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RESEARCH ARTICLE

Effects of Maize Potato Intercropping and Different Fertilization Methods on Rhizosphere Soil Microorganisms and Yield of Potato

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Abstract: A field experiment with three replicates was conducted to explore the effects of maize-potato intercropping and different nitrogen application strategies on rhizosphere soil microorganisms and potato yield. Microbial community analysis was based on relative abundance. Maize-potato intercropping improves land use efficiency, yet how differentiated nitrogen management regulates rhizosphere microecology and potato productivity in this system remains unclear. Clarifying nitrogen-mediated shifts in soil microbial communities under intercropping provides a theoretical basis for precise nutrient optimization. Five treatments were established: potato monoculture conventional fertilization (CK), intercropping intraspecific conventional nitrogen (T1), intercropping intraspecific reduced nitrogen (T2), intercropping interspecific conventional nitrogen (T3), intercropping interspecific reduced nitrogen (T4). We combined high-throughput sequencing, agronomic traits, and yield measurements to characterize rhizosphere microbial and crop responses. The findings revealed that, in terms of microbial community response, while treatment T3 significantly decreased bacterial community richness and diversity, Fungal communities were more sensitive to nitrogen reduction; Treatment T2 notably increased the relative abundance of the Proteobacteria phylum and *Sphingomonas* genus, maintaining high bacterial diversity. Fungal communities were more sensitive to nitrogen reduction; treatment T4 markedly lowered fungal richness, whereas treatment T1 promoted the proliferation of beneficial fungal groups, including those from the Mortierellomycota phylum. Regarding crop growth and yield formation, under treatment T3, the plant height of potatoes increased by 5.44% compared to CK, with both fresh and dry weights per tuber reaching their highest levels. Fresh tuber yield peaked in T3, showing a significant increase of 9.6% over CK, along with an elevation in the commercial tuber rate by 41.7%. Yield improvement was mainly attributed to larger tuber size rather than increased tuber number. The intercropping system compensated for a slight decrease in tuber number by optimizing individual tuber quality, which was associated with shifts in rhizosphere microbial community structure, achieving synergistic improvements in yield and quality. Under maize-potato intercropping, conventional interspecific fertilization (T3) can significantly enhance potato yield and commercial quality by regulating the rhizosphere microbial community structure, such as enriching functional bacteria like *Parasegetibacter*.

Although nitrogen reduction treatments (T2, T4) maintained microbial diversity to some extent, they necessitate vigilance against potential pathogen proliferation risks. This research provides a theoretical basis for the microbially-driven mechanisms underlying reduced fertilizer input and increased efficiency in intercropping systems.

Keywords: Intercropping, Nitrogen Reduction, Intraspecific, Interspecific, Rhizosphere Soil, Microorganisms, Yield

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Introduction

Research Significance

The potato (*Solanum tuberosum L.*), ranking as the fourth most significant staple crop globally after rice, wheat, and maize, boasts high nutritional and medicinal values, making it one of the crops with the most promising development prospects [1] In recent years, alongside the rapid expansion of the potato industry, its cultivation scale has been increasing annually. However, constrained by limited arable land resources, intensive potato farming has become increasingly prevalent. This has led to escalating issues of continuous cropping obstacles, which exacerbate soil-borne diseases year after year, significantly diminishing crop yield and quality, thereby severely impacting the healthy development of the potato industry. Continuous cropping obstacles have emerged as a major challenge for the sustainable growth of the potato sector [2].

Previous Research Advancements

Numerous scholars have extensively explored the mechanisms underlying continuous cropping obstacles in crops, attributing them primarily to long-term monoculture practices that result in unbalanced soil nutrients, deterioration of the soil biological environment, and allelopathic effects. As potato cultivation areas continue to expand, crop rotation becomes increasingly challenging, and the duration of continuous cropping extends, leading to a continuous decline in soil microbial diversity. This, in turn, causes severe outbreaks of pests and diseases, reduced yields, and diminished quality in potatoes [3-6]. Intercropping maize with potatoes has been validated by numerous studies as an effective strategy to mitigate continuous cropping obstacles in potatoes [7-9]. Experiments demonstrate that long-term intercropping can maintain soil chemical properties. On continuously cropped soils, intercropping maize and potatoes significantly increases organic matter content, promoting the evolution of soil into a highly fertile "bacterial-type" condition, showcasing notable alleviation of continuous cropping obstacles. In soils subjected to 10 years of continuous cropping, research indicates that intercropping maize and potatoes enhances the functional diversity of microbial communities, boosts metabolic activity among microbial groups, markedly improves crop tolerance to adverse environmental conditions and resistance to pests and diseases, while also reducing or eliminating harmful pathogenic fungi, thereby effectively improving the rhizosphere microenvironment [10,11]. Results from five consecutive years of maize-potato intercropping reveal enhanced proliferation of beneficial microbial populations, significantly elevating the resistance of intercropped crops [12]. Prior investigations found that under intercropping conditions, applying fertilizer between rows rather than within rows or uniformly across the field promotes yield advantages in the intercropping system. Under a 2:2 row ratio and 190 cm bandwidth model for maize-potato intercropping, narrow inter-row planting intensifies nutrient competition between species but paradoxically enhances intercropping benefits [13]. Additionally, heterogeneous nitrogen supply between and within rows alters the relative competitive abilities of maize and potatoes, with interspecific competition and nitrogen heterogeneity interacting to regulate crop growth processes. Furthermore, inter-row fertilization reduces weed interference on maize growth [14] Nitrogen is a crucial component of defense enzyme systems, pathogenesis-related proteins, and disease-resistant substances in plants; thus, rational nitrogen application forms the foundation for enhancing plant resistance. Extensive research shows that late blight is the primary recurrent disease affecting potatoes in maize-potato intercropping systems [15]. At nitrogen application rates ranging from 90-135 kg/ha, late blight incidence remains relatively low. However, excessive nitrogen application exacerbates late blight severity, diminishes or even negates the advantages of maize-potato intercropping, and drastically reduces yields.

Conversely, reduced nitrogen fertilization exhibits pronounced promotional effects on phosphorus and potassium uptake in intercropped potatoes [16]. Maize-potato intercropping significantly boosts organic matter content in continuously cropped soils, driving their transformation into highly fertile "bacterial-type" environments, thereby demonstrating substantial mitigation of continuous cropping obstacles [17].

Research Starting Point

Intercropping facilitates mutual benefits between species through mechanisms such as moisture supplementation, nutrient activation, and recognition of interspecific relationships, guiding root growth towards inter-species rows. Given nitrogen's vital role in plant defense systems, pathogenesis-related proteins, and disease-resistant compounds, appropriate nitrogen application serves as the cornerstone for bolstering plant resistance. Existing studies on maize-potato intercropping mostly focus on uniform nitrogen application within crop rows, and few systematically distinguish intraspecific (within row) and interspecific (between row) nitrogen placement modes. Previous microbial research in this intercropping system only compared monoculture vs. intercropping without decoupling the independent effects of nitrogen position and nitrogen reduction on rhizosphere microorganisms. Most related studies measured overall soil microbes rather than potato rhizosphere microbial communities, which cannot directly reflect the microecological feedback of target tuber crops to fertilization regulation. To fill the above research gaps, this study constructs five treatments combining monoculture, intraspecific/inter specific nitrogen placement, and conventional/reduced nitrogen input to investigate the effects of maize-potato intercropping combined with varying nitrogen application methods both intra- and inter-specific placement alongside moderate nitrogen reduction on the rhizosphere soil microbiota of potatoes.

Key Issues to Address

Research gap: Prior intercropping studies failed to separate the regulatory effects of nitrogen placement location (intraspecific vs. interspecific rows) and nitrogen reduction magnitude on potato rhizosphere bacterial and fungal community diversity, composition, and crop yield; no research has clarified whether interspecific nitrogen fertilization can optimize rhizosphere microbial structure and offset the yield loss caused by reduced nitrogen supply in maize-potato intercropping systems. Core novelty of this study:

(1) We innovatively set paired intraspecific/interspecific nitrogen placement treatments under both conventional and 50% reduced nitrogen rates, which distinguishes this work from previous single-row fertilization experiments

(2) We specifically target potato rhizosphere soil rather than bulk soil, to reveal microbe-tuber yield linkage under intercropping nutrient regulation

(3) We systematically compare divergent responses of bacteria and fungi to nitrogen position and nitrogen reduction, and identify microbial biomarkers associated with high commercial tuber yield under interspecific fertilization. Objectives: To investigate how intercropping and nitrogen management alter rhizosphere microbial communities and potato growth, yield, and quality. This paper focuses on potatoes, employing field experiments contrasting conventional nitrogen fertilization in sole potato stands. It explores the impacts of different nitrogen quantities applied within versus between rows under maize-potato intercropping conditions. By measuring rhizosphere soil microorganisms, agronomic traits, and yields across various treatments, the study seeks to elucidate how intercropping and diverse fertilization strategies influence potato cultivation, providing essential theoretical and technical support for the potato farming industry

Materials and Methods

Overview of the Experimental Site and Test Materials

The field experiment was conducted in 2024 at the Practical Training Base of Kunming University, Anning City, Yunnan Province, China (102°32'22" E, 24°56'14" N, altitude 1800 m). The site has an average annual temperature of 17.0°C, a frost-free period of 232 days, and receives 1933.2 hours of sunshine annually. The average annual precipitation is 765.1 mm, which was concentrated in June (309.7 mm), July (373.4 mm), and August (484.0 mm) of the experimental year. The previously recorded July precipitation value contained a typographical error; the annual total precipitation was revised to match the sum of monthly rainfall observations from the Anning experimental station in 2024. A summary of the experimental site is presented in Table 1.

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Table 1: Overview of experimental sites

pH	Soilorganicmatter (g kg^{-1})	Availablenitrogen content (mg kg^{-1})	Availablephosphoruscontent (mg kg^{-1})	Availablepotassium content (mg kg^{-1})	Totalphosphorus (mg kg^{-1})	Totalpotassium (mg kg^{-1})
8.06	9.21	88.95	1.76	103.93	84.77	1512.38

Potato: Virus Free Seed Tubers. Maize: The Commercial Variety 'Jingdian 8

Fertilizer Materials: Controlled-Release Nitrogen (N) Fertilizer: Composition: N ≥28%. Typically contains negligible amounts of Phosphorus (P) and potassium (K).

High-Phosphorus, High-Potassium Controlled-Release Fertilizer: N: P: K ratio of 2:15:30.

Experimental Design and Sampling

Experimental Design: A total of five treatments were established: CK: Monoculture of potatoes with conventional N fertilization (N, 150 kg ha^{-1}). T1: Maize-potato intercropping with conventional intraspecific N application (N, 150 kg ha^{-1}). T2: Maize potato intercropping with reduced intraspecific N application (N, 75 kg ha^{-1}). T3: Maize-potato intercropping with conventional interspecific N application (N, 150 kg ha^{-1}). T4: Maize-potato intercropping with reduced interspecific N application (N, 75 kg ha^{-1}). Fertilization details: Normal N rate = 150 kg·hm^{-}2, reduced N rate = 75 kg·hm^{-}2. Definition of fertilization placement: Intraspecific fertilization (T1, T2) means all nitrogen fertilizer was buried within the planting rows of maize or potato; interspecific fertilization (T3, T4) means all nitrogen fertilizer was buried in the vacant inter-row zone between maize and potato rows, with a 40 cm horizontal distance from both crop rows. For all five treatments, the total application rates of phosphorus (P_2O_5) and potassium (K_2O) were fully consistent (90 kg P_2O_5 hm^{-2} and 180 kg K_2O hm^{-2}) and applied uniformly as basal fertilizer before sowing. Only nitrogen dosage and placement position differed between treatments, which excludes differential P/K supply as a confounding factor affecting potato yield and rhizosphere microbial communities. Fertilizer was applied basally at sowing. Interspecific fertilization (T3, T4) was placed between maize and potato rows (40 cm apart); intraspecific fertilization (T1, T2) was placed within crop rows. For both monoculture and intercropping systems, the row spacing within a crop's rows (intraspecific) and between different crops (interspecific) was standardized at 40 cm, with a plant-to-plant spacing of 40 cm. The plot size was 5.5 m × 6.5 m, and the experiment was arranged in a Randomized Complete Block Design (RCBD) with three replicates, which is standard for field agronomic trials. Controlled-release compound fertilizers were applied as a basal dressing, mixed into the soil in their designated positions immediately prior to sowing. A schematic diagram of the field layout for the different planting systems is shown in Fig. 1. (Note: A: Monoculture of Potatoes, B: Intraspecific Row Fertilization in Intercropping, C: Interspecific Row Fertilization in Intercropping).

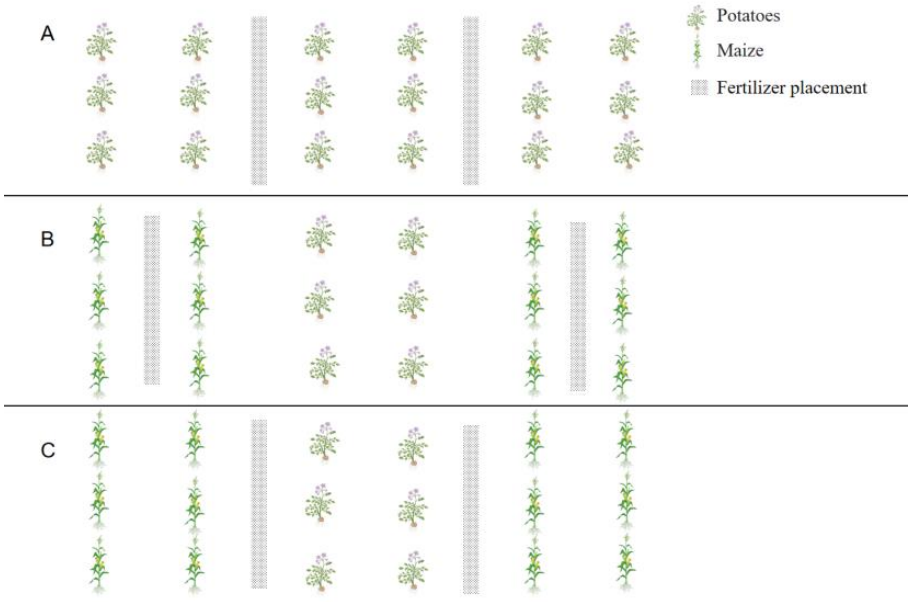

Fig. 1: Schematic diagram of the field experiment

At maize physiological maturity, five sampling points were evenly arranged in each plot via the five-point sampling method; 6 potato plants were randomly excavated at each point, resulting in 30 potato individuals per plot. Rhizosphere soil was brushed from the root surface of each plant using the root-shaking method [18] All rhizosphere soil from the 30 plants within one plot was fully homogenized to form a single composite sample per plot. Each treatment contained three independent biological replicate plots, and composite soil samples from each replicate were stored, DNA-extracted, sequenced, and analyzed separately without cross-pooling across replicates. The homogenized samples were then divided into three subsamples, sealed in self-sealing bags, and stored under different conditions. One subsample was stored at -80 °C for subsequent microbiological analysis.

Determination of Growth and Yield Indicators

During the mid to late stages of potato cultivation, measurements were taken for plant height, stem diameter, and number of main stems. Ten plants were randomly selected from each plot, with three replicates per treatment, and their average values were calculated. Plant Height (cm): Measured using a tape measure from the base of the plant to the top of the main stem (i.e., the growing point). Stem Diameter (cm): Measured at a point 3 cm above the soil surface on the main stem using a vernier caliper. Number of Main Stems: Observed by examining branching patterns; potatoes typically have branches along their main stem, each producing new stems and leaves. Yield Calculation: Potatoes were harvested, cleaned to remove surface dirt, then weighed for fresh weight. Dry weight was determined after oven-drying at 80°C to constant weight. Commercial tuber rate was defined as the proportion of tubers >50 g. Dry matter conversion rate = dry weight / fresh weight $\times$ 100%. The entire plot (5.5$\times$6.5 m) was harvested. Yield (kg· hm^{-2}) = plot fresh weight (kg) / plot area (m^2) × 10,000. Starch, protein, reducing sugar, and disease-related quality indices were not measured in this study. These data were used to calculate yield.

Soil Total DNA Extraction, PCR Amplification, and Library Construction

Total soil DNA was extracted using the CTAB-SDS method [19]. The purity and concentration of the extracted DNA were assessed via agarose gel electrophoresis. An appropriate quantity of each DNA sample was then diluted in sterile water to a final concentration of 1 ng/μL. Using the diluted genomic DNA as the template, PCR amplification was performed. For bacterial community analysis, the V4 region of the 16S rRNA gene was targeted using the barcoded primer pair 515F-806R. The reaction was conducted with Phusion® High-Fidelity PCR Master Mix with GC Buffer (New England Biolabs) and a high-efficiency, high-fidelity polymerase to ensure both amplification efficiency and accuracy. For fungal community ITS amplification: The ITS1−ITS2 hypervariable region of fungal rRNA was amplified using the barcode-tagged primer pair ITS1F (5'-CTTGGTCATTTAGAGGAAGTAA-3') and ITS2R (5'-GCTGCGTTCTTCATCGATGC-3'). PCR reaction system (20 μL): 10 μL Phusion High-Fidelity PCR Master Mix, 0.4 μL forward primer (10 μM), 0.4 μL reverse primer (10 μM), 2 μL template DNA (1 ng μL^{-1}), 7.2 μL sterile ddH_2O. PCR thermal cycling program: Initial denaturation at 98 °C for 1 min; 30 cycles of denaturation at 98 °C for 10 s, annealing at 50 °C for 30 s, extension at 72 °C for 30 s; final extension at 72 °C for 5 min. Purification, library construction, and Illumina NovaSeq 6000 sequencing followed the same protocol as bacterial 16S amplicons. Fungal OTU taxonomic annotation was performed against the UNITE 8.3 fungal ITS reference database with a confidence threshold of 0.8.

The resulting PCR products were first visualized on a 2% agarose gel. Products that passed quality control were purified using magnetic beads. Following quantification with a microplate reader, samples were pooled in equal amounts based on their concentration. The pooled mixture was again checked by 2% agarose gel electrophoresis, and the target band was excised and recovered using a Qiagen gel extraction kit.

Library construction was performed using a TruSeq® DNA PCR-Free Sample Preparation Kit. The constructed libraries were quantified using a Qubit fluorometer and quantitative real-time PCR (qPCR). After confirming library quality, sequencing was carried out on an Illumina NovaSeq 6000 platform.

Data Processing and Analysis

Raw sequencing data were demultiplexed based on barcode sequences and PCR primers. The resulting reads for each sample were then assembled using FLASH software [20]. After trimming the barcode and primer sequences, the assembled sequences, referred to as Raw Tags, underwent a stringent quality filtering process [21] to generate high-quality Clean Tags. Following the QIIME [22] (Version 1.9.1) quality control pipeline, chimeric sequences were identified and removed. This was

performed by aligning the tags against a reference database using an algorithm such as UCHIME [23] within the USEARCH suite, ultimately yielding the final Effective Tags [24].

All Effective Tags from every sample were clustered into Operational Taxonomic Units (OTUs) at a 97% sequence identity threshold using the UPARSE algorithm [25]. Representative sequences for each OTU, defined as the most frequent sequence within that cluster, were selected. These representative sequences were then taxonomically annotated by alignment against the SILVA 138 [26] SSU rRNA database [27] using the Mothur method with a confidence threshold of 0.8–1. This generated taxonomic information at various levels: Kingdom, Phylum, Class, Order, Family, Genus, and Species. A multiple sequence alignment of all OTU representative sequences was conducted using MUSCLE [28] to establish their phylogenetic relationships. Finally, all samples were normalized by subsampling to the same sequencing depth (the lowest read count among all samples) to ensure comparability for subsequent diversity analyses.

Within-sample (Alpha) diversity was assessed using QIIME (Version 1.9.1). Key metrics calculated included Observed OTUs, Chao1, Shannon, Simpson, ACE, Good's Coverage, and PD_whole_tree. Rarefaction curves, Rank abundance curves, and Species accumulation curves were generated using R software (Version 2.15.3). Differences in Alpha diversity indices between groups were statistically tested. For comparisons between two groups, a t-test or Wilcoxon rank-sum test was employed. For comparisons involving more than two groups, Tukey's HSD test and the Kruskal-Wallis H test (via the 'agricolae' package) were used.

Between-sample (Beta) diversity was evaluated. Unweighted UniFrac distances were calculated using QIIME (Version 1.9.1) to assess community dissimilarity, and a UPGMA (Unweighted Pair-Group Method with Arithmetic Mean) clustering tree was constructed. Principal Component Analysis (PCA) was performed in R (Version 2.15.3) to visualize sample clustering based on community composition.

Agronomic traits, yield, and other phenotypic data were organized using Excel 2016. Statistical analysis: Phenotypic data were analyzed by Duncan’s multiple range test. Microbial alpha diversity was analyzed by ANOVA followed by Tukey’s HSD. Beta diversity was assessed by PERMANOVA based on Bray−Curtis dissimilarity. Multiple-testing correction was performed using the False Discovery Rate (FDR). Statistical analysis was performed using IBM SPSS Statistics 26. Significant differences between treatments were determined using Duncan's Multiple Range Test (DMRT) at a significance level of P<0 05. Figures were created using Origin 2018.

Results and Analysis

Changes in Rhizosphere Soil Microorganisms

Richness and Diversity of Rhizosphere Soil Microbial Communities

As shown in Table 2, through sequencing of the bacterial 16S-V4 region in each sample, all samples had a coverage rate of over 99.6%, indicating that the library capacity was sufficiently large to reflect the true composition of the bacterial communities in the samples. From the analysis results of the Alpha diversity index: The ACE index showed that the T3 treatment (3659.39±293.31) was significantly lower than the T1 treatment (4190.23±79.57) and the T4 treatment (4219.62±265.63) (P<0.05). The Chao1 index indicated that the T3 treatment (3674.77±111.69) was significantly lower than the T1 treatment (4131.61±58.47) and the T4 treatment (4108.54±232.08) (P<0.05). The Shannon index revealed that the T3 treatment (8.61±0.29) was significantly lower than the CK treatment (9.28±0.13) (P<0.05). Although there were numerical differences in the Simpson index among various treatments, they did not reach statistical significance. These findings suggest that after maize-potato intercropping, employing conventional interspecific fertilization (T3) significantly reduces the richness (ACE, Chao1 indices) and diversity (Shannon index) of the rhizosphere soil bacterial community associated with potatoes. In contrast, the richness indices for the T1 (conventional intraspecific fertilization) and T4 (interspecific nitrogen reduction) treatments were relatively higher, while no significant differences were observed between the T2 (intraspecific nitrogen reduction) treatment and the CK treatment across all measured indices, implying that intraspecific nitrogen reduction has no notable impact on the diversity and abundance of the rhizosphere soil bacterial community in potato.

As shown in Table 3, through sequencing of the fungal ITS region in each sample, all samples had a coverage rate of over 99.6%, indicating that the library capacity was sufficiently large to reflect the true composition of the fungal communities

in the samples. From the analysis results of the Alpha diversity index: The ACE index showed that the T4 treatment (1006.32±69.21) was significantly lower than the CK treatment (1135.33±71.44) and the T2 treatment (1175.77±36.17) ($P<0.05$). The Chao1 index indicated that the T4 treatment (1011.10±68.79) was significantly lower than the CK treatment (1146.53±66.42) and the T2 treatment (1178.32±31.84) ($P<0.05$). The Simpson index revealed that the T4 treatment (0.97±0.01) was significantly lower than other treatments. Although there were numerical differences in the Shannon index among various treatments, they did not reach statistical significance. These findings suggest that after maize-potato intercropping, employing interspecific nitrogen reduction (T4) significantly reduces the richness (ACE, Chao1 indices) and evenness (Simpson index) of the rhizosphere soil fungal community associated with potatoes. In contrast, no significant differences were observed between the T1 (conventional intraspecific fertilization) and T3 (conventional interspecific fertilization) treatments and the CK treatment across all measured indices, implying that conventional intraspecific and interspecific fertilization have no notable impact on the diversity and abundance of the rhizosphere soil fungal community in potatoes. The richness indices for the T2 (intraspecific nitrogen reduction) treatment did not differ significantly from those of the CK, and this treatment exhibited the highest fungal community richness.

Table 2: Bacterial OTU abundance and alpha diversity index

Samples	Alpha diversity				
	ACE	Chao1	Simpson	Shannon	Coverage
CK	4020.48±163.45ab	3998.42±165.64ab	0.99±0.00a	9.28±0.13a	0.97±0.00a
T1	4190.23±79.57a	4131.61±58.47a	0.99±0.00a	9.22±0.03a	0.97±0.01a
T2	3941.02±231.64ab	3917.87±195.21ab	0.99±0.00a	8.84±0.42ab	0.97±0.01a
T3	3659.39±293.31b	3674.77±111.69b	0.99±0.00a	8.61±0.29b	0.97±0.00a
T4	4219.62±265.63a	4108.54±232.08a	0.99±0.00b	9.05±0.11ab	0.97±0.01a

Note: Different lowercase letters indicate significant differences at the level of 0.05. The same as below

Table 3: Fungal OTU abundance and alpha diversity index

Samples	Alpha diversity				
	ACE	Chao1	Simpson	Shannon	Coverage
CK	1135.33±71.44a	1146.53±66.42a	0.97±0.01a	6.92±0.11a	0.96±0.002a
T1	1085.04±42.94ab	1074.46±42.94ab	0.98±0.00a	6.73±0.23a	0.96±0.006a
T2	1175.77±36.17a	1178.32±31.84a	0.97±0.01a	6.00±0.63a	0.97±0.005a
T3	1099.49±80.29ab	1114.34±81.19a	0.97±0.01a	6.71±0.50a	0.96±0.003a
T4	1006.32±69.21b	1011.10±68.79b	0.97±0.01b	6.60±0.45a	0.96±0.004a

Analysis of the Impact of Different Treatments on Bacterial Community Distribution Characteristics

An analysis of the top 10 phyla in the sample information (Fig. 2) revealed that the dominant groups were Proteobacteria (32.0%-41.2%), Bacteroidota (28.0%-35.6%), Acidobacteriota (7.3%-10.3%), Actinobacteriota (3.1%-6.6%), Verrucomicrobiota (3.6%-4.3%), and Firmicutes (2.2%-3.6%). Among these, the relative abundance of the Patescibacteria phylum in the conventional fertilization treatment for monoculture potatoes (CK) was higher (3%) than in the maize-potato intercropping treatments with conventional intraspecific fertilization (T1, 2.7%) and reduced nitrogen application within species (T2, 1.7%). Following reduced nitrogen application within species in maize-potato intercropping (T2), the relative abundance of the Proteobacteria phylum (41.2%) was significantly higher than in all other treatments, while the relative abundances of Bacteroidota (0.280) and Patescibacteria (0.017) were significantly lower. Compared to conventional interspecific fertilization (T3) in maize-potato intercropping, reduced nitrogen application between species (T4) led to an increase in the relative abundance of the Acidobacteriota phylum (T4: 10.35 / T3: 8%), whereas the relative abundances of Bacteroidota (T4: 33.6% / T3: 35.6%) and Firmicutes (T4: 2.2% / T3: 3.5%) decreased. Under maize-potato intercropping, the relative abundance of the Acidobacteriota phylum in the reduced nitrogen application between-species treatment (T4) was the highest among all treatments. The above analysis indicates that under maize-potato intercropping, reduced nitrogen application within species (T2) significantly increased the relative abundance of the Proteobacteria phylum, while reduced nitrogen application between

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species (T4) elevated the relative abundance of the Acidobacteriota phylum. Different intercropping patterns and nitrogen application levels had significant effects on the bacterial community structure at the phylum level.

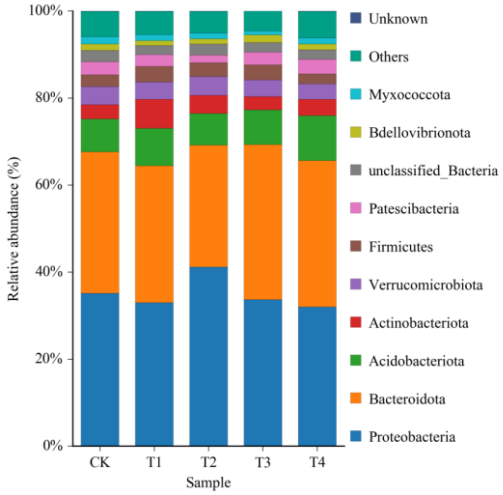

Fig. 2: The relative abundance of species at the bacterial phylum level

Analysis of the main bacterial genera in the sample information (Fig. 3) showed that the dominant groups included Terrimonas (5.3%-7.1%), *Sphingomonas* (5.2%-10.0%), Flavisolibacter (3.7%-4.9%), unclassified_Chitinophagaceae (2.8%-5.0%), Massilia (2.1%-3.6%), unclassified_Bacteria (2.1%-3.1%), Flavitalia (2.0%-2.5%), Lysinibacter (1.8%-2.4%), Ramlibacter (1.7%-2.7%), and *Parasegetibacter* (1.6%-2.4%). Among these, the relative abundances of unclassified_Chitinophagaceae and Ramlibacter in the conventional fertilization treatment for monoculture maize (CK) were higher than in some intercropping treatments. After reduced nitrogen application within species in maize-potato intercropping (T2), the relative abundances of *Sphingomonas*, Flavisolibacter, Massilia, Flavitalia, and *Parasegetibacter* were higher compared to other treatments. In the conventional interspecific fertilization treatment (T3) for maize-potato intercropping, the relative abundance of *Parasegetibacter* was higher than in other treatments. Under maize-potato intercropping, the relative abundance of the *Sphingomonas* genus in the reduced nitrogen application within-species treatment (T2) was significantly higher than in other treatments. The above analysis suggests that under maize-potato intercropping, reduced nitrogen application within species (T2) significantly increased the relative abundance of genera such as *Sphingomonas*, while conventional interspecific fertilization (T3) elevated the relative abundance of *Parasegetibacter*. Different planting patterns and nitrogen application levels produced specific effects on the bacterial community structure at the genus level.

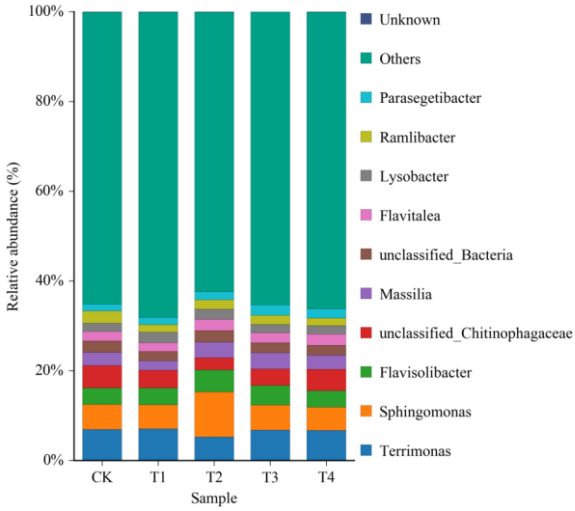

Fig. 3: The relative abundance of species at the bacterial genus level

Analysis of the Impact of Different Treatments on Fungal Community Distribution Characteristics

An analysis of the main fungal phyla in the sample information (Fig. 4) revealed that the dominant groups were Ascomycota (62.6%-70.5%), Mortierellomycota (9.6%-18.4%), Basidiomycota (7.2%-12.6%), Chytridiomycota (2.0%-6.3%), and Rozellomycota (1.3%-4.2%). Among these, the relative abundances of Basidiomycota and Rozellomycota in the conventional fertilization treatment for monoculture potatoes (CK) were higher than in the maize-potato intercropping treatments with conventional intraspecific fertilization (T1) and reduced nitrogen application within species (T2). After applying conventional intraspecific fertilization in maize-potato intercropping (T1), the relative abundance of the Mortierellomycota phylum (18.4%) was significantly higher than in all other treatments, while the relative abundances of the Basidiomycota and Chytridiomycota phyla decreased. Following reduced nitrogen application within species in maize-potato intercropping (T2), compared to conventional intraspecific fertilization (T1), the relative abundances of the Ascomycota, Chytridiomycota, and Glomeromycota phyla increased, whereas those of the Mortierellomycota and Rozellomycota phyla decreased. In the maize-potato intercropping treatment with reduced nitrogen application between species (T4), relative to conventional interspecific fertilization (T3), the relative abundances of the Ascomycota and Glomeromycota phyla rose, while those of the Chytridiomycota and Rozellomycota phyla fell. Under maize-potato intercropping, among the conventional fertilization treatments, the relative abundance of the Mortierellomycota phylum was higher in the intraspecific conventional fertilization treatment (T1) than in the interspecific conventional fertilization treatment (T3). The above analysis indicates that under maize-potato intercropping, conventional intraspecific fertilization (T1) significantly increased the relative abundance of the Mortierellomycota phylum, while reduced nitrogen application within species (T2) elevated the relative abundance of the Ascomycota phylum. Different planting patterns and nitrogen application levels had significant effects on the fungal community structure at the phylum level.

Analysis of the main fungal genera in the sample information (Fig. 5) showed that the dominant groups included Fusarium (12.3%-20.6%), Mortierella (9.6%-18.4%), Humicola (1.9%-6.3%), Botryotrichum (1.1%-4.8%), Penicillium (2.2%-3.0%), Clonostachys (1.4%-2.8%), and Fusicolla (1.3%-2.1%). Among these, the relative abundance of the Humicola genus in the conventional fertilization treatment for monoculture potatoes (CK) was higher (0.063) than in the maize-potato intercropping treatments with conventional interspecific fertilization (T3, 0.019) and reduced nitrogen application between species (T4, 0.058). After applying conventional intraspecific fertilization in maize-potato intercropping (T1), the relative abundance of the Mortierella genus (0.184) was significantly higher than in all other treatments, while the relative abundances of the Fusarium and Humicola genera decreased. Following reduced nitrogen application within species in maize-potato intercropping (T2), compared to conventional intraspecific fertilization (T1), the relative abundances of the Fusarium, Botryotrichum, Penicillium, Fusicolla, and Nagaashia genera increased. In the maize-potato intercropping treatment with reduced nitrogen application between species (T4), relative to conventional interspecific fertilization (T3), the relative abundances of the Humicola, Staphylotrichum, and Nagaashia genera rose, while those of the Fusarium, Botryotrichum, and Clonostachys genera fell. Under maize-potato intercropping, among the conventional fertilization treatments, the relative abundance of the Mortierella genus was higher in the intraspecific conventional fertilization treatment (T1) than in the interspecific conventional fertilization treatment (T3). The above analysis suggests that under maize-potato intercropping, conventional intraspecific fertilization (T1) significantly increased the relative abundance of the Mortierella genus, while reduced nitrogen application treatments (T2, T4) tended to elevate the relative abundances of genera such as Fusarium and Botryotrichum. Different planting patterns and nitrogen application levels had significant effects on the fungal community structure at the genus level.

Variations in Biological Traits and Yield Across Different Treatments

Comparison of Potato Agronomic Traits Under Diverse Planting Regimes

As evidenced by Table 4, regarding plant height, the T3 treatment notably surpassed the CK, registering a 5.44% increase. While treatments T1 and T4 also exhibited taller plants than CK, these differences did not achieve statistical significance. In terms of stem diameter and main stem count, no significant variations were observed among any treatments. This suggests that while various treatments can enhance potato plant height, their impact on stem thickness and branching is less pronounced. The response of potatoes to soil nutrients appears to prioritize vertical growth (main stem elongation) over lateral expansion or tillering, aligning with tuber crops' strategy to avoid shade competition. T3 increased plant height but not stem thickness or main stem number, indicating that height can serve as a reliable indicator of improved growth and light capture in this intercropping system.

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Table 4: Comparison of agronomic traits of potatoes under different planting patterns

Treatment	Indicator		
	Plant height (cm)	Stem thickness (cm)	Number of main stems
CK	68.91±4.43b	9.47±0.89a	4.70±1.03a
T1	72.20±5.52ab	9.82±1.01a	5.15±1.35a
T2	70.90±5.29ab	9.56±1.01a	4.85±1.31a
T3	72.66±6.21a	9.81±1.05a	5.15±1.14a
T4	71.82±4.43ab	9.65±0.88a	4.95±0.76a

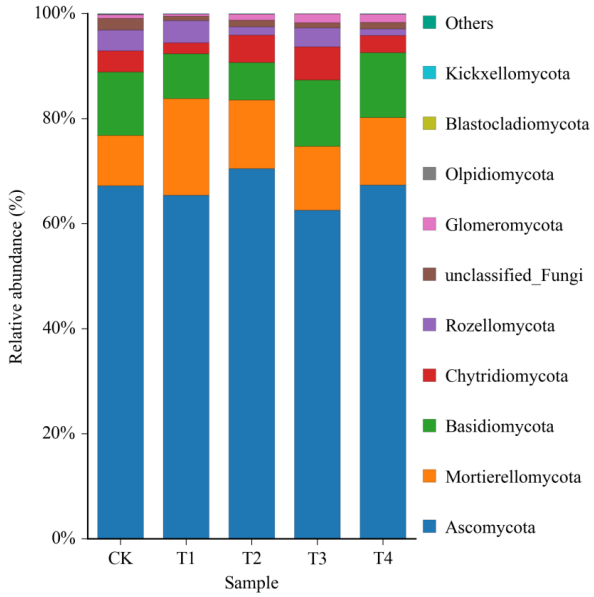

Fig. 4: The relative abundance of species at the fungal phylum level

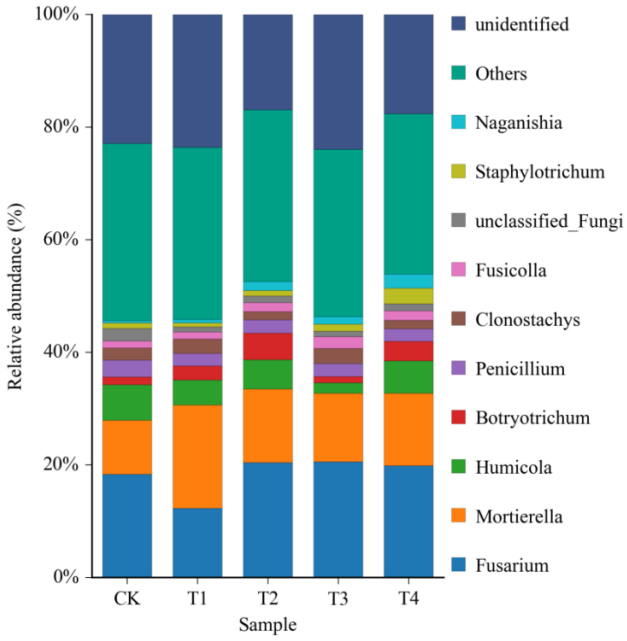

Fig. 5: The relative abundance of species at the fungal genus level

Effects of Different Cultivation Modes on the Quality Traits of Potatoes

As shown in Table 5, compared with CK (conventional nitrogen application in potato monoculture), all intercropping treatments showed improvements in certain quality traits. In terms of fresh weight per tuber, T1 (364.95 g) and T3 (380.48 g) increased by 5.3% and 9.8%, respectively, compared to CK (346.58 g), while T4 (353.37 g) showed a slight increase of 2.0%. For average dry weight per tuber, T1 (57.03 g), T2 (55.25 g), T3 (55.59 g), and T4 (54.27 g) were higher than CK (51.65 g) by 10.4%, 7.0%, 7.6%, and 5.1%, respectively. However, the number of tubers per plant was slightly lower in all intercropping treatments compared to CK, with reductions of 7.9% for T1, 9.5% for T2, 12.8% for T3, and 11.0% for T4. Regarding dry matter content, T1 and T2 were 6.7% higher than CK, while T3 and T4 were similar to CK.

Overall, maize potato intercropping had positive effects on improving the average fresh and dry weights of individual tubers as well as dry matter content particularly under treatment T3 (conventional interspecific nitrogen application). Although there was a small decrease in the number of tubers per plant, no significant differences were observed in overall potato quality traits between intercropped and monoculture systems. This suggests that intercropping allows for successful co-cultivation of maize and potatoes without significantly affecting potato quality. Treatment T3, which involves conventional interspecific nitrogen application, appears most beneficial for enhancing single-tuber weight, making it an optimal choice when considering both crops' growth requirements.

Effects of Different Cultivation Modes on Potato Yield

According to Table 6, most indicators in intercropping treatments showed significant improvements compared with CK (conventional nitrogen application in potato monoculture). Fresh tuber yields for T3 (23,792.34 kg·hm^{-2}), T1 (22,667.12 kg·hm^{-2}), and T4 (22,195.77 kg·hm^{-2}) increased by 9.6%, 4.4%, and 2.2% respectively over CK (21,716.10 kg·hm^{-2}), while T2 (21,608.76 kg·hm^{-2}) decreased slightly by 0.5%. Among these, only T3 reached a statistically significant level higher than CK. In terms of dry tuber yield, all intercropping treatments T1 (3,416.43 kg·hm^{-2}), T2 (3,438.30 kg·hm^{-2}), T3 (3,470.75 kg·hm^{-2}), and T4 (3,433.18 kg·hm^{-2}) were significantly greater than CK (3,171.65 kg·hm^{-2}), with increases ranging from 7.7% to 9.4%. Regarding the commercial tuber rate, T3 (0.68) saw a notable increase of 41.7% compared to CK (0.48), followed by T1 (0.59) at +22.9% and T4 (0.58) at +20.8%. The improvement in T2 (0.50) was minimal, just 4.2% above CK. Notably, the commercial tuber rate under T3 was significantly higher than that of CK.

Table 5: Effects of Different Cultivation Patterns on the Quality Traits of Potatoes

Treatment	Average fresh weight per potato (g)	Average weight of dried potatoes per unit (g)	The number of tubers per plant	Conversion rate
CK	346.58±43.48a	51.65±10.98a	5.25±0.87a	0.15±0.02ab
T1	364.95±43.70a	57.03±11.06a	4.83±1.03a	0.16±0.02a
T2	344.46±43.33a	55.25±8.89a	4.75±0.45a	0.16±0.01ab
T3	380.48±45.37a	55.59±7.63a	4.58±1.00a	0.15±0.01b
T4	353.37±35.36a	54.27±8.62a	4.67±0.78a	0.15±0.01ab

Table 6: Effects of Different Cultivation Patterns on the Quality Traits of Potatoes

Treatment	Fresh potato yield (kg·hm^{-2})	Dry potato yield (kg·hm^{-2})	Commercial potato rate
CK	21716.10±350.60c	3171.65±54.58b	0.48±0.01c
T1	22667.12±392.32b	3416.43±69.09a	0.59±0.01b
T2	21608.76±338.06c	3438.30±77.32a	0.50±0.02c
T3	23792.34±400.67a	3470.75±60.17a	0.68±0.01a
T4	22195.77±295.68bc	3433.18±79.03a	0.58±0.01b

Discussion

Soil microorganisms are the most dynamic component of soil ecosystems, and changes in their community structure directly reflect soil health status and ecological function stability, serving as crucial biological indicators for predicting agricultural ecosystem responses to management practices [29]. Through high-throughput sequencing analysis, this study

demonstrated that different nitrogen application strategies under maize-potato intercropping significantly altered rhizosphere soil microbial community structure and diversity. Specifically, conventional interspecific fertilization (T3) reduced overall bacterial richness and diversity while exhibiting co-occurrence with higher relative abundance of *Parasegetibacter*. T3 treatment corresponded to the maximum potato yield in this one-year trial, yet we only obtained relative abundance data and cannot confirm a direct causal linkage between *Parasegetibacter* enrichment and yield improvement; this correlation requires further functional verification via strain isolation or gene quantification. T3 reduced bacterial diversity but increased yield, indicating that lower diversity can be beneficial when the community is restructured toward beneficial functional microbes, such as *Parasegetibacter*. In contrast, intraspecific nitrogen reduction (T2) notably increased the relative abundance of the Proteobacteria phylum (41.2%) and *Sphingomonas* genus (10.0%), suggesting that nitrogen reduction may sustain soil nutrient cycling by promoting specific functional microbial groups [30]. Fungal communities were more sensitive to nitrogen reduction than bacterial communities. Reduced-N treatments (T2, T4) increased the relative abundance of Fusarium, which may pose long-term risks of soil-borne diseases. Fungal communities exhibited greater sensitivity to nitrogen application patterns, with interspecific nitrogen reduction (T4) sharply decreasing fungal richness and evenness, while intraspecific conventional fertilization (T1) elevated the abundance of Mortierellomycota (18.4%) and its genus Mortierella (18.4%) a phosphorus-solubilizing group potentially synergistic with crop growth. These findings indicate that nitrogen management in intercropping systems indirectly modulates soil ecological functions via key microbial regulators. This occurs because intercropping combined with varied nitrogen regimes alters root growth dynamics, vitality, and the quality/quantity of root exudates [31-33] differential nitrogen rates and placement directly modify soil nitrogen content, forms, and spatial distribution [34, 35]; and spatially overlapping roots of maize and potatoes with distinct nutrient demands, exudate profiles, and microbial recruitment strategies generate synergistic or antagonistic interactions [36, 37].

In terms of crop performance, intercropping substantially improved potato growth traits and yield components. Under T3 treatment, potato plant height (72.66 cm) increased by 5.44% compared to monoculture controls (CK), with peak fresh (380.48 g) and dry tuber weights (55.59 g), indicating enhanced photosynthate allocation to tubers driven by resource complementarity. Despite marginally lower tuber numbers per plant in intercropped treatments, T3 achieved significantly higher fresh tuber yield (23,792.34 $kg \cdot hm^{-2}$, +9.6%) and marketable tuber rate (0.68+41.7%) than CK, demonstrating that quality enhancement compensated for minor quantitative deficits. Yield improvement under T3 was mainly attributed to larger tuber size and higher commercial tuber rate rather than increased tuber number, suggesting that intercropping altered resource allocation toward tuber quality. Notably, while T2 maintained microbial diversity, its yield gain was minimal (−0.5% vs. CK), whereas T4 despite suppressing fungal communities still sustained relatively high productivity, revealing complex trade-offs between microbial functions and crop yields.

Theoretically, root interactions and divergent exudation in intercropping may reshape soil carbon-nitrogen availability, thereby selecting for microbial communities adapted to specific nutrient conditions. For instance, reduced bacterial diversity under T3 coincided with maximal yields, possibly due to positive regulation by *Parasegetibacter* mediated plant-soil interactions. Conversely, enrichment of potential pathogens like Fusarium under nitrogen-reduced treatments (T2, T4) suggests nitrogen limitation could elevate disease risks. The resource heterogeneity provided by intercropping likely enhances microbial functional redundancy, buffering against negative effects of fertilization shifts [38-41].

Limitations of the Study

First, this study relied solely on microbial relative abundance data; absolute abundance was not quantified, which limits mechanistic interpretation. Second, causal relationships between microbial shifts and yield remain unproven. Third, the experiment was conducted at a single site over one year; the significant increase in commercial tuber rate under T3 requires validation across different soil types and growing seasons. Fourth, no functional assays or enzyme activity measurements were performed to validate sequencing-based microbial community changes.

Conclusion

Under maize-potato intercropping, conventional interspecific fertilization (T3) was associated with improved potato yield and commercial tuber quality concurrent with restructured rhizosphere microbial community composition, whereas nitrogen reduction strategies exhibited trade-offs between microbial diversity maintenance and tuber productivity. This study only observed correlative links between microbial relative abundance shifts and crop performance, and no causal regulatory mechanisms were validated. Future multi-site, multi-season field trials are required to verify the stability of T3’s yield

advantage, and functional microbial assays (enzyme activity, absolute quantification, functional gene sequencing) are needed to clarify microbe-mediated nutrient cycling processes. Subsequent research should screen optimal nitrogen reduction thresholds that balance rhizosphere microbial community stability, tuber yield, and soil-borne disease risk, and couple microbial functional gene expression with crop nitrogen/phosphorus use efficiency to provide precise nutrient management theory for maize-potato intercropping systems.

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Li Lin: Methodology writer review and edited.
Song Jin and Qiong He: Investigation.
Huiping Xu: Methodology writer review and edited.

Ethics

This article is original and contains unpublished material. The corresponding author confirms that all of the other authors have read and approved the manuscript and no ethical issues involved.

Conflict of Interests

The authors declare that they have no competing interests.

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