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Ridge-furrow with black-film mulching enhances phosphorus transformation in rhizosheath soil and grain yield in maize-soybean intercropping systems

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ABSTRACT

Ridge-furrow with film mulching (RFM) increases grain yield by enhancing nutrient uptake and biomass accumulation in monoculture systems. However, its effects on transformation of phosphorus (P) concentration in rhizosheath soil and its role in yield enhancement in maize–soybean intercropping systems under acidic soil conditions, where low P availability in soil limits productivity, remain unclear. A 4-year field experiment with four different treatments was conducted to investigate the effects of film mulching on grain yield, root traits, P concentrations in rhizosheath soil, P-solubilising microorganisms (PSMs) and P-cycling functional genes in a maize–soybean intercropping system. The four treatments given were as follows: ridge-furrow without film mulching at 0-kg P ha^{-1} (CK), ridge-furrow without film mulching at 90-kg P ha^{-1} (P90), RFM at 0-kg P ha^{-1} (FM) and RFM at 90-kg P ha^{-1} (P90 + FM). The results showed that FM considerably enhanced seed yield, P uptake, root length, concentration of plant-available P in rhizosheath soils, acid phosphatase activity and Al-bound P in maize and soybean. FM remarkably reduced the diversity of maize rhizosheath PSMs, as indicated by a lower Shannon index. Permutational multivariate analysis revealed that FM notably altered the composition of rhizosheath PSMs in both the crops. Furthermore, FM notably increased the abundance of functional genes responsible for organic-P mineralisation, inorganic-P solubilisation, P-starvation response regulation and P transport in rhizosheath soils of maize and soybean. Structural equation modelling demonstrated that FM enhanced P transformation in rhizosheath soils, leading to increased concentrations of plant-available P, improved root morphology and better P uptake—ultimately contributing to higher maize and soybean grain yields in the maize–soybean intercropping system. In conclusion, RFM considerably improved maize and soybean productivity in acidic soils by promoting P transformation, stimulating root growth and increasing rhizosheath PSM abundance as well as increased expression of their P-cycling functional genes. These findings highlight RFM as a sustainable cultivation practice for achieving high grain yield and P-acquisition efficiency by enhancing plant–microbe interactions in maize–soybean intercropping systems.

1. Introduction

Maize and soybean, two of the most important staple food crops worldwide, play a crucial role in ensuring food security and promoting sustainable agricultural development (Li et al., 2023a; Yang et al., 2022a). Maize–soybean intercropping is a widely adopted farming practice in China. It is practiced to improve land-use efficiency—reflected in the land equivalent ratio (LER)—as well as seed yield and resource-use efficiency, including nutrient and water utilisation (Nasar et al., 2023; Shen et al., 2023; Xu et al., 2020). A global meta-analysis reported an average LER of 1.32 for maize–soybean intercropping, indicating a considerable land-sparing potential for two of the major food crops globally (Xu et al., 2020). However, low concentrations of plant-available phosphorus (P) in South China's acidic

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soils remains a key limiting factor for crop yield, particularly for maize (Luo et al., 2024) and soybean (He et al., 2019; Zhang et al., 2024). Although large quantities of P fertiliser are applied to farmland annually, much of it becomes fixed in the soil, resulting in a low P-utilisation rate (15 %–30 %) (Veneklaas et al., 2012). Furthermore, using excessive P fertiliser not only accelerates the depletion of non-renewable P reserves but also harms the environment considerably (Zou et al., 2022). Therefore, achieving high yield performance while ensuring sustainable use of P fertiliser in maize–soybean intercropping systems is a crucial requirement for maintaining sustainable agriculture in P-limited areas worldwide, including South China.

Ridge-furrow with film mulching (RFM) has been recognised as a sustainable management practice to improve crop yield in monoculture systems, including maize (Zhang et al., 2025) and soybean (Liao et al., 2022a, 2022b), particularly in arid and semi-arid regions (Liao et al., 2022b; Zhang et al., 2021). Compared with traditional flat cultivation with mulching, RFM enhances rainwater harvesting; improves soil moisture and water-use efficiency and ultimately increases yield of maize (Zheng et al., 2021), wheat (Liu et al., 2023) and soybean (Liao et al., 2022b). Although South China experiences abundant rainfall, seasonal droughts are common from July to October—during the reproductive period of crop—characterised by low rainfall, high temperatures and rapid evaporation (Yue et al., 2023). Unlike prolonged droughts, seasonal droughts are short-term, fast-developing and demonstrate clear spatiotemporal patterns (Song et al., 2020). Therefore, evaluating the impact of RFM on crop productivity in maize–soybean intercropping systems is essential for improving yield in this region.

P deficiency is a major factor that limits crop productivity (He et al., 2017; Zhang et al., 2024). In China, ~70 % of the soils are P-deficient. Despite the widespread application of P-based fertilisers, low utilisation rates persist owing to P fixation by soil particles (Lambers, 2022). Moreover, the overuse of P fertilisers accelerates the depletion of non-renewable P reserves and leads to environmental degradation (Zou et al., 2022). Therefore, enhancing P availability in soils and improving P uptake by plants have become a crucial research focus in agriculture (Ma et al., 2025). Intercropping maize with legumes, such as peanuts, increases maize yield and promotes P transformation in soils (Yang et al., 2022b). Some studies have reported that RFM improves the microbial microenvironment in soils (Huo et al., 2017). RFM can promote maize root growth, influence root exudation and alter the composition of rhizosphere microbial communities (Li et al., 2023c). P transformation in rhizosheath soils is closely associated with phosphate-solubilising microorganisms (PSMs), which enhance P availability by solubilising inorganic mineral phosphates through exuded carboxylates (He et al., 2025; Lambers, 2022) and by mineralising organic P compounds (Dodd and Sharpley, 2015; Raguet et al., 2023), thereby improving P uptake by plant (Cheng et al., 2023; Parastesh et al., 2019; Rawat et al., 2021). However, plastic film mulching has been demonstrated to reduce the abundance of P-cycling microbial functional genes in maize (Zhang et al., 2023). Despite this, the effects of RFM on P transformation in rhizosheath soils, PSM composition, P-cycling functional genes and their inter-relationships in maize–soybean intercropping systems remain poorly understood.

In summary, RFM remarkably enhances crop yield by reducing water evaporation, minimising nutrient losses and promoting P uptake in monoculture systems (Liao et al., 2022b; Zhang et al., 2025; Zheng et al., 2021). However, its application in maize–soybean intercropping systems has not yet been reported and its impact on yield enhancement and P transformation in rhizosheath soils remains unexplored. This study aimed to investigate the effects of RFM on P transformation in rhizosheath soils that is mediated by the P-cycling microbial community in a maize–soybean intercropping system. The goal was to offer insights into improving P-use efficiency and seed yield in intercropping systems. The following hypotheses were tested: (1) RFM further increases seed yield compared with non-film mulching by promoting root growth, thereby enhancing P uptake and ultimately boosting seed production. (2) RFM alters the composition of PSMs to enhance P transformation in rhizosheath soils and increase concentration of plant-available P.

2. Materials and methods

2.1. Experiment site

This experiment was conducted in Lianxing Village, Jichang Township, Xiu District, Anshun City, Guizhou Province (106°5′59″E, 26°6′29″N) in 2020. The soil type at the test site was classified as Ferrisol soil, containing 28 % sand (0.02–2 mm), 34 % silt (0.02–0.002 mm) and 38 % clay (<0.002 mm). The basic chemical properties of the surface soil layer (0–20 cm) were as follows: pH = 4.54, organic carbon = 17.06 g/kg, alkali-hydrolysed nitrogen = 126.73 mg/kg, resin P = 0.92 mg/kg and available potassium = 159.50 mg/kg. The experiment started in 2020, with the planting period spanning from April to October each year. The land remained uncultivated during the remaining months. The mean temperature varied from 20.9°C to 22.7°C while the precipitation varied from 408 to 1065 mm during the crop growth season from 2020 to 2023.

2.2. Experimental design

A randomised split-plot experimental design (film mulching × P application) was used in this field study. Only maize–soybean intercropping systems were included. Ridge-furrow with black film mulching was applied in the maize–soybean intercropping system (Fig. S1). Based on the method of Yang et al. (2022), two P application rates were used: 0- and 90-kg P ha^{-1}. Single superphosphate was used as the P fertiliser. Urea was applied as the nitrogen fertiliser at a rate of 150-kg N ha^{-1}, 50 % of which was applied before sowing and the rest at the maize silking stage. Four treatment combinations were established: maize–soybean intercropping with ridge-furrow and black film mulching at 0- (FM) and 90-kg P ha^{-1} (P90 + FM) and maize–soybean intercropping with ridge-furrow but without film mulching at 0- (CK) and 90-kg P ha^{-1} (P90). Each treatment was replicated three times, with each plot measuring 60 m^2 (6-m wide × 10-m long). The maize and soybean varieties used were Jinyu 908 and Fendou 97, respectively. The intercropping pattern consisted of two rows of maize intercropped with two rows of soybean. The row spacing was kept 30 cm (with 20 cm between plants) for maize and 40 cm (with two plants per hole) for soybean. The spacing between the maize and soybean rows was 60 cm. Planting densities in the intercropping system were 50,000 plants ha^{-1} for maize and 100,000 plants ha^{-1} for soybean. When the seedlings attained a height of 3–5 cm, thinning and replanting were performed. All other field management practices followed local farming practices.

2.3. Sample collection in 2022 and 2023

Plant samples were collected 106 days following sowing during the grain-filling stage of soybeans (R5) and the early grain-filling stage of maize (R2) in the 2022 and 2023 seasons, while soil samples were collected in the 2023 season. Five maize plants (from five holes) and 10 soybean plants (from five holes) were collected from each plot. A shovel was used to excavate the plant roots within a 20 × 20 × 20-cm soil block. Loose soil was shaken off, while the soil adhering to the root surface was considered rhizosheath soil (Pang et al., 2017). The rhizosheath soil was carefully brushed off. The soil samples from the five maize and 10 soybean plants from the same plot were mixed to obtain a single soil sample that was further divided into two portions: one stored at −80 °C for metagenomic analysis and the other used for determining P concentrations in the soil as well as acid phosphatase activity. Following rhizosheath soil collection, roots were gently washed and scanned using a flatbed scanner (Epson PV850 Pro, Epson Corporation, Long Beach, CA, USA). The root parameters, such as total length, surface area, volume and average diameter, were analysed using WinRHIZO 2019 Pro software (Regent Instruments Inc., Quebec, Canada). Next, the scanned roots were dried at 75 °C for 48 h, ground into fine powder and used to determine the P concentration, following the method of He et al. (2019). At the time of crop maturity, a 2 × 2-m subplot (4 m^2) was harvested from each plot in 2022 and 2023 to measure seed weight and calculate seed yield.

2.4. Determination of P concentrations in the rhizosheath soil and acidic phosphatase activity

The collected rhizosheath soil was air-dried and used to determine P concentration in the soil sample. Plant-available soil P (Olsen-P) was extracted using $NaHCO_3$, and P concentration was measured using the molybdenum blue colorimetric method (Olsen et al., 1954). Concentration of P in the soil—in the form of Fe–P, Ca–P, Al–P and occluded P (O–P)—were determined according to the protocol described by Hedley et al. (1982). Phosphatase activity in soil was measured using the 96-well microplate method with reagent kits provided by Suzhou Greis Biological Co., Ltd., following the manufacturer's instructions. Plant shoots were oven-dried at 75 °C for 48 h, weighed and finely ground to determine the P concentration. Samples were digested with sulphuric acid and hydrogen peroxide, and the P content was determined using the molybdenum-antimony colorimetric method (He et al., 2019).

2.5. Metagenomic analysis of P-solubilising microbes in rhizosheath soil and their P-cycle genes

One gram of rhizosheath soil was used to extract total DNA following the instructions of the E.Z.N.A.® Soil DNA Kit (Omega Bio-tek, Norcross, GA, USA). DNA concentration was measured using a NanoDrop 2000 (Thermo Fisher Scientific, Wilmington, NC, USA), and DNA purity was assessed via 1 % agarose gel electrophoresis. Metagenomic libraries were sequenced on the Illumina NovaSeq platform (PE150), generating an average of 10 GB of raw data per sample.

Raw FASTQ data were subjected to quality control using Fastp (ver. 0.20.0, https://github.com/OpenGene/fastp). All unaligned sequences were removed, and only paired-end reads were retained. Based on the high-quality sequences, single-sample assemblies were performed using MEGAHIT to obtain longer contigs. Gene abundance was quantified by aligning the clean reads from each sample to a non-redundant gene set using Bowtie 2 software. Then, the non-redundant gene set was annotated against multiple reference databases using DIAMOND to identify taxonomic and functional information. Combined with the gene abundance table, species-level taxonomic and functional abundance data were obtained. The Shannon index was calculated using the method described by Ortiz-Burgos (2016).

Seventy-two P-cycle-related genes and their corresponding KEGG Orthology numbers were retrieved, as described by Liu et al. (2024). These genes were classified into four categories based on their roles in the soil P cycle. Herein, microorganisms harbouring soil P-cycling genes were defined as P-solubilizing microorganisms (PSMs).

2.6. Statistical analysis

Data were analysed using two-way ANOVA (FM and P supply rate)) in the GenStat 19.0 statistical package (VSN International Ltd., Rothamsted, England) to assess the abundance of PSMs in rhizosheath soil and P-cycling microbial genes. Duncan's post hoc test was used to determine significant differences in the P content in soil, transcripts per million (TPM) (normalised abundance as transcripts per million) values of P-cycling functional genes, PSM diversity, root morphology, P accumulation and grain yield upon providing different treatments ($P = 0.05$). Three-way ANOVA (FM, P supply rate (P) and year (Y)) was conducted to analyse seed yield, P uptake and root traits of maize and soybean. R software (version 4.4.2) was used to perform permutation multivariate analysis of variance (PERMANOVA, vegan), random forest model analysis (randomForest) and partial least squares path modelling (plspm). Figures were generated using the online platform ChiPlot (https://www.chiplot.online) when needed. Circular heat maps displayed the standardised abundance (Z-score) of P-cycling functional genes.

3. Results

3.1. Effects of FM on the P concentration in rhizosheath soil

FM, P application and their combination considerably affected P concentrations in the soil (Fig. 1 and Table S1). In the soybean rhizosheath soil, the concentration of plant-available P increased by 193 %, 47 % and 224 % under the P90, FM and P90 + FM treatments, respectively, compared with that under the CK treatment, while Al–P increased by 207 %, 54 % and 270 %, respectively. In the maize rhizosheath soil, the concentration of plant-available P increased by 188 %, 38 % and 329 %, respectively, and acid phosphatase activity increased by 63 %, 187 % and 149 %, respectively. In the soybean rhizosheath soil, when compared with the CK treatment, the P90 and P90 + FM treatments each increased total P by 32 % and acid phosphatase activity by 250 % and 321 %, total inorganic P by 69 % and 65 %, Fe–P by 65 % and 53 %, O–P by 40 % and 32 % and Ca–P by 134 % and 143 %, respectively. In the maize rhizosheath soil, the P90 and P90 + FM treatments increased total P by 43 % and total inorganic P by 54 % and 60 %, respectively. Al–P increased by 145 % and 255 %, and Fe–P increased by 63 % and 79 %, respectively. In addition, FM significantly ($p < 0.05$) increased organic P in the soybean rhizosheath soil by 24 % but significantly ($p < 0.05$) decreased Ca–P in the maize rhizosheath soil by 44 %. When compared with the CK treatment, the proportions of Al–P and organic P increased, whereas the proportion of O–P decreased in the soybean rhizosheath soil. Furthermore, in the maize rhizosheath soil, the proportions of Al–P and Fe–P increased, while those of O–P, Ca–P and organic P decreased.

3.2. Effects of FM and P supply on PSM composition in rhizosheath soil

FM, P supply and their combination remarkably affected the diversity (Shannon index) and composition of microbial communities in the rhizosheath soil (Fig. 2). The Shannon index of P-solubilising bacteria in the maize rhizosheath soil was highly influenced by FM, while the Shannon index of P-solubilising fungi in the soybean rhizosheath soil was notably affected by P application. P application considerably reduced the Shannon index of P-solubilising bacteria in the soybean rhizosheath soil by 6.7 % (P90) and 9.0 % (P90 + FM) and of P-solubilising fungi by 27.8 % (P90 + FM) ($p < 0.05$) (Fig. 2a). Meanwhile, FM significantly decreased the Shannon index of P-solubilising bacteria in the maize rhizosheath soil by 4.8 % at P0 and 3.6 % at P90 ($p < 0.05$).

Distinct differences in the communities of P-solubilising bacteria and fungi were observed in the maize and soybean rhizosheath soils among the four treatments groups (Fig. 2b). Principal coordinates analysis revealed that the first two axes explained 60 % and 41 % of the variation in bacterial and fungal communities in the soybean rhizosheath and 58 % and 47 % in the maize rhizosheath, respectively. PERMANOVA revealed that P application and its interaction with FM remarkably affected P-solubilising bacteria in soybean and fungi in maize (Fig. 2b).

At the phylum level, the dominant P-solubilising bacteria in the maize and soybean rhizosheath soils included *Pseudomonadota*, *Acidobacteriota*, *Actinomycetota*, *Chloroflexota* and *Bacteroidota* (Fig. 2c). In soybean, nine of the top 10 P-solubilising bacterial phyla were notably affected by P application. By contrast, in maize, eight of the top 10 P-solubilising bacterial phyla were affected by FM (Fig. 2c and Table S2). Only three fungal phyla were identified in the rhizosheath soils of both the crops, and P application highly affected their relative abundance than by FM (Table S2). At the genus level, in the soybean rhizosheath, the relative abundances of *Rhodanobacter*, *Dyella*, *Phenylobacterium*, *Rhizobium*, *Trinickia*, *Mesorhizobium* and *Rudaea* considerably decreased

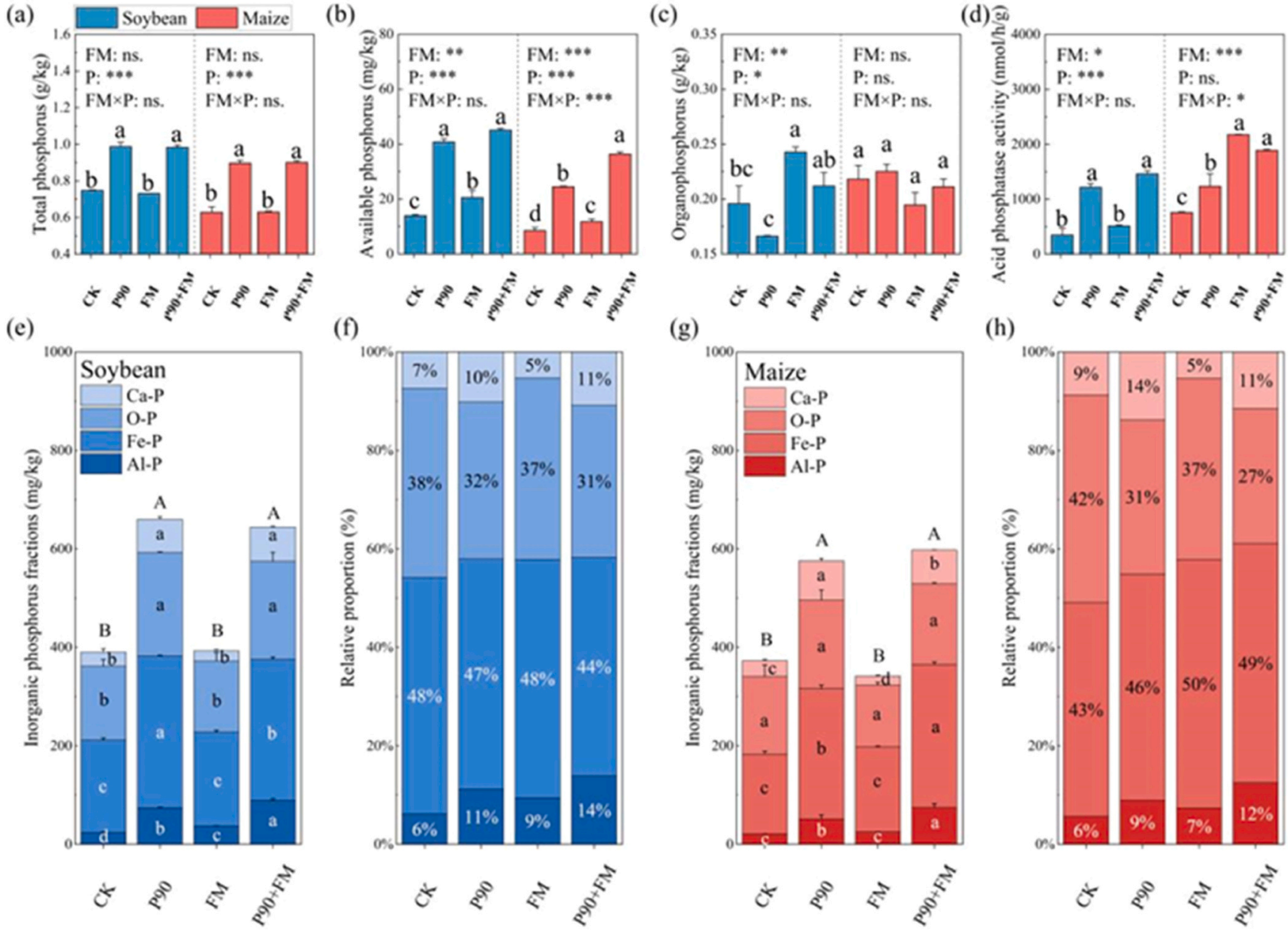

Fig. 1. Changes in the concentrations of (a) total soil P, (b) available soil P and (c) organophosphorus as well as (d) acid phosphatase activity, inorganic soil P fractions and their proportions in the rhizosheath soils of (e, f) soybean and (g, h) maize with and without film mulching (FM) under 0- (CK) and 90-kg P ha^{-1} (P90) supply in maize–soybean intercropping system. ns indicates no significance. * $P < 0.05$, ** $P < 0.01$ and *** $P < 0.001$. Different lowercase letters indicate significant differences among treatments (Duncan's test, $P < 0.05$).

upon P application, whereas those of *Ramlibacter* and *Occallatibacter* notably increased. FM considerably reduced the relative abundances of *Sphingomonas*, *Dyella*, *Rhizobium* and *Paraburkholderia* but increased those of *Rudaea* and *Ramlibacter* (Fig. 2c and Table S3). In the maize rhizosheath, P application considerably decreased the relative abundances of *Dyella*, *Trinickia*, *Rhodanobacter*, *Amycolatopsis*, *Actinocrinis* and *Catenulispora* but increased those of *Occallatibacter*, *Sphingomonas*, *Edaphobacter* and *Mucilaginibacter*. FM notably reduced the relative abundances of *Bradyrhizobium*, *Sphingomonas*, *Dyella*, *Trinickia*, *Paraburkholderia* and *Mucilaginibacter* but increased those of *Rhodanobacter* (Fig. 2c and Table S3). Among P-solubilising fungi, the relative abundance of the genus *Ambispora* notably increased in soybean but decreased in the maize rhizosheath soil upon P application (Fig. 2c and Table S4), while the relative abundance of *Colletotrichum* notably decreased in soybean but increased in maize under the FM treatment.

3.3. Effects of FM and P application on the P-cycling functional genes

Cluster analysis showed that the abundance of P-cycling functional genes in the soybean rhizosheath soil was more affected by FM than by P application, whereas in the maize rhizosheath soil, P application had a greater effect than FM (Fig. 3a). When compared with the CK treatment, the TPM values of the four P-cycling functional gene communities in the maize and soybean rhizosheath soils were significantly increased by FM and significantly reduced by P application (Fig. 3b). Furthermore, the interaction between FM and P supply did not considerably affect the TPM values of the four P-cycling gene communities.

3.4. Correlations among P-solubilising microbes, P-cycling functional genes and P concentrations in soil

Mantel correlation analysis revealed that P-solubilising bacteria in the soybean rhizosheath soil were notably affected by the total P, plant-available P in soil, acid phosphatase, Al–P, Fe–P, O–P and Ca–P, while P-solubilising fungi were considerably affected by total P, plant-available P in soil, acid phosphatase, Al–P, Fe–P and Ca–P. In the maize rhizosheath soil, P-solubilising bacteria were notably affected by total P, plant-available P in soil, acid phosphatase, Fe–P and Ca–P, while P-solubilising fungi were notably affected by total P, plant-available P in soil, acid phosphatase, Fe–P and Ca–P (Fig. 4a). The random forest model revealed that the microbial phyla contributing (mean squared error (MSE) > 6 %) to the concentration of plant-available P in soil in the soybean rhizosheath were *Nitrospirota*, *Gemmatimonadota*, *Pseudomonadota* and *Candidatus Dormibacteraeota*. In maize, *Actinomycetota* and *Mucoromycota* considerably contributed (Fig. 4b).

In soybean rhizosheath, plant-available soil P concentrations showed significant positive correlations with acid phosphatase, Al–P, Fe–P, O–P and Ca–P (Fig. 5a). Acid phosphatase was significantly positively correlated with Al–P, Fe–P, O–P and Ca–P. In the maize rhizosheath soil, plant-available soil P concentrations were significantly positively

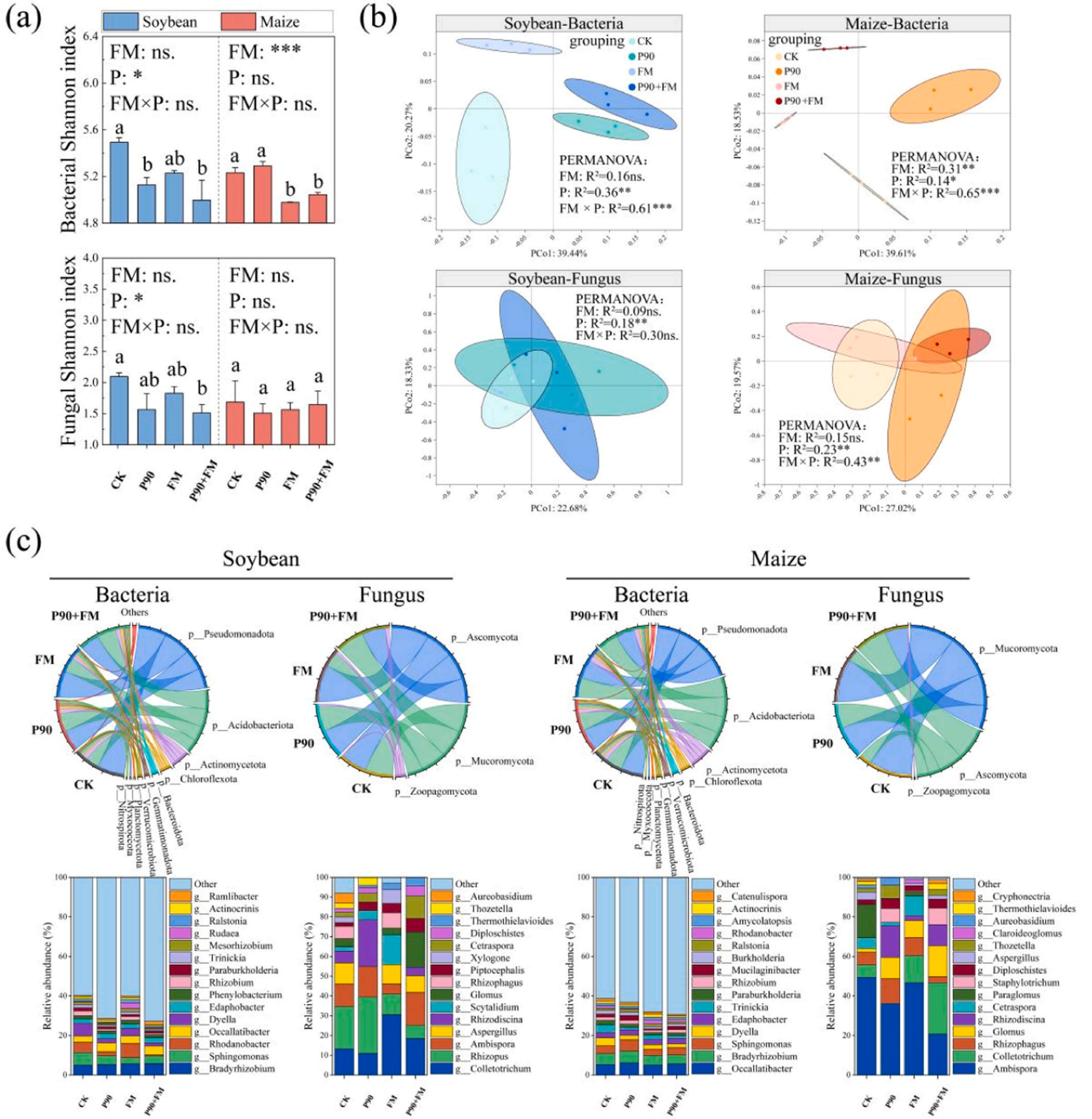

Fig. 2. Changes in the (a) Shannon index and (b) composition of P-soluble bacteria and fungi. Relative abundances of P-soluble bacteria and fungi at the phylum and genus levels of the rhizosheath soils of (c) soybean and (d) maize with and without film mulching (FM) under 0- (CK) and 90-kg P ha^{-1} (P90) supply in the maize–soybean intercropping system. ns, no significance. *$P < 0.05$, **$P < 0.01$ and *** $P < 0.001$. Different lowercase letters indicate significant differences among treatments (Duncan test, $P < 0.05$).

correlated with Al–P, Fe–P and Ca–P (Fig. 5a). Mantel analysis further indicated that in the soybean rhizosheath soil, genes involved in inorganic-P solubilisation and organic-P mineralisation were significantly correlated with concentrations of total P, plant-available P in soil, organic P, Al–P, Fe–P and Ca–P (Fig. 5a). In maize, organic-P mineralisation genes were significantly correlated with the concentrations of plant-available P in rhizosheath soil, O–P and Ca–P (Fig. 5a). Random forest analysis identified the P-cycling functional genes *phoN*, *pqqC* and *phnP* (MSE > 6 %) in soybean and *TPS* and *pepM* (MSE > 6 %) in maize as the key contributors to plant-available soil P concentrations in their respective rhizosheath soils (Fig. 5b). Among these, P-cycling gene communities involved in inorganic-P solubilisation contributed the most to plant-available soil P concentrations in the rhizosheath of maize and soybean.

3.5. Effects of FM and P application on root morphological traits and yield

Soybean root length, root surface area, root diameter and root volume under FM were 25.4 %, 46.8 %, 6.7 % and 47.6 % higher,

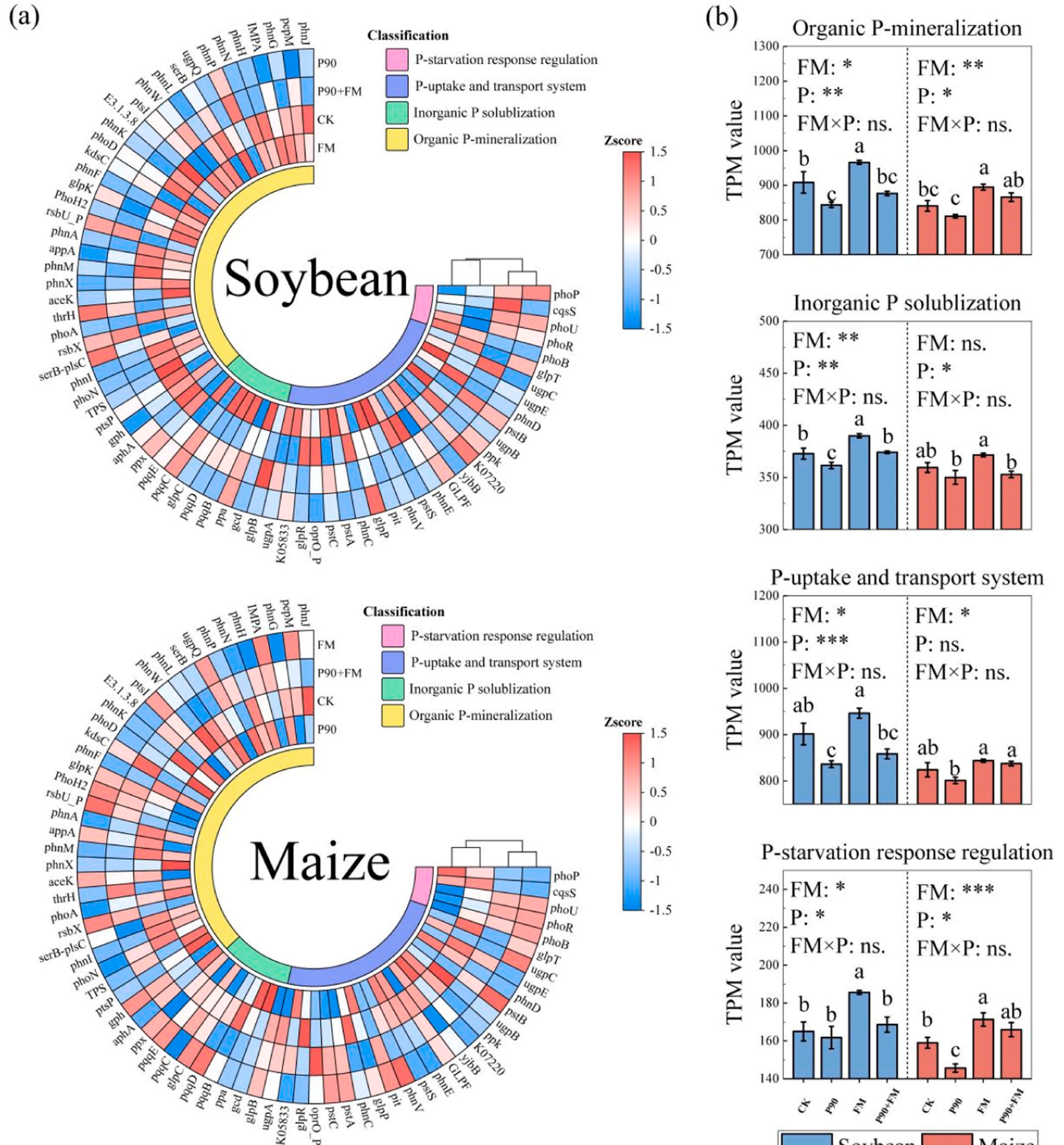

Fig. 3. Changes in the (a) normalised abundance (transcripts per million (TPM)) of P-cycling functional genes and (b) the four types genes involved in P-cycling gene in the rhizosheath soils of soybean and (d) maize with and without film mulching (FM) under 0- (CK) and 90-kg P ha^{-1} (P90) supply in the maize–soybean intercropping system. ns, no significance. *$P < 0.05$, **$P < 0.01$, *** $P < 0.001$. Different lowercase letters indicate significant differences among treatments (Duncan's test, $P < 0.05$).

respectively, than without FM across two P supply rates and 2 years (Fig. 6 and Table S5). Meanwhile, soybean root length, root surface area, root diameter and root volume under P application were 41.6 %, 35.8 %, 13.4 % and 53.0 % higher, respectively, than without P application across both managements (with and without FM) and years. Maize root length, root surface area and root volume with FM were 34.2 %, 17.3 % and 18.5 % higher, respectively, than without FM across two P supply rates and 2 years, respectively (Fig. 6 and Table S6). Maize root length, root surface area, root diameter and root volume with P application were 15.5 %, 19.4 % and 15.8 % higher, respectively, than without P application across both the managements and years.

Soybean seed yield and P uptake (P content) were 45.1 % and 30.9 %

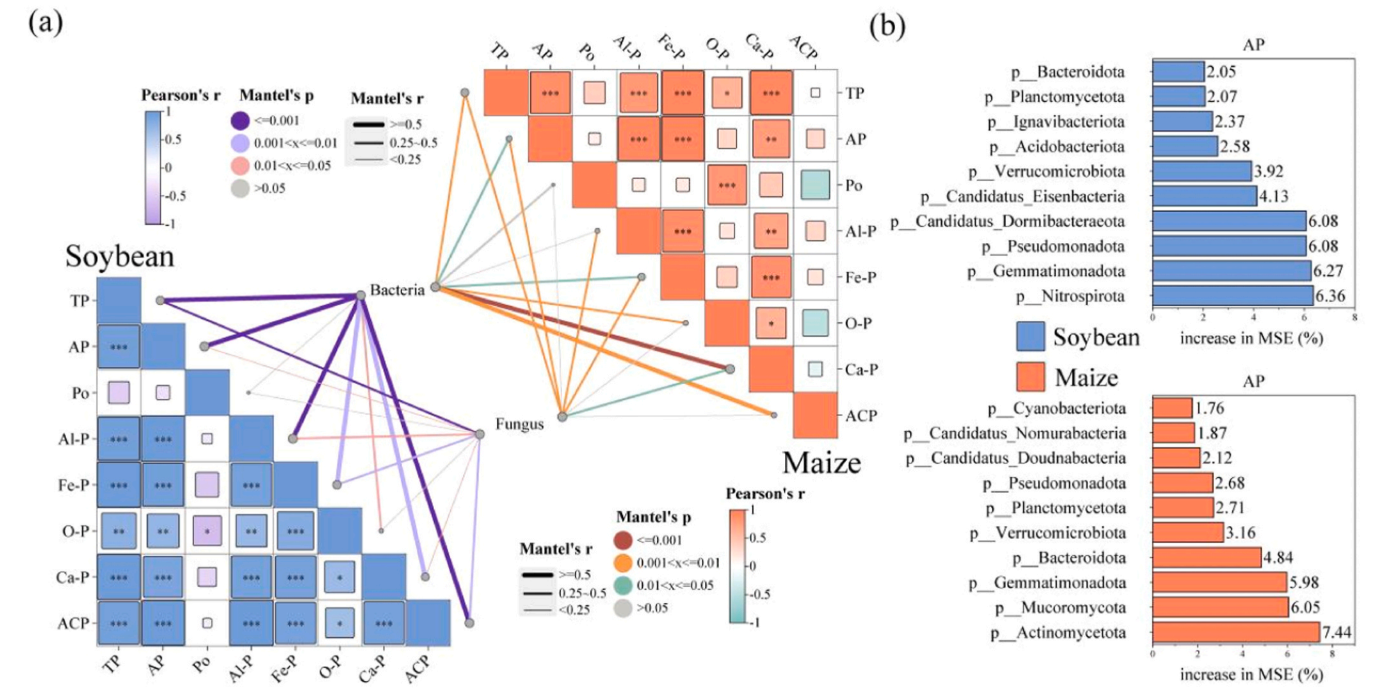

Fig. 4. (a) Relationship (Mantel test based on Pearson correlation) between soil P fractions and P-cycling microorganisms at the phylum level in the rhizosheath soils of maize and soybean. (b) Contribution ranking of P-cycling microorganisms at the phylum level to the plant-available P concentration in rhizosheath soil (AP), expressed as the percentage increase of mean squared error (MSE).

higher with FM, respectively, than without FM across two P supply rates and 2 years (Fig. 7 and Table S5). Soybean seed yield and P uptake were 79.1 % and 35.5 % higher with P application, respectively, than without P application across both the managements and years. Maize seed yield and P uptake were 23.8 % and 50.3 % higher with FM, respectively, than without FM across two P supply rates and 2 years (Fig. 7 and Table S5). Maize seed yield and P uptake were 53.7 % and 116.7 % higher with P application, respectively, than without P application across both the managements and years.

The partial least squares structural equation model (PLS-SEM) demonstrated that FM considerably affected soil P fractions, P accumulation and grain yield in the maize–soybean intercropping system (Fig. 8). The concentration of plant-available P in the rhizosheath soil was positively correlated with that of soybean ($R^2 = 0.83$, $p < 0.001$) and maize ($R^2 = 0.66$, $p < 0.001$) seed yields (Fig. 8b and d). The model further shows that RFM considerably increased the plant-available soil P concentration by enhancing the transformation of inorganic and organic P components, promoting root growth and thereby increasing P uptake and seed yield.

4. Discussion

4.1. Effects of RFM on P concentrations in rhizosheath soil

P, one of the three major soil nutrients, is highly important for crop yield and productivity (Chen et al., 2025; McDowell et al., 2024). As expected, the total soil P concentration was mainly affected by P application, with no notable effect observed upon FM application (Fig. 1a). The total P content in the rhizosheath soil following P application for the four consecutive years could be attributed to the soil's fixation of the applied P fertiliser (Li et al., 2023b), resulting in low P-use efficiency (Li et al., 2023b). The increase in total soil P upon P application was mainly related to increases in Ca–P, Al–P and Fe–P, indicating that surplus P was primarily stored as Al–P. We found that the concentration of organic P in the soybean rhizosheath soil considerably increased upon FM application than without FM, whereas P application considerably reduced organic-P concentration, highlighting the difference in effects of FM and P application on the organic-P concentration in soybean rhizosheath soil. The increase in organic P could be associated with FM-induced enhanced rhizodeposition (Hallama et al., 2022). Herein, it was observed that higher P supply could stimulate acid phosphatase activity, thereby promoting organic-P mineralisation (Raguet et al., 2023) (Fig. 1d). This effect was associated with a reduction in the organic-P concentration in the soybean rhizosheath soil.

As expected, P fertiliser application notably increased the concentration of plant-available P in soil, which is consistent with previous studies (Chen et al., 2023). In addition, FM application considerably increased the plant-available soil P concentration in the rhizosheath of maize and soybean (Fig. 1b). One possible explanation for this is that FM considerably enhances acid phosphatase activity, which converts unavailable organic P into plant-available soil P (Raguet et al., 2023). This reason was validated by the positive correlation between acid phosphatase activity and plant-available soil P in the rhizosheath (Fig. 4a). In addition, FM helped reduce P leaching along with rainwater, minimising P loss along with surface runoff, thereby resulting in higher plant-available soil P content under FM than under treatments without FM (Xu et al., 2016). However, P leaching was relatively low. Finally, FM increased the soil temperature and water content (Liao et al., 2022b), both of which were suitable for the growth of PSMs, such as bacteria and fungi, which convert unavailable soil P into plant-available forms by enhancing the abundances of microbial P-cycling genes, thereby increasing rhizosheath plant-available soil P concentration. However, more research was required to clarify the roles of PSMs in P transformation.

4.2. Effects of RFM on PSMs and its role in P transformation

Rhizosheath soil PSMs play a crucial role in regulating the soil's P cycle, promoting plant growth and sustaining agroecosystem health (Shi et al., 2024). Soil PSMs are highly sensitive to P input and management practices and are the key players in regulating plant-available soil P concentration (Prakash et al., 2018). Herein, P application considerably

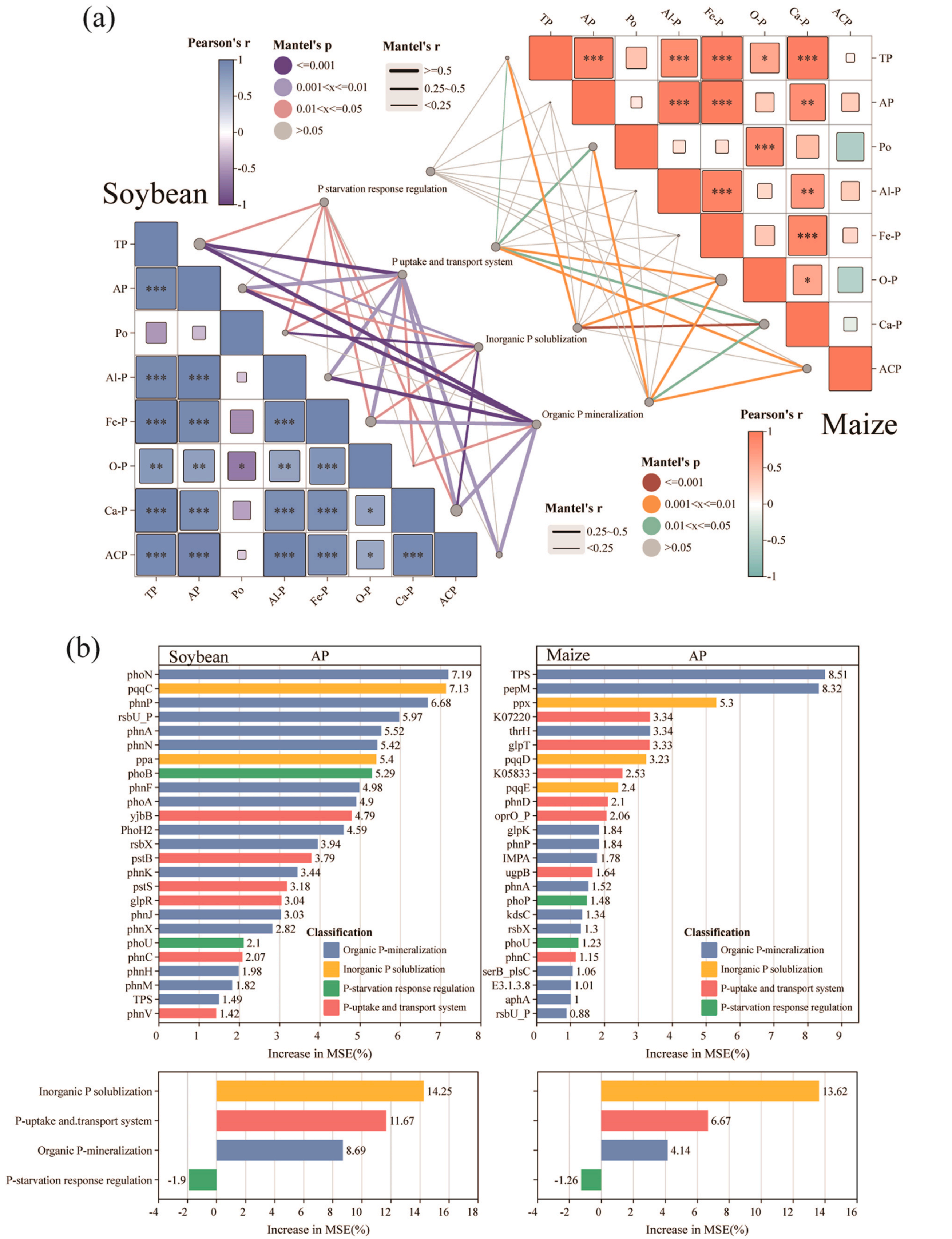

Fig. 5. (a) Relationship (Mantel test based on Pearson correlation) between P content in soil and P-cycling functional genes in the rhizosheath soils of maize and soybean. (b) Contribution ranking of P-cycling genes to P concentration (AP) in rhizosheath soil, expressed as the percentage increase of mean squared error (MSE).

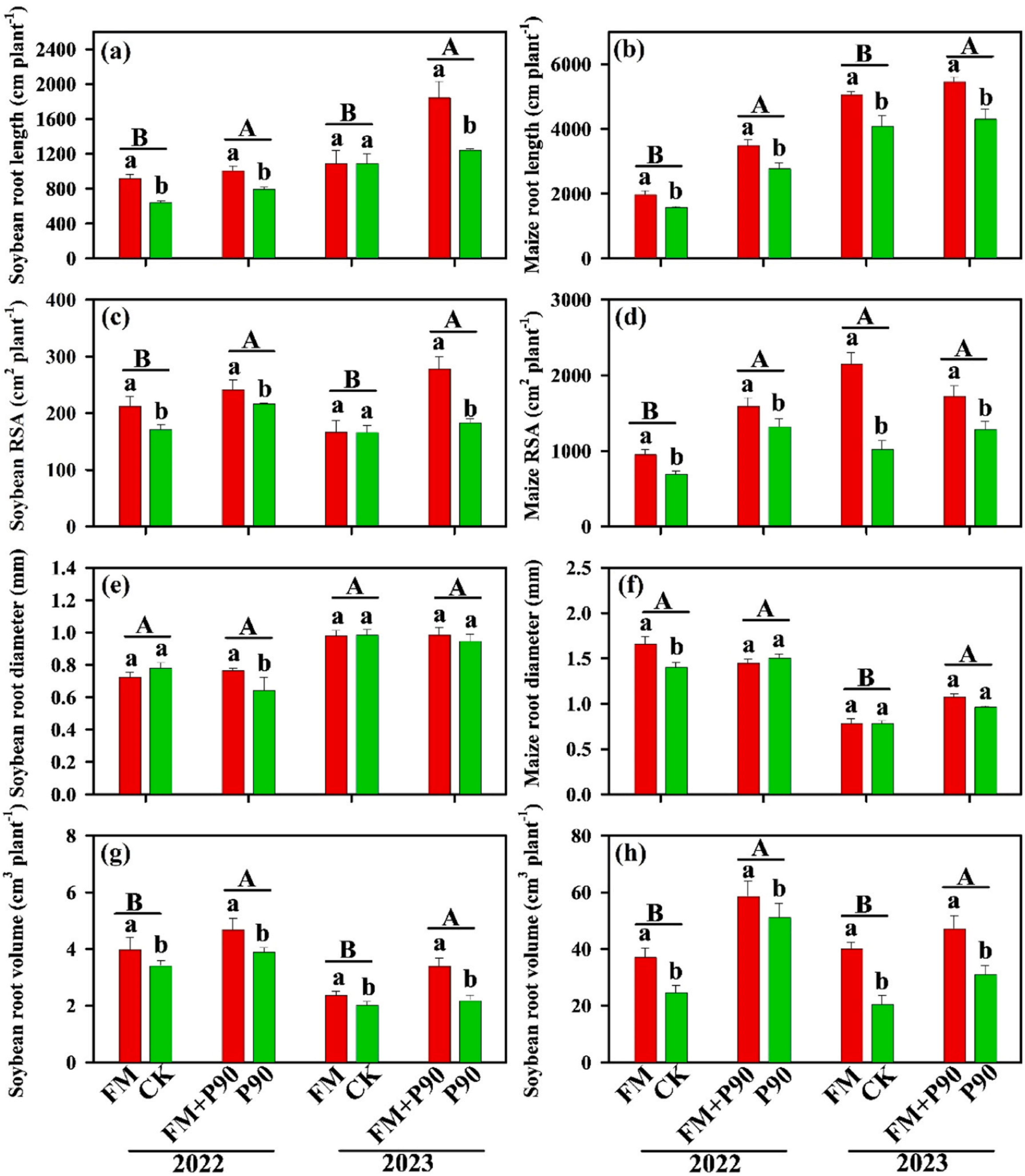

Fig. 6. Changes in (a, b) root length, (c, d) root surface area (RSA), (e, f) root diameter and (g, h) root volume of maize and soybean with and without film mulching (FM) under 0- (CK) and 90-kg P ha^{-1} (P90) supply in the maize–soybean intercropping system. Different lowercase letters indicate significant differences between with and without FM at the same P supply rate, and different uppercase letters indicate significant differences between P0 and P90 in the same year.

reduced the diversity (Shannon index) of PSMs (bacteria and fungi) in the soybean rhizosheath, while it only affected the diversity of P-solubilising bacteria in the maize rhizosheath (Fig. 2a). This difference indicates that the responses of PSMs to FM and P application are species-dependent in the maize–soybean intercropping system. One possible explanation could be that the soybean was fully covered, whereas the maize was partly covered, which led to different effects on the water content of root soil between maize and soybean, thereby affecting the composition of the PSMs. However, this needs further investigation. Changes in root exudates can alter microbial composition (Lamichhane et al., 2024; Zhalnina et al., 2018), suggesting that the differential responses of rhizosheath PSMs to FM and P application can be linked to changes in root exudates, necessitating further investigation. Changes in soil water content caused by FM (Zhang et al., 2025) can affect the composition of soil microbial communities (Długosz et al., 2024). The constructions of ridge-furrow systems alter physical traits of soils, such as bulk density, and chemical characteristics, such as soil organic matter, through soil redistribution, thereby affecting microbial communities, including PSMs (Philippot et al., 2024). However, further studies are needed to clarify the interactions between soil properties and microbial communities. Bacterial and fungal PSMs are significantly positively correlated with the concentration of plant-available P in rhizosheath soil (Fig. 4a), underscoring their important roles in transforming P concentrations in soil. In addition, the dominant microbial phyla contributing to plant-available P in rhizosheath soil were *Nitrospirota* in soybean and *Actinomycetota* in maize (Fig. 4b).

Microbial functional genes involved in soil P cycle were the key drivers of P transformation, with their expression levels directly linked

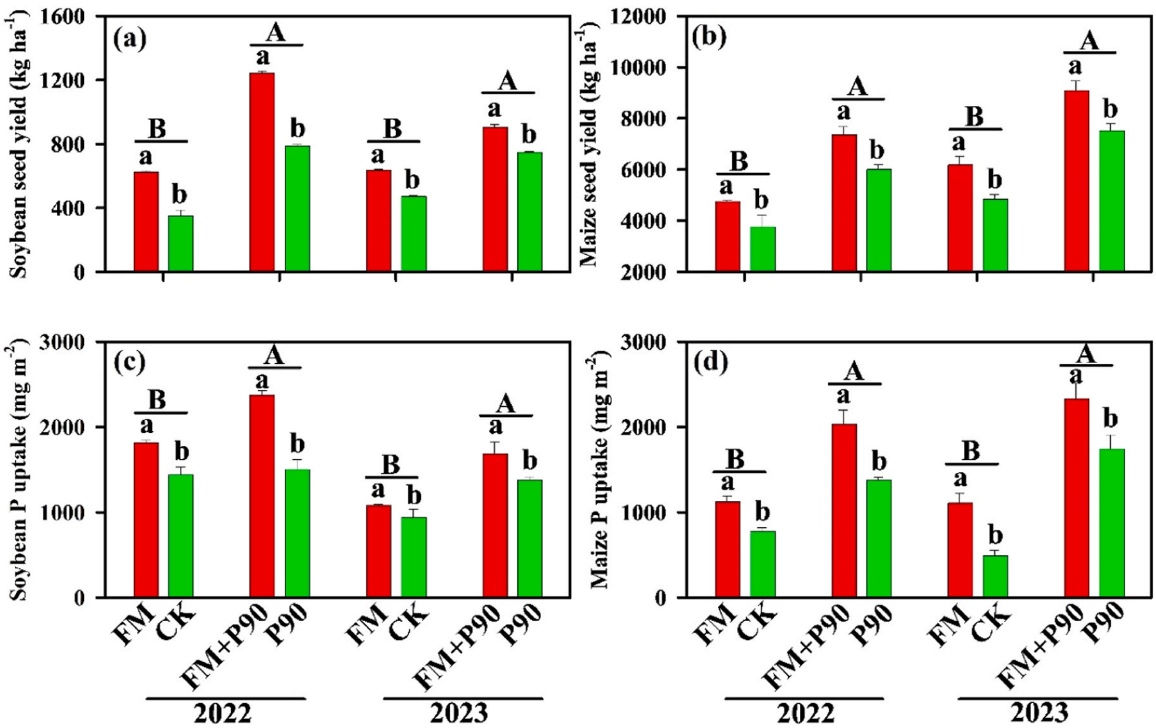

Fig. 7. Changes in (a, b) seed yield and (c, d) P uptake of maize and soybean with and without film mulching (FM) under 0- (CK) and 90-kg P ha^{-1} (P90) supply in the maize–soybean intercropping system. Different lowercase letters indicate significant differences between with and without FM at the same P supply rate, and different uppercase letters indicate significant differences between P0 and P90 in the same year.

to the intensity of each P-cycle process (Dai et al., 2020). Four types of microbial functional gene communities were involved: organic-P mineralisation, P-starvation response regulation, inorganic-P solubilisation as well as P absorption and transport systems (Hu et al., 2019). Herein, four consecutive years of FM treatment to the maize–soybean intercropping system considerably increased the abundances of all four microbial functional gene types involved in the soil P cycle in soybean and those of three types (organic-P mineralisation, P-starvation response and P absorption and transport) in the maize rhizosheath (Fig. 3b). These gene abundances were positively correlated with the plant-available soil P concentration in the crop rhizosheaths (Fig. 5). Genes involved in inorganic-P solubilisation contributed the highest to the concentration of plant-available P in rhizosheath soil (Fig. 5b). Specifically, *phoN* and *phnP* (organic-P mineralisation), *pqqC* and *phnP* (inorganic-P solubilisation) and *TPS* and *pepM* (organic-P mineralisation) contributed the highest (MSE $>$ 6 %) to plant-available soil P concentration in soybean and maize, respectively (Fig. 5). Genes involved in inorganic-P solubilisation were positively correlated with Ca–P in soybean and maize soils (Fig. 5a), indicating that Ca–P was the main inorganic-P source mobilised by these genes. This understanding was further supported by the observed reductions in the Ca–P concentration and proportion in the rhizosheath soils of soybean and maize (Figs. 1e–1h). Furthermore, FM reduced the proportion of Fe–P in the soybean rhizosheath soil, which was associated with the increased abundance of inorganic-P solubilisation genes induced by FM. This indicates an enhanced soil P cycle, particularly involving Ca–P, which contributed to the increase in P concentration in rhizosheath soil.

However, long-term (14 years) P fertiliser application has been reported to reduce the abundance of soil P-cycling functional genes (Liu et al., 2023). Herein, four consecutive years of P application markedly reduced the abundance of four types of soil P-cycling genes (except those related to P absorption and transport) in the maize and soybean rhizosheaths (Fig. 3b). This result indicates that crops could have experienced upregulated soil P-cycling microbial functional gene expression to cope with P deficiency in the maize–soybean intercropping system. However, the regulatory mechanisms underlying the changes in PSMs are still unknown and further understanding them could advance our knowledge on plant–microbe interactions related to rhizosheath soil P transformation in maize–soybean intercropping system.

4.3. Effects of RFM on maize–soybean intercropping productivity

Previous studies have confirmed that RFM is a sustainable management practice that improves yield of crops in monoculture systems, such as maize and soybean, by enhancing nutrient uptake, particularly P (Liao et al., 2022b; Zhang et al., 2025). We introduced RFM into the maize–soybean intercropping system (Fig. S1) in South China, where seasonal droughts frequently occur during the crop reproductive stage (Yue et al., 2023). Our findings demonstrated that RFM considerably increased crop productivity in this intercropping system, which was associated with enhanced P uptake under two P supply rates (Fig. 7). This increase supported higher biomass production and improved seed yield by enhancing yield components, such as seed number (He et al., 2019; Zhang et al., 2024). In addition, we observed that RFM improved root morphology—including root length, root surface area and root volume—in maize and soybean, notably enhancing P uptake by increasing soil exploration (Lynch, 2019). The alleviation of the limiting effects of P deficiency on root growth was found to be mainly associated with the FM-induced increase in the concentration of plant-available P in rhizosheath soil, which promoted P accumulation and ultimately increased seed yield in the maize–soybean intercropping system.

5. Conclusion

The introduction of RFM in maize–soybean intercropping considerably enhances crop productivity and land-use efficiency compared with conventional intercropping practices. RFM enhances P concentrations in rhizosheath soil, promotes root growth in maize and soybean and enhances P uptake and accumulation, thereby improving the overall grain yield in the maize–soybean intercropping system. RFM accelerates P

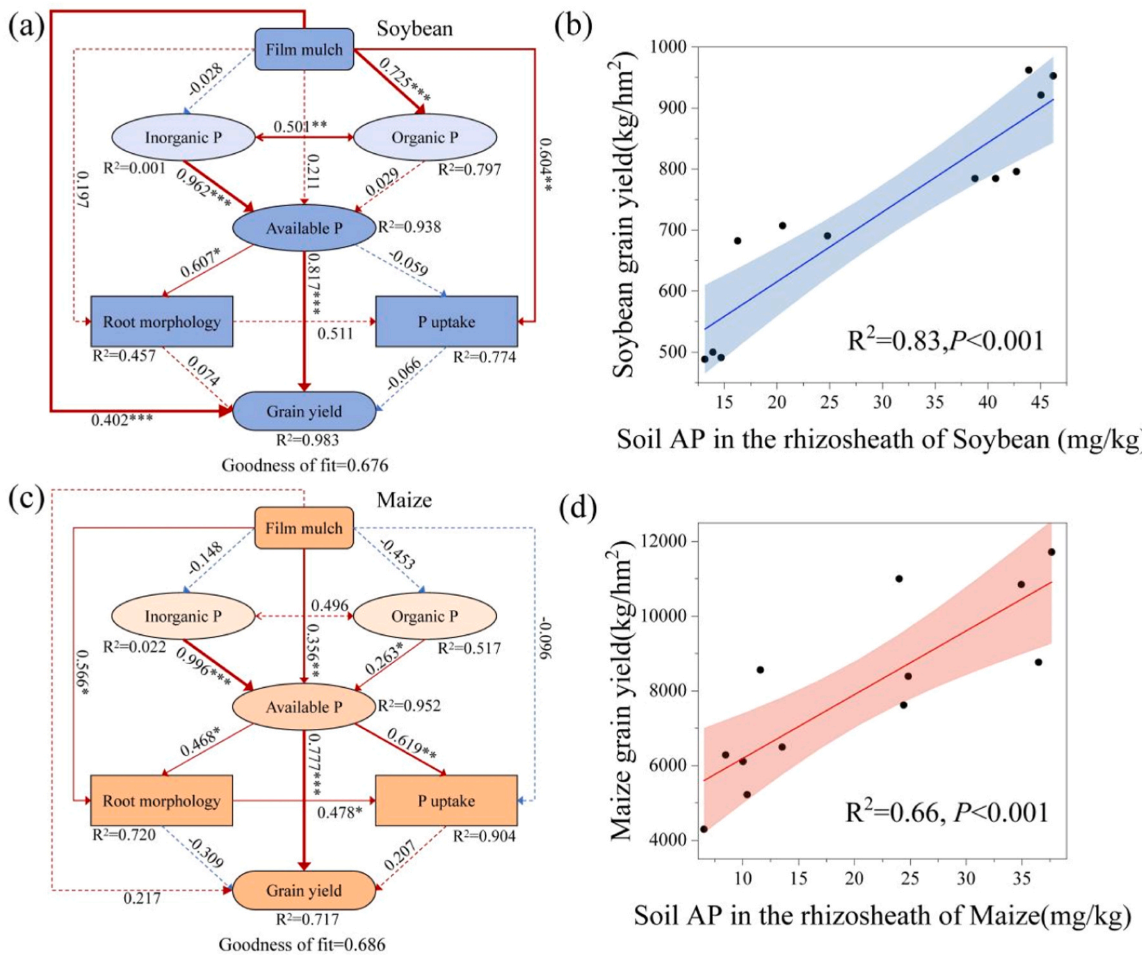

Fig. 8. Structural equation model illustrating the effects of plastic film mulching on phosphorus transformation in the rhizosheath soils of (a) soybean and (c) maize in a maize–soybean intercropping system as well as the correlation between the plant-available P concentration in rhizosheath soil and the yield of (b) soybean and (d) maize.

transformation in rhizosheath soil by upregulating P-cycling functional genes and altering the composition of PSMs, leading to an increase in the concentrations of plant-available P. This study highlights RFM as a sustainable cultivation practice for achieving high seed yield and P-acquisition efficiency in maize–soybean intercropping systems in areas with low levels of plant-available P. This underscores the crucial role of enhanced plant–microbe interactions derived by RFM in promoting sustainable P use and yield formation in acidic soils worldwide.

CRediT authorship contribution statement

Sanwei Yang: Writing – review & editing, Supervision, Funding acquisition, Conceptualization. **Jing He:** Writing – review & editing, Investigation. **Yi Jin:** Writing – original draft, Methodology, Investigation, Formal analysis. **Yu-Mei Wang:** Writing – original draft, Methodology, Investigation, Formal analysis. **Jin He:** Writing – review & editing, Writing – original draft, Supervision, Funding acquisition, Conceptualization. **Chen-Xi Yi:** Writing – review & editing, Investigation. **Yu Dai:** Writing – review & editing, Investigation. **Qiao Zhu:** Writing – review & editing, Investigation. **Long-Gui Li:** Writing – review & editing, Investigation. **Yinglong Chen:** Writing – review & editing. **Xiao-Li Wang:** Writing – review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.still.2025.106883.

Data availability

Data will be made available on request.

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