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# Bacterial community changes in the presence of AMF in the context of maize with low phosphorus content

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## Abstract

**Purpose** Arbuscular mycorrhizal fungi (AMF) perform an ancestral and essential association with plant roots, where plants provide carbohydrates and lipids, and the fungi respond by translocating water and nutrients to the roots through the hyphae. There is a need to investigate the microbial community associated with the rhizosphere of mycorrhizal plants in response to the multiple benefits (e.g., improved nutrition and stress resistance) provided by the association. In this work, we analyzed the bacterial communities associated with the rhizosphere of plants and their response to mycorrhizae in low P conditions.

**Methods** For this purpose, inoculated and non-inoculated B73 corn plants were grown with a consortium of mycorrhizal fungi under low phosphorus conditions. Mycorrhiza response in B73 and the interaction with rhizosphere microbiome were characterized by sequencing the bacterial 16S rRNA gene.

**Results** Inoculated plants showed increased greater growth in leaf and root parameters in low P conditions. Bacterial microbiome showed changes in beta diversity and some OUTs significantly regulated by AMF presence.

**Conclusion** These data confirm the importance of mycorrhizae in phosphorus stress and rhizosphere community changes as a possible mechanism to improve plant growth.

**Keywords** Mycorrhiza · Microbiome · Rhizosphere · Low P

## 1 Introduction

Food production is affected by increasing competition for land, water, and energy and the urgency to reduce environmental impacts. This presents a daunting challenge to meet the food needs of a growing population while ensuring environmental and economic sustainability (Godfray et al. 2010). Comprehensive strategies must be developed to address this challenge, for example, the interaction of plants with soil microorganisms to make better use of resources and reduce various types of stress. Some microorganisms have co-evolved with plants to mutually benefit from the soil and its multiple nutrient sources. While this approach may reduce productivity in the short term, it can ultimately maximize crop yield while minimizing resource use (Chaparro et al. 2012).

During plant growth, interaction with soil microbes in the rhizosphere is critical for optimal nutrient uptake. The rhizosphere refers to the area surrounding the root where there is increased biological and chemical activity, as defined by Hiltner (1904). Roots release low molecular weight root exudates into the soil including amino acids, vitamins, organic acids, sugars, phenolic compounds, anions, gases, and other secondary metabolites as well as high-molecular-weight root exudates such as polysaccharides and proteins (Kamilova et al. 2006; Badri and Vivanco 2009). Exudates function as a food source that attracts beneficial, neutral, and pathogenic microbes through the root.

There is growing evidence that plant-microorganism coadaptation plays an important role in enhancing both plant health and productivity, resulting in tightly intertwined and

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beneficial ecological interactions. Among the most studied interactions are those between plants and two categories of organisms: symbiotic mutualists (mycorrhizal fungi and nitrogen-fixing microorganisms) and parasites (diseases) (Lambers et al. 2009). The term mycorrhiza encompasses the symbiotic association between soil fungi and plant roots. These associations play a crucial role in terrestrial ecosystems by regulating carbon and nutrient cycles where mycorrhiza supply mineral nutrients to the plant in exchange for carbohydrates and lipids (Rich et al. 2017). One of the main advantages for plants associated with mycorrhiza is the increase in root growth, resulting in improved nutrient acquisition, including nitrogen (N) and phosphorus (P), and greater drought resistance (Subramanian and Charest 1999). AMF benefit the plant transporting nutrients and water into the root; in addition, the hyphae also release compounds to interact with soil microbiota, forming the mycorhizosphere, a zone where microbial activity and nutrient availability are enhanced (Linderman 1988). A positive correlation has been observed between changes in quantitative and qualitative patterns of root exudates induced by mycorrhiza and the microflora of the mycorrhizosphere (Bansal and Mukerji 1994). Therefore, it is important to study the interaction between mycorrhizae and other microorganisms present in the plant rhizosphere like plant growth-promoting rhizobacteria (PGPR), which are beneficial for plant growth and contribute to the development of sustainable agricultural systems. PGPR typically function in three distinct ways: synthesizing plant compounds, including phytohormones and vitamins (Dobbelaere et al. 2003); assisting in the uptake of specific soil nutrients, as observed in nitrogen-fixing bacteria (Çakmakçi et al. 2006); and aiding in the prevention or control of phytopathogens.

Through metagenomic analysis, it has become possible to obtain a comprehensive view of the rhizosphere microbiome (Gupta et al. 2018). The 16S rRNA sequence of the small subunit ribosome is a commonly used phylogenetic marker for amplicon sequencing of bacterial communities. It is highly conserved and useful for identification. Recent advances in sequencing technologies have enabled the acquisition of hundreds of thousands of sequences per sample, which can be analyzed through bioinformatics (Qin et al. 2010). This allows the assessment of bacterial diversity and species distribution for ecological sample comparisons (Birtel et al. 2015).

As several studies in maize have shown, there are different factors that influence the microbiome that colonizes the plant roots. An analysis of the bacterial communities associated with different maize cultivars showed changes in diversity and relative abundance of certain bacterial groups in the rhizosphere compared to bulk soil, because the rhizosphere serves as a selection zone (Peiffer et al. 2013). The microbiome inhabiting maize roots is influenced by microorganisms present in the soil where the crop is grown, in addition to those found in the seed (Johnston-Monje et al. 2016). When examining the effects of different maize genotypes and other Poaceae species, researchers found that genetic distance between rhizobacterial communities was associated with phenotypic distance between plants, suggesting that the evolutionary history of the host plant influences the composition of bacteria colonizing the root (Bouffaud et al. 2014). A study by Zhu et al. (2016) showed that nitrogen fertilizer application affects root exudates and bacterial communities in the maize rhizosphere, resulting in an increase in the relative abundance of Bacillales, Nitrosomonadales, and Rhodocyclales and a decrease in Chloroflexales, Gemmatimonadetes, and Phycisphaerae.

Maize plants can benefit from mycorrhizal association for enhanced growth. This is achieved through variations in phosphate content within the plant, the abundance of internal and external fungal structures of the root, facilitated phosphorus uptake by mycorrhiza, and accumulation of transcripts encoding phosphate transporters of the PHT1 family among different genotypes (Sawers et al. 2017). Dabire et al. (2007) observed that the uniformity found in the rhizosphere of sorghum (*Sorghum bicolor* L.) was positively correlated with the number of inoculated AMF propagules. To assess the microbial changes in the rhizosphere microbiome due to mycorrhizal association, bacterial diversity and composition in the rhizosphere of AMF-inoculated B73 maize plants were compared to non-mycorrhizal plants through 16S ribosomal gene analysis.

## 2 Materials and Methods

### 2.1 Greenhouse

Plants were grown under greenhouse conditions in Cinvestav Unidad Irapuato, México. PVC tubes (1 m × 15 cm) were used as pots and filled with a pasteurized mixture of sand (65%), silt (15%), and perlite (20%) to remove AMF spores. Sterilization was carried out in autoclave at 15 lbs. for 1 h in 3 days. The substratum microbiome was compensated with microorganism's inoculum extracted from native soil from Cinvestav. The Soil was suspended (1/2 v/v) in sterile water and sieved at 40 µm to avoid AMF contamination.

Treatments consisted in plants inoculated and non-inoculated with AMF spores. For plants with mycorrhiza, pots were inoculated with 5 g (approx. 300 spores) of AMF consortia spores (TM-73, Biomic). B73 maize seeds were disinfected with 1% chlorine and planted directly. Pots were watered with 200 ml sterile water every 2 days and, after plant emergence, once a week fertilized with Hoagland's solution corrected to 1/4 of the original phosphorous.

At 55 days after emergence of the plants, leaf growth was determined with the stem diameter, height to the flag

leaf, stem height, and leaf area, and the relative chlorophyll content was measured with the SPAD-502 chlorophyll meter (Konica Minolta, Japan) by placing the equipment on the third youngest leaf of the plant. At 56 days after emergence, plants were harvested, and complete roots were removed from the tubes. The roots were vigorously shaken to remove non-rhizosphere soil. Then, soil samples from the rhizosphere were taken in 16.5 cm × 14.9 cm Ziploc bags and stored in a cold room at 4 °C until analysis. Subsequently, the root was washed with tap water to remove any remaining soil. Random fragments from the entire root were cut and stored in 50-ml Falcon tubes for mycorrhizal fungi staining. The root was photographed and later evaluated for volume, fresh weight, dry weight, and root length. Leaf and root parameters were compared by Student's *t*-test using R software (v 4.2.3).

### 2.2 Root colonization

The tubes containing the roots were filled with 10% KOH solution to cover the samples for clearing. They were autoclaved treatment at 10 lb for 10 min. Roots were rinsed with tap water. Then, roots were stained with 0.1% trypan blue staining solution in a 2:1:1 mixture of acetic acid-glycerol-distilled water and placed in the autoclave at 10 lb of pressure for 10 min. The roots were rinsed with tap water. The roots were suspended in acetoglycerol for preservation. From each sample, 15 fragments of 1 cm root were mounted on slides for colonization quantification. Three technical replicates were performed for each sample. The quantification of root colonization was done using the Intersection method (McGonigle et al. 1990).

### 2.3 Sequencing and analyses

The metagenomic DNA (mDNA) from the rhizosphere of 3 plants per treatment was extracted using the DNeasy PowerSoil Kit (QUIAGEN, Germany) following the instructions provided. The mDNA was sequenced by Macrogen for the V3–V4 region using the Bakt_341F oligo: CCT ACGGGNGGCWGCAG and Bakt_805R oligo: GACTAC HVGGGTATCTAATCC, with a read size of 301 bp in a paired-end format. The libraries were prepared using the Herculase II Fusion DNA Polymerase Nextera XT Index Kit V2 following the 16 M Metagenomic Sequencing Library Preparation Part # 15044223 Rev. B protocol for sequencing on the Illumina platform.

The sequences were analyzed using the Qiime 2 platform (Quantitative Insights Into Microbial Ecology V 2018.11), an open-source pipeline for microbiome analysis from sequencing data. Data was imported with Casva 1.8. Sequence quality control was performed, and the feature table was constructed using the DADA2. The assignment of operational taxonomic units (OTUs) was performed using the Greengenes 13_8 database as a reference at a 97% similarity threshold. Alpha rarefaction curves were generated with the number of OTUs at a depth of 7000 for all samples to ensure the maximum possible diversity was captured per sample. The Shannon diversity index was calculated to compare the diversity between samples. To assess changes in community structure among treatments, as indicated by beta diversity, the weighted UniFrac distances were used, which quantitatively measure dissimilarity between communities while incorporating phylogenetic relationships among features (Lozupone et al. 2007). To find species-level differences in bacterial OTUs, the exact test of the edgeR (v 3.40.2) package in R software was used, which compares two groups of counts with negative binomial distribution.

## 3 Results

### 3.1 Leaf growth

B73 maize plants were grown under greenhouse conditions to compare mycorrhizal versus non-mycorrhizal plants. Plants inoculated with TM-73 showed the increased leaf growth parameters (Table 1). The most significant response to mycorrhizal inoculation was 152% increase in leaf dry weight and 123% increase in leaf fresh weight. The mycorrhizal association increased the physiological activity of the plant to achieve this increase seen in an increase in relative chlorophyll content. In addition, visually, the control showed a reduced growth and signs of stress in the basal leaves (Fig. 1a).

### 3.2 Root growth and colonization

Non-mycorrhizal plants were confirmed as controls because they did not show the typical structures of the symbiosis (hyphae, arbuscules, and vesicles). The mycorrhizal plants showed a colonization of 80.87% by hyphae, 57.66% by arbuscules, and 23.83% by vesicles (Fig. 1c and d).

Mycorrhiza also had a positive effect on root growth with increase of 154% in dry weight and 137% in volume (Table 2). On the other hand, there was no significant effect on length, probably because the pot was too deep for the stage at which they were harvested (Fig. 1b).

### 3.3 Microbiome analysis

The bacterial composition of the rhizosphere samples consisted mainly of the phyla Proteobacteria,

**Table 1** Maize leaf growth data

| | Stem diameter* | Flag leaf height* | Stem height* | Leaf area* | Leaf fresh mass** | Leaf dry mass** | Chlorophyll relative content* |
|---|---|---|---|---|---|---|---|
| | r(mm) | cm | | $cm^2$ | g | | |
| **Control** | 10.12 (±1.7) | 39.07 (±8.25) | 14.00 (±2.89) | 204.78 (±58.41) | 11.44 (±5.49) | 1.62 (±0.64) | 8.22 (±2.09) |
| **TM-73** | 13.29 (±1.67) | 51.55 (±9.35) | 19.00 (±2.58) | 396.57 (±91.56) | 25.55 (±6.99) | 4.09 (±1.7) | 13.13 (±2.44) |
| **p** | 0.0133 | 0.0345 | 0.0103 | 0.0022 | 0.0034 | 0.0145 | 0.004 |

Mean and *t*-test results. * 55 days after emergence. ** 56 days after emergence. Mean (±SD)

Bacteroidetes, Actinobacteria, Nitrospirae, and Cyanobacteria (Fig. 2b). Mycorrhiza influenced bacterial diversity, using beta diversity by the weighted UniFrac method to prove that samples were different by community structure between treatments which can be observed by principal component analysis in (Fig. 2a). However, for alpha diversity indicators, no significant differences were observed. Mycorrhizal fungi also had an effect at the species level. Six bacterial OTUS had a significant change compared to the control, where *Asteroleplasma* spp. and *Lysobacter brunescens* were upregulated and *Pseudoxanthomonas mexicana*, *Mycobacterium* spp., *Achromobacter* spp., and *Cyanobacteria* spp. were downregulated (Fig. 2c and d).

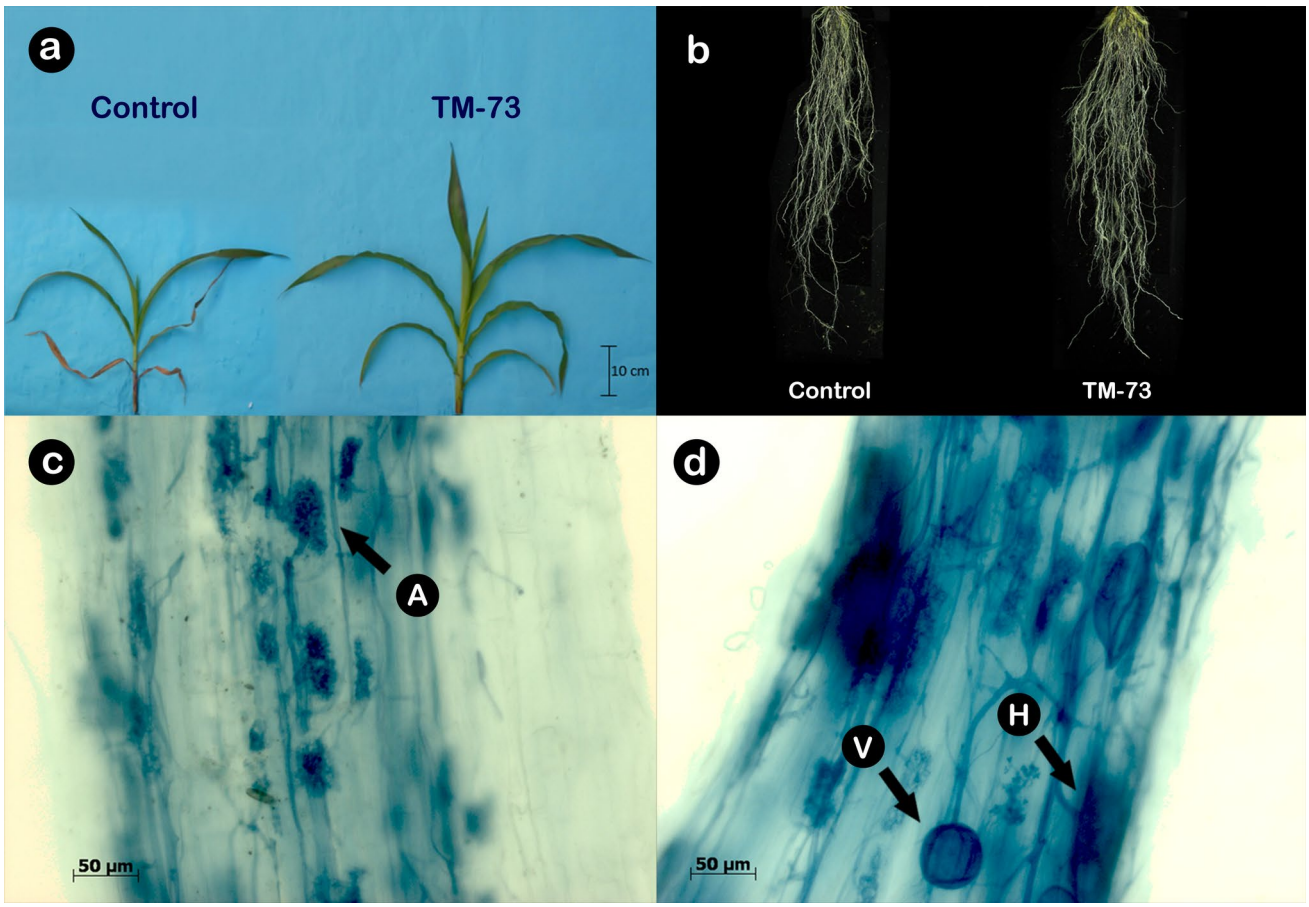


**Fig. 1** Effect of mycorrhizal fungi on the plant (**a**–**b**) with the plant closest to the average: **a** leaf growth and **b** root growth. Structures seen under the microscope of plants colonized by arbuscular mycorrhizal fungi (**c**–**d**). **c** A, arbuscules; **d** H, hyphae; and V, vesicles

**Table 2** Maize root growth data 56 days after emergence

| | Root length | Root volume | Root dry mass | Hypha | Arbuscle | Vesicula |
|---|---|---|---|---|---|---|
| | cm | $cm^3$ | g | % | % | % |
| **Control** | 92.25 (±19.26) | 3.42 (±1.11) | 1.12 (±0.5) | 0 | 0 | 0 |
| **TM-73** | 103.15 (±12.34) | 8.10 (±2.41) | 2.85 (±0.8) | 80.87 (±9.32) | 57.66 (±13.06) | 23.83 (±14.68) |
| **p** | 0.2748 | 0.0087 | 0.0018 | | | |

Mean and *t*-test results. Mean (±SD)

## 4 Discussion

Maize B73 has been shown to be susceptible to the absence of P and mycorrhizae help its performativity transporting the nutrient to the plant root by activating molecular mechanisms, such as the PT transporters for phosphorus transport in both plant and fungus (Giovannini et al. 2022; Ma et al. 2021; Giovannini et al. 2022). This study confirms the positive response of plants to the presence of a good mycorrhizal association, producing a positive response in the leaf and root growth of inoculated plants compared to non-inoculated plants in low P conditions. Ramírez-Flores (2019) demonstrated under similar P conditions that inoculating B73 maize plants with AMF *Rhizophagus irregularis* leads to an increase in mineral accumulation.

Abd El-Fattah et al. (2023) report the potential contribution of mycorrhizae on the productivity, benefit–cost ratio, and economic return of irrigation water of sweet maize, especially under inadequate water and nutrient conditions. Therefore, we suggest that mycorrhiza can potentially help

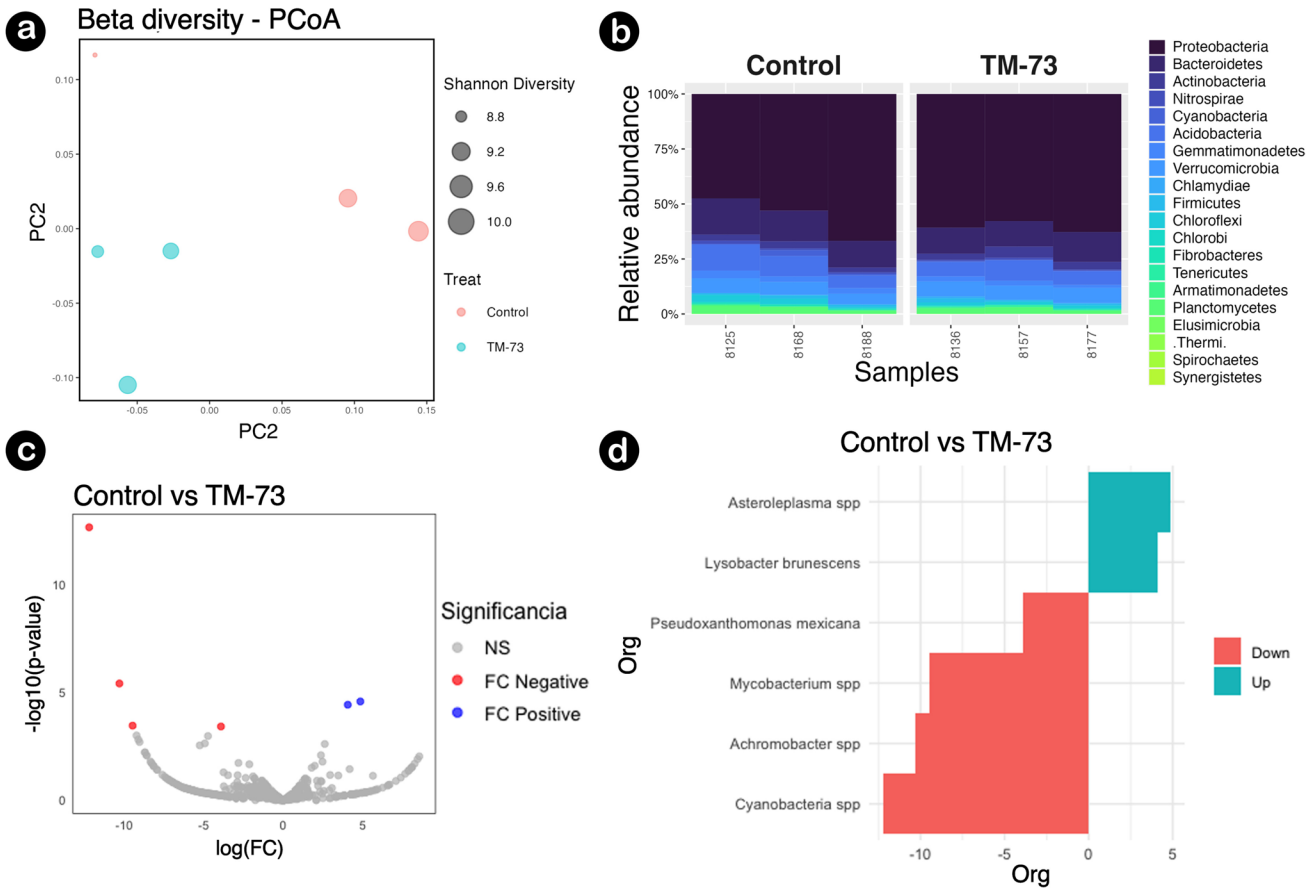


**Fig. 2** Characteristics of the rhizosphere bacterial community of inoculated and non-inoculated plants: **a** beta diversity, PCoA with weighted UniFrac distances; **b** ratio of relative abundances of bacterial phyla; **c–d** differences at species level by exact test ($p < 0.05$); **c** volcano plot with all organisms; and **d** bar chart of significant organisms

food crops to adapt to climate change and produce more sustainable and healthy food. Inoculation with efficient mycorrhizae strains can be a strategy to restore internal ecosystem processes to support agricultural production in an environmentally friendly way (Bender et al. 2019).

Chlorophyll is the main pigment used by plants to perform photosynthesis in their leaf. It is also a key component of plant stress; under high levels of stress, the concentration of the compound in the leaves is reduced, largely due to the presence of high levels of oxidative stress (Agathokleous et al. 2020). In maize, it has shown that the presence of water stress produces a decrease in the presence of chlorophyll, while the compound is recovered when the plants are inoculated with the mycorrhizal fungus *Funneliformis mosseae* (Sun et al. 2021). In this study, an increase in the relative chlorophyll content of plants inoculated with mycorrhizae was observed with respect to the control at a low dose of phosphorus fertilization. Further research is required to find out the role of chlorophyll in the context of phosphorus concentration in plants inoculated with mycorrhizae.

In this study, the plants were grown under low phosphorus conditions, controlling irrigation nutrients and sterilizing the substrate to achieve mycorrhiza-free controls and homogenize the rhizosphere conditions. Under these conditions, changes in the bacterial community structure and a response to P stress conditions were observed. Lu et al. (2023) also observed changes in rhizosphere bacteria community using B73 maize and a mycorrhizal-deficient mutant as control. They observed that in addition to declining plant P uptake, bacterial communities were affected in the rhizosphere by the mycorrhizal absence.

It is known that AMF interact synergistically with other microorganisms. For example, bacteria isolated from mycorrhizal fungal spores contributed to increased phosphorus transport into the plant (Battini et al. 2017). The change in communities in plants benefited by mycorrhizae has also been seen in other types of stresses, such as in the presence of rare earth elements like La where bacterial diversity was modified (Hao et al. 2021). Changes in beta diversity were observed in the rhizosphere of corn B73, indicating a difference in community structure between mycorrhizal and non-mycorrhizal plants. Additionally, six bacterial OTUs showed significant differential abundance. There is no information that can explain the presence of the two upregulated bacteria *Asteroleplasma* spp. and *Lysobacter brunescens* with maize rhizosphere, but their abundance could be determined by the niche formed in stressed plants under the low phosphorus conditions of non-inoculated plants.

It is intriguing to consider information within the down-regulated bacterial OUTS (*Pseudoxanthomonas mexicana*, *Mycobacterium* spp., *Achromobacter* spp., and *Cyanobacteria* spp.) that potentially explain their preferential presence in roots with mycorrhizal fungi. Cyanobacteria is capable of increasing soil fertility around roots by fixing nitrogen (Srivastava et al. 2021) Furthermore, it can facilitate the solubilization of phosphorus (Afkairin et al. 2021), which could contribute to the phosphorus deficit response affecting plants. Therefore, cyanobacteria can constitute a group that can act synergistically with mycorrhizal fungi to alleviate phosphorus stress by making it rapidly assimilated by the fungal hyphae, complementing functions for a better utilization of soil nutrients. Huda et al. (2022) described the strain *Pseudoxanthomonas mexicana* S254, resistant to arsenic, not only facilitates plant growth but also synthesizes hydrogen cyanide, auxin, and nitrogen, thereby promoting plant health. The *Achromobacter piechaudii* ARV8 strain, which was isolated from arid and saline environments, exhibited a beneficial impact on tomato growth when exposed to drought stress (Mayak et al. 2004). Additionally, *Achromobacter* species have been found in cowpea nodules (Azarias Guimarães et al. 2012). It is possible that these microorganisms perform other beneficial functions for the plant, in addition to mitigating stress (e.g., N fixation, hormone production) and complement AMF function in low P conditions. Mycobacteria constitute a widespread group of ubiquitous microorganisms found in both aquatic and terrestrial systems. They are commonly associated with animal and plant diseases. Nevertheless, an extensive knowledge of remaining members that have not been explored is needed (Walsh et al. 2019).

These changes imply that the symbiotic association may be modifying the microbiome to achieve the higher growth observed in mycorrhizal plants, which could be a strategy to fulfill functions necessary to alleviate phosphorus stress. However, further information is required to understand the functions performed by these bacteria and the functions that are favored or suppressed by mycorrhizal symbiosis, in order to better understand the role of the fungi in the selection of the microbiome that colonizes the rhizosphere.

## 5 Conclusions

This study confirms the positive effect of AMF on plant growth and chlorophyll relative content compared to non-inoculated plants under low phosphorus conditions. Changes in the bacterial community indicate that mycorrhiza interacts with the soil microbiome in the rhizosphere, and this may support plant performance under P stress. The significant influence of mycorrhiza on 6 operational taxonomic units suggests a specific communication to shape the rhizosphere microbiome with preferential taxa. These findings highlight the role of mycorrhizal interactions in solving plant stress problems with a perspective of sustainable solutions for agriculture.

## Declarations

**Conflict of interest** The authors declare no conflict of interest.



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