

Postprint of a Study on Developmental Differences of Moss Crusts in *Artemisia ordosica* and *Salix psammophila* Shrublands

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Date: 2023-08-25T00:00:00+00:00

Abstract

To address the phenomenon that moss crust development in *Artemisia ordosica* shrublands of the Mu Us Sandy Land is consistently significantly superior to that in *Salix psammophila* shrublands, this study reveals the reasons for the substantial differences in moss crust development between the two shrubland types based on observational analysis of soil properties and moss crust development indicators, combined with allelopathy experiments using aqueous extracts from different organs of the two shrubs on moss crust development. The results show: (1) Significant differences in moss crust coverage exist between the two shrubland types ($P < 0.05$), with total coverage as well as under-canopy and between-canopy coverage all following the pattern: *Artemisia ordosica* > *Salix psammophila*. The total moss crust coverage and the under-canopy and between-canopy moss crust coverage in *Artemisia ordosica* shrublands are 1.6 times, 2.9 times, and 1.1 times the corresponding moss crust coverage in *Salix psammophila* shrublands, respectively; (2) Pearson correlation analysis reveals that under-canopy moss crust coverage is significantly positively correlated with soil water content, and thickness is significantly positively correlated with silt content; between-canopy moss crust coverage is significantly positively correlated with soil water content and clay content ($P < 0.05$). The higher soil water content and clay and silt contents in *Artemisia ordosica* shrublands significantly promoted moss crust development; (3) Allelopathy experiments demonstrate that aqueous extracts from roots, stems, and leaves of both *Artemisia ordosica* and *Salix psammophila* inhibited moss crust development, i.e., the comprehensive allelopathic effect (SE) values were all negative. Among these, the $0.2 \text{ g} \cdot \text{mL}^{-1}$ aqueous leaf extract of *Salix psammophila* exhibited the strongest allelopathic inhibition, with an SE value of -0.95, which was significantly higher than that of *Artemisia ordosica* leaves (SE value of -0.65) ($P < 0.05$). These results

indicate that the higher soil water content, clay and silt contents in *Artemisia ordosica* shrublands, together with the significant allelopathic inhibition of moss crust development by *Salix psammophila* leaves, collectively lead to superior moss crust development conditions in *Artemisia ordosica* shrublands compared to *Salix psammophila* shrublands.

Full Text

Differences in Moss Crust Development Between *Artemisia ordosica* and *Salix psammophila* Shrubs

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Abstract

Moss crust development in *Artemisia ordosica* shrubland is consistently superior to that in *Salix psammophila* shrubland in the Mu Us Sandy Land. To reveal the underlying causes of this substantial difference, we analyzed soil properties and moss crust development indicators in both shrubland types, combined with allelopathic experiments using aqueous extracts from different shrub organs. The results showed: (1) Moss crust coverage differed significantly between the two shrubland types ($P < 0.05$). Total moss crust coverage and sub-canopy and inter-canopy coverage followed the pattern: *A. ordosica* > *S. psammophila*, with values in *A. ordosica* shrubland being 1.6, 2.9, and 1.1 times higher than those in *S. psammophila* shrubland, respectively. (2) Pearson correlation analysis revealed that sub-canopy moss crust coverage was significantly positively correlated with soil water content, while thickness was significantly positively correlated with silt content. Inter-canopy moss crust coverage was significantly positively correlated with both soil water content and clay content ($P < 0.05$). The higher soil water content and clay and silt contents in *A. ordosica* shrubland clearly promoted moss crust development. (3) Allelopathic tests demonstrated that aqueous extracts from roots, stems, and leaves of both shrub species inhibited moss crust development, with negative allelopathic synthesis effect (SE)

values. The $0.2 \text{ g} \cdot \text{mL}^{-1}$ *S. psammophila* leaf extract showed the strongest inhibitory effect ($\text{SE} = -0.95$), significantly higher than that of *A. ordosica* leaves ($\text{SE} = -0.65$) ($P < 0.05$). These findings indicate that the superior moss crust development in *A. ordosica* shrubland results from the combined effects of higher soil water content, greater clay and silt fractions, and significant allelopathic inhibition by *S. psammophila* leaves.

Keywords: *Artemisia ordosica*; *Salix psammophila*; moss crusts; allelopathy; comparative research; Mu Us Sandy Land

Introduction

Biological soil crusts are composite structures formed by algae, lichens, mosses, and microorganisms cemented with soil particles. They are widely distributed in arid and semi-arid regions, covering approximately 12% of Earth's terrestrial surface. Biocrusts play crucial roles in promoting nutrient cycling, stabilizing surfaces, resisting wind erosion, regulating surface runoff and rainfall infiltration, and are often used as important indicators of ecosystem stability and recovery status in degraded ecosystems. Previous research has extensively investigated factors influencing biocrust development and distribution. At the global scale, climate is the key factor affecting biocrust distribution. For example, in the Negev Desert of Israel, crust communities change along rainfall gradients, shifting from cyanobacterial crusts in areas with <100 mm annual rainfall to mixed cyanobacterial, lichen, and moss crusts in areas receiving >200 mm. At regional scales, topography, soil properties, vegetation, and disturbance are closely related to biocrust development. Current studies on vegetation effects have primarily focused on vegetation coverage, canopy structure, and litter impacts on biocrust development. For instance, research has shown that moss crusts develop better under shady, moist canopies compared to inter-canopy spaces. However, the relationship between vegetation and biocrusts is extremely complex, and studies on how different vegetation types affect biocrust growth remain limited. Revealing the factors influencing moss crust development in vegetation-crust systems is crucial for understanding crust formation, maintaining desert ecosystem functions, and combating desertification in the Mu Us Sandy Land.

As one of China's four major sandy lands, the Mu Us Sandy Land lies in the ecological transition zone between forest and desert, serving as an important ecological barrier in northern China. Biocrusts are important biological components in this region, coexisting with higher plants such as *A. ordosica* and *S. psammophila* on the surface and influencing ecological processes. Field investigations reveal that moss crusts in *A. ordosica* shrubland develop well with high coverage, often forming patchy distributions centered on shrub canopies and extending into inter-canopy spaces. In contrast, adjacent *S. psammophila* shrublands with similar habitats often lack or have minimal moss crust development. To investigate the causes of this difference, this study measured soil properties and moss crust development indicators in both shrubland types and conducted allelopathic experiments using extracts from different shrub organs,

aiming to elucidate the mechanisms of biocrust development under different shrub influences from both soil properties and plant allelopathy perspectives.

Methods

1.1 Study Area

The study area is located in Hengshan District, Yulin City, Shaanxi Province (37°21'–38°14' N, 108°56'–110°01' E), on the southern edge of the Mu Us Sandy Land, in the transition zone between the Ordos Plateau and the Loess Plateau. The region has a temperate semi-arid continental monsoon climate with distinct seasons. Spring features large diurnal temperature variations, frequent cold waves and frost, strong winds, and occasional sandstorms. Summer is hot with relatively abundant rainfall and occasional heavy rains. Autumn has frequent precipitation, rapid cooling, and early frost. Winter is cold with little snow. The multi-year average temperature is 8.9°C, with an average frost-free period of 175 days and annual precipitation of 352.2 mm, concentrated from June to September. The dominant vegetation includes *A. ordosica* and *S. psammophila*, with the moss crust dominated by *Bryum argenteum*, accompanied by *Bryum rutilans* and *Gymnostomum calcareum*.

1.2 Sample Plot Setup and Sample Collection

Undisturbed shrublands with minimal grazing and gentle topography were selected as experimental sites for both *A. ordosica* and *S. psammophila*. For each shrub type, three 5 m × 5 m sample plots were randomly established. Within each plot, five 20 cm × 20 cm moss crust investigation quadrats were randomly placed under shrub canopies and in inter-canopy spaces at different angles. From May to September 2022, moss crust thickness, coverage, and underlying soil properties (0–5 cm depth) were measured monthly. Soil samples were collected between 9:00–10:00 AM, ensuring at least three days without rainfall before sampling. Soil water content, bulk density, total nitrogen, total phosphorus, organic matter, and particle size composition were analyzed. The geographical location and real scene of the sample plots are shown in [Figure 1: see original paper], and basic plot information and background soil properties are provided in .

1.3 Allelopathic Tests

1.3.1 Extract Preparation Fresh roots, stems, and leaves of *A. ordosica* and *S. psammophila* were collected from the study sites, transported to the laboratory at low temperature and protected from light, then washed with distilled water and dried with filter paper. Each organ type (200 g) was cut into pieces, placed in a wide-mouth bottle with 1000 mL distilled water, and soaked at room temperature for 48 h in darkness. The extracts were filtered through four layers of filter paper to obtain 0.20 g · mL⁻¹ stock solutions, which were stored at low

temperature. Some stock solution was diluted to $0.02 \text{ g} \cdot \text{mL}^{-1}$. If flocculent precipitate appeared, the solution was discarded and freshly prepared.

1.3.2 Moss Crust Allelopathic Experiment The allelopathic experiment was conducted in a phytotron at Northwest A&F University's Institute of Soil and Water Conservation (RGL-P1000-C4) under constant environmental conditions (temperature: 25°C ; light intensity: 6000 lx ; photoperiod: $12 \text{ h}/12 \text{ h}$; air humidity: 60%). The soil substrate and moss crusts were collected from the study sites. The substrate was sand soil from beneath moss crusts, and moss crusts were selected for good development, integrity, and uniform growth. Collected crusts were air-dried and crushed. A $700 \text{ g} \cdot \text{m}^{-2}$ inoculum of crushed moss crust was spread on sterilized soil substrate in culture boxes ($9 \text{ cm} \times 9 \text{ cm} \times 4 \text{ cm}$) and lightly pressed to ensure contact. During cultivation, 20 mL of different organ extracts at various concentrations was applied with a pipette every two days, with distilled water as control. There were 13 treatments with three replicates each (see for details). Moss density, height, and coverage were measured continuously after crusts turned green. Cultivation ended when coverage stabilized, with consistent duration across treatments (60 days). Allelopathic index (RI) was calculated as: $\text{RI} = \{1 - \text{CK}/\text{T} (\text{T} \geq \text{CK}); \text{T}/\text{CK} - 1 (\text{T} < \text{CK})\}$, where CK is the control value and T is the treatment value. Positive RI indicates promotion, negative indicates inhibition. The allelopathic synthesis effect index (SE) is the arithmetic mean of all test indicators' RI values for the same donor-receptor combination.

1.4 Measurement Indicators

Moss indicators: Coverage was measured using point-frame method (recorded as 1 if moss present at grid intersection, 0 if absent). Thickness and height were measured with vernier calipers.

Soil indicators: Total nitrogen by Kjeldahl method; total phosphorus by $\text{H}_2\text{SO}_4\text{-HClO}_4$ digestion and molybdenum antimony colorimetry; organic matter by $\text{K}_2\text{Cr}_2\text{O}_7$ heating; water content by oven-drying; pH with DELTA320 pH meter (soil:water ratio 1:2.5); particle size composition by Mastersizer 2000 laser particle size analyzer, with fractions classified as clay ($<0.002 \text{ mm}$), silt ($0.002\text{--}0.02 \text{ mm}$), fine sand ($0.02\text{--}0.2 \text{ mm}$), and coarse sand ($0.2\text{--}2 \text{ mm}$).

Statistical analysis: Independent samples t-test was used to analyze differences in vegetation coverage, height, soil properties, and moss crust coverage and thickness between shrub types. Pearson correlation analyzed relationships between soil properties and moss crust characteristics. One-way ANOVA with LSD multiple comparisons tested allelopathic effects of different organ extracts. Origin 2023 and R 4.1.2 with ggplot2 were used for graphics. All data are presented as means \pm standard error, with significance at $P = 0.05$.

Results

2.1 Differences in Moss Crust Development Between Two Shrubland Types

As shown in , moss crust coverage differed significantly between the two shrubland types during the study period ($P < 0.05$), while thickness differences were not significant ($P > 0.05$). Total moss crust coverage and sub-canopy and inter-canopy coverage all showed the pattern: *A. ordosica* > *S. psammophila*. The total moss crust coverage in *A. ordosica* shrubland, as well as sub-canopy and inter-canopy coverage, were 1.6, 2.9, and 1.1 times higher than corresponding values in *S. psammophila* shrubland, respectively. Sub-canopy moss crust thickness in *A. ordosica* shrubland (12.22 mm) was greater than in *S. psammophila* shrubland (10.44 mm), and inter-canopy thickness in *A. ordosica* (11.11 mm) was greater than in *S. psammophila* (10.56 mm), though these differences were not significant ($P > 0.05$). The data in represent averages of sub-canopy and inter-canopy values for each shrub type.

2.2.1 Differences in Soil Physicochemical Properties Between Two Shrubland Types

As shown in , soil nutrient contents (total nitrogen, total phosphorus, organic matter) beneath moss crusts in *S. psammophila* shrubland were higher than in *A. ordosica* shrubland, but differences were not significant ($P > 0.05$). Compared with *S. psammophila*, *A. ordosica* shrubland had higher soil water content and clay and silt contents beneath moss crusts. Specifically, inter-canopy soil water content in *A. ordosica* shrubland was 3.80% and 4.70% under canopies, significantly higher than *S. psammophila*'s 2.70% (under canopy) and 3.10% (inter-canopy) ($P < 0.05$). Inter-canopy clay and silt contents in *A. ordosica* shrubland were approximately 2.1 times those in *S. psammophila* shrubland. Fine sand content under *A. ordosica* canopies was 66.10%, significantly higher than *S. psammophila*'s 54.60% ($P < 0.05$). There were no significant differences in coarse sand content or pH values between shrub types or positions ($P > 0.05$).

2.2.2 Correlations and Allelopathic Effects

The correlation heatmap ([Figure 2: see original paper]) shows that relationships between soil factors and moss crust coverage and thickness vary by position. Sub-canopy moss crust thickness was significantly positively correlated with soil silt content, and coverage was significantly positively correlated with soil water content ($P < 0.05$). Inter-canopy moss crust coverage was significantly positively correlated with soil water content and clay content ($P < 0.05$), while thickness showed no significant correlation with soil factors ($P > 0.05$).

As shown in [Figure 3: see original paper], aqueous extracts from different organs of both shrubs inhibited moss crust development, with SE values all negative. Inhibitory effects varied by shrub species, organ type, and extract concentration. At $0.02 \text{ g} \cdot \text{mL}^{-1}$, inhibition strength was: *A. ordosica* roots > *A. ordosica* leaves

> *S. psammophila* leaves > *S. psammophila* roots. At $0.20 \text{ g} \cdot \text{mL}^{-1}$, inhibition strength was: *S. psammophila* leaves > *A. ordosica* leaves > *A. ordosica* stems > *S. psammophila* roots. The $0.2 \text{ g} \cdot \text{mL}^{-1}$ *S. psammophila* leaf extract showed the strongest inhibition ($SE = -0.95$), significantly greater than other treatments ($P < 0.05$). For moss density and height, inhibition increased with concentration. For coverage, $0.02 \text{ g} \cdot \text{mL}^{-1}$ *A. ordosica* stem extract showed slight promotion, which shifted to inhibition at higher concentration, while *S. psammophila* root extract showed the opposite pattern.

Discussion

3.1 *Artemisia ordosica* Promotes Moss Crust Development by Improving Soil Moisture and Particle Composition

Numerous studies indicate that higher soil water content and clay and silt contents favor biocrust colonization and development. This study found significant positive correlations between sub-canopy moss crust coverage and soil water content ($P < 0.05$), sub-canopy thickness and silt content ($P < 0.05$), and inter-canopy coverage with both soil water and clay contents ($P < 0.05$), consistent with previous research. Studies have reported large differences in soil water content beneath moss crusts under different shrub canopies. This study found higher soil water content in both sub-canopy and inter-canopy positions in *A. ordosica* shrubland compared to *S. psammophila* shrubland. This is because *A. ordosica*, with its dense, low-growing foliage, reduces wind-driven evaporation from shallow soils more effectively than the tall *S. psammophila*, thus better preserving surface soil moisture. Consequently, moss crust coverage is highest in *A. ordosica* shrubland with its higher soil water content.

While some studies suggest *S. psammophila* has stronger soil particle refining effects than *A. ordosica*, our results show higher clay and silt contents beneath *A. ordosica* canopies and in inter-canopy spaces. This discrepancy may arise because abundant litter in *S. psammophila* shrubland intercepts fine particles captured by shrubs, preventing their movement downward to the soil surface beneath crusts. The higher clay and silt content in *A. ordosica* shrubland enhances soil surface stability and water retention, promoting moss crust colonization and development. Additionally, litter decomposition releases allelochemicals and nutrients, resulting in higher soil nutrient contents under *S. psammophila* canopies. However, the low soil water content in *S. psammophila* shrubland creates a dry environment unfavorable for moss colonization, and water deficiency may override any positive effects of nutrients. Therefore, moss crust coverage and thickness showed no significant correlation with total nitrogen, total phosphorus, or organic matter content ($P > 0.05$).

3.2 Allelopathic Inhibition of Moss Crust Development by Aqueous Extracts from Different Organs

Plant allelopathy refers to the harmful effects of chemicals released by plants on other plants (including microorganisms). This study found that extracts from all organs of both shrubs inhibited moss crust development ([Figure 3: see original paper]), with SE values varying among organs even at the same concentration, likely due to differences in allelochemical composition and content. At low concentration ($0.02 \text{ g} \cdot \text{mL}^{-1}$), inhibition strength was: *A. ordosica* roots > *A. ordosica* leaves > *S. psammophila* leaves > *S. psammophila* roots. However, under natural conditions, stem and leaf allelochemicals affect surrounding plants through rain and fog leaching, while root exudates influence seed banks and root activity underground, with minimal direct impact on surface moss crusts. As concentration increased ($0.2 \text{ g} \cdot \text{mL}^{-1}$), inhibition by *A. ordosica* and *S. psammophila* leaves strengthened significantly, with *S. psammophila* leaves showing the strongest inhibition ($\text{SE} = -0.95$). Due to lower litter accumulation, *A. ordosica* shrubland exerts lighter allelopathic pressure. In contrast, *S. psammophila*, with its dense, slender branches and high litter production, creates strong allelopathic inhibition, resulting in scarce moss crust growth. Thus, allelopathy is a key factor causing differences in moss crust development between the two shrubland types.

Conclusion

Total moss crust coverage and sub-canopy and inter-canopy coverage in *A. ordosica* shrubland were significantly higher than in *S. psammophila* shrubland, being 1.6, 2.9, and 1.1 times greater, respectively. Soil water content and clay and silt contents are key soil factors causing these differences, with *A. ordosica* promoting moss crust development by improving these properties. Additionally, high-concentration ($0.2 \text{ g} \cdot \text{mL}^{-1}$) *S. psammophila* leaf aqueous extract showed the strongest inhibitory effect on moss crust development. We infer that the superior moss crust development in *A. ordosica* shrubland results from the combined effects of higher soil water content, greater clay and silt fractions, and significant allelopathic inhibition by *S. psammophila* leaves. These findings suggest that vegetation type effects on biocrust development must be considered in arid region ecological restoration. The *A. ordosica*-moss crust combined protection configuration shows promising prospects for engineered sand fixation and desertification control in the Mu Us Sandy Land.

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