Effects of biological soil crusts on plant growth and nutrient dynamics in the Minqin oasis-desert ecotone, Northwest China (Postprint)

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Abstract

Biological soil crusts (BSCs) play crucial roles in improving soil fertility and promoting plants settlement and reproduction in arid areas. However, the specific effects of BSCs on growth status and nutrient accumulation of plants are still unclear in different arid areas. This study analyzed the effects of three different BSCs treatments (without crust (WC), intact crust (IC), and broken crust (BC)) on the growth, inorganic nutrient absorption, and organic solute synthesis of three typical desert plants (Grubovia dasyphylla (Fisch. & C. A. Mey.) Freitag & G. Kadereit, Nitraria tangutorum Bobrov, and Caragana koraiensis Kom.) in the Minqin desert-oasis ecotone of Northwest China. Results showed that the effects of three BSCs treatments on seed emergence and survival of three plants varied with seed types. The IC treatment significantly hindered the emergence and survival of seeds, while the BC treatment was more conducive to seed emergence and survival of plants. BSCs significantly promoted the growth of three plants, but their effects on plant growth varied at different stages of the growth. Briefly, the growth of G. dasyphylla was affected by BSCs in early stage, but the effects on the growth of G. dasyphylla significantly weakened in the middle and late stages. However, the growth of N. tangutorum and C. koraiensis only showed differences at the middle and late stages, with a significant enhancement in growth. Analysis of variance showed that BSCs, plant species, growth period, and their interactions had significant effects on the biomass and root: shoot ratio of three plants. BSC significantly affected the nutrients absorption and organic solute synthesis in plants. Specifically, BSCs significantly promoted nitrogen (N) absorption in plants and increased plant adaptability in N poor desert ecosystems, but had no significant effects on phosphorus (P) absorption. The effects of BSCs on inorganic nutrient absorption and organic solute synthesis in plants varied significantly among different plant species. The results suggest that BSCs have significant effects on the growth and nutrient accumulation of desert plants, which will provide theoretical basis for

exploring the effects of BSCs on desert plant diversity, biodiversity conservation, and ecosystem management measures in arid and semi-arid areas.

Full Text

Preamble

Effects of Biological Soil Crusts on Plant Growth and Nutrient Dynamics in the Minqin Oasis-Desert Ecotone, Northwest China

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Abstract

Biological soil crusts (BSCs) play crucial roles in improving soil fertility and promoting plant establishment and reproduction in arid areas. However, the specific effects of BSCs on growth status and nutrient accumulation in plants remain unclear across different arid regions. This study analyzed the effects of three BSC treatments (without crust (WC), intact crust (IC), and broken crust (BC)) on the growth, inorganic nutrient absorption, and organic solute synthesis of three typical desert plants (*Grubovia dasyphylla* (Fisch. & C. A. Mey.) Freitag & G. Kadereit, *Nitraria tangutorum* Bobrov, and *Caragana koraiensis* Kom.) in the Minqin desert-oasis ecotone of Northwest China. Results showed that the effects of BSC treatments on seed emergence and survival varied with seed type. The IC treatment significantly hindered emergence and survival, while the BC treatment was more conducive to seed emergence and plant survival. BSCs significantly promoted the growth of all three plants, though their effects varied across growth stages. Specifically, *G. dasyphylla* growth was affected by BSCs in the early stage, but these effects weakened significantly in middle and late stages. In contrast, *N. tangutorum* and *C. koraiensis* only showed growth differences in middle and late stages, with significant enhancement during this period. Analysis of variance revealed that BSCs, plant species, growth period, and their interactions significantly affected biomass and root:shoot ratio. BSCs significantly influenced nutrient absorption and organic solute synthesis, promoting nitrogen (N) uptake and increasing plant adaptability in N-poor desert ecosystems, but had no significant effects on phosphorus (P) absorption. The effects of BSCs on inorganic nutrient absorption and organic solute synthesis varied significantly among plant species. These results suggest that BSCs substantially affect desert plant growth and nutrient accumulation, providing a theoretical basis for exploring BSC effects on desert plant diversity, biodiversity conservation, and ecosystem management in arid and semi-arid regions.

Keywords: biological soil crusts (BSCs); desert oasis; desert plants; growth; nutrient accumulation

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1. Introduction

Drought is considered one of the major abiotic factors that inevitably causes desertification, coupled with decreased vegetation coverage and rapid soil degradation in many arid and semi-arid areas (Kang et al., 2020a). Therefore, desertification control is of great significance to countries with severe desertification hazards. Biological soil crusts (BSCs), known as "desert ecosystem engineers" and "desert biological carpets," play important roles in the restoration and stability maintenance of desert vegetation in arid and semi-arid areas worldwide, including polar regions (Gao et al., 2017; Lu et al., 2022). BSCs are complex systems composed of various microorganisms (including microalgae, cyanobacteria, bacteria, fungi, etc.) and soil particles, widely distributed in arid and semi-arid areas with coverage exceeding 40%, and accounting for up to 70% of surface area in some regions (Su et al., 2007). Based on successional stages, researchers have divided BSCs into algal crust, lichen crust, and moss crust (Belnap et al., 2016; Tang et al., 2018; Liu et al., 2020). The presence of BSCs contributes significantly to increasing nitrogen (N) nutrition in plants and improving N availability in soil and long-term response to N deposition in arid and semi-arid areas (Zhuang et al., 2015; Li et al., 2016; Tang et al., 2018; Rong et al., 2022). Additionally, BSCs serve as important carbon (C) sinks in terrestrial ecosystems because global soil algae absorb approximately 3.6 Pg C/a, equivalent to 6% of the net primary production of terrestrial vegetation. They also release CO_2 into the atmosphere through their own organic components and respiration, thereby affecting C cycling in drylands (Bi et al., 2022; Jassey et al., 2022; Li and Zhang, 2023).

Microbial communities, as important components of BSCs, play crucial roles in BSC formation, improvement of soil physicochemical properties, soil aggregate stability, and vegetation development (Li et al., 2017, 2018; Liu et al., 2020; Zhou et al., 2023). In particular, N-fixing microorganisms play significant roles in seed germination and plant growth, directly affecting these processes by accumulating C and N, and indirectly promoting plant growth and development by regulating soil environmental factors (Zhang et al., 2022). Due to their unique physio-ecological processes and strong adaptability to adversity, BSC formation and succession profoundly change the structural characteristics and physicochemical properties of the soil surface, including nutrient status, micro-topography, water and heat conditions, and rapid infiltration of precipitation and runoff, thereby affecting seed germination, seedling survival, and plant growth stages in arid and semi-arid areas (Li, 2012; Chen et al., 2017; Li et al., 2017, 2018; Luo et al., 2020; Nevins et al., 2021). Therefore, it is necessary to clarify and reveal the specific impact processes and mechanisms of BSCs on seed reproduction, germination, seedling survival, and plant growth in arid and semi-arid areas.

Controversies exist regarding the effects of BSCs on seed germination, survival, nutritional condition, and plant growth, which can be broadly summarized as inhibitory effects, promoting effects, and no significant effects (Li et al., 2002, 2005; Aguilar et al., 2005; Chen et al., 2008; Zhang and Nie, 2011; Wang et al., 2021). Currently, research on BSC effects on plant growth and nutrient absorption has concentrated in the Gurbantunggut Desert, Tengger Desert, Mu Us Sandy Land, and Loess Plateau in China. In the Gurbantunggut Desert, BSC effects on herb growth were highly time-dependent, significantly increasing plant N and potassium (K) absorption but showing no significant effect on phosphorus (P) absorption, with effects on other elements varying among plant species (Zhuang et al., 2017; Zhuang and Zhang, 2017). In the Tengger Desert, mutual complementary effects of BSCs and sand burial (BSCs inhibit seed germination, while sand burial improves soil water and nutrient availability to reduce BSC inhibitory effects) promoted establishment and overall recruitment success of annual herbs (Gao et al., 2023). BSCs had significantly different effects on seed germination and survival of different plant life forms in the Tengger Desert, playing ecological filtering roles in the invasion and settlement process of plant species (Song et al., 2022). In the Mu Us Sandy Land, BSCs played important roles in nutrient turnover of *Artemisia ordosica* Krasch communities, improving soil C and N availability and thus promoting nutrient absorption by *A. ordosica* communities (Sun et al., 2020). Moreover, BSC presence did not negatively affect water absorption by *A. ordosica* in the Mu Us Sandy Land. BSCs improved soil moisture under drought conditions and alleviated drought stress on *A. ordosica*, with the degree of effect on water absorption depending on BSC developmental stage and rainfall variation (Guan, 2023). In the Loess Plateau, BSCs positively affected seed emergence and plant growth through indirect effects, and seedling survival and growth were mainly affected by penetration resistance and soil chemical properties of BSCs (Zhang et al., 2024).

It should be noted that different results exist regarding BSC effects on plant growth and nutrient absorption across different arid areas. Although extensive studies have examined BSC effects on plant growth and nutrient accumulation in various arid regions, systematic studies on BSC effects on beneficial element accumulation and organic solute synthesis in plants, especially under different vegetation types and climates, remain insufficient. BSCs play important roles in protecting the ecological environment of the Minqin Desert (He et al., 2017). In recent years, studies on BSCs in the Minqin Desert have mainly focused on developmental stages, soil physicochemical properties, hydrological characteristics, soil seed banks, microorganisms, and precipitation infiltration (Li et al., 2002; Jia et al., 2003; Qiao et al., 2015; He et al., 2017; Tao et al., 2023). However, systematic studies on BSC effects on plant growth and nutrient accumulation are less well developed in the Minqin Desert, which is important for desert conservation.

Grubovia dasyphylla (Fisch. & C. A. Mey.) Freitag & G. Kadereit (Amaranthaceae), *Nitraria tangutorum* Bobrov (Zygophyllaceae), and *Caragana koraiensis* Kom. (legume) are three drought-tolerant plants widely distributed in the Minqin oasis-desert ecotone. However, the effects of BSCs on seedling growth and nutrient absorption of these three species have received limited attention.

In this study, we hypothesize that: (1) BSCs significantly hinder seed emergence and survival, but broken BSCs are more conducive to seed emergence and seedling survival; (2) BSCs can promote plant growth and increase biomass accumulation, with temporally variable effects; and (3) BSCs affect not only inorganic nutrient absorption from soil but also organic solute synthesis in plants, with effects varying significantly among species. The results will provide theoretical support for exploring BSC effects on plant diversity and a scientific basis for biodiversity conservation in the Minqin desert-oasis ecotone.

2.1 Study Area

The study area is located in Minqin County, Gansu Province, China (38°03 - 39°28 N, 101°49 -104°12 E; 1400 m a.s.l.). This area is surrounded by the Badain Jaran Desert to the west and north, and by the Tengger Desert to the east. The total area is 1.6$×10^{4}$ km^{2}, with desertified and oasis areas accounting for 91% and 9% of the total area, respectively. The region is characterized by an arid climate, with average annual precipitation, evaporation, and temperature of 115.4 mm, 2644.0 mm, and 8°C, respectively. The average accumulated temperature of $ $10°C is 3036°C, with a frost-free period of 189 days and an average wind speed of 2.5 m/s (Zhao et al., 2023). The soil consists of loose and barren sand, with stable soil moisture content ranging from 2% to 3%. This area is dominated by algal crust, followed by lichen crust. Due to unreasonable human activities and global climate change, the ecological environment has severely degraded, making it a typical desert-oasis ecotone in Northwest China (Li et al., 2021a).

2.2 Methods

In early May 2022, well-developed algal crusts at 4–6 mm depth were collected from the Minqin desert-oasis ecotone. Samplers (40 cm in height and 30 cm in diameter) were made using polyvinyl chloride (PVC) pipes. When collecting crust soil samples, we vertically pressed the sampler into the soil to collect intact soils covered with algal crusts. Soils at the bottom of the sampler were then flattened and transported back to the laboratory as culture substrates. To ensure crust integrity, we moistened the samples before collection and kept them intact for experimental use.

Mature seeds of *N. tangutorum*, *C. koraiensis*, and *G. dasyphylla* were collected in mid-August, early July, and mid-October 2021, respectively, and stored in a stable environment (4°C) for experimental use. *N. tangutorum*, a typical succulent xerophyte with high seed dormancy, is recognized as one of the most drought-resistant plants for desert afforestation. Before the experiment, *N. tangutorum* seeds were treated as follows: first, seeds were soaked in 98% H_2SO_4 for 55 min, then treated with 150 mg/L gibberellin (GA_3) for 48 h, and finally germinated at 25°C/5°C in darkness for 8 days. The seed germination rate reached up to 69% (Kang et al., 2016). *C. koraiensis*, a typical less-succulent xerophyte, is an important plant for constructing windbreak and sand-fixation forests. *G. dasyphylla*, a typical annual herb, is used for the herb layer construction of windbreak and sand-fixation forests in the Minqin desert-oasis ecotone.

2.3 Experimental Design

The experiment was conducted in a greenhouse in mid-May 2022. Before the experiment, we watered the collected BSCs daily to remove all sprouted seedlings until no seedlings appeared for 7 days. To prevent damage to crust integrity, we cut all sprouted plants at the roots with scissors. Preprocessed seeds of *N. tangutorum*, *C. koraiensis*, and *G. dasyphylla* were selected for germination experiments in late May. The soil samples in the samplers were then divided into three parts. The first part had the crust completely removed from the surface using a flat shovel until bare sand was exposed in the lower layer (without crust; WC). The second part maintained the intact crust surface (intact crust; IC), and the remaining part was broken as a control (broken crust; BC), which was evenly rolled with cylindrical tools on the crust to form similarly sized particles. A total of 15 mature seeds of each plant were sown (1.0–1.5 cm burial depth) in the samplers with 20 replicates per treatment, then covered with IC, BC, and bare sand, respectively. Water was sprayed on the crust surface every noon for 8 days to maintain moisture, and seedling emergence numbers and initial emergence time were recorded every morning. After 10 days, seedling survival numbers were counted in each treatment, and all seedlings were thinned to 8 uniform seedlings per sampler. Soil water content (SWC) in all treatments was maintained at 70% of field water holding capacity by irrigation, then water was withheld for 5 days to gradually induce drought stress. SWC was subsequently maintained at 30% of field water holding capacity by irrigation. As this was a control experiment conducted in a greenhouse, we divided the growth processes into three stages based on cultivation days: early growth stage (late May to 1 July), middle growth stage (1 July to 1 August), and late growth stage (1 August to the end of the growing period). After the growth period ended, 10 healthy uniform plants per treatment were excavated and separated into roots, stems, and leaves for physiological and morphological analysis. Soil sampling of each treatment (IC, BC, and WC) was performed after the experiment. Soils were sampled as 5 sub-samples at different layers (0-5, 5-10, and 10-15 cm), then mixed, and all soil samples were placed in sealed plastic bags and taken to the laboratory for nutrient analysis.

2.4.1 Seed Germination and Plant Growth

Plant height was measured with a ruler, fresh weight was estimated using an electronic scale, and root:shoot ratio was calculated. Seed emergence rate (SER) was calculated using the following formula:

$$SER = SEN/TSM$$

where SEN is seed emergence number and TSM is total sowing number. Seed emergence speed (SES) was calculated as:

$$SES = (\sum QDCC)/n \times FER \times 10$$

where QDCC is the quotient obtained by dividing the cumulative number of seedlings per day by the corresponding number of seedling emergence days, n is the number of days from emergence to end, and FER is final emergence rate (%) (Wang et al., 2011).

2.4.2 Plant Nutrients

We measured Na^+, K^+, Ca^{2+}, Mg^{2+}, N, and P contents in plants according to the method described by Kang et al. (2020b). Na^+, K^+, Ca^{2+}, and Mg^{2+} contents were measured by atomic absorption spectrophotometry. Si concentration ($SiO_3{}^{2-}$) was determined by the molybdate-blue method, and total N and total P were determined by acid standard solution titration and vanadium-molybdenum-yellow spectrophotometry, respectively. Free proline and soluble sugars contents were analyzed by the acidic indene three ketone method and hydrochloric acid (HCl) transformation-copper reduction-iodimetry, respectively (Kang et al., 2020b).

2.4.3 SWC and Soil Nutrients

SWC was determined by weighing. We measured soil nutrient indices according to the methods of Bao (2000). Briefly, soil organic carbon (SOC) was measured by the $K_2Cr_2O_7$-H_2SO_4 oxidation method, total N by the Kjeldahl procedure, and total P by molybdenum-antimony anti-colorimetric method. Available N was measured by alkali-hydrolyzable diffusion and available P by the Bray method. Available K included the sum of soluble, exchangeable, and available non-exchangeable K, with concentration measured by ammonium acetate extraction.

2.5 Data Analysis

All experimental data were analyzed using SPSS v.13.0 (SPSS Inc., Chicago, USA) and Excel v.2010 software. One-way analysis of variance (ANOVA) examined the effects of three BSC treatments on soil nutrients, growth indices, inorganic nutrient absorption, and organic solute synthesis of three desert plants. Multivariate variance analysis examined the interactive effects of BSC treatments, plant types, and growth periods on seed emergence rate, biomass, and root:shoot ratio. Duncan' s multiple range tests detected significant differences between means at $P<0.05$.

3.1 Effects of BSCs on SWC and Nutrients

Different BSC treatments significantly affected SWC [Figure 1: see original paper]. Under all three treatments, SWC in the 0–5 and 5–10 cm soil layers during the early growth stage was significantly lower than in middle and late stages, while the trend in the 10–15 cm layer was opposite. Moreover, SWC in the 0–5 and 5–10 cm layers under WC and BC treatments was consistently higher than under IC treatment throughout the growth period. However, SWC in the 10–15 cm layer under IC and BC treatments was higher than under WC treatment in the early growth stage, with the opposite trend in middle and late stages.

Soil nutrients showed no significant changes across growth stages of the three desert plants, but significant differences were observed among BSC treatments . In the 0–5 cm layer, SOC, total N, total K, available N, and available K under IC and BC treatments were significantly higher than under WC treatment. In the 5–10 cm layer, SOC, total N, and available N under IC and BC treatments were significantly higher than under WC treatment. However, the three treatments did not significantly affect nutrient content in the 10–15 cm layer.

3.2 Effects of BSCs on Seed Emergence and Seedling Survival

Both plant seed types and crust treatments (IC, WC, and BC) significantly affected seed emergence rate, while the interaction between seed types and crust treatments was not significant, indicating that crust effects on emergence rate varied with seed type . Seed emergence and seedling survival rates of the three desert plants under WC and BC treatments were significantly higher than under IC treatment, indicating that IC treatment hindered emergence and survival. *C. koraiensis* and *G. dasyphylla* had significantly higher emergence and survival rates than *N. tangutorum*, with no significant difference between WC and BC treatments, indicating that BC treatment had no significant effects on germination and was more conducive to emergence and survival [FIGURE:2a and b]. Different BSC treatments also affected seed emergence speed differently. Under all treatments, *C. koraiensis* had the fastest emergence speed, followed by *G. dasyphylla*, with *N. tangutorum* the slowest. Emergence speed under the three treatments ranked as WC > BC > IC, indicating that BSC presence decreased emergence speed [Figure 2c: see original paper].

3.3 Effects of BSCs on Growth Status of Desert Plants

Different BSC treatments significantly affected plant height . Plant heights under IC and BC treatments were higher than under WC treatment, with weaker promoting effects on *N. tangutorum* and *C. koraiensis* than on *G. dasyphylla*. *G. dasyphylla* height was affected by BSCs in the early growth stage, but these effects weakened significantly in middle and late stages. In contrast, *N. tangutorum* and *C. koraiensis* heights only showed differences in middle and late stages, with significant increases during this period .

BSCs had different effects on fresh weight and root:shoot ratio of the three desert plants [FIGURE:3a and b]. Effects on fresh weight varied by species, with all three plants showing significantly higher fresh weight under BC treatment than under IC and WC treatments, and the lowest fresh weight under WC treatment [Figure 3a: see original paper]. Changes in root:shoot ratio under different treatments were consistent with fresh weight trends [Figure 3b: see original paper]. ANOVA results showed that BSCs, plant species, growth stages, and their interactions all significantly affected single-plant fresh weight accumulation, and BSCs, plant species, growth periods, and their interactions significantly affected aboveground-belowground biomass and root:shoot ratio .

3.4 Effects of BSCs on Inorganic Nutrient Absorption and Organic Solute Synthesis of Desert Plants

BSC treatments had different effects on inorganic nutrient absorption and organic solute synthesis of the three desert plants, with effects varying among species [TABLES:5 and 6]. Inorganic nutrient absorption was highest under BC treatment and lowest under WC treatment . BSCs significantly promoted N absorption but had no significant effect on P absorption. BC treatment significantly promoted Na^+, Ca^{2+}, Mg^{2+}, and $SiO_3{}^{2-}$ absorption in *N. tangutorum* but had no significant effect on K^+ absorption, while significantly promoting K^+, Ca^{2+}, Mg^{2+}, and $SiO_3{}^{2-}$ absorption in *C. koraiensis* but little effect on Na^+ absorption. Inorganic nutrient absorption by *G. dasyphylla* was similar to *C. koraiensis*, with BSCs having stronger effects on promoting nutrient accumulation in *C. koraiensis* than in *G. dasyphylla* .

Organic solute synthesis (except in *N. tangutorum*) was highest under BC treatment and lowest under WC treatment. BC treatment significantly promoted organic solute synthesis (especially soluble sugars) in *C. koraiensis* and *G. dasyphylla*, with no significant difference observed in *N. tangutorum* .

4.1 Effects of BSCs on Seed Germination and Plant Growth of Desert Plants

In arid and semi-arid ecosystems, BSCs exhibit a mosaic distribution pattern with herbs and woody vegetation, forming a small ecosystem together with surrounding plants (Zhou et al., 2019; Bi et al., 2022). BSCs affect seed germination and growth of coexisting plants through various effects on soil nutrients, structure, hydrological processes, and surface roughness (Li et al., 2021b). Our results showed that both seed types and crust treatments (IC, WC, and BC) significantly affected seed emergence and seedling survival, with emergence rate and growth height under BC treatment higher than under IC and WC treatments, indicating that BSCs inhibited germination and seedling growth, with effects varying by seed type [FIGURE:2; TABLE:2].

BSCs had different effects on seed germination of different desert plant types, resulting in spatial heterogeneity of germination and affecting plant distribution and diversity. Our results are consistent with Song et al. (2022), Gao et al. (2023), and Zhang et al. (2024), who found that BSCs, as key biological factors in vegetation succession, significantly affected germination and survival of different plant life forms. Thus, BSCs play important roles in species composition and establishment of plant communities in arid areas.

The binding effects of crust microorganisms and their secretions on surface soil particles significantly enhanced soil adhesion, making it difficult for seeds to penetrate the crust for emergence and lacking habitat space for colonization and survival (Zhao et al., 2006; Wang et al., 2011). Results also showed that BSCs provided a suitable hydrothermal microenvironment for germination and growth, which was conducive to seeds with small size and simple morphological structure, but unfavorable for seeds with large size and complex structure (Song et al., 2017). We found that BSCs promoted germination and emergence of *C. koraiensis* and *G. dasyphylla* but were not conducive to *N. tangutorum* [Figure 2a: see original paper], similar to Song et al. (2017). This result can be attributed to the large particle size, thick and impermeable seed coat, and complex structure of *N. tangutorum* seeds. Additionally, *N. tangutorum* seeds exhibit severe morphological and physiological dormancy; even after dormancy breaking, germination and emergence rates remain very slow (Kang et al., 2016). This makes it difficult for *N. tangutorum* seeds to quickly absorb water and nutrients from soil under the BSC isolation layer, ultimately leading to low emergence rates. In contrast, *C. koraiensis* and *G. dasyphylla* seeds are relatively small with simple morphological structure, making them less susceptible to BSC barrier effects and instead protected in the relatively stable microenvironment provided by BSCs, thereby promoting germination, emergence, and growth (Zhang and Belnap, 2015; Havrilla et al., 2019; Wang et al., 2021).

Our results indicated that growth height, fresh weight, and root:shoot ratio under BC treatment were higher than under IC treatment, with the worst growth status under WC treatment [FIGURE:2; TABLES:2 and 3], indicating that BSCs affected seed growth in lower soil layers by influencing water and nutrient transport and transfer. This occurred because IC treatment hindered soil water infiltration and light penetration, while BC treatment promoted water and nutrient transfer through cracks beneficial for germination and growth. WC treatment had significant inhibitory effects due to poor water retention and nutrient deficiency. Similarly, studies in tropical deserts found high densities of perennial plants under BC treatment, indicating that BC did not inhibit growth. On the contrary, the rough BSC surface can capture organic matter, water, and fine soil particles, increasing soil micro-environment fertility (Happer and Marble, 1988; Prasse and Bornkamm, 2000; Wang et al., 2011). Notably, BSCs showed positive effects on *G. dasyphylla* in the early growth stage but negative effects in middle and late stages, while effects on *N. tangutorum* and *C. koraiensis* were opposite . The positive effect on *G. dasyphylla* occurred because soil moisture and nutrients in lower BSC layers were relatively sufficient, benefiting its growth and development. The lack of promoting effect on *N. tangutorum* and *C. koraiensis* may be attributed to their deep-rooted nature, making growth less affected. The negative effect on *G. dasyphylla* and positive effects on *N. tangutorum* and *C. koraiensis* in later stages may relate to soil moisture deficiency. During this period, deep soil moisture was severely lacking, and *G. dasyphylla* could not utilize deep moisture. However, *N. tangutorum* and *C. koraiensis* are extreme xerophytes; under drought stress, BSC presence significantly reduced soil moisture content, allowing them to exert normal physiological drought resistance functions by improving various metabolic activities (Kang et al., 2020b; Wang et al., 2023; Feng et al., 2024).

4.2 Effects of BSCs on Inorganic Nutrient Absorption and Organic Solute Synthesis of Desert Plants

BSCs can change soil surface chemical properties, resulting in corresponding changes in essential elements contained in plants (Zhou et al., 2023). BSC effects on plant nutrient absorption may be due to increased organic matter on the soil surface, which is transferred to plants, allowing them to absorb more nutrients (Zhang and Nie, 2011; Zhuang et al., 2017). Results showed that BSC presence increased soil organic nutrient content, and blue-green algae in BSCs have N-fixation effects that can be utilized by plants (Wu et al., 2009; Wang et al., 2021). Additionally, decomposition products of various BSC components increase soil organic nutrient content and can promote essential nutrient absorption by plants (Zhuang et al., 2017; Wang et al., 2021). Our results indicated that N content in plants under IC and BC treatments was significantly higher than under WC treatment, but no significant difference in P content existed between treatments . These results are consistent with Zhuang et al. (2017), who found that regardless of BSC type, BC treatment promoted N uptake and inhibited P uptake, contrary to DeFalco’ s (1995) conclusion that BSCs promoted P uptake. Different P content in desert plants with BSC presence can be attributed to differences in plants, research areas, and crust types. Moreover, in many arid desert areas, calcareous and sandy soils often lack P, and BSC organisms may compete with plants for P, which may be the main reason for negative BSC effects on plant P content (Harper and Belnap, 2001).

Increasing evidence shows that increased plant nutrients when BSCs are present may be due to fungi’ s role in nutrient transfer between soil and plant (Green et al., 2008; Maestre et al., 2011; Zhuang et al., 2015). BSCs may also promote nutrient absorption in other ways. For example, soil covered by BSCs often contains more clay, and clay components are more conducive to binding nutrients, especially under humid conditions. These soil particles are more likely to adsorb sticky sheath substances, and negatively charged sheath substances chelate with positively charged plant nutrients, thereby increasing plant nutrient content (Verrecchia et al., 1995; Zhuang et al., 2017). Interestingly, our results indicated that BSC presence had consistent effects on inorganic nutrient absorption and organic solute synthesis, exhibiting significant selectivity among the three desert plants but not significantly altering their nutrient characteristics [TABLES:5 and 6]. The difference lies in varying amounts of inorganic nutrient absorption and organic solute synthesis among the three species under different treatments. This occurred because BSC presence increased soil water content, leading to increased plant water use efficiency and enhanced physiological metabolic activities, thereby promoting growth and drought resistance (He et al., 2017; Zhuang and Zhang, 2017; Guan, 2023). This further confirms our previous findings that accumulation of high concentrations of inorganic nutrients was one of the most effective physiological adaptation strategies for *N. tangutorum* to cope with drought stress, as it did not rely on K^+ and organic solute accumulation to enhance drought resistance. However, accumulation of large amounts of inorganic nutrients and moderate organic solutes was an important mechanism for *C. koraiensis* to adapt to arid habitats. Inorganic nutrient and organic solute accumulation in *G. dasyphylla* was similar to *C. koraiensis*, but nutrient accumulation in *G. dasyphylla* was significantly lower than in *C. koraiensis*. Thus, due to unique nutrient accumulation characteristics for drought resistance, succulent xerophytes (*N. tangutorum*) had stronger drought resistance than less-succulent xerophytes (*C. koraiensis*), and mesophytes (*G. dasyphylla*) had the weakest drought resistance in arid areas (Wang et al., 2004; Kang et al., 2020b).

5. Conclusions

In this study, BSC presence significantly affected seed emergence, seedling survival, and growth of three desert plants in the Minqin desert-oasis ecotone, Northwest China. Overall, the positive effects of BSCs on emergence, survival, growth, and nutrient accumulation were significantly greater than negative effects. BSC effects on emergence and survival varied with seed type and growth stage. Effects on inorganic nutrient accumulation and organic solute synthesis showed interspecific differences, indicating complex interactions between desert plants and BSCs. The internal mechanism can be attributed to different desert plants having evolved unique strategies and mechanisms to adapt to environmental changes and ensure survival under adverse conditions. Therefore, further study is needed to clarify the specific mechanisms of long-term BSC effects on seed emergence, seedling survival, and growth of desert plants in different arid areas.

Conflict of Interest

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

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Author Contributions

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References

Aguilar V R, Alvarez H G, Cacheux I M, et al. 2005. Physical effect of biological soil crusts on seed germination of two desert plants under laboratory conditions. *Journal of Arid Environments*, 63(1): 344–352.

Bao S D. 2000. *Soil Chemical Analysis of Agriculture* (4th ed.). Beijing: Agriculture Press, 12–21. (in Chinese)

Belnap J, Weber B, Büdel B. 2016. *Biological Soil Crusts as an Organizing Principle in Drylands*. Switzerland: Springer International Publishing.

Bi Y L, Guo Y, Liu F, et al. 2022. Ecological restoration effect and carbon neutrality contribution of biological soil crusts in western mining area. *Journal of China Coal Society*, 47(8): 2883–2895. (in Chinese)

Chen M C, Zhang J G, Liu L C, et al. 2017. Advances and prospects for the effects of biological soil crusts on annual plants. *Journal of Desert Research*, 37(3): 483-490. (in Chinese)

Chen R Y, Wei W S, Zhang Y M, et al. 2008. Effect of biological soil crust on plant diversity in arid area. *Journal of Desert Research*, 28(5): 868-873. (in Chinese)

DeFalco L A. 1995. Influence of Cryptobiotic Crusts on Winter Annuals and Foraging Movements of the Desert Tortoise. Fort Collins: Colorado State University.

Feng L, Teng F, Li N, et al. 2024. A reference-grade genome of the xerophyte *Ammopiptanthus mongolicus* sheds light on its evolution history in legumes and drought-tolerance mechanisms. *Plant Communication*, 5(7): 100891, doi: 10.1016/j.xplc.2024.100891.

Gao L Q, Bowker M A, Xu M X, et al. 2017. Biological soil crusts decrease erodibility by modifying inherent soil properties on the Loess Plateau, China. *Soil Biology and Biochemistry*, 105: 49–58.

Gao Y H, Jia R L, Liu Y P, et al. 2023. Biocrust and sand burial together promote annual herb community assembly in an arid sandy desert area. *Plant and Soil*, 491(1–2): 645–663.

Green L E, Porras-alfaro A, Sinsabaugh R L. 2008. Translocation of nitrogen and carbon integrates biotic crust and grass production in desert grassland. *Journal of Ecology*, 96(5): 1076–1085.

Guan H J. 2023. Biocrust effects on root water uptake of shrubs in the Mu Us Desert. *Acta Ecologica Sinica*, 43(14): 5875–5889. (in Chinese)

Happer K T, Marble J R. 1988. A role for nonvascular plants in management of arid and semi-arid rangelands. In: Tueller P T. *Application of Plant Sciences to Rangeland Management*. Amsterdam: Martinus Nijhoff, 135–169.

Harper K T, Belnap J. 2001. The influence of biological soil crusts on mineral uptake by associated vascular plants. *Journal of Arid Environments*, 47(3): 347–357.

Havrilla C A, Chaudhary V B, Ferrenbe S, et al. 2019. Towards a predictive framework for biocrust mediation of plant performance: A meta-analysis. *Journal of Ecology*, 107(6): 2789–2807.

He F L, Guo C X, Wu H, et al. 2017. Effect of biological soil crust succession on soil texture, nutrient contents, and microbial populations of dune surfaces at the edge of the Minqin Oasis. *Acta Ecologica Sinica*, 37(18): 6064–6073. (in Chinese)

Jassey V E J, Walcker R, Kardol P, et al. 2022. Contribution of soil algae to the global carbon cycle. *New Phytologist*, 234(1): 1–3.

Jia B Q, Zhang H Q, Zhang Z Q, et al. 2003. The study on the physical and chemical characteristics of sand soil crust in the Minqin County, Gansu Province. *Acta Ecologica Sinica*, 23(7): 1442–1448.

Kang J J, Yue L J, Wang S M, et al. 2016. Na compound fertilizer stimulates growth and alleviates water deficit in the succulent xerophyte *Nitraria tangutorum* (Bobr) after breaking seed dormancy. *Soil Science and Plant Nutrition*, 62(5–6): 489–499.

Kang J J, Zhang X W, Zhang J Q, et al. 2020a. Special organic fertilizer for improving soil fertilization and xerophyte *Haloxylon ammodendron* growth in the nursery and afforestation in desert regions of China. *Journal of Soil Science and Plant Nutrition*, 20(9): 2241–2252.

Kang J J, Zhao W Z, Wang Z W, et al. 2020b. The features of main osmolytes, silicon and their coupling effects in improving drought resistance of the typical xerophytes in the desert areas of Northwest China. *Land Degradation and Development*, 31(17): 2720–2733.

Li J H, Chen Y, Yang G J, et al. 2021a. The aeolian desertification process and driving mechanism of Minqin Oasis from 1975 to 2018. *Journal of Desert Research*, 41(3): 44–55. (in Chinese)

Li X R, Wang X P, Li T, et al. 2002. Microbiotic soil crust and its effect on vegetation and habitat on artificially stabilized desert dunes in Tengger Desert, Northern China. *Biology and Fertility of Soils*, 35(3): 147–154.

Li X R, Jia X H, Long L Q, et al. 2005. Effects of biological soil crusts on seed bank, germination and establishment of two annual plant species in the Tengger Desert. *Plant and Soil*, 277(1–2): 375–385.

Li X R. 2012. *Eco-hydrology of Biological Soil Crusts in Desert Regions of China*. Beijing: Higher Education Press. (in Chinese)

Li X R, Zhou H Y, Wang X P, et al. 2016. Ecological restoration and recovery in arid desert regions of China: A review for 60-year research progresses of Shapotou desert research and experiment station, Chinese Academy of Sciences. *Journal of Desert Research*, 36(2): 247–264. (in Chinese)

Li X R, Hui R, Zhao Y. 2017. *Eco-physiology of Biological Soil Crusts in Desert Regions of China*. Beijing: Higher Education Press. (in Chinese)

Li X R, Tan H J, Hui R, et al. 2018. Biological soil crusts in deserts and sandy lands of China. *Science Bulletin*, 63(23): 1503–1505.

Li X R, Hui R, Tan H J, et al. 2021b. Biocrust research in China: Recent progress and application in land degradation control. *Frontiers in Plant Science*, 25(12): 751521, doi: 10.3389/fpls.2021.751521.

Li Y G, Zhang Y M. 2023. Response of carbon flux of different moss biocrust patches to rainfall in arid desert. *Acta Ecologica Sinica*, 43(4): 1584–1595. (in Chinese)

Liu Y B, Wang Z R, Gao T P. 2020. Succession of microbial community structure and their functions of biological soil crusts in temperate desert: A review. *Microbiology China*, 47(9): 2974-2983.

Lu Q, Xiao Y, Lu Y J. 2022. Employment of algae-based biological soil crust to control desertification for the sustainable development: A mini-review. *Algal Research*, 65(4): 102747, doi: 10.1016/j.algal.2022.102747.

Luo Z P, Kang N X, Liu X X. 2020. Study on the role of biological soil crust in ecological restoration and its enlightenment to the control of rocky desertification. *Research of Soil and Water Conservation*, 27(1): 394-404. (in Chinese)

Maestre F T, Bowker M A, Cantón Y, et al. 2011. Ecology and functional roles of biological soil crusts in semi-arid ecosystems of Spain. *Journal of Arid Environments*, 75(12): 1282-1291.

Nevins C J, Inglett P W, Strauss S L. 2021. Biological soil crusts structure the subsurface microbiome in a sandy agroecosystem. *Plant and Soil*, 462(2): 311-329.

Prasse R, Bornkamm R. 2000. Effect of microbiotic soil surface crusts on emergence of vascular plants. *Plant Ecology*, 150(1-2): 65-75.

Qiao Y, Xu X Y, Fu G Q, et al. 2015. Characteristics of soil crusts of different development years and their impact on soil hydrological processes in Minqin Oasis fringe. *Journal of Soil and Water Conservation*, 29(4): 1-6. (in Chinese)

Rong X Y, Zhou X B, Li X Z, et al. 2022. Biocrust diazotrophs and bacteria rather than fungi are sensitive to chronic low N deposition. *Environmental Microbiology*, 24(11): 5450-5466.

Song G, Li X R, Hui R. 2017. Biological soil crusts determine the germination and growth of two exotic plants. *Ecology and Evolution*, 7(22): 9441-9450.

Song G, Hui R, Yang H T, et al. 2022. Biocrusts mediate the plant community composition of dryland restoration ecosystems. *Science of the Total Environment*, 844: 157135, doi: 10.1016/j.scitotenv.2022.157135.

Su Y T, Li X R, Huang G, et al. 2007. Effects of two types of biological soil crusts on the germination of desert vascular plants under laboratory conditions. *Acta Ecologica Sinica*, 27(5): 1845-1851. (in Chinese)

Sun Y Q, Feng W, Zhang Y Q, et al. 2020. Effects of biological soil crusts on soil enzyme activities of *Artemisia ordosica* community in the Mu Us Desert of northwestern China. *Journal of Beijing Forestry University*, 42(11): 82-90. (in Chinese)

Tang K, Gao X D, Jia L J, et al. 2018. Community structure and diversity of diazotrophs in biological soil crusts and soil underneath crust of Hunshandake Deserts. *Microbiology China*, 45(2): 293-301. (in Chinese)

Tao H X, Guo C X, Ma J M, et al. 2023. Influences of soil crust development on soil seed bank of herbaceous plants in arid desert area. *Journal of Desert Research*, 43(4): 89-97. (in Chinese)

Verrecchia E, Yair A, Kidron G J, et al. 1995. Physical properties of the psammophile cryptogamic crust and their consequences to the water regime of sandy soils, north-western Negev Desert, Israel. *Journal of Arid Environments*, 29(4): 453-460.

Wang N, Liu J E, Zhou Z C. 2021. Research progress on the effect of biological soil crust on seed germination and seedling establishment. *Acta Ecologica Sinica*, 41(18): 7464-7474. (in Chinese)

Wang R, Zhu Q K, Zhao L L, et al. 2011. Effects of biological soil crusts on seed emergence and seedling growth in Loess Plateau, North Shaanxi Province. *Arid Zone Research*, 28(5): 800-807. (in Chinese)

Wang S M, Wan C G, Wang Y R, et al. 2004. The characteristics of Na^+, K^+ and free proline distribution in several drought-resistant plants of the Alxa Desert, China. *Journal of Arid Environments*, 56(3): 525-539.

Wang S Y, Liu Y H, Hao X, et al. 2023. *AnWRKY29* from the desert xerophytic evergreen *Ammopiptanthus nanus* improves drought tolerance through osmoregulation in transgenic plants. *Plant Science*, 336(15): 111851, doi: 10.1016/j.PLANTSCI.2023.111851.

Wu N, Zhang Y M, Downing A. 2009. Comparative study of nitrogenase activity in different types of biological soil crusts in the Gurbantunggut Desert, Northwestern China. *Journal of Arid Environments*, 73(9): 828-833.

Zhang L Y, Zhang M L, Huang S Y, et al. 2022. A highly conserved core bacterial microbiota with nitrogen-fixation capacity inhabits the xylem sap in maize plants. *Nature Communications*, 13(1): 3361-3373.

Zhang X, Xiao B, Han F M. 2024. The effect of biological crust on seed emergence, seedling survival and growth in the Loess Plateau. *Acta Ecologica Sinica*, 44(20): 9354-9363. (in Chinese)

Zhang Y M, Nie H L. 2011. Effects of biological soil crusts on seedling growth and element uptake in five desert plants in Junggar Basin, western China. *Chinese Journal of Plant Ecology*, 35(4): 380-388.

Zhang Y M, Belnap J. 2015. Growth responses of five desert plants as influenced by biological soil crusts from a temperate desert, China. *Ecological Research*, 30(6): 1037-1045.

Zhao P, Xu X Y, Zhang Y N, et al. 2023. Age structure and its dynamics of artificial *Haloxylon ammodendron* population in Minqin oasis-desert ecotone. *Acta Ecologica Sinica*, 43(13): 6069-6079. (in Chinese)

Zhao Y G, Xu M X, Wang Q J, et al. 2006. Physical and chemical properties of soil bio-crust on rehabilitated grassland in hilly Loess Plateau of China. *Chinese*

Journal of Applied Ecology, 17(8): 1429-1434.

Zhou S J, Han B H, Jiang J C, et al. 2023. Influence of biological soil crust development on soil nutrients in typical grasslands of Loess Plateau in central Gansu province. *Acta Botanica Boreali-Occidentalia Sinica*, 43(1): 147-154. (in Chinese)

Zhou X J, An X L, De Philippis R, et al. 2019. The facilitative effects of shrub on induced biological soil crust development and soil properties. *Applied Soil Ecology*, 137(12): 129-138.

Zhuang W W, Downing A, Zhang Y M. 2015. The influence of biological soil crusts on ^{15}N translocation in soil and vascular plant in a temperate desert of Northwestern China. *Journal of Plant Ecology*, 8(4): 420-428.

Zhuang W W, Zhang Y M. 2017. Effects of biological soil crusts on the photosynthetic characteristics of three desert herbs in Gurbantunggut Desert. *Plant Science Journal*, 35(3): 387-397. (in Chinese)

Zhuang W W, Zhou X B, Zhang Y M. 2017. Effects of biological soil crusts on growth and nutrient uptake in three desert herbs in the Gurbantunggut Desert, Northwestern China. *Bulletin of Botanical Research*, 37(1): 37-44. (in Chinese)

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