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The influence of biological soil crusts on ^{15}N translocation in soil and vascular plant in a temperate desert of northwestern China

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Abstract

Aims

Desert ecosystems are often characterized by patchy distribution of vascular plants, with biological soil crusts (BSC) covering interplant spaces. However, few studies have comprehensively examined the linkage between BSC and vascular plants through nitrogen (N) or element translocation. The objective of this study was to evaluate the ecological roles of BSC on N translocation from soil to the dominant herb *Erodium oxyrrhynchum* Bieb. (Geraniaceae) in a temperate desert in China.

Methods

Isotopes (including ^{15}N-Glu, ^{15}N-NH_4Cl and ^{15}N-$NaNO_3$) were used as a tracer to detect translocation of N in two types of desert soil (BSC covered; bare) to the dominant herb *E. oxyrrhynchum*. Three different forms of ^{15}N-enriched N compounds were applied as a point source to small patches of BSC and to bare soil. And we measured isotopes (^{14}N and ^{15}N) and obtained the concentration of labeled-^{15}N in both vascular plants and soils at different distances from substrate application

Important Findings

Plants of *E. oxyrrhynchum* growing in BSC-covered plots accumulated more $\delta^{15}N$ than those growing in the bare soil. Similarly, soil from BSC-covered plots showed a higher concentration of labeled-N irrespective of form of isotope, than did the bare soil. The concentration of dissolved organic N (^{15}N-Glu) in *E. oxyrrhynchum* was higher than that of dissolved inorganic N (^{15}N-NH_4Cl and ^{15}N-$NaNO_3$). Soil covered by BSC also accumulated considerably more dissolved organic N than bare soil, whereas the dominant form of ^{15}N concentrated in bare soil was dissolved inorganic N. Correlation analysis showed that the concentration of labeled-N in plants was positively related to the concentration of labeled-N in soils and the N% recorded in *E. oxyrrhynchum*. Our study supports the hypothesis that BSC facilitates ^{15}N translocation in soils and vascular plants in a temperate desert of northwestern China.

Keywords: biological soil crusts, nitrogen translocation, *Erodium oxyrrhynchum*, temperate desert

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INTRODUCTION

Arid ecosystems are patch mosaics of both vascular plants and biological soil crusts (BSC), described respectively as 'islands of fertility' and 'mantles of fertility' (Schlesinger *et al.* 1996). BSC are common assemblages of lichens, fungi, cyanobacteria and mosses that colonize the soil surface, which can represent up to 70% of the living cover in these areas (Belnap and Lange 2001). These crusts are common in water-limited systems between widely spaced vascular plants (Belnap and Lange 2001), representing a physical barrier between soil and atmosphere (Belnap and Eldridge 2003). It has confirmed that BSC plays an important role in enhancing soil stability and fertility (Belnap and Harper 1995; Li *et al.* 2005), increasing the possibility of vascular plant colonization (Belnap and Eldridge 2003; Hawkes 2003), contributing to protect the

soil surface from wind and water erosion (Zhang *et al.* 2006) and affecting seed germination and plant growth (Godínez-Alvarez *et al.* 2012; Li *et al.* 2005). However, few studies have comprehensively examined the linkage between BSC and vascular plants through nutrient or element translocation. The contribution of BSC to N input in arid regions is rarely considered in studies on the biotic controls on N cycling and transformation in semi-arid ecosystems (Castillo-Monroy *et al.* 2010; Schlesinger *et al.* 1996). And the only studies have been carried out in arid and semi-arid ecosystems of Australia, USA and Spain (Delgado-Baquerizo *et al.* 2013; Eldridge and Greene 1994; Green *et al.* 2008). Little is known about N in interactions between BSC and vascular plants in temperate, low rainfall (<200 mm per annum) regions such as the deserts of central Asia.

Water is generally considered to be the most important determinant of the composition, diversity and productivity of plant species in semi-arid and arid ecosystems but this is closely followed by N (Martínez-Alcántara *et al.* 2012; Xia and Yan 2011). In arid regions, input rates of N from both the atmosphere and substrate are extremely low, and vegetation in these systems can be dependent on N fixed by BSC (Belnap 2002). N fixed or transformed by free-living soil microbes could provide abundant sources of N for plants (Harte and Kinzig 1993). Numerous studies have reported that the presence of BSC increases N content of surrounding soil by up to 200% (Harper and Belnap 2001) and that use of stable isotopes can demonstrate that BSC can be the principal source of N for desert plants and desert soils (Evans and Belnap 1999). Microorganisms in BSC produce extracellular mucilaginous polysaccharides and these, together with fungal hyphae, aggregate surface soil particles, absorb water and add organic matter to the surface layers of soil (Evans and Johansen 1999). The soil microbial community and the interactions between soil microorganisms and plants effectively control N cycling in ecosystems (Knops *et al.* 2002). Hawkes (2003) reported that soil microorganisms act as sources and sinks of nutrients and are crucial to the analysis of N transformations in soil. Later, Whiteside *et al.* (2009) using fluorescent nanoscale semiconductors, demonstrated direct uptake and translocation of quantum dot-labeled N through fungal hyphae to roots and shoots of the annual grass *Poa annua* L. Although these studies have demonstrated the role of fungi in N uptake and transfer to vascular plants, reports on the effects these organisms have on the status of plant N are quite controversial (Delgado-Baquerizo *et al.* 2013; Hawkes 2003).

The contribution of BSC to soil fertility has been demonstrated in disturbed areas where loss of BSC was found to decrease soil N content by 25–75% (Evans and Belnap 1999) and also decrease the N and micronutrient content of nearby plants (Harper and Belnap 2001). In this study, our objective was to evaluate the ecological role of BSC on N translocation in soils and plants in the Gurbantunggut Desert, northwestern China. To do this, we quantified the spatial variability in concentration of ^{15}N in plants and soils collected from BSC and bare soil plots. To better understand the form of N absorbed and used by plants and retained by soil in both types of plots, we used three different forms of ^{15}N-enriched N compounds as a tracer. These isotopes were injected into the BSC and into the bare soil to observe the preference of plant and soils to organic and inorganic N. Given the role of BSC as N fixers and as a sink for N (Belnap 2002), we hypothesized that more ^{15}N would be accumulated in the soil and vascular plant samples from plots covered with BSC than from bare soil plots.

MATERIALS AND METHODS

Site description

The Gurbantunggut Desert is located in the center of the Junggar Basin (44°11′–46°20′N, 84°31′–90°00′E) in the Xinjiang Uygur Autonomous Region of northwestern China. It is the largest fixed and semi-fixed desert in China, with an area of 4.88×10^4 km^2. The Himalayan Range effectively blocks moist Indian Ocean air currents from reaching the area, resulting in the vast expanse of arid terrain. Our experiment was conducted in the southern part of the Gurbantunggut Desert (44°87′N, 87°82′E). Mean annual precipitation of 79.5 mm is predominantly in spring; mean potential annual evaporation is 2606.6 mm. Mean annual temperature is 7.26°C. Such a temporal allocation pattern of water and heat creates a favorable condition for the growth and development of ephemeral plants (Zhang and Chen 2002). In the study area, both ephemeral plants and ephemeroids grow vigorously in spring and early summer after snowmelt and rain, resulting in up to 40% increase in vegetation cover. Desert plants *Ephedra distachya*, *Erodium oxyrrhynchum*, *Alyssum linifolium*, *Hyalea pulchella* and *Malcolmia africana* mainly appear in the interdune and middle to lower slopes of dunes. BSC are widely distributed on soil between vascular plants, usually with a cover of ~40% (Zhang *et al.* 2007). Lichen-dominated crusts are usually present in the interdune areas, on the lower and middle slopes of dunes but are absent from the crests of the highest dunes. The most common lichens include *Collema tenex*, *Psora decipiens*, *Xanthoria elegans*, *Acarospora strigata* and *Lecanora argopholis*. Other less common lichens include *Diploschistes muscorum*, *Heppia lutosa*, *Catapyrenium sp*. and *Caloplaca songoricum* (Zhang *et al.* 2007).

Arrangement of field plots

In May 2013, 18 circular plots each with a radius of 1.0 m were established in interdune areas, at a minimum distance of 10 m from each other. Nine were centered on lichen-dominated BSC; the remaining nine were centered on bare soil. All plots marking were done from outside the plot perimeters to avoid disturbance. Relevant soil properties of both types of plots (BSC-covered and bare soil) were given in Table 1. *Erodium oxyrrhynchum*, the dominant species within the herbaceous plant community in this desert in spring, was selected as the target species for measurement of the differences in the concentrations of labeled-N in vascular plants distributed throughout BSC-covered soils and bare soils.

Table 1: main soil characteristics of crust covered soil and bare soil (n = 5, mean ± standard deviation)

	0–5 cm		5–10 cm		10–15 cm	
	BSC	Bare soil	BSC	Bare soil	BSC	Bare soil
pH	7.4 ± 0.2	7.2 ± 0.1	7.2 ± 0.3	7.1 ± 0.4	7.1 ± 0.2	7.1 ± 0.4
Silt (%)	18.26 ± 1.49	16.16 ± 1.34	16.69 ± 1.27	15.11 ± 0.22	16.16 ± 1.24	15.22 ± 0.31
Clay (%)	2.63 ± 0.49	2.42 ± 0.32	2.45 ± 0.45	2.52 ± 0.35	2.64 ± 0.25	2.33 ± 0.47
Sand (%)	79.11 ± 1.02	81.41 ± 1.66	80.85 ± 1.42	82.36 ± 0.37	81.20 ± 1.06	82.44 ± 0.26
Organic matter	5.41 ± 0.17**	3.44 ± 0.63	3.02 ± 0.17**	1.48 ± 0.13	1.88 ± 0.24	1.43 ± 0.18
Total N	0.137 ± 0.063*	0.101 ± 0.022	0.081 ± 0.006*	0.067 ± 0.009	0.073 ± 0.004*	0.053 ± 0.007
C:N	13.41 ± 1.52	15.74 ± 6.34	11.81 ± 0.68	12.88 ± 0.62	10.12 ± 2.02	12.16 ± 3.65
NH_4^+–N	18.27 ± 2.31	14.73 ± 0.91	15.71 ± 1.80	13.60 ± 3.53	13.20 ± 1.42	11.03 ± 1.64
NO_3^-–N	36.43 ± 3.07*	22.00 ± 4.84	32.13 ± 2.45*	20.26 ± 3.94	25.70 ± 3.85*	16.76 ± 2.02
Dissolved organic N	26.26 ± 3.89*	16.23 ± 2.31	22.20 ± 1.44*	14.73 ± 1.96	20.43 ± 4.38	13.13 ± 1.61

Organic matter and total N were measured in units of $g \cdot kg^{-1}$; NH_4^+–N, NO_3^-–N and dissolved organic N were measured in units of $mg \cdot kg^{-1}$. Data are expressed as mean ± standard deviation (n = 5).
Significant differences between plots in the initial concentrations of the soil variables are as follows: $^*P < 0.05$ and $^{**}P < 0.01$.

^{15}N addition treatment

On 9 May 2013, three N-isotope forms (^{15}N-Glu, ^{15}N-NH_4Cl and ^{15}N-$NaNO_3$) were added as N tracers to the surface of both BSC-covered plots and bare soil plots. Each form of N isotope was applied to three randomly selected circular plots in each of the two areas, resulting in three BSC-centered plots and three bare soil-centered plots for each of the three treatments (^{15}N-Glu, ^{15}N-NH_4Cl and ^{15}N-$NaNO_3$ application), making a total of 18 plots.

The nitrate and ammonium applications were prepared as follows: 0.58 g of 99 atom% ^{15}N-$NaNO_3$ and 0.37 g of 99 atom% ^{15}N-NH_4Cl, respectively, were dissolved in 10 ml of deionized water to make a 0.68 M solutions. Then, 1.25 ml of the nitrate solution (total ^{15}N/site = 12.5 mg) was applied to the centre of each of six plots (three BSC-centered plots and three bare soil-centered plots) as a fine spray using an atomizer, ~3 cm in diameter. The ammonium applications to the other six plots were the same as nitrate applications. Glutamate was prepared using the following procedure: 1.0 g of ^{15}N-glutamic acid (99 atom% ^{15}N) was dissolved in 40 ml of deionized water (0.34 M). A 5-ml solution (total ^{15}N/site = 12.5 mg) was applied to each of the rest six plots as described previously for nitrate and ammonium applications. In each process, care was taken to ensure all labeled isotope was applied to the soil surface within an area ~3 cm in diameter in each BSC and bare soil plot (Green *et al.* 2008).

The N isotopes were added to the plots at midday, in full sunlight, when surface temperatures were ~25°C. There was no precipitation recorded during the experiment. The plots were carefully monitored and there were no incursions by animals, no predation by insects or detritivores and no moisture condensation.

Sample collection

Green *et al.* (2008) reported that, during peak growth periods, point sources of organic and inorganic N can disperse through BSC at rates of up to 1 m per day. So in this study, plant and soil samples were collected from each BSC plot and each bare soil plot ~24 h after the addition of labeled-N. To avoid disturbance, the centers of each plot where the tracers had been applied were not sampled. Thus, no sample was collected within a 15 cm radius from the central application point. Plant and soil samples were collected along concentric circles marking 20, 40, 60 and 100-cm radii from the central application point of each plot. All the plants (one circle would typically have four or five stems) from each concentric circle were collected and combined to produce one sample, thus providing three replicates from the three plots for each treatment. The entire plants, including roots, shoots and leaves, were sampled. Soil samples were randomly collected at three depths (0–5, 5–10 and 10–15 cm) along the same concentric circles marking the 20-, 40-, 60- and 100-cm radii from the central application point. Soil samples were extracted from the ground using a circular soil corer (diameter, 5 cm; height, 5 cm). Besides sampling plants and soils from ^{15}N-applied plots, samples from BSC and bare soil plots without ^{15}N application were also collected to examine the background δ^{15}N and N %. The plot design showing pattern of plant and soil sampling points was given in Fig. 1.

Sample analyses

Plant and soil samples were placed in individual plastic bags and returned to the laboratory where they were dried at 60°C for 48 h then pounded using a rolling grinder. Approximately 50–100 mg from each sample was placed in tin capsules and analyzed for ^{15}N signals using dry combustion gas chromatography–isotope ratio mass spectrometry (Thermo Finnigan Delta Plus XP, Flash EA 1112) at the Stable Isotope Laboratory, Institute of Botany, Chinese Academy of Sciences, Beijing, China. The level of δ^{15}N in samples collected 24 h after application and within 100-cm radius of the center of each plot was determined. Analyses of selected properties of BSC-covered soil and bare soil, and plant N content (N %) were conducted at the central laboratory, Xinjiang Institute of Ecology and

Geography, Chinese Academy of Sciences, Urumqi, China, using high-temperature combustion (ThermoQuest CE Instruments NC2100 Elemental Analyzer).

Isotope ratios are expressed in δ-notation as parts per thousand (‰):

$$\delta^{15}\mathrm{N}(‰) = [(\mathrm{R}_{sample} / \mathrm{R}_{standard}) \quad 1] \times 1000$$

where R is the ratio of $^{15}N/^{14}N$ (atom%) of the sample and standard, and the standard is atmospheric N_2 (Lajtha and Michener 1994). The $\delta^{15}N$ value (‰) of atmospheric N_2 (0.0036764 ^{15}N abundance) is the standard for $\delta^{15}N$ analysis.

The background $\delta^{15}N$ in plant and soils from our plots was extremely low, with average values ranging from ~0.05 to 0.3 ‰. And the ending values of $\delta^{15}N$ shown in Figs 2 and 3 were labeled $\delta^{15}N$ (calculated as: $\delta^{15}N_{labeled} = \delta^{15}N_{sample} \quad \delta^{15}N_{background}$).

Statistical analyses

All statistical analyses were conducted using SPSS 17.0 software (SPSS, Chicago, IL, USA). The differences in soil properties and the $\delta^{15}N$ values for plant and soil between BSC and bare soil plots were compared using multiple comparison and one-way analysis of variance procedures. The least significant difference test (at $P < 0.05$) was used to compare means of soil properties

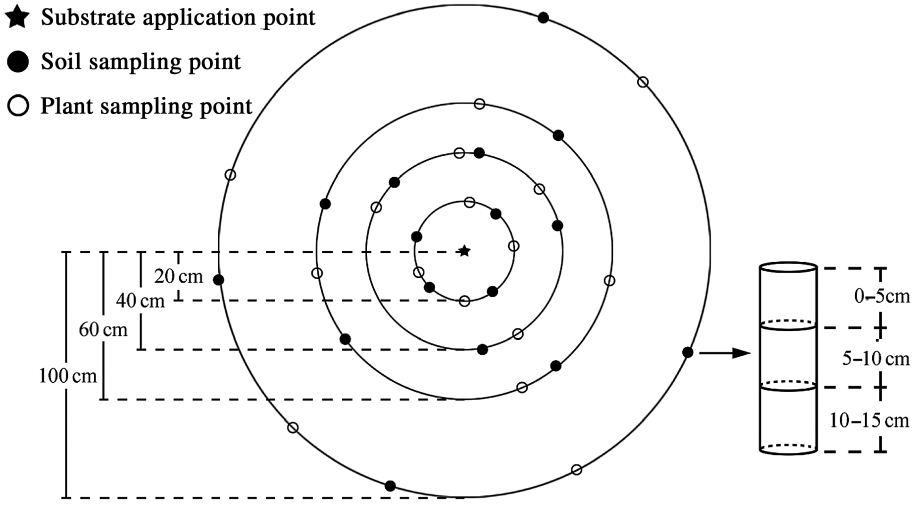

Figure 1: mode pattern for plant and soil sampling.

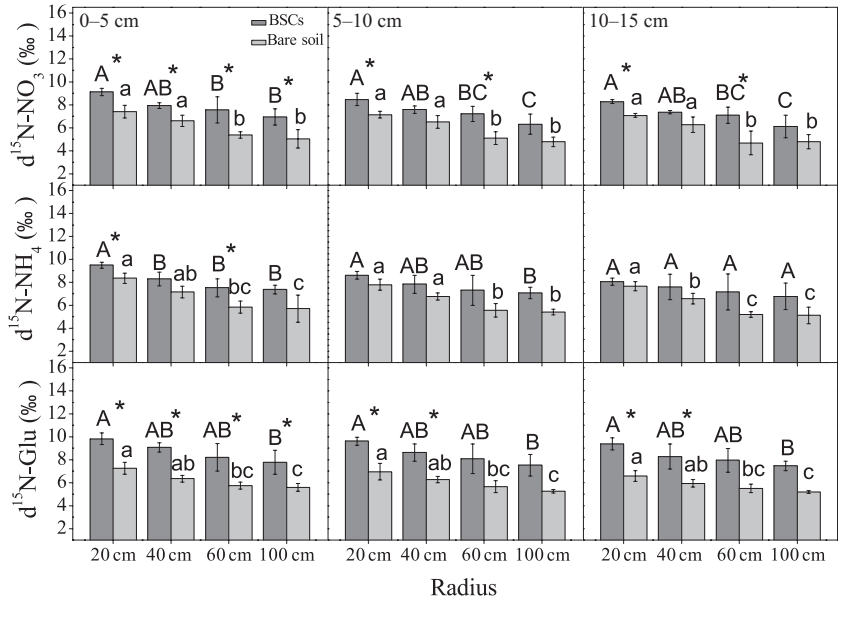

Figure 2: concentration of $\delta^{15}N$-$NaNO_3$, $\delta^{15}N$-NH_4Cl and $\delta^{15}N$-Glu in soil samples from BSC covered and from bare soil plots. Asterisks indicate significant pairwise differences between BSC and bare soil plots (*$P < 0.05$). Uppercase and lowercase letters represent statistical differences among soil samples at four radii (20, 40, 60 and 100 cm) used for plant samples at both locations. The letters indicate the differences for $P < 0.05$. Vertical bars represent ±standard deviation ($n = 3$).

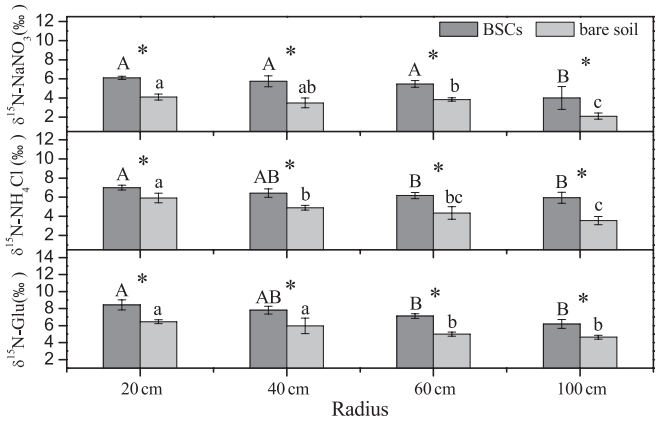

Figure 3: concentration of δ^{15}N-$NaNO_3$, δ^{15}N-NH_4Cl and δ^{15}N-Glu in plant samples from BSC covered and from bare soil plots. Asterisks indicate significant pairwise differences between plants grown in BSC and bare soil microsites (*$P < 0.05$). Uppercase and lowercase letters represent the differences at four radii (20, 40, 60 and 100 cm) used for plant samples at both locations. The letters indicate the differences for $P < 0.05$. Vertical bars represent ±standard deviation ($n = 3$).

and the δ^{15}N values. Simple linear regression and correlation analysis were performed to identify the relationships between plant δ^{15}N and soil δ^{15}N, moreover, plant δ^{15}N and plant N%. Pearson correlation coefficient and two-tailed test were used to distinguish the correlation and significant differences.

RESULTS

Spatial variation of ^{15}N concentration in soils

In general, the δ^{15}N values for soil samples from BSC-covered plots were greater than those from bare soil plots (Table 2, $P < 0.01$). In both BSC-covered plots and bare soil plots, the δ^{15}N signals declined both with increase in horizontal distance from the central application points and with greater depth (Fig. 2). In the vertical translocation, soil δ^{15}N varied widely in the three soil layers. The value of δ^{15}N for soil from 0 to 5 cm was always the highest among the three depths in both BSC-covered and bare soil plots (Fig. 2). The depth significantly affected the value of δ^{15}N for ^{15}N-$NaNO_3$, ^{15}N-NH_4Cl and ^{15}N-Glu ($P = 0.013$, 0.002 and 0.031, respectively). The presence of BSC appears to facilitate the ^{15}N translocation and concentration in the top 0–5 cm soil layer and also to enable horizontal movement of ^{15}N across the plots, up to 100 cm from the point of N application. The effects of BSC on the δ^{15}N translocation in soils at greater depths and distances from N application points were not always significant (Fig. 2). Different levels of substrate enrichment (^{15}N-$NaNO_3$, ^{15}N-NH_4Cl and ^{15}N-Glu) were also observed between BSC-covered soil and bare soil. The concentration of ^{15}N-Glu was higher than that of either ^{15}N-NH_4Cl or ^{15}N-$NaNO_3$ in BSC-covered soil. In contrast, soil samples from bare soil plots were enriched with more ^{15}N-$NaNO_3$ than ^{15}N-NH_4Cl or ^{15}N-Glu (Fig. 2). BSC had the least effect on the concentration and diffusion of ^{15}N-NH_4Cl compared to the effect on ^{15}N-$NaNO_3$ and ^{15}N-Glu (Fig. 2). The interaction between soil surface type (whether BSC-covered or bare soil), radius (distance from central application point) and form of labeled-N (^{15}N-$NaNO_3$, ^{15}N-NH_4Cl and ^{15}N-Glu) did not significantly affect soil δ^{15}N (Fig. 2, $P > 0.05$).

Differences in ^{15}N uptake by plants

In both BSC-covered and bare soil plots, δ^{15}N signals in plants declined with increasing distance from the application points (Fig. 3). After 24 h, point sources of labeled-N were absorbed by plants up to 100 cm from the central application points. Variation within and between plots was high (Fig. 3, Table 2, $P < 0.01$). Plant δ^{15}N was differed significantly among three different forms of labeled-N (^{15}N-$NaNO_3$, ^{15}N-NH_4Cl and ^{15}N-Glu) (Table 2, $P < 0.01$). Plants from both BSC-covered plots and bare soil plots recorded higher levels of ^{15}N-Glu than either ^{15}N-NO_3 or ^{15}N-NH_4 (Fig. 3). The δ^{15}N values of all three forms of labeled-N in plants growing in BSC-covered plots were significantly higher than those of plants occurred in bare soil plots (Fig. 3, Table 2, $P < 0.01$). The interaction among soil surface type (whether BSC-covered or bare soil), radius (distance from central application point) and form of labeled-N (^{15}N-$NaNO_3$, ^{15}N-NH_4Cl and ^{15}N-Glu) did not significantly affect plant δ^{15}N (Fig. 3, $P > 0.05$).

Relationship of plant δ^{15}N with soil δ^{15}N and plant N%

In both BSC-covered and bare soil plots, the concentration of δ^{15}N in soil samples was greater than that found in plant samples (Figs 2 and 3). The mean δ^{15}N values in plants from BSC-covered plots and bare soil plots were 5.26‰ and 3.06‰, respectively ($n = 9$), with an average distance from point of application of 100 cm. By comparison, the mean δ^{15}N values in soil samples from the same plot were 7.92 ‰ and 6.11 ‰, respectively. The total ^{15}N translocated from the application points to the soil was much greater than that concentrated in plants from both BSC-covered and bare soil plots. Significant positive correlations were observed between plant δ^{15}N and soil δ^{15}N at all three soil layers. The δ^{15}N values of all three forms of labeled-N in plants were similarly affected by soil δ^{15}N; all were positively and strongly correlated with soil δ^{15}N (Fig. 4, $P < 0.01$). Positive correlations were also observed between plant δ^{15}N and plant N% (Fig. 5, $P < 0.01$), with the strongest relationship being a strong positive relationship between δ^{15}N-NH_4Cl and N% (Fig. 5, $R^2 = 0.408$).

DISCUSSION

Our results confirmed that BSC can facilitate N translocation both in soils and vascular plants, a finding similar to those recorded for other terrestrial systems (Green *et al.* 2008; Hawkes and Flechtner 2002). The acquisition by BSC of labeled-N applied to the crust surface demonstrates the ability of BSC to immobilize such sources (Hawkes 2003). In this

Table 2: multivariate analysis of variance results (*P* value) for the effects of site of application (*S*), nitrogen form (*N*), radius (*R*) and their interaction (*S* × *N*, *S* × *R*, *S* × *R* and *S* × *N* × *R*) on $\delta^{15}N$ in plants and soils

Factor	*df*	Plant $\delta^{15}N$	Soil $\delta^{15}N$ (0–5 cm)	Soil $\delta^{15}N$ (5–10 cm)	Soil $\delta^{15}N$ (10–15 cm)
S	1	267.43**	150.97**	135.99**	102.48**
N	2	120.12**	4.18	5.73**	3.76
R	3	49.94**	39.98**	35.69**	24.75**
S × *N*	2	1.48	4.21	5.21	4.57
S × *R*	3	0.79	0.29	0.81	1.19
N × *R*	6	0.78	0.36	0.27	0.34
S × *N* × *R*	6	0.99	0.34	0.41	0.69

Data are expressed as mean ± standard deviation ($n = 3$).
Variables are as follows: $^{**}P < 0.01$.

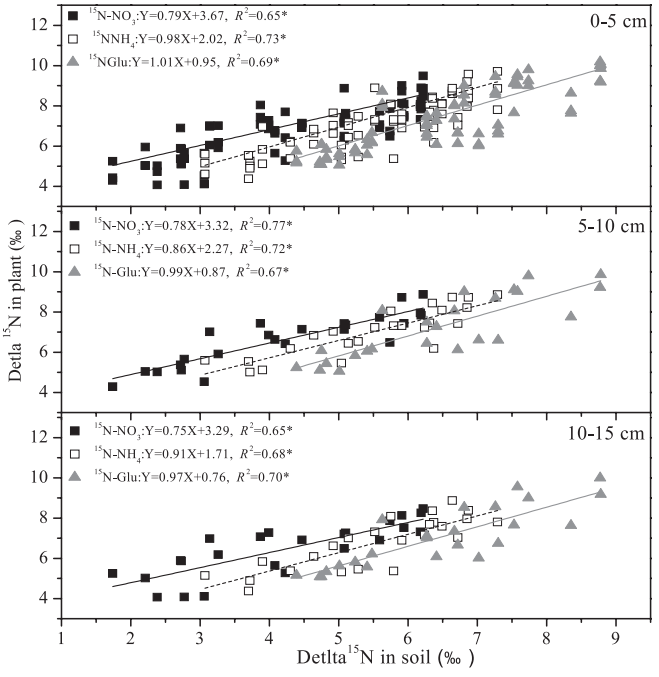

Figure 4: linear correlation between $\delta^{15}N$-$NaNO_3$, $\delta^{15}N$-NH_4Cl and $\delta^{15}N$-Glu in plant and in soil samples from three soil depths. The data from three experimental plots per treatment are plotted in each graph. Asterisks indicate the differences for $^{*}P < 0.05$. Data are expressed as mean ± standard deviation ($n = 3$).

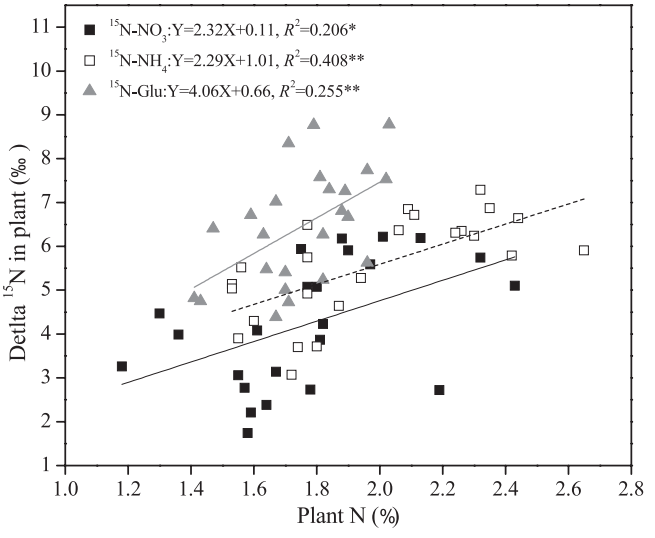

Figure 5: linear correlation between $\delta^{15}N$-$NaNO_3$, $\delta^{15}N$-NH_4Cl and $\delta^{15}N$-Glu in plants and N% in plants. The data from three experimental plots per treatment are plotted in each graph. Asterisks indicate the differences for $^{*}P < 0.05$ and $^{**}P < 0.01$. Data are expressed as mean ± standard deviation ($n = 3$).

process, capture of N by BSC organisms probably inhibits N loss from the system and ultimately benefits vascular plants. In our study, consideration of N leaching is irrelevant as no rainfall events occurred during the course of the experiment. The soil microbial community can also act as a buffer for N in other ecosystems. For example, in Californian hardwood rangelands characterized by an oak overstory and annual grass understory, microbial uptake of N during autumn rains prevented leaching losses (Herman *et al.* 2003). However, in the Gurbantunggut Desert, where N is severely limited, survival of all plants and microorganisms associated with BSC are profoundly dependent on optimum uptake of all available forms of N, including ^{15}N.

We recorded significant differences in the preliminary chemical properties (C, N, C:N ratio and dissolved organic N) between BSC and bare soils (Table 1). Given the high C:N ratios of both BSC and bare soils, heterotrophic bacteria and fungi were far more likely to be limited by N than C (Kaye and Hart 1997). Therefore, a higher value for $\delta^{15}N$ in soil compared to that found in plants is predictable. Once accumulated N is mineralized and held in the soil, and this increased availability has the potential to benefit vascular plants in the N-limited ecosystem. The N content in plant tissues of naturally N-limited ecosystem is usually closely correlated with soil N (Pérez-Soba *et al.* 1994). We found that plant $\delta^{15}N$ was positively correlated with soil $\delta^{15}N$ (Fig. 4), evidence of the importance of soil N to plant nutrition in an N-poor ecosystem. In contrast, both in BSC and in bare soil plots, the concentration of $\delta^{15}N$ in soil was greater than that found in plant samples (Figs 2 and 3). In short-term studies,

the higher levels of the N isotope recorded in soils is explained by the much greater affinity of soils for the isotope and by the much greater surface area-to-volume ratios of soils (Schimel and Bennett 2004).

Levels of $\delta^{15}N$ in both plants and soil were higher from BSC-covered plots than from bare soil plots (Figs 2 and 3), implying that the existence of BSC may facilitate ^{15}N translocation in soils and N uptake by plants. Our results also showed that there was a significant difference between plant $\delta^{15}N$ in BSC-covered plots and plant $\delta^{15}N$ in bare soil plots along four comparative radii, even when levels of soil $\delta^{15}N$ were the same at the identical sampling points (Figs 2 and 3), indicating that not all N is translocated from soil to plant. There may be other pathways to explain this translocation capacity. Recent studies on the contribution of BSC to ecosystem productivity have suggested that vascular plant centred 'islands of fertility' and BSC 'mantles of fertility' may be functionally integrated by a common fungal network (Green *et al.* 2008; Schlesinger *et al.* 1996), which may be responsible for the higher rates of N translocation in BSC than in bare soil (Castillo-Monroy *et al.* 2010; Hawkes 2003). In this study, N-isotope solution could infiltrate into a depth of 2.5–3 cm and a horizontal distance ~3 cm, where few fine roots could be found. The roots of *E. oxyrrhynchum* in this growing period (9 May) mainly distributed in the depth of 5–10 cm. In addition, the distance between plant individuals was so far that the roots barely connected each other. Specially, plant-to-plant transfer of ^{15}N via roots was unlikely in our study. Thus, fungi, to some extent, play an important role in ^{15}N translocation in soils and from soils to plants. Studies have proved that primary producers (e.g. grasses and BSC) have extensive symbioses with mycorrhizal fungi in arid area (Barrow 2003; Johnson *et al.* 2006). These symbioses enhance resistance to desiccation during dry periods and act as networks for water and nutrient transport during pulses of water availability (Allen 2007). There is an extensive literature relating to N translocation by fungal hyphae, including dark-septate endophytes, and a variety of saprotrophic and parasitic fungi (Barrow 2003; Corkidi *et al.* 2002; Green *et al.* 2008; Johnson *et al.* 2006).

Increasingly, studies of biogeochemistry and fungal communities support the hypothesis that patch mosaics of BSC and grass tussocks in semi-arid grasslands are functionally integrated by fungal networks (Maestre *et al.* 2011). Fungi are a key component of BSC of the Gurbantunggut Desert so their role in translocation of N to vascular plants should not be underestimated. On the other hand, plant $\delta^{15}N$ correlated positively with plant N%, and plant N% in BSC-covered site was higher than that in the bare soil (Fig. 5). Higher leaf N content results in strong positive correlation between photosynthesis and leaf N content for many C3 and C4 species (Connor *et al.* 1993) and up to 75% of leaf nitrogen is found in chloroplasts (Hak *et al.* 1993). Thus, higher leaf N content is reflected in increased chlorophyll content and Rubisco activity, with corresponding higher rates of photosynthesis with the potential to augment uptake of ^{15}N from crusted soil (Verhoeven *et al.* 1997).

We recorded uptake of both organic and inorganic ^{15}N by *E. oxyrrhynchum*; however, levels of ^{15}N originating from the organic source (^{15}N-Glu) were much higher than those from the inorganic sources (^{15}N-NH_4Cl and ^{15}N-$NaNO_3$; Fig. 2). Our findings were consistent with that found by Öhlund and Näsholm (2001), which showed uptake rate of NH_4^+ and NO_3^- seem to be decreased more than rates of uptake of amino acids when several N sources are present simultaneously. This study also provided information regarding the capacities of BSC-covered soils and bare soils to translocate various N forms from the environment (Fig. 3). Availability of soil N is the principal factor controlling plant N uptake (Jones and Kielland 2002) and the spatial distribution of ^{15}N in soil is also considered in the context of plant N uptake because soils are highly heterogeneous with respect to nutrients available to plants (Augustine and Frank 2001). Intact lichens can directly absorb inorganic NH_4^+–N and NO_3^-–N (Gaio-Oliveira *et al.* 2005), and some have the capacity for organic N uptake (Dahlman *et al.* 2004). We found the ^{15}N-amino acid was the dominant form of N in BSC, but bare soil appears to access to ^{15}N-NH_4 and ^{15}N-NO_3 (Fig. 3) more readily. Our results suggested that amino acid uptake was active for lichen-dominated BSC. It is known that BSC could synthesize polysaccharide and anionic fractions of the polysaccharide increase concentration of cation (Parker *et al.* 1996; Reddy *et al.* 1996). For the NH_4^+ and NO_3^-, NH_4^+ can be held by soils through bonding to the overall negatively charged colloids and then more mobile NO_3^- may leach through soil. Thus, BSC-covered soils concentrated more ^{15}N-NH_4 than ^{15}N-NO_3 in this study. It indicated that the performance of cations and anions in soils might be related to the specific translocation of ^{15}N. Therefore, variation in N transfer capacity of soils could thus be dependent on either a difference in N acquisition strategies (Lang *et al.* 1976; Valladares and Sancho 2000), and/or even the soil bonding ability to cation or anion (Parker *et al.* 1996; Reddy *et al.* 1996).

CONCLUSIONS

The function of the BSC in N translocation among the plant patches is crucial for the ecological evaluation of their functions. N translocation was strongly affected by BSC; thus, the plants and soils were more enriched with ^{15}N for isotope injections made into crusts rather than into bare soils. This study supported the assumption that the symbiotic fungal network in BSC can facilitate ^{15}N translocation in soil and vascular plants in a temperate desert of northwestern China. However, more studies examining the various components of the soil microbial community and their interactions of vascular plants will be necessary if we are to understand the regulation of vascular plant distributions and ecosystem processes.

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