Postprint: Facilitative Effects of Caragana brachypoda Shrubs on Plant Communities and Soil Microbial Communities

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Date: 2021-04-23T00:00:00+00:00

Abstract

Taking Caragana brachypoda shrubs in the desert area of Inner Mongolia as the research object, field survey methods were used to analyze the effects of shrubs on plant communities, and traditional culture methods combined with molecular identification techniques were used to analyze the effects of shrubs on soil microbial communities. The results showed that: (1) The abundance and total biomass of plant communities within shrubs were significantly greater than those outside shrubs, but there was no significant difference in species richness and Shannon-Wiener index between inside and outside shrubs; (2) With increasing soil depth, there was no significant difference in culturable bacterial abundance and fungal abundance between surface soil and deep soil, while all other soil microbial community diversity characteristics showed that surface soil was significantly greater than deep soil; (3) Shrubs had a positive effect on soil microbial communities, and the positive effect was greatest in surface soil; (4) The promoting effect of shrubs on plant communities was greater than that on soil microbial communities.

Full Text

The Positive Effect of *Caragana brachypoda* Shrubs on Plant Communities and Soil Microbial Communities in the Inner Mongolia Desert Region

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Abstract

In this study, we used *Caragana brachypoda* shrubs in the Inner Mongolia desert region as our research subject. We employed field investigation methods to analyze the effects of shrubs on plant communities, and combined traditional cultivation methods with molecular identification techniques to analyze the effects of shrubs on soil microbial communities. The results showed that: (1) Both the abundance and total biomass of plant communities under shrub canopies were significantly greater than outside the canopies, but there was no significant difference in species richness and Shannon-Wiener index between inside and outside shrub canopies; (2) With increasing soil depth, there was no significant difference in soil culturable bacterial richness and fungal abundance between surface and deep soil layers, while all other soil microbial community diversity characteristics showed that surface soil was significantly greater than deep soil; (3) Shrubs had positive effects on soil microbial communities, and these positive effects were greatest in the surface soil layer; (4) The promoting effect of shrubs on plant communities was greater than that on soil microbial communities.

Keywords: *Caragana brachypoda*; shrub encroachment; soil culturable microorganisms; fertile island effect; plant community

Introduction

Woody encroachment, defined as the gradual increase in density, coverage, and biomass of shrubs in natural grasslands, has become a widespread phenomenon of vegetation succession in global arid and semi-arid regions. In Inner Mongolia grasslands of China, shrub expansion dominated by *Caragana* species represents a major landscape change. This expansion inevitably leads to interactions with inherent herbaceous plants, thereby affecting plant community structure and function. Consequently, the effects of shrubs on herbaceous plants have remained a central focus of shrub encroachment research.

Previous studies have reported varied impacts of shrub expansion on plant communities. Some research indicates that shrub encroachment significantly reduces species diversity, biomass, and cover of grassland communities. Other studies demonstrate facilitative effects, showing that herbaceous plant density, height, coverage, and biomass decrease progressively from shrub centers to peripheries, disappearing completely just beyond shrub boundaries. Conversely, some evidence suggests that woody plant invasion can enhance species diversity in certain contexts. These contrasting results highlight that shrub effects depend on specific community attributes and environmental conditions.

Soil microbial communities, as primary drivers of ecological processes such as soil organic matter decomposition and nutrient mineralization, have become increasingly important in shrub encroachment research. Studies reveal that shrubs create distinct "fertile island" effects, resulting in significantly higher soil microbial numbers beneath canopies compared to open areas, which improves soil microbial community structure and function. While shrub invasion significantly affects both plant and soil microbial communities, the relative importance of these effects and how they vary with soil depth remain unclear.

Caragana brachypoda, a leguminous deciduous shrub with short, dense, thorny branches, forms compact canopies that play crucial roles in water conservation and sand fixation in desert grasslands while providing food and shelter for animals. Distributed primarily in western Inner Mongolia (eastern and western Alxa, western Ordos, and northern Bayannur League) with additional populations in Ningxia and Gansu, *C. brachypoda* is a dominant shrub species in desert steppe ecosystems. In typical desert regions of Inner Mongolia, its biomass, coverage, and density have increased significantly, forming distinct patterns of shrub and herbaceous patches.

This study investigates *C. brachypoda* shrub patches and adjacent shrub-free grassland patches in a typical desert region of Inner Mongolia to address three key questions: (1) How do shrubs influence plant communities? (2) How do shrub effects on soil microbial communities vary with soil depth? (3) What is the relative importance of shrub effects on plant versus soil microbial communities? This research aims to enhance understanding of the ecological consequences of grassland shrub encroachment.

Materials and Methods

1.1 Study Area

The study was conducted in the Alxa Left Banner desert region of the Inner Mongolia Plateau (37.87°N, 105.34°E, elevation 800-1500 m). The climate is typical continental, characterized by strong winds, aridity, low rainfall, and intense evaporation. The mean annual temperature is 7.2°C; annual evaporation is 2900–3300 mm; annual precipitation is 80–220 mm; annual sunshine duration is 120–180 days; and total annual radiation is 628.1–669.9 $kJ \cdot cm^{-2}$. The dominant shrub is *C. brachypoda*, accounting for 20%–30% of total plant coverage. Other plant species include shrubs such as *Caragana tibetica*, *Caragana roborovskyi*, *Nitraria tangutorum*, *Artemisia desertorum*, *Atraphaxis frutescens*, *Helianthemum songaricum*, and *Oxytropis aciphylla*, and herbaceous plants including *Stipa glareosa*, *Asparagus cochinchinensis*, *Salsola ruthenica*, *Cynanchum thesioides*, and *Astragalus membranaceus*. Soils are primarily loose sandy loam or sandy soils.

1.2 Field Surveys

1.2.1 Plant Community Survey In July 2019, we selected 10 *C. brachypoda* shrubs and established 50 cm × 50 cm quadrats both inside shrub canopies and outside (more than 50 cm from canopy edges). We recorded species composition and density for all plants within each quadrat, then clipped all aboveground biomass at ground level, bagged it, transported it to the laboratory, oven-dried it at 65°C to constant weight, and measured aboveground biomass.

1.2.2 Soil Microbial Community Survey We selected 10 shrubs and collected approximately 300 g of soil samples from both inside and outside shrub canopies at three depths: 0–10 cm, 10–20 cm, and 30–40 cm. Samples were sealed in plastic bags, transported to the laboratory as quickly as possible, and stored at 4°C for soil microbial analysis.

We used traditional cultivation methods to analyze soil microbial community diversity. Soil bacteria were cultured on beef extract peptone medium, fungi on Martin' s medium, and actinomycetes on Gause' s No. 1 medium. After incubation, colonies were counted and classified according to morphological characteristics, then isolated and purified using plate streaking. Soil microbial numbers were expressed as colony-forming units per gram of dry soil.

For molecular identification, we extracted bacterial and fungal genomic DNA using a DNA extraction kit. Universal primers 27F (5 -AGAGTTTGATCCTGGCTCAG-3) and 1492R (5 -GGTTACCTTGTTACGACTT-3) were used to amplify bacterial 16S rRNA genes (including actinomycetes), while GeoA2 (5 -CCAGTAGTCATATGCTTGTCTC-3) and Geo11 (5 -ACCTTGTTACTTTTACTTCC-3) were used to amplify fungal 18S rRNA genes. Amplification products were sequenced by Beijing Genomics Institute and identified to genus level by BLAST comparison with the GenBank database (www.ncbi.nlm.nih.gov).

1.3 Data Analysis

We calculated plant community diversity using species richness (number of species), abundance (total number of individuals), biomass, and Shannon-Wiener index. Soil microbial community diversity was assessed using microbial richness, abundance, and Shannon-Wiener index.

Two-way ANOVA was used to test the effects of shrub presence and soil depth on soil microbial indicators, with Tukey HSD tests for differences among soil layers. Independent samples t-tests were used to analyze significant differences between inside and outside shrub canopies. All analyses were performed using SPSS 20.0.

The Shannon-Wiener index was calculated as:

$$H' = -\sum_{i=1}^{S} P_i \ln P_i$$

where P_i represents the proportion of individuals belonging to the ith species ($P_i = N_i/N$), N_i is the number of individuals of the ith species, and N is the total number of individuals in the community.

We used the Relative Interaction Index (RII) to assess shrub effects on plant communities (richness and biomass) and soil microbial communities (richness and abundance):

$$\mathrm{RII} = \frac{X_{\mathrm{in}} - X_{\mathrm{out}}}{X_{\mathrm{in}} + X_{\mathrm{out}}}$$

where X_{in} and X_{out} represent response variables inside and outside shrub canopies, respectively. RII ranges from -1 to +1, with positive values indicating facilitative effects and negative values indicating inhibitory effects.

For soil microbial communities, RII was calculated separately for each soil layer as:

$$\text{RII}_{\text{microbial}} = \frac{\text{Abundance}_{\text{in}} - \text{Abundance}_{\text{out}}}{\text{Abundance}_{\text{in}} + \text{Abundance}_{\text{out}}}$$

Results

2.1 Shrub Effects on Plant Communities

Caragana brachypoda shrubs affected different dimensions of plant community diversity differently. Plant community abundance and total biomass were significantly greater inside shrub canopies than outside ($P < 0.05$), while species richness and Shannon-Wiener index showed no significant differences between shrub canopies and open areas.

2.2 Shrub Effects on Soil Microbial Communities

Shrub presence significantly affected soil bacterial richness and Shannon-Wiener index but not bacterial abundance (richness: $F_{1,12} = 19.45$, $P < 0.01$; Shannon-Wiener index: $F_{1,12} = 2.47$, $P = 0.14$). Both bacterial richness and Shannon-Wiener index were higher inside shrub canopies than outside, with significant differences in the subsurface soil layer (Figure 2). Soil depth significantly affected bacterial abundance, richness, and Shannon-Wiener index (abundance: $F_{2,12} = 5.37$, $P < 0.05$; richness: $F_{2,12} = 8.39$, $P < 0.01$; Shannon-Wiener index: $F_{2,12} = 20.09$, $P < 0.01$).

Shrub presence significantly affected soil fungal abundance and richness but not the Shannon-Wiener index (abundance: $F_{1,12} = 6.627$, $P < 0.05$; richness: $F_{1,12} = 32.31$, $P < 0.01$; Shannon-Wiener index: $F_{1,12} = 0.276$, $P = 0.609$). Fungal abundance in deep soil layers was significantly greater inside shrub canopies than outside, while fungal richness in subsurface soil was significantly greater outside than inside shrub canopies (Figure 2). Soil depth significantly affected fungal abundance, richness, and Shannon-Wiener index (abundance: $F_{2,12} = 6.537$, $P < 0.01$; richness: $F_{2,12} = 19.043$, $P < 0.05$; Shannon-Wiener index: $F_{2,12} = 5.933$, $P < 0.05$). Both inside and outside shrub canopies, fungal abundance, richness, and Shannon-Wiener index were highest in the surface soil layer (Figure 2).

Shrub presence significantly affected soil actinomycete abundance but not richness or Shannon-Wiener index (abundance: $F_{1,12} = 74.1$, $P < 0.01$; richness: $F_{1,12} = 1.719$, $P = 0.214$; Shannon-Wiener index: $F_{1,12} = 0.565$, $P = 0.467$). At the same soil depth, actinomycete abundance was greater inside shrub canopies than outside (Figure 2). Soil depth significantly affected actinomycete abundance, richness, and Shannon-Wiener index (abundance: $F_{2,12} =$

92.122, $P < 0.01$; richness: $F_{2,12} = 26.746$, $P < 0.01$; Shannon-Wiener index: $F_{2,12} = 40.071$, $P < 0.01$). Both inside and outside shrub canopies, actinomycete abundance, richness, and Shannon-Wiener index decreased progressively with increasing soil depth.

2.3 Shrub Effects on Relative Abundance of Dominant Microbial Genera

The dominant bacterial genera inside and outside *C. brachypoda* shrub canopies were *Bacillus*, *Curtobacterium*, and *Paenibacillus* (Figure 3). Bacterial abundance decreased gradually with soil depth inside shrub canopies, while richness showed a unimodal pattern peaking in subsurface soil. The Shannon-Wiener index showed no significant difference between surface and subsurface soils but was lowest in deep soil. *Paenibacillus* was unique to deep soil layers (Figure 3). Soil depth significantly affected the relative abundance of *Bacillus* ($F_{2,6} = 9.339$, $P < 0.05$), which increased significantly with soil depth (Figure 3).

The dominant fungal genera were *Fusarium*, *Aspergillus*, *Microascaceae*, and *Chaetomium* (Figure 3). *Fusarium* and *Aspergillus* occurred at all soil depths both inside and outside shrub canopies. Soil depth significantly affected the relative abundance of *Fusarium* ($F_{2,6} = 5.933$, $P < 0.05$). The RII values for soil microbial communities showed a unimodal pattern with soil depth, with surface soils having significantly higher RII values than subsurface soils (Figure 4).

The dominant actinomycete genera were *Streptomyces* and *Nocardia* (Figure 3). *Nocardia* occurred only in surface and subsurface soils. Soil depth significantly affected the relative abundance of *Streptomyces$ both inside ($F_{2,6} = 37.041$, $P < 0.01$) and outside ($F_{2,6} = 4.911$, $P < 0.05$) shrub canopies, with relative abundance decreasing as soil depth increased.

2.4 Relative Importance of Shrub Effects on Plant vs. Soil Microbial Communities

The RII values for plant community richness and biomass were both positive (Figure 5), indicating that shrubs had significant facilitative effects on aboveground plant communities. The RII values for soil microbial communities were also positive across all soil depths (Figure 4), demonstrating positive shrub effects on microbial communities. However, RII values for plant communities were greater than those for soil microbial communities for both community richness and abundance, indicating that shrub effects on plant communities were stronger than those on soil microbial communities.

Discussion

3.1 Mechanisms of Shrub Effects on Plant and Soil Microbial Communities

Shrubs often function as "benefactors" that influence surrounding plants. Our study found that *C. brachypoda* shrubs significantly increased plant community abundance and total biomass. These facilitative effects can be attributed to two main mechanisms. First, shrubs improve microenvironmental conditions: lower temperatures and wind speeds, higher humidity, and improved soil nutrient environments beneath canopies promote plant growth. Second, shrubs provide shelter for seed germination and seedling establishment, protecting them from herbivory by livestock and wildlife, thereby increasing species abundance. Additionally, as a deciduous legume, *Caragana* species can promote nitrogen uptake by understory grasses and enhance nitrogen mineralization from soil organic matter, increasing understory productivity.

Caragana brachypoda shrubs also facilitated soil microbial communities, similar to their effects on plant communities. These positive effects are attributable to the "fertile island"effect created by shrubs. Furthermore, higher plant abundance and biomass beneath shrub canopies produce greater quantities of higher-quality litter, providing abundant food resources for soil microorganisms and promoting their growth. This explains why both aboveground plant communities and soil microbial communities showed positive RII values even in this strongly arid environment.

Numerous studies have demonstrated vertical heterogeneity in soil microbial abundance, richness, and Shannon-Wiener diversity indices. For example, soil microbial numbers beneath *Sophora alopecuroides*, *Achnatherum splendens*, and *Artemisia ordosica* decrease with soil depth. Similarly, soil microbial diversity indices in three forest types in the Lesser Khingan Mountains decline significantly with increasing soil depth. Our results are consistent with these findings: regardless of shrub presence, soil culturable bacteria, fungi, and actinomycetes showed highest abundance, richness, and Shannon-Wiener indices in surface or subsurface soils. This pattern occurs primarily because abundant surface litter increases nutrient content in topsoil, which decreases with depth, altering resource availability for soil microorganisms and consequently affecting their vertical distribution. Our results also showed that soil microbial community RII values differed significantly among soil layers, with the highest values in surface soils (Figure 4), indicating that shrub effects on surface soil microbial communities were strongest.

Although *C. brachypoda* shrubs had clear facilitative effects on both plant and soil microbial communities, the effects on plant communities were stronger (Figure 5). This may be because plant communities can more directly and easily benefit from shrub-mediated microenvironmental improvements.

3.2 Differential Effects on Different Community Attributes

Shrub effects vary among different plant community attributes (e.g., richness, abundance, Shannon-Wiener index, evenness). Our study found that shrubs significantly affected plant community abundance and biomass but not richness or Shannon-Wiener index (Figure 1), indicating that different diversity attributes show specific responses to shrub presence. Similarly, shrub effects on soil microbial communities varied among different attributes (richness, abundance, Shannon-Wiener index), microbial groups (bacteria, fungi, actinomycetes), and dominant genera.

Bacillus is one of the most active bacterial groups in soil, with low nutritional requirements, rapid growth, and resistance to adverse environments, playing important roles in soil nutrient cycling and plant growth promotion. Our study found *Bacillus* as the dominant genus both inside and outside shrub canopies, with relatively high abundance (Figure 3). *Bacillus* can colonize plant roots and form biofilms, primarily utilizing root exudates for rapid growth and reproduction. The well-developed root systems of *C. brachypoda* (roots can exceed 2–3 m in length) in deep soil layers provide abundant food resources for *Bacillus*, explaining why its relative abundance was highest in deep soils (Figure 3).

Nocardia is widely distributed in soil, decaying vegetation, and animal waste. As an aerobic saprophytic bacterium, it can degrade plant litter and obtain carbon and nitrogen sources for growth. Since surface soils contain abundant litter that directly provides required nutrients, *Nocardia* was primarily distributed in surface and subsurface soils (Figure 3).

Conclusion

Caragana brachypoda shrubs had significant facilitative effects on both plant communities and soil microbial communities, but the positive effects on plant communities were stronger than those on soil microbial communities. The effects of *C. brachypoda* on plant and soil microbial communities depended on specific community attributes, with different responses observed among microbial groups (bacteria, fungi, actinomycetes), diversity attributes (richness, abundance, diversity), and dominant genera. Soil microbial communities showed clear surface aggregation, and shrub effects on surface soil microbial communities were strongest.

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