IRSTI 68.03.07; 68.05.45 https://doi.org/10.26577/EJE208830526

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EFFECTS OF A TEN-BACTERIAL CONSORTIUM ON RICE GROWTH AND RHIZOSPHERE MICROBIAL COMMUNITY COMPOSITION

Rice production needs sustainable strategies that reduce dependence on chemical inputs while maintaining growth and yield. In this study, we assembled a ten-bacterial consortium (B10) from dominant rice-associated isolates and evaluated its effects on rice growth and rhizosphere bacterial communities under pot conditions. Compared with the control (CK), inoculation significantly enhanced rice growth, with dry biomass, fresh weight, shoot height, and stem height increasing by 50.7%, 47.6%, 18.2%, and 14.8%, respectively. High-throughput 16S rRNA sequencing showed that the consortium did not significantly alter alpha diversity, but clearly shifted beta diversity and community composition. B10 enriched taxa positively associated with rice growth, including *Azospirillum brasilense*, *Delftia tsuruhatensis*, *Bdellovibrio*, *Paracoccus*, and *Pseudomonas*, while reducing several negatively associated taxa. Functional prediction analyses indicated that B10 reshaped the rice rhizosphere into a more favorable microbiome than CK by enriching beneficial predicted metabolic functions and reducing undesirable phenotypes. These results indicate that the consortium promoted rice growth partly through rhizosphere microbiome restructuring. This work shows the potential of multi-strain inoculants in agroecosystems.

Keywords: rice, consortium, rhizosphere, microbiome, inoculation.

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Күріштің өсуіне және ризосфералық микробтық қауымдастық құрамына он бактериядан тұратын консорциумның әсері

Күріш өндірісіне өсім мен өнімділікті сақтай отырып, химиялық енгізілімдерге тәуелділікті азайтатын тұрақты стратегиялар қажет. Осы зерттеуде біз күрішпен ассоциацияланған басым изоляттардан он бактериядан тұратын консорциумды (B10) құрастырып, оның күріштің өсуіне және ризосферадағы бактериялық қауымдастықтарға әсерін вегетациялық ыдыстар жағдайында бағаладық. Бақылаумен (CK) салыстырғанда, инокуляция күріштің өсуін едәуір жақсартты: құрғақ биомасса, жаңа салмақ, өркен биіктігі және сабақ биіктігі тиісінше 50,7%, 47,6%, 18,2% және 14,8%-ға артты. 16S rRNA жоғары өнімді секвенирлеу нәтижелері консорциумның альфа-алуантүрлілікке айтарлықтай әсер етпегенін, бірақ бета-алуантүрлілік пен қауымдастық құрамын анық өзгерткенін көрсетті. B10 күріштің өсуімен оң байланысты таксондарды, соның ішінде *Azospirillum brasilense*, *Delftia tsuruhatensis*, *Bdellovibrio*, *Paracoccus* және *Pseudomonas* туыстарын байытты, сонымен қатар өсуге теріс байланысты бірнеше таксондардың үлесін азайтты. Функционалдық болжау талдауы B10 нұсқасының CK-пен салыстырғанда күріш ризосферасының микробиомын пайдалы болжанған метаболикалық функцияларды байыту және қолайсыз фенотиптерді азайту арқылы анағұрлым қолайлы күйге өзгерткенін көрсетті. Бұл нәтижелер консорциумның ризосфера микробиомын қайта құрылымдау арқылы күріштің өсуін ішінара

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дырғанын көрсетеді. Бұл жұмыс көпштаммды инокулянттардың агроэкожүйелердегі әлеуетін көрсетеді.

Түйін сөздер: күріш, консорциум, ризосфера, микробиом, инокуляция.

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Влияние консорциума из десяти бактерий на рост риса и состав микробного сообщества ризосферы

Производству риса необходимы устойчивые стратегии, позволяющие снизить зависимость от химических средств при сохранении роста и урожайности. В данном исследовании мы сформировали консорциум из десяти бактерий (B10) на основе доминирующих изолятов, ассоциированных с рисом, и оценили его влияние на рост риса и бактериальные сообщества ризосферы в условиях вегетационного опыта. По сравнению с контролем (CK) инокуляция значительно улучшила рост риса: сухая биомасса, свежая масса, высота побега и высота стебля увеличились на 50,7%, 47,6%, 18,2% и 14,8% соответственно. Высокопроизводительное секвенирование 16S rRNA показало, что консорциум не оказывал значимого влияния на альфа-разнообразие, однако заметно изменял бета-разнообразие и состав сообщества. B10 способствовал обогащению таксонов, положительно связанных с ростом риса, включая *Azospirillum brasilense*, *Delftia tsuruhatensis*, *Bdellovibrio*, *Paracoccus* и *Pseudomonas*, одновременно снижая представленность нескольких таксонов, отрицательно связанных с ростом. Анализ функционального прогнозирования показал, что B10 перестроил микробиом ризосферы риса в более благоприятное состояние по сравнению с CK за счёт обогащения полезных прогнозируемых метаболических функций и снижения нежелательных фенотипов. Эти результаты показывают, что консорциум способствовал росту риса отчасти за счёт реструктуризации ризосферного микробиома. Данная работа демонстрирует потенциал многоштаммовых инокулянтов в агроэкосистемах.

Ключевые слова: рис, консорциум, ризосфера, микробиом, инокуляция.

Introduction

Rice (*Oryza sativa* L.) is one of the most important food crops in the world and remains central to global food security. FAO and IRRI describe rice as a staple food for more than half of the world's population, and in Asia alone more than 2 billion people obtain 60–70% of their dietary energy from rice and rice-derived products (Food and Agriculture Organization of the United Nations [FAO], 2003). Beyond its nutritional importance, rice cultivation also supports the livelihoods of hundreds of millions of farmers and rural households, especially in developing countries (Fukagawa & Ziska, 2019).

Conventional rice production has relied heavily on chemical fertilizers and other external inputs to maintain yield, but this strategy raises concerns about production costs, nutrient losses, environmental contamination, and long-term soil health. For this reason, microbial inoculants have attracted increasing attention as a sustainable alternative or complement to chemical inputs. Recent works describe plant growth-promoting rhizobacteria and related bioinoculants as promising tools for improving nutrient availability, phytohormone production, stress tolerance, and crop performance while reducing dependence on synthetic fertilizers. For example, Ríos-Ruiz et al. (2020) reported that selected native bacterial consortia increased rice productivity while allowing nitrogen fertilizer inputs to be reduced by up to 25% in field conditions in Peru. Likewise, Huang et al. (2024) showed that microbial inoculation significantly increased rice yield and seed-setting rate, with co-inoculation increasing yield by up to 13.7%. In another study, Wang et al. (2023) found that inoculants promoted rice growth mainly by regulating the rhizosphere microbiome rather than simply acting alone or only increasing soil nutrient availability.

Although many studies have focused on single beneficial strains, increasing evidence suggests that microbial consortia may be more effective because different members can contribute complementary functions and improve colonization stability in the rice rhizosphere. For example, Etesami and Alikhani (2016) showed that co-inoculation of rhizosphere and endophytic *Pseudomonas* strains improved rice growth and nutrient uptake while allowing a 25% reduction in N fertilizer. In addition, Moronta-Barrios

et al. (2018) demonstrated that a 10-strain simplified bacterial community could colonize rice seedlings together for 30 days, indicating that multispecies inoculants can persist as coordinated assemblages. Also, Xiao et al. (2022) found that co-inoculation improved rice yield and altered the resident soil bacterial community, particularly rare taxa associated with crop performance.

A closely related concept is that beneficial inoculants may not act only through direct plant-growth-promoting traits, but also by reshaping the indigenous rhizosphere microbiome in ways that support crop performance. This mechanism is especially important in rice because introduced strains must establish and function within an already complex root-associated microbial community. For example, Islam et al. (2023) reported that inoculation of rice with *Paraburkholderia fungorum* BRRh-4 and *Delftia* sp. BTL-M2 significantly improved growth and yield, while 16S-based analysis showed clear changes in the diversity, structure, and composition of the root and rhizosphere bacteriome; the authors concluded that these probiotic strains likely promoted rice performance partly by modulating associated bacterial communities. Likewise, Li et al. (2024) showed that inoculation with the nitrogen-fixing bacterium R3 (*Herbaspirillum*) increased rice yield by 8.81% and altered the native nitrogen-fixing microbiome, increasing the abundance of key genera such as *Ralstonia*, *Azotobacter*, *Geobacter*, *Streptomyces*, and *Pseudomonas*. Yang et al. (2025) found that *Bacillus amyloliquefaciens*-modified bio-organic fertilizer increased rice yield by 9.6% and markedly restructured the rhizosphere bacterial community, enriching beneficial taxa such as *Sphingomonas* that were positively associated with soil nutrient status and crop performance.

The present study evaluated whether a consortium of high-abundance bacterial isolates could improve rice growth and modify rhizosphere bacterial communities. We hypothesized that high-abundance bacteria would promote rice growth not only through their own colonization, but also by enriching beneficial soil bacteria and shifting community composition toward taxa positively associated with plant performance.

Materials and methods

Sample preparation, isolation, and DNA preparation

Forty plates each of TSA (Doyle et al., 1968), PDA (de Wet & Brink, 2021), and LB (Bertani, 1951) media were prepared. Root-adjacent soil (1 g), rhizosphere soil (0.1 g) from the Daan region of China, and rice roots treated with microbial agent N were used for microbial isolation. Soil samples were suspended in 9 mL sterile water, while roots were rinsed twice with sterile water, blotted dry, weighed (1 g), and homogenized in 9 mL sterile water. Seven replicate samples were pooled for each treatment. Suspensions were serially diluted 10-fold in PBS to $10^{-}5$, and 100 µL aliquots of the $10^{-}2$ to $10^{-}5$ dilutions were spread onto TSA, PDA, and LB plates using glass beads. Plates were labeled and incubated inverted at 30°C for 24 h. Plates containing 30–100 colonies were selected for further analysis. For colony isolation, 1 mL TSB (Perchetti et al., 2020) was dispensed into each well of 96-well deep plates using an automated liquid handler. Single colonies of appropriate size were picked using a QPix 420 automated colony picker (Molecular Devices, USA) and transferred into 96-well plates, which were then sealed and incubated overnight at 30°C with shaking.

DNA extraction and PCR

Following enrichment, a Biomek i7 (Beckman Coulter, California, USA) automated workstation was employed. For each well in a 96-deep well plate, 10 µL of bacterial suspension was collected and centrifuged at 4000 rpm for 5 min at room temperature. After discarding the supernatant, 10 µL of lysis buffer (TaKaRa Bio, Shiga, Japan) was added. The plate was then incubated at 80°C for 15 minutes in a PCR machine to lyse the cells and extract the DNA.

The PCR mixture was prepared in the sample loading slot of the workstation with the following components: 7875 µL Taq MasterMix (Kangwei Century, China), 5250 µL dH_2O, 525 µL 1492R primer, and 525 µL 27F primer. After thorough mixing, the PCR mixture was aliquoted into a 96-well PCR plate, with each well receiving 27 µL. An additional 3 µL of the extracted DNA was then added to each well, bringing the total volume to 30 µL per well. The PCR amplification program was set as follows: denaturation- 94°C for 5 min, denaturation – 94°C (35 cycles) for 30 secs, annealing – 56°C for 30 secs, and extension – 72°C for 10 min. After amplification, the samples were sent to BGI Genomics Co., Ltd. (Shenzhen, China) for sequencing. The sequencing results were then compared with the NCBI database to determine the taxonomic classification of each bacterial strain.

Soil collection and sterilization

Rhizosphere soil was collected from the upper 30 cm of a weed field in the Tianjin, China. The sampled soil was air dried and thoroughly mixed, followed by a sieving step (0.5-cm mesh) to remove plant debris. 10 plastic pots (diameter 10 cm, height 9 cm) were sterilized using 1.5% sodium hypochlorite and 100% ethanol and then exposed to UV-C light for 2 hours by turning sides every 30 min. Soil was sterilized in an autoclave at 121°C for 2 h with help of autoclave bags. 10 pot bags were filled with soil, each containing 300 g of soil.

Rice pot experiment

High-throughput sequencing identified 603 isolates/strains representing 24 genera and 56 species. High abundance ten PGPB (*Pseudomonas kilomensis* 520-20*, Stutzerimonas chloritidismutans, Kosakonia sacchari* strain SP1, *Enterobacter mori* strain YIM Hb-3*, Atlantibacter hermannii* strain CIP 103176*, Cronobacter dublinensis* subsp. lausannensis strain E515*, Salmonella enterica* subsp. salamae strain DSM 9220*, Bacillus aerius* strain 24K*, Halomonas lutescens* strain Q1U*, Aeromonas hydrophila* strain JCM 1027) from identified species were grown in TSB medium at 30°C for 48 hours on a rotary shaker (180 rpm). The bacterial broth was washed three times with 0.9% NaCl solution and resuspended with sterile deionized water. The number of bacteria was counted by microscopy and was adjusted to about 3×10^8 CFU/mL with sterile deionized water. The resuspended bacteria were verified by TSB plates.

The glume of rice seeds (Ledao 111, Wuchang Fangyuan Institute of Agricultural Sciences cross-breeding, Heilongjiang, China) were removed by a rice huller (Taizhou Grain Instrument Factory, Taizhou, China). Intact rice seeds were sterilized with 3.7% sodium hypochlorite (wt/vol) for 15 min, 75% ethanol for 5 min. The seeds were stirred with a glass rod throughout the sterilization period. Then the seeds were washed six times with sterile water. Rice seeds were soaked for 10 min when washing them for the last three times. The sterile water used to wash rice seeds for the last time was used to verify the sterilization.

Twenty rice seeds were sown in each pot. Each pot was drenched with 50 mL sterile water. There were 2 treatments (Table 1). In order to prevent microbial contamination, after sowing on the ultra-clean table, the mouth of the sealing bottle was wiped with alcohol cotton ball. Five replications of each treatment were set up. Pots were placed randomly in a growth chamber (CIMO, Shanghai, China) with 75% relative humidity and 16/8 h day/night. Before seedling emergence, the temperature was controlled at 30°C. Then, the temperature was set at 28°C day/24°C night for one leaf stage, 28°C day/25°C night for two-leaf stage, and 28°C day/22°C night for other stages. The cultured pots were watered 50 ml every 48 h, and the position of the rice pots was randomly changed.

Table 1
The treatments of the rice pot experiment

#	Name	Supernatant (50 mL)	Inoculation (50 mL)
1	CK	sterilized dH_2O	sterilized dH_2O
2	10B	sterilized dH_2O	10 bacterial suspensions

Amplicon sequencing analysis

Soil bacterial communities were analyzed using high throughput sequencing. The bacterial hypervariable regions (V3-V4) of the 16S rRNA genes were amplified using primers 338F (5'-ACTCCTACGGGAGGCAGCAG-3') – 806R (5'-GGACTACHVGGGTWTCTAAT-3') respectively. PCR products were purified and then sequenced using the MiSeq platform at Majorbio Co., Ltd. (Shanghai, China). Raw data were processed and analyzed (ACE α-diversity, PCoA β-diversity, taxonomic composition, detection of inoculated taxa, Spearman correlations, linear regression, and a correlation network) using Majorbio. Alpha-diversity (Sobs) was compared using the Wilcoxon rank-sum test. Spearman correlation, linear regression, and correlation network analyses were performed in R. PCoA was used to evaluate beta-diversity.

Biosafety statement

All procedures involving bacterial isolates were performed under approved institutional biosafety practices in designated laboratory facilities. Appropriate personal protective equipment was used throughout, and all cultures, media, and contaminated materials were decontaminated by sterilization before disposal. No live microbial material was intentionally released into the environment.

Data analysis

To evaluate differences between the data presented in figures, we conducted a one-way analysis of variance (ANOVA) with Tukey's honestly

significant differences (HSD) as a post-hoc test in IBM SPSS Statistics. Correlation analyses were conducted using R (version 3.1.1). Figures and one-way analysis of variance (ANOVA) with Tukey's of pot experiments were generated with GraphPad Prism.

Results and their discussion

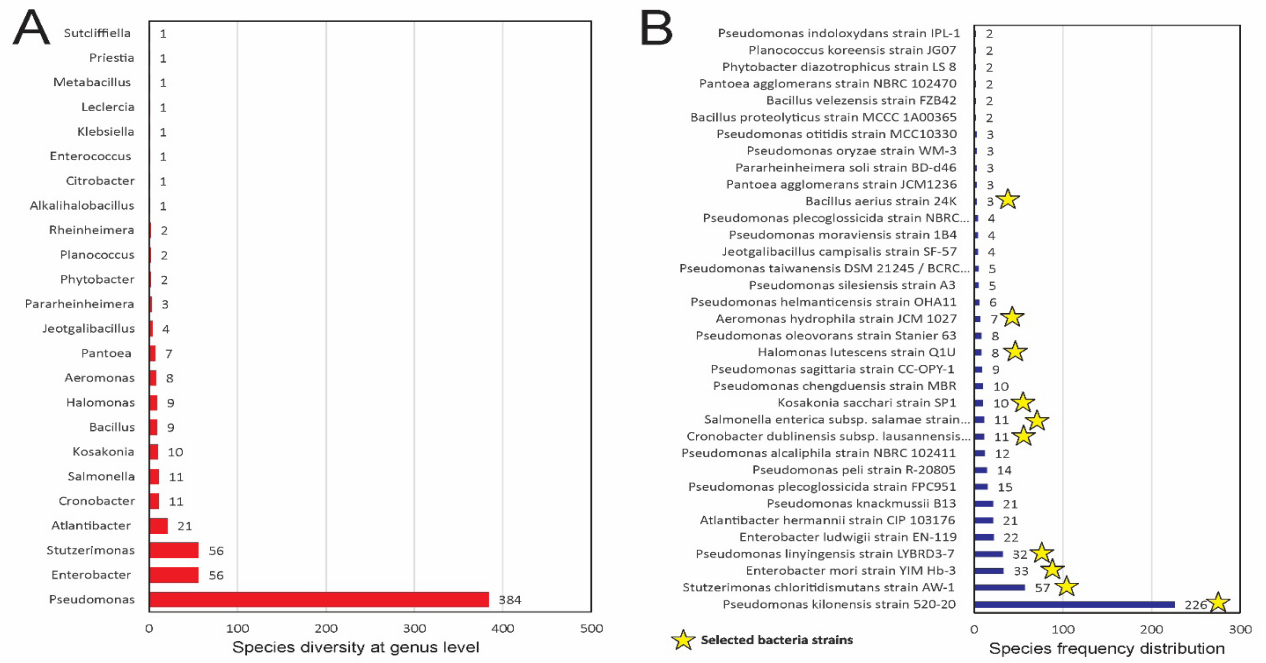
Isolation and selection of bacterial species

Sequencing results showed that there were 603 strains belonging to 24 genera. The ten strains were selected as the most representative species from the dominant genera based on isolation frequency, while avoiding repeated selection of closely related taxa; Bacillus aerius was additionally included because Bacillus is a well-known plant growth-promoting genus (Figure 1). These 10 selected species are common rhizosphere-associated bacteria of agricultural plants. *Pseudomonas* species contained 63.68% (384) of total isolated samples, so total number were 384. *Enterobacter* and *Stutzerimonas* were 9.29% (56) of total isolated strains. Other species were as follows: *Atlantibacter* – 3.48% (21), *Cronobacter* and *Salmonella* 1.82% – (11), *Kosakonia* – 1.66% (10), *Bacillus* and *Halomonas* – 1.49% (9), *Aeromonas* – 1.33% (8), *Pantoea* – 1.16% (7), *Jeotgalibacillus* – 0.66% (4), *Pararheinheimera* – 0.50% (3), *Phytobacter*, *Planococcus* and *Rheinheimera* – 0.33%, *Alkalihalobacillus*, *Citrobacter*, *Enterococcus*, *Klebsiella*, *Leclercia*, *Metabacillus*, *Priestia* and *Sutcliffiella* – 0.17% (1) (Fig. 1A).

There were 56 different species at species level with different strain names. We took 1 from each dominated species. For example, among *Pseudomonas* species, *Pseudomonas kilomensis* frequency was 226, so we took this one. From *Stutzerimonas* species *Stutzerimonas chloritidismutans* had frequency 57, so we took this species. *Enterobacter mori* (33), *Atlantibacter hermannii* (21), *Salmonella enterica* subsp. salamae (11), *Cronobacter dublinensis* subsp. ausannensis (11), *Kosakonia sacchari* (10), *Halomonas lutescens* (8), *Aeromonas hydrophila* (7) and *Bacillus aerius* (3) (Fig. 1B).

Following 10 species were chosen for next experiments based on their high abundance: *Pseudomonas kilomensis* G1, *Enterobacter mori strain* H1, *Stutzerimonas chloritidismutans* E1, *Atlantibacter hermannii* C10, *Cronobacter dublinensis* C11, *Salmonella enterica* F7, *Kosakonia sacchari* H9, *Bacillus aerius* D4, *Halomonas lutescens* D3, *Aeromonas hydrophila* G3.

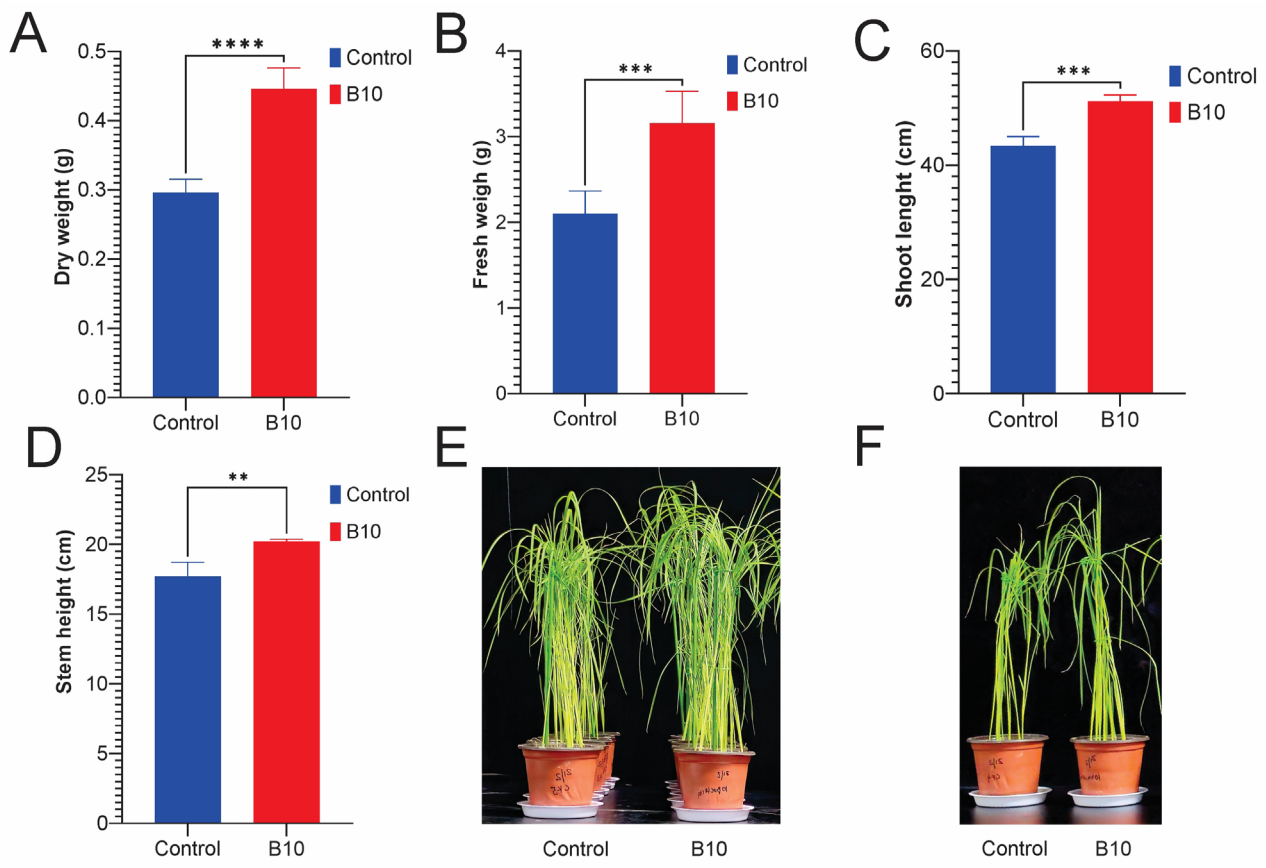
Figure 1
Total number of isolated bacterial taxa at the genus (A) and species (B) levels



The effect of inoculants on rice

The effect of 10 newly isolated bacterial strains on rice growth was evaluated in a subsequent experiment. Compared with the uninoculated CK, the rice plants treated with the B10 exhibited improved growth performance. After 31 days under laboratory conditions, dry biomass, fresh biomass, shoot height, and stem height were measured. Dry biomass was significantly higher in B10 (0.446 g) than in CK (0.296 g), corresponding to an increase of 50.7% (Fig. 2A; $P < 0.0001$, $R = 0.9912$). In addition, fresh biomass was significantly higher in B10 (3.1 g) than in CK (2.1 g) (Fig. 2B; $P = 0.0010$, $R = 0.9491$). Likewise, shoot height increased significantly from 43.3 cm in CK to 51.2 cm in B10 (Fig. 2C; $P = 0.0003$, $R = 0.9724$). Stem height was also significantly greater in B10 (20.2 cm) than in CK (17.6 cm) (Fig. 2D; $P = 0.0087$, $R = 0.8519$). Representative images of individual pots and grouped pots are presented in Fig. 2E and Fig. 2F, respectively.

Figure 2
Effect of inoculants on rice growth



(A) Dry weight; (B) fresh weight; (C) shoot height, (D) stem height; (E) five pots for each treatment; (F) a representative pot from each treatment

Effect of inoculants on microbial diversity and composition

Community diversity analysis

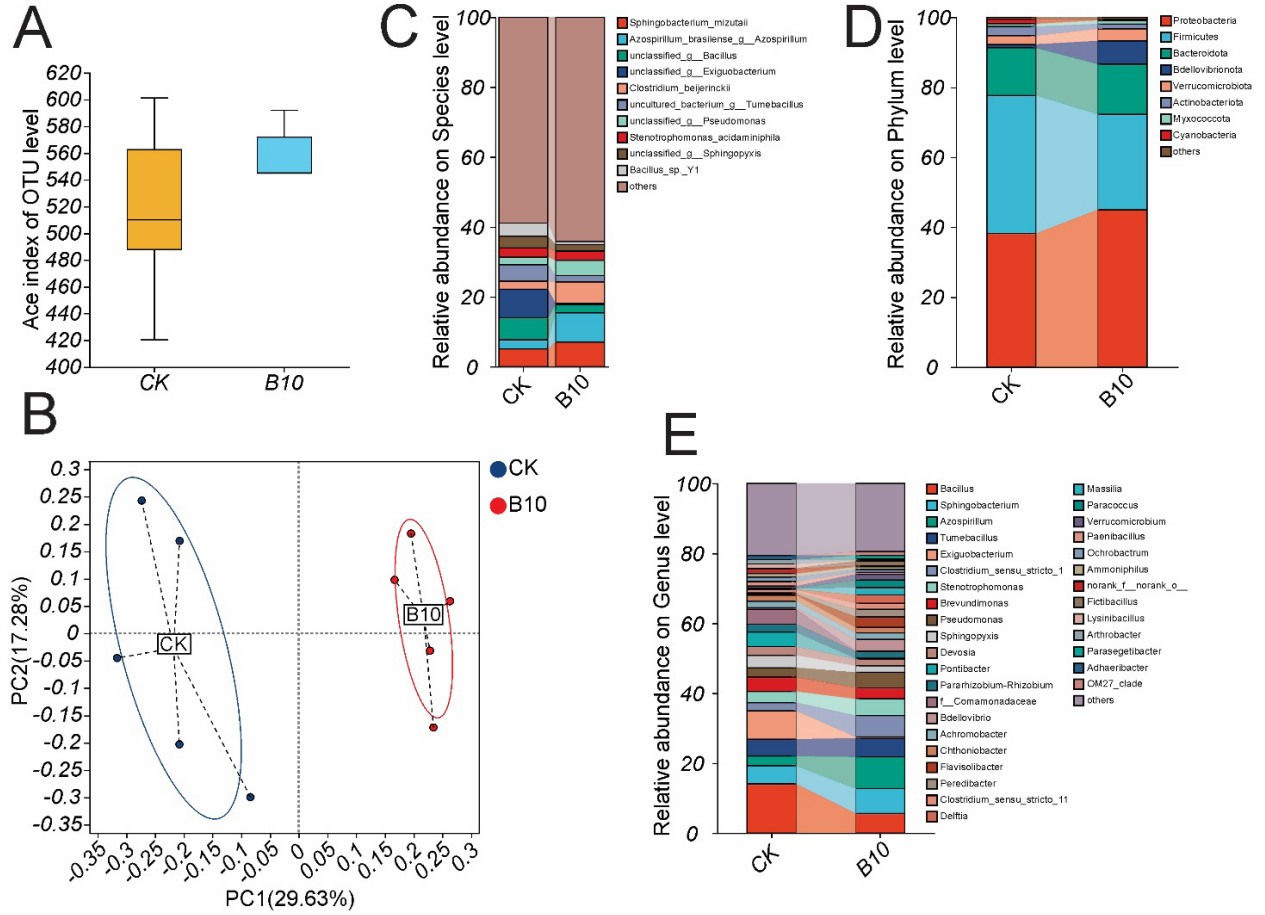
There was no significant difference in bacterial α-diversity between the B10 treatment and the CK based on the ACE index (Wilcoxon rank-sum test, $p = 0.5309$; Fig. 3A). Although the median ACE value was slightly higher in B10 (544.94) than in CK (509.94), the difference was not statistically significant, indicating that inoculation with the 10-bacterial consortium did not markedly change overall bacterial richness in the rice rhizosphere.

In contrast, the bacterial community structure differed between B10 and CK in the β-diversity analysis (Fig. 3B). Principal coordinate analysis (PCoA) at the species level showed a clear separation between the two treatments. PC1 and PC2 ex-

plained 29.63% and 17.28% of the total variation, respectively. All B10 replicates were distributed on the positive side of PC1, whereas all CK replicates were located on the negative side of PC1, indicating that the inoculation shifted the bacterial community composition in the rhizosphere soil.

Figure 3

Effects of B10 inoculation on bacterial diversity and community composition in the rice rhizosphere



(A) Between-group difference test of the ACE index based on the Wilcoxon rank-sum test; (B) Principal coordinate analysis (PCoA) of bacterial communities at the species level; (C–E) Community composition analysis showing the relative abundance of bacterial taxa at the species, phylum, and genus levels, respectively

Community composition analysis

At 31 days after inoculation, the bacterial community composition of the rice rhizosphere differed between the B10 treatment and the CK. At the species level (Fig. 3C), the B10 treatment was mainly dominated by *Azospirillum brasilense* (8.37%), *Sphingobacterium mizutaii* (7.04%), *Clostridium beijerinckii* (6.07%), unclassified *Pseudomonas* (4.37%), and *Tumebacillus ginsengisoli* (3.48%). In contrast, the CK treatment was dominated by unclassified *Exiguobacterium* (8.11%), unclassified *Bacillus* (6.30%), *Sphingobacterium mizutaii* (5.13%), uncultured *Tumebacillus* (4.74%), unclassified Comamonadaceae (4.22%), and *Pontibacter populi* (3.72%). Compared with CK, B10 markedly increased the relative abundance of *Azospirillum brasilense*, *Clostridium beijerinckii*, *Tumebacillus ginsengisoli*, uncultured *Flavisolibacter*, unclassified *Pseudomonas*, and *Delftia tsuruhatensis*. By contrast, unclassified *Exiguobacterium*, unclassified Comamonadaceae, unclassified *Bacillus*, *Pontibacter populi*, and uncultured *Tumebacillus* were clearly reduced in the B10 treatment.

At the phylum level (Fig. 3D), Proteobacteria was the most abundant phylum in both treatments, but its relative abundance was higher in B10 than

in CK (44.99% vs. 38.20%). In contrast, Firmicutes was less abundant in B10 than in CK (27.32% vs. 39.51%), showing a clear decline after inoculation. Bacteroidota remained one of the dominant phyla in both treatments and showed a slight increase in B10 (14.35%) compared with CK (13.57%). A notable enrichment was also observed for Bdellovibrionota, which increased strongly in B10 (6.61%) relative to CK (0.98%). In addition, Verrucomicrobiota increased from 2.51% in CK to 3.49% in B10. In contrast, Actinobacteriota and Cyanobacteria decreased in B10, dropping from 2.57% to 1.37% and from 1.31% to 0.28%, respectively. Overall, the phylum-level profile suggests that B10 shifted the rhizosphere microbiome toward Proteobacteria- and Bdellovibrionota-dominated communities, while reducing the contribution of Firmicutes.

At the genus level (Fig. 3E), the B10 treatment was dominated by Azospirillum (9.10%), Sphingobacterium (7.13%), Clostridium_sensu_stricto_1 (6.10%), Bacillus (5.58%), Tumebacillus (5.29%), Stenotrophomonas (4.78%), and Pseudomonas (4.39%). In CK, however, Bacillus (14.04%) and Exiguobacterium (8.15%) were the most dominant genera, followed by Sphingobacterium (5.19%), Tumebacillus (4.79%), unclassified Comamonadaceae (4.22%), and Pontibacter (4.13%). Compared with CK, B10 strongly enriched Azospirillum, Clostridium_sensu_stricto_1, Bdellovibrio, Flavisolibacter, Delftia, Paracoccus, Massilia, and Pseudomonas. In contrast, Bacillus, Exiguobacterium, unclassified Comamonadaceae, Pontibacter, and Sphingopyxis decreased in the B10 treatment. Among the inoculated genera, Pseudomonas, Kosakonia, and Enterobacter were more abundant in B10 than in CK, while Halomonas was detected only in B10 and Bacillus showed a lower relative abundance in B10 than in CK.

Inoculation

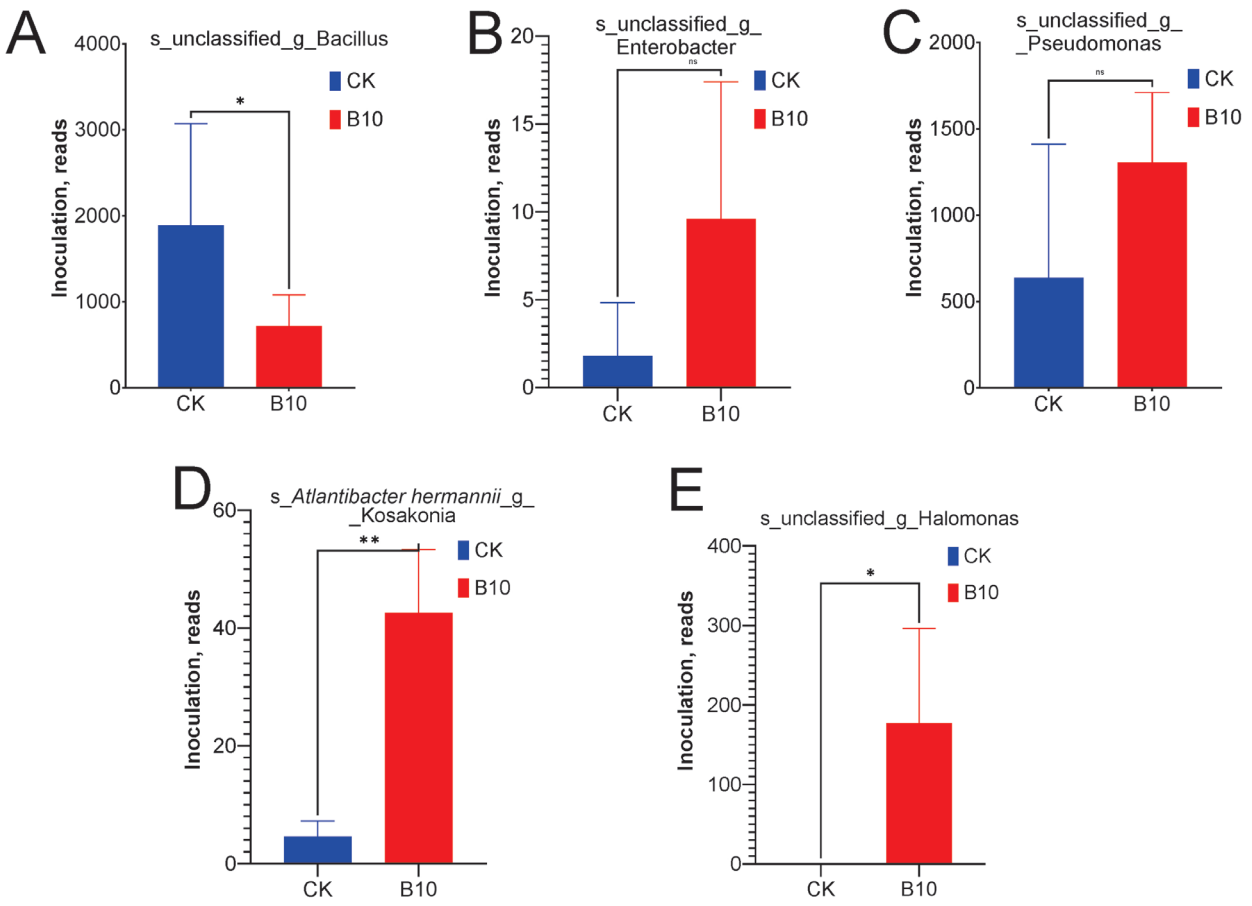
Among the inoculated taxa, five were detected in the sequencing dataset, including Bacillus, Pseudomonas, Enterobacter, Halomonas, and *Atlantibacter hermannii*/Kosakonia. Their abundance patterns differed between the CK and B10 treatments.

Bacillus was detected in both treatments but was significantly more abundant in CK (9,434 total reads) than in B10 (3,593 total reads), indicating that inoculation did not increase the abundance of this taxon under the experimental conditions ($P = 0.0453$, $R = 0.6737$; Fig. 4A). Enterobacter was detected at very low abundance in CK (9 total reads) and showed a higher total abundance in B10 (48 total reads). However, this difference was not statistically significant ($P = 0.1276$, $R = 0.4791$; Fig. 4B). Pseudomonas was enriched in B10, with total read counts increasing from 3,193 in CK to 6,532 in B10. This increase showed a marginal trend but did not reach statistical significance ($P = 0.0549$, $R = 0.6434$; Fig. 4C). Similarly, *Atlantibacter hermannii*/Kosakonia was present at low abundance in CK (23 total reads) and increased in B10 (213 total reads), although this difference was not statistically significant ($P = 0.1276$, $R = 0.4791$; Fig. 4D). Halomonas was not detected in CK but was consistently detected in all B10 replicates, with a total of 885 reads. This taxon showed a significant association with B10 inoculation ($P = 0.0028$, $R = 0.9142$; Fig. 4E).

Correlation analysis

Spearman correlation analysis between bacterial taxa and rice growth traits revealed clear associations between rhizosphere community composition and plant performance (Fig. 5A). Across the CK and B10 samples, several taxa showed strong positive correlations with both shoot height and shoot dry weight. The strongest positive correlations with shoot height were observed for Bdellovibrio ($r = 0.906$, $p < 0.001$), Peredibacter ($r = 0.869$, $p = 0.001$), Paracoccus ($r = 0.805$, $p = 0.005$), *Azospirillum brasilense* ($r = 0.778$, $p = 0.008$), and *Delftia tsuruhatensis* ($r = 0.736$, $p = 0.015$). Similarly, shoot dry weight was positively correlated with *Delftia tsuruhatensis* ($r = 0.828$, $p = 0.003$), *Azospirillum brasilense* ($r = 0.816$, $p = 0.004$), Paracoccus ($r = 0.794$, $p = 0.006$), and Bdellovibrio ($r = 0.791$, $p = 0.006$). In addition, *Sphingobacterium mizutaii*, Flavisolibacter, Pseudomonas, and *Clostridium beijerinckii* also showed positive correlations with shoot traits, although these associations were weaker. In contrast, several taxa were negatively correlated with plant growth. Shoot height showed strong negative correlations with unclassified Sericytochromatia ($r = -0.894$, $p < 0.001$), Adhaeribacter ($r = -0.853$, $p = 0.002$), Exiguobacterium ($r = -0.741$, $p = 0.014$) and Sphingopyxis ($r = -0.687$, $p = 0.028$). Shoot dry weight was most negatively correlated with *Methylorubrum extorquens* ($r = -0.890$, $p < 0.001$), Adhaeribacter ($r = -0.829$, $p = 0.003$), unclassified Sericytochromatia ($r = -0.779$, $p = 0.008$) and unclassified Comamonadaceae ($r = -0.767$, $p = 0.010$). The correlation heatmap suggests that taxa positively associated with rice growth were more closely linked with the improved performance observed under B10 inoculation, whereas negatively correlated taxa were associated with poorer plant growth.

Figure 4
Detection and abundance of inoculated bacterial taxa

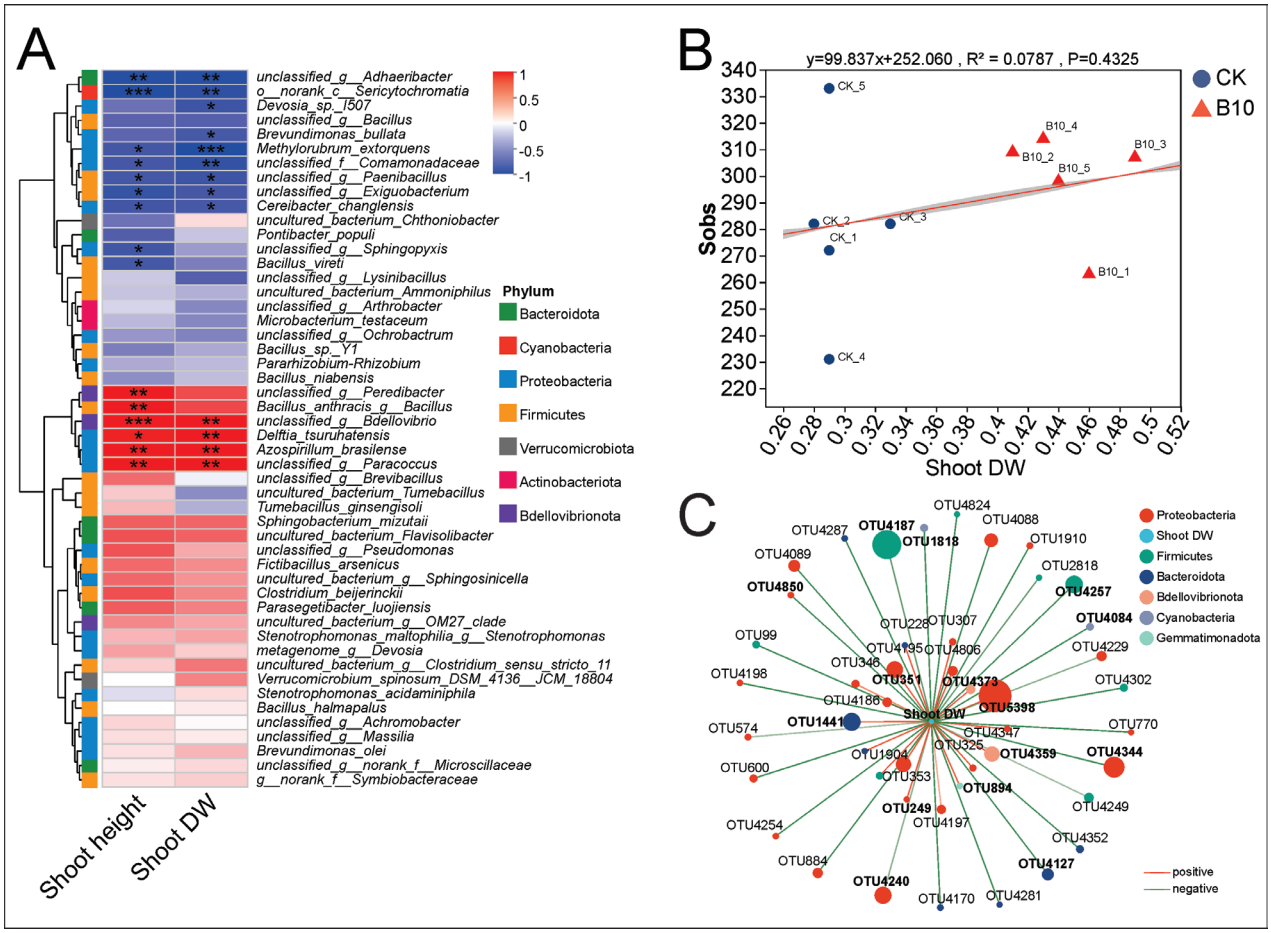


(A) Bacillus, (B) Enterobacter, (C) Pseudomonas, (D) Atlantibacter hermannii, (E) Halomonas

Linear regression analysis was performed to evaluate the relationship between shoot dry weight and bacterial richness (Sobs) across the CK and B10 treatments (Fig. 5B). The regression model showed a positive slope ($y = 99.837x + 252.060$), indicating that Sobs tended to increase slightly with increasing shoot dry weight. However, this relationship was weak and not statistically significant ($R^2 = 0.0787$, $P = 0.4325$), showing that shoot dry weight explained only a small proportion of the variation in bacterial richness. Although B10 samples were generally distributed at higher shoot dry weight values than CK, the overall regression analysis suggested that bacterial richness was not significantly associated with shoot dry weight under the conditions of this experiment.

Figure 5

Correlation analysis of rice biomass and rhizosphere bacterial communities

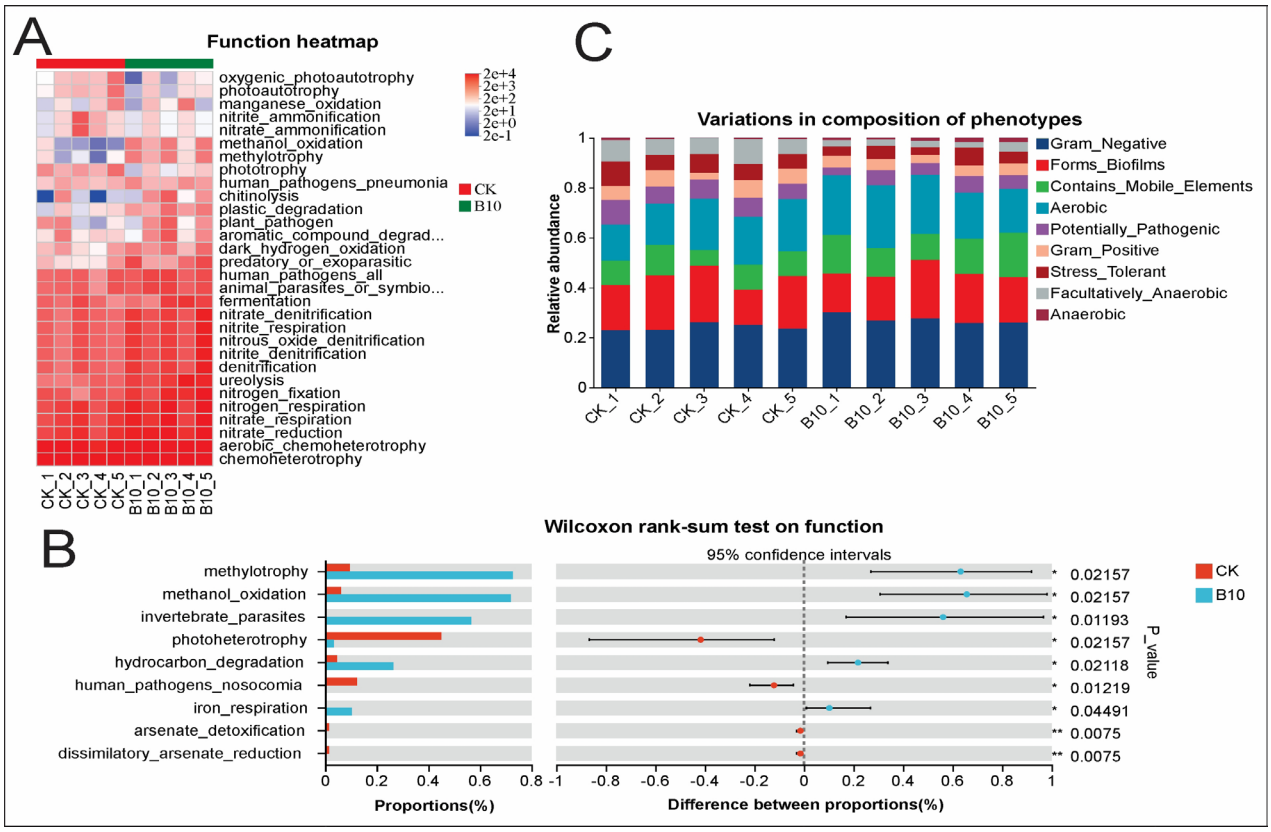


*(A) Spearman correlation heatmap showing relationships between bacterial taxa and rice growth traits; (B) Linear regression analysis between shoot dry weight and observed bacterial richness (Sobs); (C) Two-way correlation network diagram showing associations between shoot dry weight and bacterial taxa. Asterisks indicate significant correlations ($p < 0.05$, **p** < 0.01, **p** < 0.001)*

The two-way correlation network analysis showed significant associations between shoot dry weight (Shoot DW) and multiple bacterial OTUs (Fig. 5C). The network contained 46 nodes and 45 edges, with Shoot DW as the central node connected to all significant taxa. Network topology showed a diameter of 2, an average shortest path length of 1.96, and zero transitivity/clustering, indicating a simple star-like structure centered on plant performance rather than a highly interconnected microbial network. Consistent with the Spearman correlation results, several taxa were positively associated with Shoot DW, including Halomonas (OTU351, $r = 0.910$, $p < 0.001$), Paracoccus (OTU353, $r = 0.903$, $p < 0.001$), Bdellovibrio (OTU4359, $r = 0.897$, $p < 0.001$), *Azospirillum brasilense* Sp245 (OTU4806, $r = 0.880$, $p < 0.001$), *Delftia tsuruhatensis* (OTU4195, $r = 0.828$, $p = 0.003$), and another Azospirillum OTU (OTU4373, $r = 0.816$, $p = 0.004$). Positive links were also observed for unclassified Enterobacteriaceae, Lutispora, Bdellovibrio (OTU4347), and Flavisolibacter. In contrast, the strongest negative correlations with Shoot DW were found for *Methylorubrum extorquens* (OTU4089, $r = -0.890$, $p < 0.001$), Pontibacter (OTU4352, $r = -0.844$, $p = 0.002$), Adhaeribacter (OTU4127, $r = -0.829$, $p = 0.003$), Bacillus (OTU4257, $r = -0.804$, $p = 0.005$), and *Comamonas terrigena* (OTU884, $r = -0.766$, $p = 0.010$). Overall, the network indicates that taxa belonging mainly to Proteobacteria and Bdellovibrionota were positively linked with improved shoot dry weight, whereas several members of Firmicutes, Bacteroidota, and Cyanobacteria showed negative associations.

Functional prediction analysis

Figure 6
Functional potential and phenotype distribution of rhizosphere bacterial communities



Functional annotation based on FAPROTAX; (B) comparison of significantly different functional groups; (C) BugBase phenotype composition. Asterisks indicate significant differences ($p < 0.05$, $p < 0.01$, $p < 0.001$).

Integrated FAPROTAX analysis revealed a clear functional separation between B10 and CK (Fig.6A,B). Relative to CK, B10 was significantly enriched in predicted functions associated with carbon utilization and respiratory activity, including methanol oxidation and methylotrophy (both p = 0.02157), plastic degradation (p = 0.01219), hydrocarbon degradation (p = 0.02118), and iron respiration (p = 0.04491). By contrast, CK was significantly associated with phototrophy-related functions, including phototrophy (p = 0.02157), photoautotrophy and oxygenic photoautotrophy (both p = 0.03671), as well as cyanobacteria and ammonification-related functions (both p = 0.03671). These results support that B10 established a functionally superior rhizosphere environment compared with CK.

The predicted phenotype composition differed markedly between treatments, with B10 favoring a more aerobic and Gram-negative community, while suppressing several undesirable phenotypes relative to CK (Fig.6C). Specifically, B10 had significantly higher proportions of Gram-negative, aerobic, anaerobic, and mobile-element-containing bacteria, whereas CK was enriched in facultatively anaerobic, biofilm-forming, Gram-positive, potentially pathogenic, and stress-tolerant phenotypes. Notably, the lower abundance of potentially pathogenic (p = 0.0046) and stress-tolerant (p = 0.0052) phenotypes in B10 suggests that inoculation with the ten-bacterial consortium reshaped the rhizosphere toward a more favorable microbial phenotype profile than the uninoculated control.

In the present pot experiment, inoculation with the ten-bacterial consortium (B10) significantly promoted early rice growth, increasing shoot dry weight by 50.7% (0.446 vs. 0.296 g), shoot height

from 43.3 to 51.2 cm, stem height from 17.6 to 20.2 cm, and fresh weight from 2.1 to 3.1 g after 31 days (Fig. 2A). At the same time, bacterial richness did not differ significantly between treatments (Fig. 3A), whereas β-diversity and taxonomic composition shifted markedly (Fig. 3B), with enrichment of Proteobacteria and Bdellovibrionota, reduction of Firmicutes, and positive correlations of Azospirillum, Delftia, Paracoccus, Bdellovibrio, Halomonas, and related OTUs with shoot performance (Fig. 5). These results indicate that the growth-promoting effect of B10 was associated less with a general increase in microbial richness than with selective restructuring of the rhizosphere community toward taxa linked to improved plant performance. This interpretation is strengthened by the inoculant detection data: only part of the introduced taxa showed clear enrichment, and Halomonas was the only inoculated member with a strong treatment-specific signal (Fig. 4E), whereas Pseudomonas and Enterobacter increased only weakly and Bacillus was more abundant in CK (Fig. 4A-D), suggesting that the observed plant response cannot be explained simply by persistence of all introduced strains, but rather by consortium-driven reassembly of a functionally favorable microbiome (Sherpa et al., 2021). This pattern is consistent with previous studies showing that rice bacterial consortia can enhance plant growth and agronomic traits, as reported for native rhizobacterial consortia under organic rice cultivation, and that inoculation may simultaneously reshape the associated microbiome, as shown for *Azospirillum* sp. B510, which recruited other N_2-fixing bacteria and altered bacterial community structure under field conditions (Yasuda et al., 2022). It also agrees with field evidence that coinoculation with growth-promoting bacteria can improve nitrogen-use efficiency in irrigated rice, supporting the practical value of multistrain inoculants beyond single-strain effects (Turino Mattos et al., 2023). More recent SynCom work in rice further suggests that rational selection of small, functionally complementary communities can improve biomass and nutrient acquisition through multiple pathways (Ma et al., 2024), which provides a useful framework for future refinement of the B10 consortium. Because the present study was conducted at the seedling stage under pot conditions, the next step should be to test whether these early microbiome shifts persist through later developmental stages and translate into stable yield benefits under field conditions.

These functional predictions suggest that B10 did not merely alter taxonomic composition, but redirected the rhizosphere microbiome toward functions more closely associated with nutrient turnover and active heterotrophic metabolism, especially nitrogen fixation, nitrate reduction, denitrification, methanol oxidation, methylotrophy, ureolysis, and chemoheterotrophy. In contrast, the greater representation of phototrophy-, photoautotrophy-, cyanobacteria-, and ammonification-related functions in CK suggests that the uninoculated rhizosphere retained a less plant-beneficial functional profile than the B10 treatment. The BugBase results strengthen this interpretation by showing that B10 was associated with reduced potentially pathogenic and stress-tolerant phenotypes, indicating that consortium inoculation promoted a functionally and ecologically more favorable rhizosphere environment, which is consistent with the improved rice growth observed in the B10 treatment.

Conclusion

This study demonstrates that a consortium composed of high-abundance B10 can enhance rice growth and reshape the rhizosphere microbiome. Compared with the uninoculated CK, B10 significantly increased dry biomass, fresh weight, shoot height, and stem height, confirming a clear plant growth-promoting effect under pot conditions. Although inoculation did not significantly change bacterial richness, it strongly altered community structure and favored the enrichment of taxa positively associated with plant performance, including *Azospirillum*, *Pseudomonas*, *Delftia*, *Paracoccus*, and *Bdellovibrio*. At the same time, several taxa negatively correlated with growth declined in relative abundance. B10 established a functionally superior predicted rhizosphere microbiome compared with CK, supporting its potential as an effective rice growth-promoting bacterial consortium. These results suggest that the beneficial effect of the consortium was mediated not only by direct colonization of introduced strains but also by broader microbiome modulation in the rice rhizosphere. B10 represents a promising candidate microbial inoculant for sustainable rice production. However, further work is needed to validate its performance under field conditions, determine the stability of its effects across growth stages, and confirm the biosafety of the selected strains before practical application.

Funding

This work was supported by the Ministry of Science and Higher Education of the Republic of Kazakhstan (AP26193911). Also supported by the Tianjin Municipal Science and Technology Program (23YFYSHZ00050, 24PTLYHZ00300), the Central Guidance Fund for Local Scientific and Technological Development (Establishment and key technologies of agricultural microbial resource library of Xinjiang, 2024YD009), the Xinjiang Agricultural Microorganisms and Fertilizer Creation Key Laboratory Open Project (SYS2024-01), the Tianjin Synthetic Biotechnology Innovation Capacity Improvement Project (TSBICIP-BRFI-009, TSBICIP-IJCP-001).

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Received May 21, 2026
Accepted September 23, 2026