Soil Fungal Community Structure and Function in Pinus tabuliformis Sand-Fixation Forests in the Horqin Sandy Land Postprint

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Abstract

This study investigates the relationship between soil fungal community structure and function and soil chemical properties and enzyme activities in Pinus sylvestris var. mongolica sand-fixation forests of different stand ages, providing a theoretical basis for the rational management and maintenance of these forests. Using mobile sandy land in the Horqin Sandy Land as the control (0 a), Pinus sylvestris var. mongolica forest stands aged 18 a, 34 a, 48 a, and 56 a were selected as research objects, and high-throughput sequencing technology was employed to analyze differences in soil fungal community structure and functional groups. The results showed that: (1) A total of 2,517 OTUs were obtained from the soil of Pinus sylvestris var. mongolica sand-fixation forests, belonging to 14 phyla, 48 classes, 127 orders, 286 families, and 579 genera of fungi; the dominant fungal phyla were Ascomycota (47.91%-67.34%), Basidiomycota (18.45%-43.70%), and Mortierellomycota (1.41%-8.36%); the dominant genera were Biappendiculispora, Scleroderma, Tomentella, Knufia, and Amphinema. (2) Venn diagram and NMDS analysis indicated that afforestation had a significant impact on soil fungal community structure, with the richness of soil fungi (ACE index, Chao index) increasing significantly at each stand age ($P < 0.05$); and showing significant positive correlations with organic matter, total nitrogen, total phosphorus, urease, dehydrogenase, catalase, neutral phosphatase, sucrase, and neutral protease ($P < 0.05$). (3) Fungal communities were dominated by symbiotrophic and saprotrophic trophic types; after afforestation, the relative abundance of symbiotrophic types increased compared with the control, while the relative abundance of saprotrophic types remained relatively stable. Afforestation plays an important regulatory role in soil fungal community structure and function; the research findings enrich the study of soil microbial communities in sand-fixation forests and provide a basis for soil health assessment of Pinus sylvestris var. mongolica sand-fixation forests in the Horqin Sandy Land.

Full Text

Structure and Function of Soil Fungal Community in *Pinus tabuliformis* Sand-Fixing Forests in Horqin Sandy Land

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Abstract

This study investigated the relationship between soil fungal community structure and function and soil chemical properties and enzyme activities in *Pinus tabuliformis* sand-fixing forests of different stand ages, aiming to provide a theoretical basis for rational management and protection of these forests. Taking mobile sandy land in the Horqin Sandy Land as the control (0 year), *P. tabuliformis* forests established for 18, 34, 48, and 56 years were selected as research objects. High-throughput sequencing technology was employed to analyze differences in soil fungal community structure and functional groups. The results showed: (1) A total of 2,517 operational taxonomic units (OTUs) were obtained from the soil of *P. tabuliformis* sand-fixing forests, belonging to 14 phyla, 48 classes, 127 orders, 286 families, and 579 genera. The dominant phyla were Ascomycota (47.91%-67.34%), Basidiomycota (18.45%-43.70%), and Mortierellomycota (1.41%-8.36%). The dominant genera included *Biappendiculispora*, *Scleroderma*, *Tomentella*, *Knufia*, and *Amphinema*. (2) Venn diagram and nonmetric multidimensional scaling (NMDS) analysis revealed that afforestation significantly impacted soil fungal community structure. The ACE and Chao indices of soil fungi at each stand age increased significantly ($P < 0.05$) and showed significant positive correlations with organic matter, total nitrogen, total phosphorus, urease, dehydrogenase, catalase, neutral phosphatase, sucrase, and neutral protease ($P < 0.05$). (3) Fungal communities were primarily composed of symbiotrophic and saprotrophic types. After afforestation, the relative abundance of symbiotrophic fungi increased compared with the control, while the relative abundance of saprotrophic fungi remained relatively stable. Afforestation plays an important regulatory role in soil fungal community structure and function. These findings enrich the understanding of soil microbial communities in sand-fixing forests and provide a basis for soil health evaluation of *P. tabuliformis* sand-fixing forests in the Horqin Sandy Land.

Keywords: Horqin Sandy Land; *Pinus tabuliformis*; soil fungi; community structure; ecological function; stand age

Introduction

Microorganisms are the most active components of soil, and their communities are extremely sensitive to environmental changes. In adapting to the environment, the structure, activity, and diversity of soil microbial communities undergo certain changes [1]. As one of the main components of soil microorganisms, fungi possess rich species, genetic, and functional diversity. They play crucial roles in promoting the decomposition of animal and plant residues, organic matter accumulation, and maintaining soil quality and productivity, thereby making important contributions to material and energy cycling in terrestrial ecosystems [2]. Soil fungi serve as important indicators for evaluating soil health, and their functional groups can effectively respond to external environmental changes. They are closely related to plant nutrient absorption, organic matter decomposition, and disease mediation [3]. Symbiotrophic fungi can form mycorrhizal symbioses with plant roots, promoting plant nutrient absorption, enhancing plant stress resistance, and improving plant adaptability to the environment [4]. Saprotrophic fungi are the main decomposers of litter and roots and play vital roles in key processes of soil nutrient cycling. Pathotrophic fungi can infect certain plant tissues, thereby limiting plant growth or even causing death, representing an important factor in vegetation degradation [5]. Therefore, studying soil fungal community structure and functional characteristics is essential for understanding their distribution patterns in response to stand age and environmental factors.

The Horqin sandy land covers an area of approximately 5.27×10^4 km^2 and features a fragile ecological environment. As an important region for ecological restoration in northern China, significant achievements have been made through years of sand-fixing vegetation construction. Establishing stable artificial vegetation plays a strong role in improving soil quality [6]. *Pinus tabuliformis* is widely used as an important sand-control and afforestation tree species in northern China due to its wind resistance, cold tolerance, and drought resistance advantages. It has played important roles in climate regulation, soil and water conservation, changing natural landscapes, and promoting sandland management [7]. Stand age is a key factor determining soil fungal communities in *P. tabuliformis* sand-fixing forests. As stand age increases, forest structure, understory vegetation composition, and forest microclimate change significantly [8], which further affects soil microbial community structure and composition, driving changes in soil fungal communities and forming specific fungal communities adapted to environmental changes [9]. Previous studies on *P. tabuliformis* forests have mainly focused on understory vegetation, soil physicochemical characteristics, enzyme activities, and microbial community structure [10-12], with microbial research concentrating primarily on bacteria, while fungal studies remain relatively scarce [13]. Given this context, this study employed high-throughput sequencing to analyze soil fungal community structure and functional group changes in *P. tabuliformis* sand-fixing forests of different stand ages in the Horqin Sandy Land, using mobile sandy land as a control. The study also explored the driving effects of soil chemical factors and enzyme activities on soil fungi to provide a theoretical basis for rational management of *P. tabuliformis* sand-fixing forests.

1. Materials and Methods

1.1 Study Area Overview

The study area is located at the Zhanggutai Experimental Site of the Liaoning Provincial Sand Control and Afforestation Research Institute (42°63 -42°74 N, 122°47 -122°58 E). The region has a pronounced continental monsoon climate, with an average annual temperature of 6.2 °C, annual precipitation of approximately 450 mm, annual evaporation of approximately 1,700 mm, and a frost-free period of 154 days. The site is situated on the southeastern edge of the Horqin Sandy Land. The main native plant species include *Chloris virgata*, *Elymus dahuricus*, *Digitaria sanguinalis*, and *Cleistogenes songorica*.

1.2 Sample Collection

Based on field surveys conducted in August 2023, mobile sandy land was used as the control (0 year), and *P. tabuliformis* sand-fixing forests of different stand ages (18, 34, 48, and 56 years) were selected as research objects, with areas of 4.5 hm^2 each. According to principles of representativeness, typicality, and similar site conditions, three 20 m × 20 m sample plots were established in each *P. tabuliformis* sand-fixing forest. Following the "S"sampling method, five sampling points were selected in each plot. After removing surface cover, soil samples from the 0–20 cm layer were collected, with stones and roots removed. Samples were placed in sealed bags, labeled, and transported to the laboratory. One portion was stored at -80 °C for soil fungal community structure and diversity analysis, while another portion was air-dried for determination of soil enzyme activities and chemical properties.

1.3 Determination of Soil Enzyme Activities and Chemical Properties

Soil organic matter was determined using the potassium dichromate volumetric method. Available nitrogen was measured by the alkali diffusion method. Available phosphorus was determined using the molybdenum antimony colorimetric method. Available potassium was measured by atomic absorption spectrometry. Total nitrogen was determined by the Kjeldahl method. Total phosphorus was measured using the HF-$HClO_4$ digestion method. Total potassium was determined by the H_2SO_4-$HClO_4$ digestion method. Neutral protease activity was measured using the Gales method. Neutral phosphatase activity was determined by the p-nitrophenyl phosphate colorimetric method. Sucrase activity was measured using the 3,5-dinitrosalicylic acid colorimetric method. Urease activity was determined by the indophenol blue colorimetric method. Dehydrogenase activity was measured using the triphenyltetrazolium chloride (TTC) colorimetric method. Catalase activity was determined by spectrophotometry. Specific experimental procedures followed the methods described by Zhang [14].

1.4 Soil Fungal Sequencing and Functional Group Classification

Soil DNA extraction was performed using the Tiangen Biotech Genomic DNA Isolation Kit. Purity and concentration were analyzed using a Nanodrop 2000 spectrophotometer and agarose gel electrophoresis. The ITS1F (5 -CTTGGTCATTTAGAGGAAGTAA-3) and ITS2R (5 -GCTGCGTTCTTCATCGATGC-3) fungal universal primers were used for amplification. Sequencing was completed by Shanghai Meiji Biomedical Technology Co., Ltd. using the Illumina MiSeq high-throughput sequencing platform. The UPARSE software was used to cluster effective sequences and generate operational taxonomic units (OTUs). The Fungi Functional Guild (FUNGuild) database was used to predict and classify the nutritional types and functional groups of soil fungi in *P. tabuliformis* sand-fixing forests. Results with confidence levels of "highly probable" and "probable" were retained. Communities with compound trophic types or compound functional groups were classified as "other trophic types" or "other pathotrophic types," respectively.

1.5 Data Processing

Microsoft Excel 2010 was used for data organization. SAS 9.1 was employed for analysis of variance (ANOVA). The Mothur software was used to calculate alpha diversity indices. Origin 2021 was used to generate bar stacking charts and correlation heatmaps. The Heat Map with Dendrogram plugin was used to create cluster heatmaps at the genus level. The CorrelationPlot version 3.3.1 plugin was used to generate association heatmaps. RDA analysis and plotting were performed using the "vegan" package in R.

2. Results

2.1 Soil Fungal Community Alpha Diversity

High-throughput sequencing of soil samples from different stand ages revealed that sequencing coverage exceeded 99.85% in all cases (Table 1), indicating that the sequencing depth adequately represented the diversity of soil fungal communities. Compared with the control, the ACE and Chao indices increased significantly at all stand ages, demonstrating that afforestation significantly enhanced soil fungal community richness. However, the Shannon and Simpson diversity indices and Pielou evenness index were not significantly affected by afforestation.

2.2 Soil Fungal Community Structure

2.2.1 Distribution of Soil Fungal Communities Venn diagrams visually represent the shared and unique OTUs among soil fungal communities at different stand ages. As shown in [Figure 1: see original paper], distinct differences existed in the number of unique OTUs across stand ages. The five treatments shared 1,007 OTUs, while the unique OTUs at each stand age were 98, 65, 52, 45, and 73, respectively. With increasing stand age, the number of unique soil fungal OTUs initially decreased and then gradually increased, suggesting that mobile sandy land harbored more unique fungal taxa.

Non-metric multidimensional scaling (NMDS) analysis showed that the first two axes of the Bray-Curtis algorithm effectively characterized fungal community differences among stand ages. As illustrated in [Figure 2: see original paper], soil fungal communities in mobile sandy land were distinctly separated from those in forested plots, with a stress value of 0.183, indicating good representation in two-dimensional space. This further demonstrates significant divergence between mobile sandy land and afforestation sites ($P = 0.001$), confirming that afforestation substantially influences soil fungal community structure.

[Figure 1: see original paper]
[Figure 2: see original paper]

2.2.2 Composition of Soil Fungal Communities Soil fungi belonged to 14 phyla across all treatments. At the phylum level ([Figure 3: see original paper]), phyla with average relative abundance >1% in any stand age were defined as dominant groups. The dominant phyla in *P. tabuliformis* forests were Ascomycota (47.91%-67.34%), Basidiomycota (18.45%-43.70%), and Mortierellomycota (1.41%-8.36%), with cumulative relative abundances of 93.87%, 98.60%, 97.98%, 97.52%, and 98.11% across stand ages. With increasing stand age, Ascomycota and Mortierellomycota showed initial decreases followed by increases, while Basidiomycota showed the opposite trend.

At the genus level ([Figure 4: see original paper]), dominant and common genera accounted for 70.12%-74.63% of total sequences. The dominant genus in the control was *Amphinema*. At 18 years, the dominant genera were *Biappendiculispora* and *Scleroderma*. At 34 years, the dominant genus was *Tomentella*. At 48 years, the dominant genera were *Tomentella* and *Knufia*. At 56 years, the dominant genera were *Knufia* and *Amphinema*. Compared with the control, the relative abundances of *Tomentella*, *Scleroderma*, *Tomentella*, *Knufia*, and *Amphinema* increased significantly ($P < 0.05$). The relative abundances of *Wilcoxina* and *Knufia* at 48 years and *Knufia* at 56 years increased extremely significantly ($P < 0.01$). Conversely, the relative abundances of *Biappendiculispora* and *Fusarium* decreased extremely significantly at 18 years ($P < 0.01$), while *Aspergillus* decreased extremely significantly at 34 and 48 years ($P < 0.01$). The relative abundances of *unclassified_{o___}{Capnodiales}* and *unclassified_{o___}{Trechisporales}* increased extremely significantly at 56 years ($P < 0.01$). Soil fungal communities at 34 and 48 years showed good aggregation, indicating high similarity.

[Figure 3: see original paper]
[Figure 4: see original paper]

2.3 Ecological Functions of Soil Fungi

Based on FUNGuild classification, fungal nutritional types and functional groups were predicted with confidence levels of "highly probable" and "probable." After screening, three nutritional types were identified ([Figure 5: see original paper]): symbiotrophic (10.78%-35.87%), saprotrophic (19.92%-27.50%), and pathotrophic (2.80%-10.63%). All treatments were dominated by symbiotrophic and saprotrophic fungi. The main ecological functional group of symbiotrophic fungi was ectomycorrhizal fungi, whose relative abundance increased with stand age and exceeded 24.54% at 56 years. The main functional group of saprotrophic fungi was undefined saprotrophs, which were relatively evenly distributed across stand ages, reaching minimum abundance at 48 years. Pathotrophic fungi were dominated by plant pathogens and animal pathogens, both of which accounted for less than 7.98% across all stand ages. Among other nutritional types, pathotrophic-saprotrophic fungi constituted the main component.

[Figure 5: see original paper]

2.4 Correlations Between Soil Fungal Communities and Soil Nutrients

Soil organic matter, total nitrogen, and total phosphorus in *P. tabuliformis* sand-fixing forests increased significantly compared with the control (Table 2). Available nitrogen content decreased significantly at 18 years but gradually increased with stand age. Available phosphorus showed the opposite trend, being highest at 18 years ($P < 0.05$), indicating high nitrogen demand during the rapid growth period of *P. tabuliformis*. Soil urease, dehydrogenase, catalase, neutral phosphatase, sucrase, and neutral protease activities increased significantly at all stand ages ($P < 0.05$), demonstrating that afforestation promoted nutrient transformation in Horqin Sandy Land soils. With increasing stand age, soil urease and dehydrogenase activities increased, indicating enhanced nitrogen transformation and redox processes. Sucrase and neutral protease activities at 56 years were significantly higher than at other stand ages ($P < 0.05$), indicating significantly enhanced transformation and decomposition of soil organic carbon and nitrogen in mature *P. tabuliformis* forests.

Correlation analysis revealed that the ACE and Chao indices were significantly positively correlated with organic matter, total nitrogen, total phosphorus, and all measured enzyme activities ($P < 0.05$). Symbiotrophic fungi were significantly positively correlated with organic matter, total nitrogen, total phosphorus, and all enzyme activities ($P < 0.05$). Saprotrophic fungi were significantly positively correlated with organic matter, total nitrogen, total phosphorus, and most enzyme activities ($P < 0.05$). Pathotrophic fungi were significantly negatively correlated with organic matter, total nitrogen, total phosphorus, and all enzyme activities ($P < 0.05$). The correlation heatmap ([Figure 6: see original paper]) visualized relationships between soil chemical variables, enzyme activities, and the top 30 fungal genera. *Wilcoxina* was significantly negatively correlated with organic matter and dehydrogenase ($P < 0.05$). *Metarhizium* was significantly negatively correlated with organic matter ($P < 0.05$). *Scleroderma* was significantly negatively correlated with available phosphorus ($P < 0.05$). *Biappendiculispora* and *Aspergillus* were significantly negatively correlated with most soil nutrients and enzyme activities ($P < 0.05$). *Tomentella* was significantly positively correlated with organic matter, total nitrogen, and dehydrogenase ($P < 0.05$). *Sagenomella* was significantly positively correlated with total nitrogen ($P < 0.05$). *Russula* was significantly positively correlated with organic matter and total nitrogen ($P < 0.05$). *Knufia* was significantly positively correlated with total nitrogen and dehydrogenase ($P < 0.05$).

[Figure 6: see original paper]

3. Discussion

3.1 Characteristics of Soil Fungal Community Structure in *Pinus tabuliformis* Sand-Fixing Forests

Fungi are widely distributed in deserts and represent important components of soil microorganisms with strong ecological adaptability. Alpha diversity indices effectively reflect the evenness, diversity, and richness of microbial communities, which are crucial for ecosystem stability and sustainability. In this study, the diversity and evenness indices of soil fungal communities in *P. tabuliformis* sand-fixing forests were not significantly affected by stand age or environmental factors. However, the richness indices (ACE and Chao) increased significantly and were strongly correlated with soil chemical properties and enzyme activities. This may be because soil nutrients and enzyme activities increased with stand age, promoting vegetation and soil fertility recovery, thereby increasing fungal community abundance and complexity. This enhanced environmental adaptability and strengthened soil ecological stability [15], positively contributing to the growth and development of *P. tabuliformis* sand-fixing forests.

At the genus level, soil fungal communities at 34 and 48 years showed good aggregation and similarity, indicating that community stability and homogeneity gradually increased with stand age, becoming more similar in later successional stages [16]. Soil chemical properties and enzyme activities were correlated to varying degrees with both dominant and common fungal genera. *Wilcoxina* is a mycorrhizal symbiotic fungus with good adaptability to special saline-alkali environments [17]. *Metarhizium* is an entomopathogenic fungus that can colonize plant roots and promote plant growth as a biocontrol agent [18]. *Knufia* has strong adaptability to nutrient-poor soils [19]. *Scleroderma* exhibits salt stress tolerance, and its decreasing relative abundance with stand age suggests that afforestation regulates soil pH [20]. *Tomentella* belongs to Ascomycota, has saprotrophic functions, and shows good adaptability to extreme environments and symbiotic lifestyles, promoting plant survival under harsh conditions [21]. *Tomentella* was absent in mobile sandy land but reached maximum relative abundance at 34 years (24.54%), then gradually decreased. This is likely because during early afforestation, when soil nutrients were poor, *Tomentella* adapted by altering its survival strategy to utilize saprotrophic functions. *Russula* is an ectomycorrhizal fungus that must form symbiotic associations with hosts to grow normally. This mutualistic symbiosis increases root absorption area and enhances nutrient and micronutrient uptake [22]. *Russula* was absent in mobile sandy land, indicating that establishing *P. tabuliformis* sand-fixing forests improved the soil microenvironment in Horqin Sandy Land.

3.2 Functional Characteristics of Soil Fungi in *Pinus tabuliformis* Sand-Fixing Forests

Fungi can adopt multiple nutritional strategies to adapt to environmental changes, with different substrate preferences and ecological strategies [23]. Studies have shown that soil fungi become more efficient and specialized in decomposing specific substances with increasing stand age [24]. This study found that symbiotrophic and saprotrophic types dominated across all treatments. Symbiotrophic fungi improve plant nutrient absorption and promote growth through symbiotic relationships, while saprotrophic fungi are important decomposers in soil nutrient cycling [25]. The relative abundance of symbiotrophic fungi increased with stand age compared with mobile sandy land, showing an increasing trend. This may be because during early afforestation (18 years), *P. tabuliformis* forests are in a rapid growth stage with high nutrient demand, requiring more ectomycorrhizal fungi to enhance nutrient absorption. As soil nutrients gradually increased, symbiotrophic fungal abundance declined, but increased again at 56 years due to increased herbaceous vegetation quantity and diversity, which led to higher symbiotrophic fungal abundance.

Saprotrophic fungi showed the opposite pattern to symbiotrophic fungi, reaching maximum abundance at 18 years. This is because afforestation provided more organic material for saprotrophs, while their decomposition of litter provided more carbon sources to the soil, increasing soil nutrients. This aligns with the maximum soil nutrient content observed at 18 years (Table 2), indicating that specific fungal groups became more efficient at litter decomposition [26]. Pathotrophic fungal relative abundance decreased compared with mobile sandy land across all stand ages, possibly due to antagonistic interactions among different nutritional types. The enrichment of symbiotrophic fungi reduced pathotrophic colonization, positively affecting *P. tabuliformis* forest growth [27]. These results demonstrate that establishing *P. tabuliformis* sand-fixing forests improved soil fungal community structure, and that soil fungi can adapt to environmental changes by regulating functional groups at different stand ages, which is closely related to the stability of the sandy ecosystem.

4. Conclusion

Artificial afforestation is an important means of sandland management. Soil fungal community structure and functional characteristics can effectively indicate soil health status. Establishing *Pinus tabuliformis* sand-fixing forests in the

Horqin Sandy Land significantly increased soil fungal richness. The dominant fungal phyla were Ascomycota, Basidiomycota, and Mortierellomycota. At the genus level, *Tomentella*, *Knufia*, and *Sagenomella* showed significant positive correlations with soil chemical properties and enzyme activities. Symbiotrophic and saprotrophic fungi were the main nutritional types, and their enrichment promoted the decomposition of animal and plant residues and plant nutrient absorption. Soil fungal communities at 34 and 48 years showed good aggregation and structural similarity. Overall, soil nutrient status peaked at 18 years and stabilized at 56 years, indicating that *P. tabuliformis* sand-fixing forests showed no signs of decline. In conclusion, the structure and functional characteristics of soil fungal communities in *P. tabuliformis* sand-fixing forests can effectively reflect soil fertility and plantation growth status, providing important guidance for rational management and protection of these forests.

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Note: Figure translations are in progress. See original paper for figures.