3/2S and 2S treatments, respectively.

#### Photosynthetic C fixation

After different snowfall manipulations in winter, both  $P_n$  and  $R_d$  first decreased and then increased as the snow depth increased. Both  $P_n$  and  $R_d$  were strongly affected by a decrease or increase in snow depth in March ( $P < 0.001$ ; Table 1) and October ( $P < 0.001$ ; Table 2). The variation in the net photosynthetic ( $P_n$ ) and respiratory ( $R_d$ ) rates in algae, lichen, and moss crusts in March and October 2014 after the 0S, 1/2S, S, 3/2S, and 2S treatments is shown in Fig. 4. In March,  $P_n$  decreased by 59.4, 41.8, 11.5, and 55.3 % in the lichen crust (Fig. 4a); by 74.6, 34.5, 16.7, and 50.8 % in the algae crust (Fig. 4b); by 68.3, 47.1, 7.8, and 44.8 % in the moss crust (Fig. 4c) in 0S, 1/2S, 3/2S and 2S when compared with S. The highest values of  $P_n$  and  $R_d$  (0.72 and 4.15  $\text{mg cm}^{-2}$ , respectively, for the lichen crust; 0.74 and 1.41  $\text{mg cm}^{-2}$ , respectively, for the algae crust; and 0.79 and 3.43  $\text{mg cm}^{-2}$ , respectively, for the moss crust) were obtained for the 2S treatment in October (Fig. 4). Over the whole summer period, there was no significant difference in  $R_d$  for all snow treatments compared with the control condition (S).

#### Biomass accumulation

Biomass accumulation was significantly affected by snow manipulations ( $P < 0.001$ ), type of BSCs



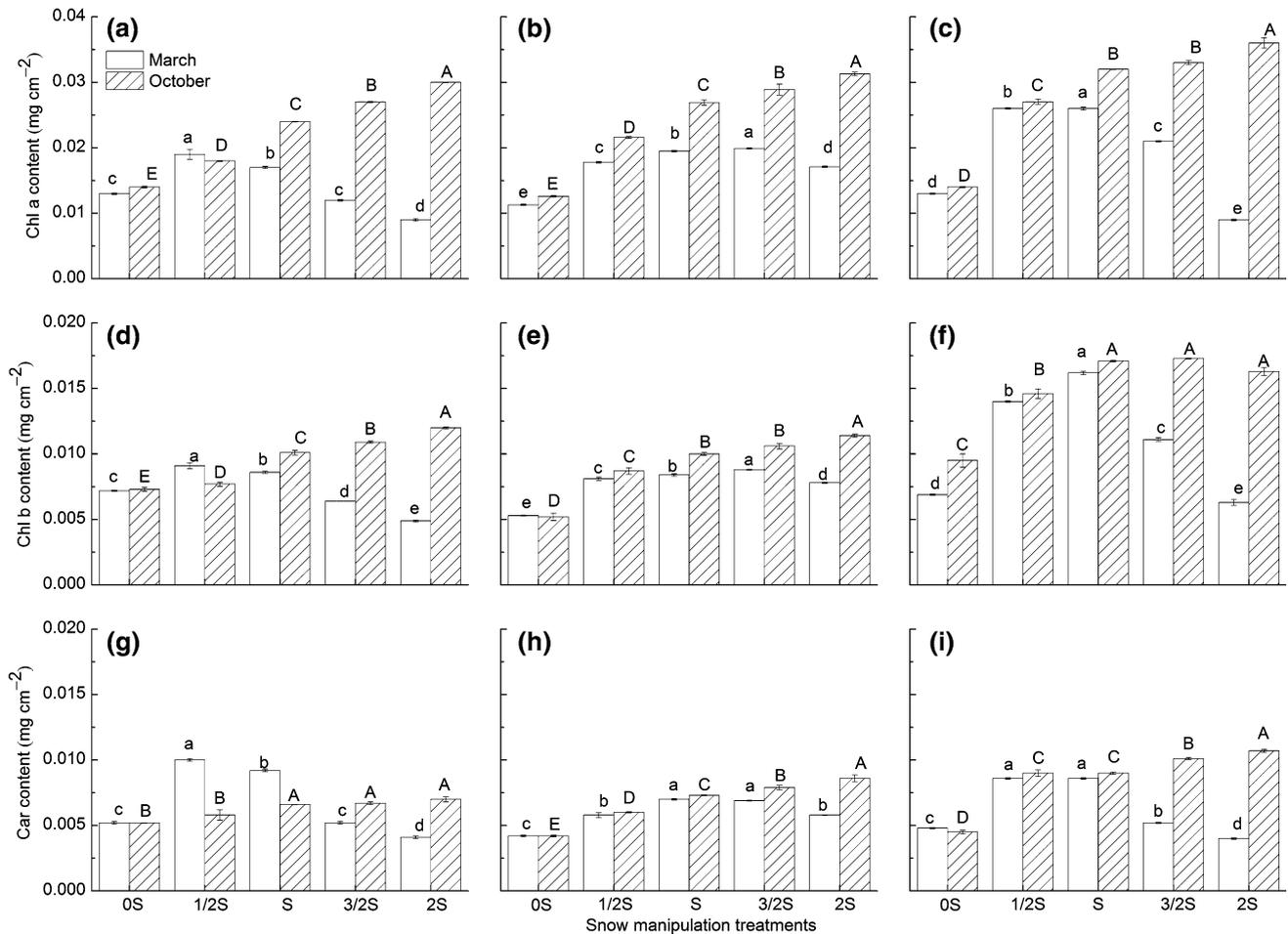
**Fig. 2** Variation in  $F_v/F_m$  (a, b, and c), yield (d, e, and f), and ETR (g, h, and i) of lichen (a, d, and g), algae (b, e, and h) and moss (c, f, and i) crusts in March 2014 (after snow) and October 2014 (the growing period) after the 0S, 1/2S, S, 3/2S, and 2S treatments. Data are mean values  $\pm$  standard deviation ( $N = 3$ ). Different letters between samples indicate significant differences using

Duncan's test ( $P < 0.05$ ). The maximal quantum yield of PSII photochemistry, the effective quantum yield of PSII photochemistry, and the electron transport rates are indicated as  $F_v/F_m$ , yield, and ETR, respectively

( $P < 0.001$ ), and the interaction between snow manipulations and type of BSCs ( $P < 0.001$ ; Fig. 5). There was a highly significant positive correlation between biomass accumulation and increase in snow depth, and a significant negative correlation between biomass accumulation and decrease in snow depth. Over the whole summer period, biomass increased by 51.9 and 64.7 % for the lichen crust; 17.7 and 48.1 % for the algae crust; and 536.6 and 1376.6 % for the moss crust (Fig. 5) in the two increased snowfall treatments (3/2S and 2S), respectively. The largest biomass accumulation was observed in the 2S treatment, with significant increases to maxima of 0.063, 0.043, and 0.081  $\text{mg cm}^{-2}$  for the lichen, algae, and moss crusts, respectively (Fig. 5). In contrast, decreased biomass accumulation was observed for the lichen and algae crusts under the decreased snowfall treatments (0S and 1/2S).

## Discussion

The results clearly indicated differences in the chlorophyll fluorescence parameters, chlorophyll content, moisture content, biomass, and net photosynthetic and respiratory rates between treatments with different snowfall depths after winter, and suggest that the sensitivity of BSCs to snow removal/reduction differed between the three BSCs. The chlorophyll fluorescence parameters, chlorophyll content, and photosynthesis and respiration rates of the three crust types declined because of the lower soil water content associated with decreased snow cover, and this effect would be greater under conditions of decreased precipitation. Increased depth of snowfall resulted in a lower rate of photosynthesis and respiration in March but a higher rate in October. The data clearly indicate that



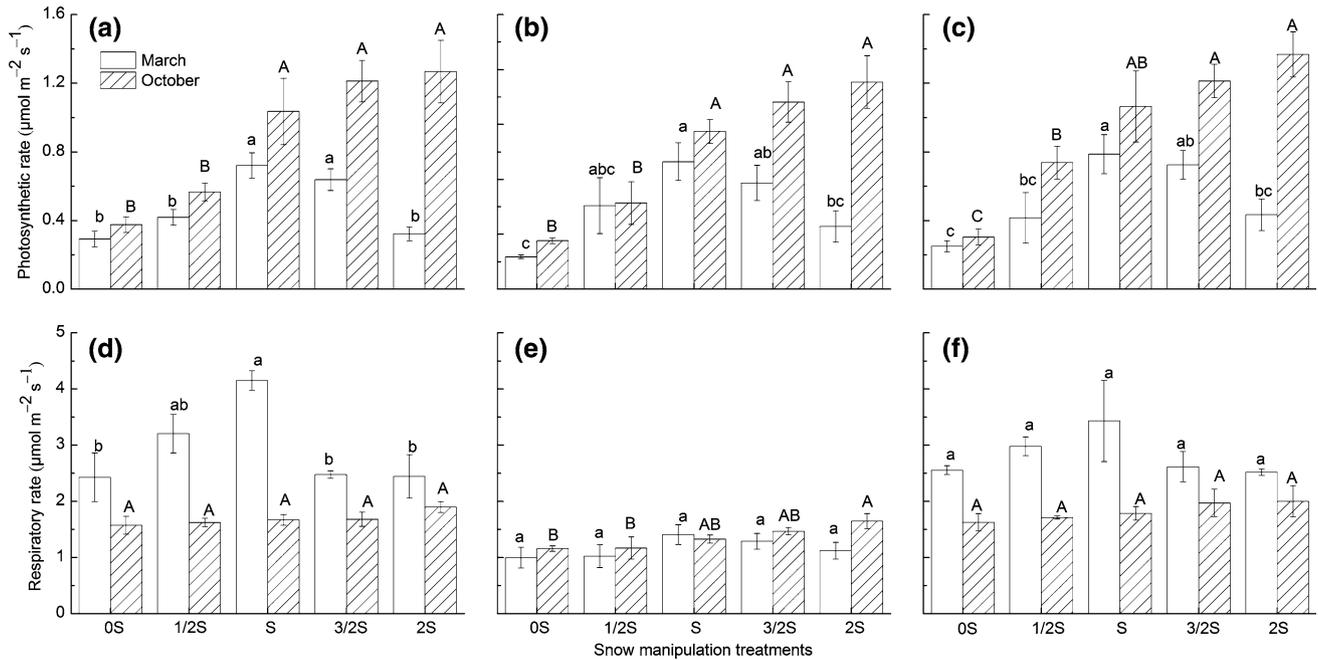
**Fig. 3** Variation in the photosynthetic pigment content of lichen, algae, and moss crusts in March 2014 (after snow) and October 2014 (the growing period) after the 0S, 1/2S, S, 3/2S, and 2S

treatments. Data are mean values  $\pm$  standard deviation ( $N = 3$ ). Different letters between samples indicate significant differences using Duncan's test ( $P < 0.05$ )

changes in winter snowfall would affect the photosynthesis and respiration of the main types of BSC in the Gurbantunggut Desert. Snowfall had a significant positive effect on the biomass accumulation of all three BSCs. There were also long-term impacts on photosynthetic C fixation and biomass accumulation in the snowfall treatments. Below, we consider the differences in the responses of the different BSCs to snowfall manipulation, the possible sources of these differences and the long-term impact of snowfall variation.

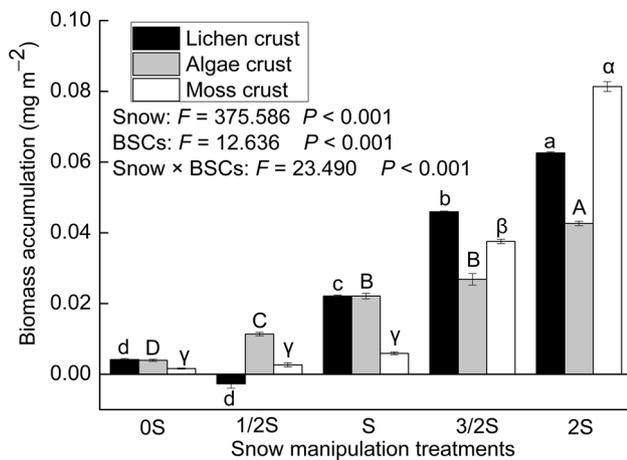
Moisture is the key abiotic factor for the growth and succession of BSCs in arid and semi-arid lands. Some studies have indicated that the structure and composition of BSCs are determined to a large extent by the precipitation patterns of desert regions, which then influences their photosynthetic and respiratory metabolism (Belnap et al. 2004; Sponseller 2007). Increased precipitation can produce significant changes in the structure and composition of the plant community at functional levels in harsh environmental conditions (Stevens et al. 2010). Moreover, the melting of snowfall

can change soil water content and help plant growth and development as a special form of precipitation (Wang et al. 2006). Our results showed that the water content of the sand beneath the three types of BSCs increased with an increase in the snow depth during March. This change might be the basis for changes in growth and metabolism of BSCs. For most poikilohydric plants (which are the main constituents of BSCs), there is physiological activity only when they grow under wet conditions (Grote et al. 2010; Lindo et al. 2013). The soil moisture content has previously been shown to differ between snow-covered and snow-free areas (Fassnacht et al. 2006). Plants in BSCs face water restrictions because of the dry conditions of the Gurbantunggut Desert. Timely snowmelt and the availability of water during the growing season are important factors regulating plant growth (Li et al. 2012). Our research showed that snowfall influenced the moisture content of sand below the crusts at depths of 0–2 cm and 2–5 cm in March, although there was no obvious change after one growing season (Fig. 1). This means that snowmelt



**Fig. 4** Variation in the net photosynthetic ( $P_n$ ) and respiratory ( $R_d$ ) rates of lichen (a and d), algae (b and e), and moss (c and f) crusts in March 2014 (after snow) and October 2014 (the growing period) after the 0S, 1/2S, S, 3/2S, and 2S treatments.

Data are mean values  $\pm$  standard deviation ( $N = 3$ ). Different letters between samples indicate significant differences using Duncan's test ( $P < 0.05$ ).



**Fig. 5** Relationships between biomass accumulation and the snow treatments for lichen, algae, and moss crusts at the end of the growing period. Data are mean values  $\pm$  standard deviation ( $N = 3$ ). Different letters between the samples indicate significant differences using Duncan's test ( $P < 0.05$ ). BSCs biological soil crusts

provided sufficient water for plant growth and prevented water limiting conditions during the snowmelt season.

Increasing or decreasing snow depth and soil water availability should have caused a change in water relations and photosynthesis based on established relationships between precipitation and plant production (Knapp and Smith 2001; Huxman et al. 2004). Previous studies reported complex results on relationships be-

tween plant photosynthesis or growth and the amount of snowfall manipulation, which includes positive correlations (Starr et al. 2008; Torp et al. 2010) and negative correlations (Lundell et al. 2010; Pattison and Welker 2014). We found that there were negative effects of both increased and decreased snow manipulation in March on the BSCs (Figs. 2, 3). There are two explanations for the decrease in photosynthetic physiological indices with snow manipulation. On the one hand, decreased snow depth might cause a decrease in soil moisture from snowmelt (Fig. 1), leading to drought stress in plants and reduced photosynthetic performance of plants (Schimel et al. 2004). On the other hand, increased snow depth might cause an increase in soil moisture from snowmelt (Fig. 1), leading to flood stress in plants and inhibition of photosynthesis (Perata et al. 2011). Our results demonstrated that there was a significant correlation between the ecophysiological parameters and the type of BSCs in March and October (Tables 1, 2). The differences in the responses of BSCs to snowfall might be partially attributed to differences in the species composition and morphological characteristics of the photosynthetic organisms forming BSCs. Each of these organisms has a coordinated suite of anatomical and physiological mechanisms that facilitate growth in arid and semi-arid environments (Zhang and Zhang 2014). The algae crusts in the Gurbantunggut desert were dominated by the cyanobacterium *Microcoleus vaginatus*, lichen crusts were dominated by *Collema tenax* (with *Psora decipiens*, *Xanthoria elegans*, *Acarospora strigata* and *Lecanora argopholis* also commonly present), and

moss crusts were dominated by *Syntrichia caninervis*, with *Crossidium squamiferum* and *Bryum argenteum* also present (Zhang et al. 2009; Zhang and Zhang 2014). Thus, differences in the species composition of BSCs are a likely basis for the differences in the responses to snowfall. Additionally, we found that a decrease/increase in the winter snow depth and the associated soil water content affected photosynthesis and respiration processes in all three BSCs, as shown by the net photosynthetic and respiratory rates in March (Fig. 4). Moisture is an important factor restricting the growth and development of poikilohydric species, with physiological activity only possible under wet conditions (Grote et al. 2010; Lindo et al. 2013). Soil moisture of BSCs will change in response to increased or decreased snow depth, leading to increased or decreased photosynthetic activity of plants (Perata et al. 2011). Once plants have recovered from inhibition by drought or flood stress, photosynthetic activity could be increased or decreased during March (Schimel et al. 2004; Leffler and Welker 2013). Our results implied that the respiration rate of the three BSCs increased with increased precipitation in March, but did not change in October (Fig. 4). The differences between March and October might be the result of variations in sand moisture, soil temperatures, and soil microbial activity (Buckeridge and Grogan 2008; Johansson et al. 2013). Johnson et al. (2012) reported that summer precipitation was more important for BSCs on dry land than snowmelt water in October. But equally important is that snowmelt provided sufficient water for plant growth in March (Figs. 1, 4), and plants can benefit from a deep snowpack that insulated plants and soil from freezing stress in winter (Elise et al. 2015).

Snow cover and snowmelt water directly or indirectly affect ecosystems, especially arid and semi-arid ecosystems, in different ways, and the influence is not only limited to the winter. Snowmelt can change the soil water content and promote plant growth and development as a special form of precipitation (Wang et al. 2006). Snowfall and cover is also a pre-condition for survival under harsh environmental conditions, such as those experienced in arid and semi-arid ecosystems. Snow cover can lead to a higher CO<sub>2</sub> flux, provide sufficient conditions for physiological activity, and sustain microbial activity and mineralization processes by increasing the soil temperature in winter (Rogers et al. 2011). Our results indicated that moisture content, photosynthesis and respiration of the three typical BSCs from the Gurbantunggut Desert changed after snowmelt (March 2014), and their biomass accumulation was affected by snowfall depth at the end of the growing period (October 2014). A deep snowpack has been shown to induce a high photosynthetic rate in plants (Leffler and Welker 2013) and lead to increased biomass accumulation. The increase in biomass will in turn alter photosynthetic C fixation. Although previous studies have reported that altered summer precipitation can have important effects on BSC C exchange process in the ecosystems of arid regions (Johnson et al. 2012; Ze-

likova et al. 2012; Angel and Conrad 2013; Drahorad et al. 2013; Miralles et al. 2013), and it is suggested that summer precipitation is more important for BSCs on dry land than snowmelt water in October (Johnson et al. 2012), the effects of changes in snowfall in arid regions on the photosynthetic C fixation of BSCs should not be ignored. At the same time, the biomass of the three types of BSC from the Gurbantunggut Desert did not increase during the early melting season (in March), but continued to increase in October. Similar results were found by Segawa et al. (2005) for the biomass of *Variovorax paradoxus*, which did not increase rapidly during the early melting season, but continued to increase from June until October.

Our data indicate that changes in winter snowfall changed the photosynthesis and respiration rates of the main types of BSCs in the Gurbantunggut Desert, leading to long-term impacts of altered snowfall on photosynthetic C fixation and biomass accumulation. The effects of increased/decreased snowfall on BSCs could have profound effects on the functioning of arid and semi-arid ecosystems. Biological soil crusts are the main contributor to the total C released by soil respiration (Castillo-Monroy et al. 2011), therefore our data provide a foundation for future studies to assess the potential effects of snowfall on the C sequestration of BSCs in arid and semi-arid regions.

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