Soil Microbial Community Response to Spartina alterniflora Invasion in Min River Estuary Mangroves: Postprint

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Abstract

Phospholipid fatty acid (PLFA) analysis was employed to investigate the effects of the invasive plant Spartina alterniflora on soil microbial community structure in mangrove wetlands of the Min River estuary and to explore its main influencing factors. The results showed that a total of 22 PLFA biomarkers were detected in soils from three different vegetation communities (mangrove community MC, mangrove-Spartina alterniflora mixed community MS, and Spartina alterniflora community SC), with the total PLFA biomass in MS soil being significantly higher than in other vegetation communities, while the variation trend of soil physicochemical properties and enzyme activities among the three vegetation communities was: MC > MS > SC, indicating that Spartina alterniflora invasion increased soil microbial biomass but significantly decreased physicochemical properties and enzyme activities, leading to obvious degradation of soil quality in mangrove wetlands. The most abundant PLFA biomarkers in soils of the three vegetation communities were 16:0, 16:1w7c, 9Me15:0w, and 18:1w12c. Significant differences existed in the relative biomass of characteristic microorganisms in soils, with bacteria being the most abundant, followed by fungi and actinomycetes, and protozoa being the least abundant. Community diversity indices showed similar patterns, with microbial group diversity indices in MS soil being lower than those in MC, indicating that Spartina alterniflora invasion reduced soil microbial community diversity indices. Principal component analysis (PCA) could basically distinguish the characteristics of microbial communities among the three different vegetation communities. Correlations existed among soil physicochemical properties and enzyme activities, with organic carbon, total nitrogen, sucrase, and catalase showing significant or extremely significant positive correlations with Gram-negative bacteria and actinomycetes. The study results indicate that Spartina alterniflora invasion has the potential to affect soil nutrient cycling in mangrove communities, particularly regarding

carbon, nitrogen, and phosphorus cycling and enzyme activities, by altering the abundance of microbial groups associated with soil environments conducive to its own growth, thereby competing for favorable environments and rapidly expanding to achieve invasion.

Full Text

Preamble

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Soil Microbial Community of Mangrove Forests and Its Responses to the Invasion of *Spartina alterniflora* in the Minjiang River Estuary

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Abstract

This study employed phospholipid fatty acid (PLFA) analysis to investigate the effects of the invasive plant *Spartina alterniflora* on soil microbial community structure in mangrove wetlands of the Minjiang River estuary. Soil physicochemical properties and enzyme activities were measured across three vegetation communities: mangrove community (MC), mangrove-*Spartina alterniflora* mixed community (MS), and *Spartina alterniflora* community (SC). The results revealed 22 distinct PLFAs across all samples. The MS soil exhibited significantly higher total PLFA content than the other vegetation types. Soil physicochemical properties and enzyme activities followed the trend MC > MS > SC, indicating that *S. alterniflora* invasion increased soil microbial biomass while simultaneously decreasing physicochemical properties and enzyme activities, leading to significant degradation of mangrove wetland soil quality.

The PLFA biomarkers with highest concentrations were 16:0, 16:1 7c, 9Me15:0 , and 18:1 12c. Significant differences in relative microbial biomass were observed among communities, with bacteria showing the highest abundance, followed by fungi, actinomycetes, and protozoa. Community diversity indices exhibited similar patterns, with MS soil microbial community diversity indices lower than

those of MC. All diversity indices decreased following *S. alterniflora* invasion. Principal component analysis distinguished microbial community characteristics across vegetation types. Soil physicochemical properties showed close correlations with enzyme activities, and SOC, TN, sucrose, and catalase were significantly correlated with Gram-positive bacteria and actinomycete PLFAs.

These findings demonstrate that *S. alterniflora* invasion can affect nutrient metabolism cycles in mangrove communities, particularly carbon and phosphorus cycling and enzyme activities. The invader may alter microbial biomass to create soil environments favorable for its own growth, thereby facilitating rapid expansion and successful invasion.

Keywords: *Spartina alterniflora*; mangrove; soil microbial community; PLFA; exotic plant invasion

1. Introduction

Rhizosphere soil microorganisms represent one of the most active and influential components in vegetation ecosystems, participating in soil energy flow, nutrient cycling, and organic matter transformation. The tripartite interaction and regulatory mechanisms among plants, soil, and microorganisms play crucial functional roles in regulating ecological processes and plant growth and development. Exotic plants can selectively shape rhizosphere microbial community structure through root exudates and litter-derived allelochemicals, while changes in microbial communities subsequently influence allelochemical release, soil nutrient cycling, and information transfer, thereby affecting plant growth processes. Investigating the mechanisms through which exotic plant invasion affects soil nutrient metabolism cycles and rhizosphere microorganisms is therefore essential.

Spartina alterniflora, as an exotic invasive species, exhibits broad ecological adaptability and strong reproductive capacity. Since its introduction, it has spread explosively across coastal mudflats in China, occupying native species' ecological niches, altering local growth environments, forming monospecific dominant communities, reducing local biodiversity, and severely damaging the structure and function of original ecosystems. Previous research has focused primarily on *S. alterniflora* reproductive characteristics, competitive traits with native species, ecosystem impacts, invasion mechanisms, and control technologies. Increasing attention has been directed toward its effects on soil ecosystem processes and soil biodiversity. Studies by Zhang et al. and others have examined impacts on soil carbon and nitrogen properties, while Zhou et al. investigated effects on microbial diversity in coastal salt marshes using plate culture techniques. Research indicates that *S. alterniflora* can alter bacterial community structure, increasing abundances of ammonia-oxidizing bacteria, methanogens, and sulfate-reducing bacteria. However, studies on how *S. alterniflora* affects

rhizosphere soil microbial community structure and function in invaded vegetation remain limited.

Fujian Province, with 941.9 hm² of mangroves, represents the northernmost distribution of natural mangroves in China. Since *S. alterniflora* introduction, mangrove wetlands have suffered continuous invasion, with wetland area 萎缩 and severe degradation. By 2016, *S. alterniflora* coverage had reached 4,166 hm². Investigating changes in mangrove rhizosphere microbial community structure following invasion and developing effective protection strategies have become urgent priorities. This study focuses on mangrove communities in the Minjiang River estuary wetland, employing PLFA analysis to examine soil microbial community structural characteristics across different vegetation types and explore relationships among microbial community composition, soil enzyme activities, and physicochemical properties following *S. alterniflora* invasion. The objectives are to reveal the soil science mechanisms of *S. alterniflora* invasion and provide theoretical foundations for understanding allelopathic interactions between *S. alterniflora* and mangrove rhizosphere microorganisms, thereby informing wetland ecosystem protection and restoration.

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2. Study Area Overview

The study area was located in the Shanyutan Wetland, the largest component of the Minjiang River estuary wetland (119°34 12 -119°41 40 E, 26°00 36 - 26°03 42 N). Situated in a transitional zone between tropical and mid-subtropical regions, the area features a typical monsoon climate with warm, humid conditions, annual precipitation of approximately 1,350 mm, and mean annual temperature of 19.3°C. The wetland, formed by sediment deposition in the Minjiang River, experiences regular semidiurnal tides and year-round tidal influence. Soils are primarily coastal saline soils and sandy soils with high salt content and pH ranging from acidic to neutral.

Vegetation types include coastal salt marshes, psammophytic communities, and mangroves. Dominant native species include *Kandelia candel*, *Phragmites communis*, and *Cyperus malaccensis*. Since *S. alterniflora* invasion, it has rapidly spread, competing with native dominant populations and forming invasion patches of varying sizes around *K. candel* communities. By 2016, approximately 306.94 hm² of *S. alterniflora* salt marsh had formed, occupying mangrove ecological niches, inhibiting seedling growth, and slowing community expansion and self-renewal.

[Figure 1: see original paper] Location of the study area and sampling sites in the Minjiang River estuary tidal marsh

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3. Field Sampling and Soil Property Measurements

In August 2015, three vegetation communities were selected in the Shanyutan Wetland based on different invasion degrees: non-invaded mangrove community (MC), mixed mangrove-*S. alterniflora* community (MS), and pure *S. alterniflora* community (SC). Rhizosphere soils from vigorously growing vegetation were collected from each community (20 m sampling plots). Five typical plots (10–20 m² each) were established per community. Soils were transported to the laboratory, where samples from each community were thoroughly mixed.

Due to high water content, one portion was air-dried in a ventilated, shaded area for 2–3 days until slightly dry for microbial community and enzyme activity analysis, while another portion was naturally air-dried and sieved for physicochemical property analysis. Soil organic carbon (SOC) was measured by potassium dichromate oxidation, total nitrogen (TN) by semi-micro Kjeldahl digestion, total phosphorus (TP) by perchloric acid digestion, and total potassium (TK) by flame photometry. pH was determined by potentiometry (1:2.5 soil:water ratio).

Enzyme activities were measured as follows: sucrase (Suc) by 3,5-dinitrosalicylic acid colorimetry, urease (Ure) by indophenol blue colorimetry, catalase (CAT) by potassium permanganate titration, acid phosphatase (PHO) by disodium phenyl phosphate colorimetry, and polyphenol oxidase (PPO) by pyrogallol colorimetry. All treatments included substrate-free controls, and each experiment included sample- and substrate-free controls.

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4. PLFA Extraction and Gas Chromatography Detection

PLFA analysis was conducted following established methods. Briefly, 5 g fresh soil was placed in 50 mL centrifuge tubes with 20 mL of 0.2 mol/L KOH-methanol solution for fatty acid release and methylation. Samples were incubated in a 37°C water bath for 1 hour with vortexing every 5 minutes, then cooled. After adding 3 mL of 1.0 mol/L acetic acid and 10 mL hexane, samples were vortexed for 10 minutes and centrifuged at 2,600 rpm for 15 minutes. The upper hexane layer was transferred to clean tubes, evaporated to dryness under N , and redissolved in methyl tert-butyl ether containing the internal standard (i19:0, 1 g/mL).

Analysis was performed on a Varian 240 GC-MS system with an autosampler. Chromatographic conditions: injector temperature 170°C, initial oven temperature 170°C for 2 minutes, ramped at 5°C/min to 280°C, held for 5 minutes, then ramped at 40°C/min to 300°C, held for 1.5 minutes. All organic solvents were chromatographic grade.

PLFA biomarker nomenclature followed Frostegård et al. Microbial groups were identified based on characteristic profiles: i15:0, a15:0, i16:0, a16:0, i17:0, a17:0 for Gram-positive bacteria; cy17:0, cy19:0, 16:1 5c, 16:1 7, 18:1 5c, 18:1 7c for

Gram-negative bacteria; 10Me16:0, 10Me17:0, 10Me18:0 for actinomycetes; 18:2 6c, 18:1 9c, 18:3 6c for fungi; and 20:4 6c for protozoa. Concentrations were calculated using peak areas and internal standard curves (g/g dry soil).

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5. Data Processing and Statistical Analysis

Data processing and mapping were performed using Excel 2010 and SPSS 22.0. Variance analysis, diversity indices, principal component analysis (PCA), and correlation analysis were conducted using DPS v7.05. Diversity indices were calculated as follows:

Shannon-Wiener index (H):

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

Pielou evenness index (J):

$$J = \frac{H'}{\ln S}$$

Simpson dominance index (D):

$$D = 1 - \sum_{i=1}^{S} P_i^2$$

Brillouin index (H):

$$H = \frac{1}{N} \ln \left(\frac{N!}{\prod_{i=1}^{S} n_i!} \right)$$

McIntosh index (D_{Mc}):

$$D_{Mc} = \frac{N - \sqrt{\sum_{i=1}^{S} n_i^2}}{N - \sqrt{N}}$$

Where P_i is the proportion of individuals in the ith species, S is the total number of species, N is the total number of individuals, and n_i is the number of individuals of the ith species.

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6. Results

6.1 Comparison of Soil Physicochemical Properties and Enzyme Activities Among Vegetation Communities

Soil physicochemical properties varied significantly among the three vegetation communities (Table 1). pH values showed no significant differences (5.89–5.87). SOC content ranged from 15.91±0.35 to 24.39±0.96 g/kg, TN from 1.24±0.08 to 1.84±0.07 g/kg, TP from 0.71±0.04 to 1.02±0.04 g/kg, and TK from 13.82±0.34 to 16.89±0.42 g/kg. All nutrients differed significantly among communities, following the trend MC > MS > SC, indicating degraded soil nutrient status following invasion.

Basic soil physicochemical properties at different vegetation communities

Enzyme activities also showed significant variation (Table 2). Sucrase, catalase, and phosphatase activities were significantly higher in MC than in MS and SC. The overall trend MC > MS > SC was observed for all enzymes, with MC showing the highest activities and SC the lowest.

Soil enzyme activities at different vegetation communities

6.2 Types and Total Content of Soil Microbial PLFAs

A total of 22 PLFAs were detected across the three vegetation communities. Total PLFA content varied significantly: 89.40±6.15 g/g in MC, 97.31±18.88 g/g in MS, and 33.94±6.47 g/g in SC. While PLFA types were similar among communities, their abundances differed markedly. The biomarkers 16:0, 16:1 7c, 9Me15:0 , and 18:1 12c dominated across all soils, comprising 21.67%, 22.81%, and 17.50% of total PLFAs in MC, MS, and SC, respectively.

Types and contents of PLFAs in soils of different vegetation communities

6.3 Characteristic Microbial Group PLFAs

Bacterial PLFAs showed the highest abundance, followed by fungi, actinomycetes, and protozoa. Gram-positive bacteria accounted for 54.07%, 54.35%, and 51.86% of total PLFAs in MC, MS, and SC, respectively. Gram-negative bacteria showed the trend MS > MC > SC. The ratio of Gram-negative to Gram-positive bacteria followed MC > SC > MS, while the fungi:bacteria ratio was SC > MC > MS.

Contents and ratios of microbial group PLFAs in soils of different vegetation communities

6.4 Microbial Community Diversity Indices

Diversity indices revealed significant differences among communities (Table 5). Shannon-Wiener, Brillouin, and McIntosh indices followed the trend MC > MS > SC, while Simpson index showed SC > MC > MS. Pielou evenness was highest

in MC and lowest in SC. These patterns indicate reduced microbial community diversity following *S. alterniflora* invasion.

Soil microbial communities' diversity indices of different vegetation types

6.5 Principal Component Analysis of Microbial Communities

PCA of PLFA data showed the first two components explained 93.19% of variance (PC1: 63.58%, PC2: 29.61%). MC soils clustered on the positive PC1 axis, MS soils on the positive PC2 axis, and SC soils on the negative PC1 axis. Key PLFAs loading on PC1 included i14:0, 9Me15:0 , a15:0, 16:1 7c, cy17:0, 16:0, 18:1 9c, and 18:0, while PC2 was characterized by 20:0 and 24:0.

[Figure 2: see original paper] Principal components analysis of different microbial groups PLFA in soils of different vegetation communities

6.6 Correlations Among Soil Properties, Enzyme Activities, and Microbial Groups

Soil physicochemical properties showed significant positive correlations with enzyme activities (Table 6). SOC, TN, sucrose, and catalase were significantly or highly significantly correlated with Gram-positive bacterial and actinomycete PLFAs. These relationships indicate that soil nutrient status and microbial function are closely linked.

Correlation analysis of soil physicochemical properties and enzyme activities at different vegetation communities

Microbial group PLFAs showed varying correlations with soil properties (Table 7). Gram-positive bacteria were significantly positively correlated with SOC, sucrose, catalase, and polyphenol oxidase. Gram-negative bacteria showed significant positive correlations with TN and polyphenol oxidase. These patterns suggest that *S. alterniflora* invasion alters microbial community functional relationships with soil nutrients.

Correlation analysis of microbial groups PLFA and physicochemical properties and enzyme activities

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7. Discussion

7.1 Effects of *S. alterniflora* Invasion on Soil Physicochemical Properties and Enzyme Activities

Vegetation succession alters soil nutrient pools. Soil enzymes, as active substances secreted by microbial metabolism, play crucial roles in material cycling and energy transformation. Soil nitrogen content serves as a biological indicator of soil quality, while enzyme activities reflect soil fertility. Our results show that SOC, TN, TP, TK, and enzyme activities in mangrove soils were significantly

higher than in mixed or pure *S. alterniflora* communities, indicating degraded soil quality following invasion. These results align with Zhang et al., suggesting that mangrove soil carbon sequestration functions have declined. The decrease in enzyme activities reflects altered microbial community function, as enzyme activities mirror microbial functional capacity. Soil microbial community diversity results from comprehensive interactions among soil nutrients, litter, and root exudates, reflecting close relationships with soil fertility and nutrient cycling. Ehrenfeld et al. demonstrated that exotic plant invasion is closely related to soil nutrient cycling processes, with *S. alterniflora* spread altering microbial community composition and consequently nutrient cycling.

7.2 Relationships Between Soil Physicochemical Properties and Enzyme Activities Under Invasion

In the Minjiang River estuary, soil physicochemical properties and enzyme activities showed significant or highly significant positive correlations. Sucrase and catalase were significantly correlated with TN, TP, and TK, indicating that carbon, nitrogen, and potassium supply and transformation are influenced by sucrase and acid phosphatase activities. Catalase affects organic matter transformation rates. Urease reflects nitrogen supply status, while acid phosphatase influences organic phosphorus decomposition. The positive correlations between soil properties and enzyme activities suggest that *S. alterniflora* invasion disrupts these functional relationships. Correlations between microbial groups and soil properties indicate that microorganisms play central roles in ecosystem nutrient cycling. For instance, nitrifying bacteria are crucial in nitrogen cycling, while pseudomonads can decompose organic matter as carbon sources, and phosphate-solubilizing bacteria enhance phosphorus availability. The altered microbial community structure under invasion likely affects these functional capacities.

7.3 Impacts of *S. alterniflora* Invasion on Mangrove Soil Microbial Communities

Rhizosphere microbial community structure and diversity are closely related to plant growth and development and play important roles in exotic plant invasion success. Native plants and soil microorganisms develop balanced symbiotic relationships over time. Exotic plant invasion disrupts this balance by altering soil microbial communities, affecting native species growth and community succession. Invasion impacts occur through two primary pathways: (1) microbial communities change with aboveground vegetation succession as invaders modify habitats and reduce biodiversity, and (2) invaders release allelochemicals through root exudates and litter that directly affect rhizosphere microbes, subsequently influencing native plant growth. For example, invasive *Centaurea* species in North America secrete antimicrobial allelochemicals, while *Ageratina adenophora* in China alters soil fungal communities and increases ammonia-oxidizing bacteria to accelerate invasion.

Our PLFA analysis revealed that *S. alterniflora* invasion increased total microbial biomass in mixed communities compared to pure mangrove stands, consistent with Zhou et al. The invasion increased Gram-positive bacterial, fungal, and protozoan biomarkers while decreasing Gram-negative bacterial and actinomycete biomarkers, indicating altered community structure that may affect nutrient cycling and energy flow. Reduced diversity indices in invaded soils suggest that changes in functional microbial groups involved in nutrient cycling and interplant competition may affect mangrove nutrient uptake, thereby favoring *S. alterniflora* competition and expansion. The allelopathic interactions between *S. alterniflora* and mangrove rhizosphere microorganisms require further investigation.

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8. Conclusion

This study demonstrates that *S. alterniflora* invasion degrades mangrove soil habitats in the Minjiang River estuary, with significant negative impacts on soil physicochemical properties, enzyme activities, and microbial community structure. The invasion significantly increased Gram-positive bacterial and fungal biomarkers while decreasing Gram-negative bacterial and actinomycete biomarkers. Soil microbial community diversity indices declined following invasion. The altered microbial community structure has the potential to affect carbon, nitrogen, and phosphorus cycling and enzyme activities, creating soil conditions favorable for *S. alterniflora* growth while disadvantaging mangroves. Given that mangrove ecosystems have low species diversity and poor stability, they are particularly vulnerable to exotic species invasion. This study provides insights into invasion mechanisms from a microbial perspective and molecular level, offering a foundation for understanding allelopathic interactions between *S. alterniflora* and mangrove rhizosphere microorganisms. PLFA analysis proved effective for characterizing soil microbial community structure and provided accurate information on microbial diversity.

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