Plant Interactions with Changes in Coverage of Biological Soil Crusts and Water Regime in Mu Us Sandland, China

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Abstract

Plant interactions greatly affect plant community structure. Dryland ecosystems are characterized by low amounts of unpredictable precipitation as well as by often having biological soil crusts (BSCs) on the soil surface. In dryland plant communities, plants interact mostly as they compete for water resources, and the direction and intensity of plant interaction varies as a function of the temporal fluctuation in water availability. Since BSCs influence water redistribution to some extent, a greenhouse experiment was conducted to test the hypothesis that the intensity and direction of plant interactions in a dryland plant community can be modified by BSCs. In the experiment, 14 combinations of four plant species (Artemisia ordosica, Artemisia sphaerocephala, Chloris virgata and Setaria viridis) were subjected to three levels of coverage of BSCs and three levels of water supply. The results show that: 1) BSCs affected plant interaction intensity for the four plant species: a 100% coverage of BSCs significantly reduced the intensity of competition between neighboring plants, while it was highest with a 50% coverage of BSCs in combination with the target species of A. sphaerocephala and C. virgata; 2) effects of the coverage of BSCs on plant interactions were modified by water regime when the target species were C. virgata and S. viridis; 3) plant interactions were species-specific. In conclusion, the percent coverage of BSCs affected plant interactions, and the effects were species-specific and could be modified by water regimes. Further studies should focus on effects of the coverage of BSCs on plant-soil hydrological processes.

Introduction

Plant interactions can greatly affect plant community structure. Dryland ecosystems are characterized by low amounts of unpredictable precipitation as well as by often having biological soil crusts (BSCs) on the soil surface. In dryland plant communities, plants interact mostly as they compete for water resources, and the direction and intensity of plant interaction varies as a function of the temporal fluctuation in water availability. Since BSCs influence water redistribution to some extent, a greenhouse experiment was conducted to test the hypothesis that the intensity and direction of plant interactions in a dryland plant community can be modified by BSCs. In the experiment, 14 combinations of four plant species were subjected to three levels of percent BSCs coverage and three levels of water supply. The results show that: 1) BSCs affected plant interaction intensity for the four plant species: a 100% coverage of BSCs significantly reduced the intensity of competition between neighboring plants, while it was highest with a 50% coverage of BSCs in combination with the target species of A. sphaerocephala and C. virgata; 2) effects of the coverage of BSCs on plant interactions were modified by water regime when the target species were C. virgata and S. viridis; 3) plant interactions were species-specific. In conclusion, the percent coverage of BSCs affected plant interactions, and the effects were species-specific and could be modified by water regimes. Further studies should focus on effects of the coverage of BSCs on plant-soil hydrological processes.

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**Materials and Methods**

**Study site**

We conducted a greenhouse experiment at the Ordos Sandland Ecological Station (OSES) (39°02′N, 109°21′E), Institute of Botany, Chinese Academy of Sciences, located in the Mu Us Sandland, China. This semiarid area has a typical continental climate with a mean annual precipitation of ca. 300 mm, occurring mostly (60–70%) between July and September. The annual mean temperature is 6.2–8.5°C, with monthly means of 22°C in July and –1°C in January [25–27].

**Study species**

*Artemisia ordosica* Krasch. (Asteraceae) is a dominant shrub species in the fixed and semi-fixed sand dunes with plumose, linearly lobate leaves. Its branch roots are mainly distributed in the upper 30 cm of the sand soil profile, while its primary roots may reach 1–3 m deep [28]; *Artemisia sphaerocephala* Krasch. (Asteraceae) is one of the most important pioneer plants on the moving and semi-fixed sand dunes, with strong resistance to drought, cold and saline-alkaline soil conditions [29]. *Chloris virgata* Swartz (Poaceae) and *Setaria viridis* (L.) Beauv. (Poaceae) are annual grass species, widely distributed in roadides, abandoned land and sandy soils.

Seeds for the experiment were collected near the OSES as they matured in September 2007 for *C. virgata* and *S. viridis* and in November 2007 for *A. ordosica* and *A. sphaerocephala*.

**Experimental design and measurements**

A total of 882 containers (15 cm diameter and 13 cm height) were prepared; each was filled with 1,100 ml sand which had been collected near the OSES, and sieved to remove the soil’s seed bank. We planted 5–10 seeds of the four species in these pots on June 12, 2008. Fifteen days later, we selected similar sized seedlings for our experiment and removed any large or small plants. Fourteen species combinations were set up as follows: four had a single seedling of one of the four test species in one pot, four had two seedlings of one of the test species in one pot, and the other six combinations had two seedlings, with one seedling of each of two different species in one pot. For each of these 14 species combinations, three levels of water supply and three levels of BSCs coverage were set up for a total of 126 treatment types, each with seven replicates or a grand total of 882 test pots. The three water levels were 80 ml, 120 ml and 160 ml every 3 days, and three levels of BSCs coverage were set up; each was filled with 1,100 ml sand which had been prepared; each was filled with 1,100 ml sand which had been collected near the OSES, and sieved to remove the soil’s seed bank. We planted 5–10 seeds of the four species in these pots on June 12, 2008. Fifteen days later, we selected similar sized seedlings for our experiment and removed any large or small plants. Fourteen species combinations were set up as follows: four had a single seedling of one of the four test species in one pot, four had two seedlings of one of the test species in one pot, and the other six combinations had two seedlings, with one seedling of each of two different species in one pot. For each of these 14 species combinations, three levels of water supply and three levels of BSCs coverage were set up for a total of 126 treatment types, each with seven replicates or a grand total of 882 test pots. The three water levels were 80 ml, 120 ml and 160 ml every 3 days, and three levels of BSCs coverage were set up; each was filled with 1,100 ml sand which had been

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**Table 1.** F-values of three-way ANOVA for effects of water regime (WR), percent coverage of biological soil crusts (BSCs), neighboring plants (NP) and their interactions on the relative interaction index (RII) of the target species of *Artemisia ordosica*, *Artemisia sphaerocephala*, *Chloris virgata* and *Setaria viridis*.

| Effects          | A. ordosica | A. sphaerocephala | C. virgata | S. viridis |
|------------------|-------------|-------------------|------------|------------|
|                  | F  | P  | F  | P  | F  | P  | F  | P  |
| WR               | 1.545 | 0.216 | 16.809 | <0.001 | 14.417 | <0.001 | 2.009 | 0.139 |
| BSCs             | 0.849 | 0.430 | 8.931 | <0.001 | 7.183 | <0.001 | 5.242 | 0.007 |
| NP               | 47.051 | <0.001 | 55.538 | <0.001 | 69.595 | <0.001 | 36.697 | <0.001 |
| WR * BSCs        | 1.318 | 0.265 | 5.467 | <0.001 | 9.608 | <0.001 | 6.925 | <0.001 |
| WR * NP          | 2.657 | 0.017 | 2.780 | 0.013 | 1.182 | 0.319 | 2.396 | 0.032 |
| BSCs * NP        | 2.185 | 0.047 | 2.630 | 0.019 | 1.641 | 0.139 | 0.862 | 0.525 |
| WR * BSCs * NP   | 1.655 | 0.081 | 1.777 | 0.056 | 0.759 | 0.692 | 3.700 | <0.001 |

P<0.05 is shown in boldface as significant.

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**Figure 1.** Relative interaction index (RII) (mean ± SE, n = 84) of *Artemisia ordosica*, *Artemisia sphaerocephala*, *Chloris virgata* and *Setaria viridis* in different treatments of biological soil crusts (BSCs) coverage. The plant interaction is (positive) facilitative as RII>0, (negative) competitive as RII<0 and neutral as RII=0. A greater absolute value of RII indicates a greater intensity of plant interaction. Different letters indicate significant difference at P<0.05.

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calculated an RII as a measure of plant interaction intensity and direction [24]. RII has strong mathematical and statistical properties, which overcome problems experienced with other frequently used indices [30], Equation (1) was used:

\[ RII = (B_w - B_o) / (B_w + B_o) \]  

(1)

where \( B_w \) is the biomass of target plant growing with a neighbor, noting that the neighbor plants may be either the same or a different species in our experiment, and the mean value is used while the neighbor plants belong to the same species; \( B_o \) is the biomass of a target plant growing in absence of inter- or intra-specific interactions, that is, the biomass of a single seedling planted by itself in our experiment.

The target plant is said to have experienced a (positive) facilitative effect from a neighbor plant if RII>0 and a (negative) competitive effect if RII<0. A greater absolute value of RII indicates a greater intensity of plant interaction.

Statistical analyses

Three-way ANOVA was used to test effects of BSCs coverage, water regime and neighboring plants on RII of each target plant species. Two-way ANOVA was used to analyze the effects of BSCs coverage and water regime on RII of each target plant species. The effects of percent BSCs coverage on RII, the effects of neighboring plants on RII, and the effects of percent BSCs coverage on biomass of each target plant species were analyzed separately using one-way ANOVA. Data were transformed to meet normality and homogeneity of ANOVA, if necessary. All statistical analyses were performed using SPSS 17.0 (SPSS, Chicago, IL, USA).

Results

Effects of BSCs coverage on plant interactions

The percent coverage of BSCs had a significant effect on RII value of three target species, \textit{A. sphaerocephala}, \textit{C. virgata} and \textit{S. viridis}, but not for \textit{A. ordosica} (Table 1). BSCs coverage did not change the direction of plant interactions between the four plant species studied here; however, RII was significantly influenced by coverage of BSCs for \textit{A. sphaerocephala} and \textit{C. virgata} (Figure 1). A coverage of BSCs of 100% significantly increased the RII value for \textit{A. sphaerocephala} as well for \textit{C. virgata} (Figure 1). Also, the RII value of \textit{C. virgata} was the lowest with 50% coverage of BSCs (Figure 1).

Interactive effect between BSCs coverage and water regime on plant interactions

Water regime and BSCs coverage had a significant interactive effect on the RII value for \textit{A. sphaerocephala}, \textit{C. virgata} and \textit{S. viridis} (Figure 2). Under low and high simulated rainfall conditions, BSCs coverage decreased the RII value for \textit{C. virgata}, while it significantly increased the RII value under medium simulated rainfall condition (Figure 2); BSCs coverage also decreased the RII value for \textit{S. viridis} under high simulated rainfall condition, but no significant effect was observed under low and medium simulated rainfall conditions. Furthermore, under medium simulated rainfall condition, neighbor plant had a facilitative effect for \textit{C. virgata} when BSCs coverage was 100% (RII>0) (Figure 2).

![Figure 2. Relative interaction index (RII) (mean ± SE, n = 28) of Artemisia ordosica, Artemisia sphaerocephala, Chloris virgata and Setaria viridis in different treatments of simulated rainfall and biological soil crusts (BSCs) coverage.](https://plosone.org/figures-transgenic.png)
Plant inter- and intra-specific interactions

For all the pairwise combinations of the four plant species studied here, neighbor plant species had significant influences on the RII value (Table 1), while they had no effect on plant interaction direction except for inter-specific interaction between plants of *C. virgata* and the neighbor plant *S. viridis* (Figure 3). As a neighbor species, *A. sphaerocephala* had a minor effect on all four target plant species as indicated by a higher RII value, while *C. virgata* intensified the competitive effect on the four target species except for *A. sphaerocephala* with the lowest RII value (Figure 3).

**Effect of BSCs coverage on plant biomass**

Coverage of BSCs significantly reduced total biomass in all four plant species grown without any neighbor plant (Figure 4). Biomass of *S. viridis* was smallest; while *C. virgata* had the highest biomass (Figure 4).

**Discussion**

BSCs coverage can play an important role in affecting individual plants at different stages of their life history, including seed germination [31,32], seedling survival and establishment [33,34] and plant growth [35]. Our results showed that percent BSCs coverage had a strong effect on plant interactions (Table 1). Percent BSCs coverage in our experiment did not benefit the growth of individual plants (Figure 4); instead it behaved like a stress factor. This might occur because BSCs sealed the soil surface, inhibiting plant root respiration and reducing water availability. Other studies have shown that stress factors can moderate inter-specific competition intensity [36,37]. This was partially supported by our results. In our experiment, RII of all four target plant species except *A. ordosica* were significantly affected by BSCs coverage (Table 1). High level of BSCs coverage generally reduced inter-specific competition levels for *A. sphaerocephala* while medium level of BSCs coverage had no significant effects (Figure 1). For the other species (*C. virgata*), effects of BSCs were more complex and did not fit well with the prediction that increased stress caused by BSCs would result in inter-specific interactions being more neutral and less negative. For example, inter-specific competition levels were greatest for *C. virgata* plants with medium BSCs coverage relative to high levels and no BSCs coverage (Figure 1).

Results showed that there were significant interactions between water regime and BSCs coverage when the target species were *A. sphaerocephala*, *C. virgata* or *S. viridis* (Table 1), and high level of BSCs coverage shifted the inter-specific competition to facilitation for *C. virgata* under medium simulated rainfall (Figure 2). Some of the results supported our hypothesis that the effects of BSCs coverage on plant interactions can be modified by water regime. Since BSCs coverage can promote water shortages [38] and increased abiotic stress may shift plant-plant interactions from competitive to facilitative [16,21], we suspect that annual variation in rainfall amount and variation in BSCs coverage have the potential to produce varied plant-plant interactions. BSCs coverage increased the intensity of competition from neighboring plants for *C. virgata* under both the low and high simulated rainfall conditions, but decreased competition under the medium simulated rainfall conditions (Figure 2). Our current study did not investigate the mechanism (such as plant-soil hydrological processes) of the effects of BSCs coverage.

Size-asymmetric competition appears likely in the experimental plantation [39], because target plant species’ competitive stress

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**Figure 3. Relative interaction index (RII) (mean ± SE, n = 63) of Artemisia ordosica, Artemisia sphaerocephala, Chloris virgata and Setaria viridis with different neighboring plant species.** The plant interaction is (positive) facilitative as RII> 0, (negative) competitive as RII< 0 and neutral as RII = 0. A greater absolute value of RII indicates a greater intensity of plant interaction. Different letters indicate significant difference at P< 0.05.

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appeared related to the size of the neighboring plants in our experiment. Neighboring plant species significantly influenced the neighboring plant’s competitive intensity or target plant species’ competitive stress, and plant interaction was species-specific (Figure 3). When the neighboring plant species was *S. viridis*, which had the smallest plant size due to its low rate of biomass accumulation during the experiment (Figure 4), all four target plant species had lower competitive stress (Figure 3). In contrast, pots with *C. virgata* consistently had negative effects on all target plant species (Figure 3). This strong competitive effect is likely the result of *C. virgata* having the largest plant size of species tested here (Figure 4). This result was consistent with previous research [40,41], and it fits with the belief that competition can be scaled to the grams of the competitor.

In conclusion, percent coverage of BSCs often had significant effect on plant interactions in our experiment. Also, this effect was species-specific and could be modified by simulated rainfall conditions. Further studies are needed to focus on plant-soil hydrological processes to show how BSCs coverage works ecologically.

**Author Contributions**

Conceived and designed the experiments: SG XY MD. Performed the experiments: SG QC XY. Analyzed the data: SG XY QC MD YH. Contributed reagents/materials/analysis tools: SG XY XP MD. Wrote the paper: SG XY MD. Manuscript revision: SG XY XP MD.

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