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Occurrence of Mycorrhizal Spores and Phosphate Solubilizing Potential of Rhizosphere Mycoflora of Seagrass *Thalassia hemprichii* (Ehrenb.) Asch.

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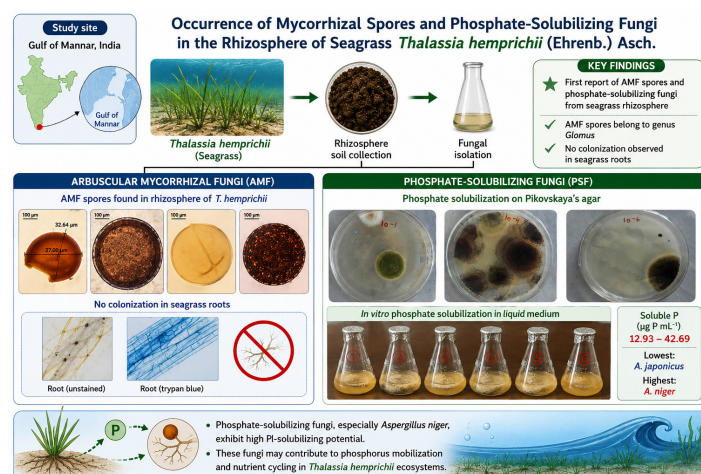
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ABSTRACT: Phosphorus is one among the chief macronutrients that take part in the various biological processes of plants, and it cannot be replaced by other elements. We examined the arbuscular mycorrhizal fungi (AMF) colonization and phosphate solubilizing potential of fungi from seagrass *T. hemprichii* (Ehrenb.) Asch., which belongs to the family Hydrocharitaceae collected from the Gulf of Mannar, India. For the first time, we reported the occurrence of AMF spores and phosphate-solubilizing potential of fungal species from the seagrass rhizosphere soil. A total of six mineral phosphates solubilizing fungi were isolated from rhizosphere of seagrass *Thalassia hemprichii*—five of them belong to the genus *Aspergillus* and one is from *Fusarium*. The concentration of soluble-P in the fluid medium ranged between 12.93 ± 0.39 and 42.69 ± 0.22 $\mu\text{g P mL}^{-1}$, with the lowest by *Aspergillus japonicus* and the highest by *Aspergillus niger*. The AMF spores isolated from the rhizosphere belong to genus *Glomus*, whereas no colonization was found in the roots.

GRAPHICAL ABSTRACT



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1. INTRODUCTION

Seagrasses are a challenging, rapidly vanishing, limited group of vascular plants that are rarely found, capable of finishing their life cycles submerged completely in seawater. They tend to flourish in estuaries, salt-marshes, and shallow coastal marine regions (Reynolds et al., 2016) and also serve as the habitat for many marine species and are an ecotone between a mangrove forest and coral reefs (Fortes, 2013; Jumawan et al., 2015). According to several studies (Brodersen et al., 2017; Fraser et al., 2018; Redondo et al., 2017; Ugarelli et al., 2017; Vinson et al., 2016), seagrass ecosystems are among the most valuable ecosystems in the marine environment because they provide a range of ecological benefits, such as stabilizing coastlines, sequestering carbon, and circulating nutrients in coastal habitats.

Among the main macronutrients, phosphorus is involved in several biological processes in plants, including growth and reproduction, nucleic acids (DNA and RNA) and membrane (phosphoproteins and phospholipids) synthesis, oxidation, respiration (ATP synthesis), cell division, and enzyme regulation (Khan et al., 2009) as well as linked with disease resistance in plants (Bargaz et al., 2018; Kaur et al., 2019). Individual ecosystems, such as soil, streams, forests, and marine environments, all comprise the P cycle, which is directly associated with significant environmental and human security issues (Lu et al., 2017; Liu et al., 2020; McMahon and Read, 2013; Onodera et al., 2020). Phosphorus content in soil ranged between 0.02 and 0.5%, and it exists in both organic and inorganic forms. Phosphate concentration in water depends upon different parameters, of which sediments occupy an important role (Pomeroy et al., 1965; Promod and Dhevendaran, 1987) where they exist in insoluble organic and inorganic forms. In natural environments, solubilization and mobilization of mineral phosphates are carried out by many soil-borne microorganisms such as bacteria, fungi, and actinomycetes through enzymatically or by acid hydrolysis (Chung et al., 2005; Silva and Vidor, 2001; Zaidi and Khan, 2005). This may enhance the availability of insoluble phosphates to the plants from the rhizosphere (Richardson et al., 2001; Rodriguez et al., 2006).

Seagrasses take up phosphate through their leaves and roots/rhizomes. They mobilize phosphorus in tropical carbonate-rich sediments by dissolving carbonates, acidifying their rhizosphere, and promoting microbial metabolism that liberates phosphate from organic matter and iron compounds (Brodersen et al., 2017; Fraser et al., 2018; Long et al., 2008). Sediment-bound phosphate is further released by organic acid exudation from roots, allowing for absorption (Brodersen et al., 2017; Long et al., 2008). By decomposing organic phosphorus, microbial communities in seagrass sediments also increase phosphate availability, particularly in high

salinity and low phosphate environments (Fraser et al., 2018). According to Brodersen et al. (2017), tropical seagrasses need between 60 and 175 $\mu\text{mol P m}^{-2} \text{ d}^{-1}$. Furthermore, due to their thick root systems and adaptation to the marine environment, seagrasses can facilitate the transformation and discharge of both organic and inorganic phosphorus from the substrate (Yuan et al., 2015). Recent studies by Ghosh et al. (2012), Zhao et al. (2020), and Saranya et al. (2022) mainly focused on isolation and characterization of phosphate solubilizing bacteria from the seagrass environment.

The symbiotic relationship of soil fungi and root of higher plants is known as mycorrhiza. These kinds of symbioses have been essential for the evolution and terrestrialization of plants for more than 400 million years (Genre et al., 2020; Kalamulla et al., 2022; Strullu-Derrien et al., 2018). Mycorrhizae promote the absorption of water and nutrients (phosphorus and nitrogen) by plants and provide resistance against biotic and abiotic stresses. They govern hormone signaling, plant defense, and growth. Mycorrhizae also enhance soil structure, promote sequestration of carbon, and support beneficial microbial communities (Ahmed et al., 2025; Begum et al., 2019; Das et al., 2022; Diagne et al., 2020; Khaliq et al., 2022; Kuyper and Jansa, 2023; Martin and Van Der Heijden, 2024; Nanjundappa et al., 2019; Shi et al., 2022; Shukla et al., 2025; Umer et al., 2025; Wahab et al., 2023; Zhang et al., 2023).

Our literature survey could ascertain that there are no reports on the presence of arbuscular mycorrhizal fungi (AMF) and very meager reports on phosphate-solubilizing fungi from seagrasses. Therefore, the present investigation was carried out and we here report the presence of mycorrhizal spores and phosphate-solubilizing potential of fungi from the sediments of seagrass *T. hemprechii* (Ehrenb.) Asch. collected from the Gulf of Mannar, India. Further this is the first finding reporting the occurrence of AMF spores from seagrass sediments.

2. MATERIALS AND METHODS

2.1. Sample collection

The roots and sediments of *T. hemprechii* (Ehrenb.) Asch. were collected from the Gulf of Mannar (latitude 8°35'–9°25'N; 78°08'–79°30'E), Tamil Nadu, India. Sediment nutrients were analyzed at the Sugarcane Breeding Research Institute, Cuddalore, Tamil Nadu, India.

2.2. AMF spore isolation and root clearing

Roots were excised and stored separately in FAA (formalin–acetic acid–alcohol–10% formalin, 5% glacial acetic acid,

50% ethanol (95%), and 35% distilled water) until examined for AMF colonization. One hundred root segments of 1 cm length were randomly selected for microscopic observation to assess AMF colonization. The clearing and staining of root segments were carried out following Phillips and Hayman (1970) and Brundrett et al. (1984). Temporary mounts of root segments were prepared and were observed for the occurrence of fungal structures (e.g., vesicles, arbuscules, and hyphae) under stereomicroscope at 100–400× magnification. Spores were recovered from soil samples by the wet sieving and decanting method (Gerdeemann and Nicolson, 1963).

2.3. Determination of phosphate-solubilizing potential *in vitro*

For isolation and determination of phosphate-solubilizing potential of fungi under *in vitro* condition, the method prescribed by Subba Rao (1988) was followed. Pikovskaya's agar medium was used to study the phosphate solubilization of fungi, and Potassium di-hydrogen phosphate was used as standard. Plating was done in triplicate and incubated at $30 \pm 5^\circ\text{C}$ for 48–96 h. The phosphate solubilization ability of fungi was shown by the development of a clear zone around the fungal colonies. Individual colonies possessing clear solubilization zones were picked up and plated on to fresh medium and incubated at $30 \pm 5^\circ\text{C}$. A medium with no microbial inoculation served as the control.

3. RESULTS AND DISCUSSION

3.1. Soil quality parameters

The sediment samples had sand as the major component followed by silt and clay. The soil had low levels of P (0.39%) compared to N (2.14%), K (2.46%), and organic matter (8.47%). The pH of the soil was near neutral (6.68) and electrical conductivity (EC) was 170 dS m^{-1} (Table 1). According to Islam et al. (2019) and Adeleke et al. (2017), tricalcium phosphate (Ca_3PO_4)₃ is formed in alkaline or high pH soils, which ultimately reduces the soil phosphorous availability to plants, while iron and aluminum react with phosphorous in low pH or acidic soil, resulting in a reduction of soil phosphorus.

3.2. AMF spore isolation and root clearing

The seagrass roots were screened for AMF association and no clear AMF colonization was found in roots examined, but some vesicle-like structures were found in the roots of *T. hemprichii*. According to Fusconi and Mucciarelli (2018), Marins

Table 1

Soil quality parameters.

Parameters	Value
OM (%)	8.47
N (%)	2.14
P (%)	0.39
K (%)	2.46
pH	6.68
EC (dS m^{-1})	170
Sand (%)	96.05
Silt (%)	2.39
Clay (%)	1.56

and Carrenho (2017), and Yu et al. (2020), hydrology, oxygen availability, and soil chemistry are crucial factors controlling AMF colonization in aquatic habitats. Recent genomic studies, showed that some aquatic plant lineages may be less able to form AMF associations because they have lost or diverged important symbiosis genes, while others still have genes for alternative fungal symbioses (Ettinger et al., 2025). In the present study, mycorrhizal spore-like structures were isolated from the sediment but not identified at the species level. All the isolated spores in the sediment may belong to the genus *Glomus* (Figure 1). In support of the present result, molecular studies have identified various AMF taxa in aquatic environments, with genera like *Glomus* and *Acaulospora* being common (Kohout et al., 2012; Xu et al., 2021). Aliasgharzadeh et al. (2001) recorded fairly high spore numbers (mean of 100 g^{-10} soil) in the high saline soils ($\text{EC} \sim 162 \text{ dS m}^{-1}$) in the Tabris Plain. Conversely, Barrow et al. (1997), Hirrel et al. (1978), and Kim and Weber (1985) reported low or even no spore populations where EC is higher than 45 dS m^{-1} . In the present study, the EC was determined as 170 dS m^{-1} . Several studies report a negative correlation between AMF spore density and soil EC, demonstrating that higher salinity or ion concentration tends to reduce spore numbers in various ecosystems, including sugarcane fields, semi-arid regions, and saline coastal soils (Sivakumar, 2013; Zhang et al. 2020). It has been documented that mycorrhiza requires oxygen to survive and thus the hypoxic conditions and high salinity in the sediment of seagrasses may prevent their establishment in the roots of seagrasses (Nielsen et al. 1999). However, Miller and Bever (1999) acknowledged two possible mechanisms by which AMF could survive in hypoxic conditions. One, the fungi may avoid oxygen stress by concentrating on the well-oxygenated part of the root system. Second, there may be some degree of fungal tolerance to conditions imposed by flooding, which is species specific (Brown and Bledsoe, 1996).

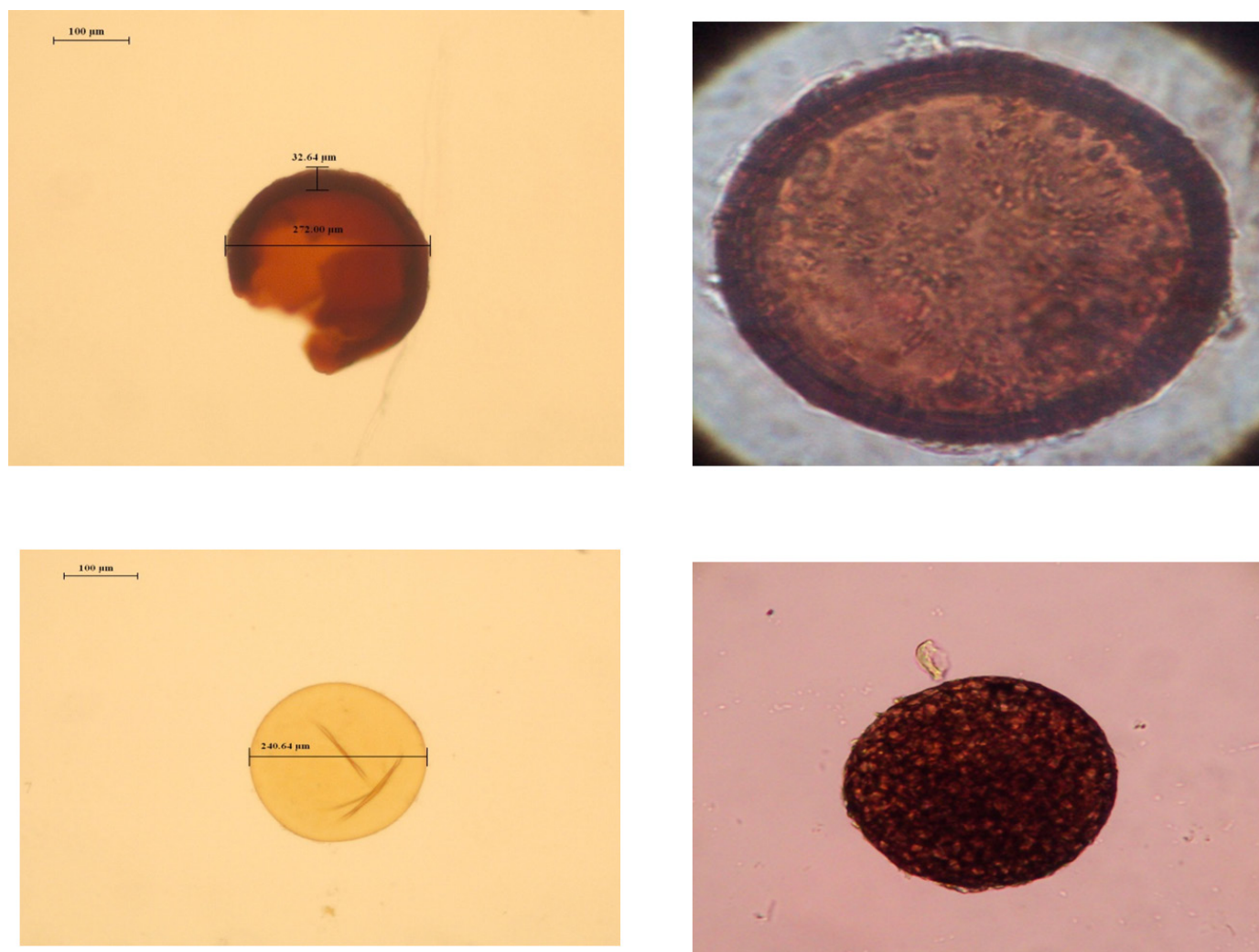


Figure 1. AMF spores found in rhizosphere of *T. hemprichii*.

According to [Le Tacon et al. \(1983\)](#), *Glomus mosseae* spores fail to germinate under the anaerobic condition, but the condition was reversed when they were exposed to air. During the sample collection, we found that seagrass meadows were completely exposed to air during low tides. Several investigations documented fungal establishment to salt and flood conditions ([Carvalho et al. 2004](#); [Landwehr et al. 2002](#)). In support of our results, [Hirrel \(1981\)](#) reported that salt-stress conditions encouraged the sporulation of AMF. [Khan and Belik \(1995\)](#) and [van Duin et al. \(1990\)](#) recognized lower AMF colonization in halophytic salt marsh plants found, respectively, in anoxia waterlogged soils and plants growing closer to the water edge where salt water flooding is more frequent. As suggested by [Bowen \(1987\)](#), salinity induced by sodium chloride may be different from natural salinity, due to the presence of different salts in the sea water logging soil beds. In the present study, this may be one of the possible reasons for the non-establishment of mycorrhizal colonization in seagrasses.

3.3. Isolation of phosphate-solubilizing fungi

Phosphorus is the second most essential element needed for plant growth along with nitrogen and potassium, and it cannot be replaced by other nutrients ([Glaser and Lehr, 2019](#); [Li et al., 2015](#); [Ram et al., 2015](#)). Phosphate-solubilizing microbes are important to the soil phosphorus cycle because they mineralize organic phosphorus, solubilize inorganic phosphorus minerals, and store significant amounts of phosphorus in biomass ([Gross et al., 2020](#); [Liang et al., 2020](#)). Numerous bacteria and fungi are known to be capable of solubilizing elemental phosphorus; in addition, fungi are known to have persistent genetic features and a more pronounced ability to dissolve insoluble phosphorus compounds than bacteria ([Joseph and Jisha 2009](#)). In the present study, phosphate solubilization was specified by the development of clear halo zone surrounding the fungal colonies on Pikovskaya's agar medium. Individual colonies showing clear solubilization

zones were isolated and plated on a fresh Pikovskaya's agar medium, and incubated at $30 \pm 5^\circ\text{C}$. Colonies exhibiting 6–15 mm halo solubilization zone on the medium after 7 days of incubation were elected for quantitative estimations of P-solubilization. Totally, six different fungal colonies such as *Aspergillus flavus*, *Aspergillus terreus*, *Aspergillus japonicus*, *Aspergillus fumigatus*, *A. niger*, and *Fusarium sp.* were identified as potential P solubilizers from the sediments of *T. hemprechii*. The maximum zone was recorded for *A. niger* and minimum for *A. japonicus* (Table 2). Phosphate solubilization by *Aspergillus* was reported very commonly (Gaur and Sachar, 1980; Narsian and Patel, 1997; Reddy et al., 2002). Gupta et al. (2010) reported 14 P solubilizing fungi, which include 10 *Aspergillus sp.*, 3 *Penicillium sp.*, and 1 *Alternaria sp.* from phyllosphere of Bhitarkanika mangrove. Thirteen phosphate-solubilizing bacterial strains and one fungal (*A. niger*) were isolated from rhizosphere of mangroves in a semiarid coastal lagoon (Vazquez et al., 2000). According to Singh (2011), filamentous nonmycorrhizal fungi such as *Aspergillus* spp. and *Penicillium* spp. have potential phosphate solubilization capacity. For instance, *A. niger* (Wang et al., 2018) have been reported as a potential fungal phosphate solubilizer. It is also evident from the present study that among the six fungal isolates, the genus *Aspergillus* is dominant and *A. niger* has more potential to solubilize inorganic phosphate compared to other fungal isolates.

3.4. Determination of phosphate-solubilizing potential *in vitro*

Marine and coastal environments, such as seagrass meadows, and phosphate-solubilizing fungi (PSF) are essential for increasing the availability of phosphorus. In nutrient-limited sediments typical of seagrass habitats, these fungi support plant growth by converting insoluble forms of phosphate into bioavailable forms. The phosphate-solubilizing potential of six isolated fungi species are presented in Table 2. In the present study, the concentration of soluble-P in the fluid medium ranged between 9.93 ± 0.39 and 42.69 ± 0.22 $\mu\text{g P ml}^{-1}$, and no soluble-P was noticed in the blank. The highest P solubilization was found in *A. niger* (42.69 ± 0.22 $\mu\text{g P ml}^{-1}$) followed by *A. fumigatus* with phosphate-solubilizing ability of 37.25 ± 0.23 $\mu\text{g P ml}^{-1}$, and *A. japonicus* had the minimum soluble-P concentration (12.93 ± 0.39 $\mu\text{g P ml}^{-1}$) in the culture medium. According to recent research, fungi, especially those belonging to the phylum Ascomycota, have a greater impact on the forms and cycling of phosphorus in seagrass meadow sediments than bacteria. P-cycling fungi, such as *Aspergillus*, *Trichoderma*, and *Penicillium*, are significantly more prevalent than bacteria, and their activity is strongly correlated with the presence of different P compounds in sediments (Zhao et al.,

Table 2

P-solubilization with respect to zone of solubilization, *in vitro* activity, and pH decline.

Isolates	P-solubilization zone (mm)	$\mu\text{g P ml}^{-1}$	pH
<i>Aspergillus flavus</i>	8	24.27 ± 0.40	4
<i>Aspergillus terreus</i>	12	25.72 ± 1.16	4.1
<i>Aspergillus japonicus</i>	6	12.93 ± 0.39	5
<i>Aspergillus fumigatus</i>	12	37.25 ± 0.23	3.8
<i>Aspergillus niger</i>	15	42.69 ± 0.22	3.4
<i>Fusarium sp.</i>	11	23.15 ± 0.27	4.1

2020). These fungi secreting organic acids (such as oxalic, citric, and gluconic acids) acidify their environment and chelate metal ions to release phosphate from mineral complexes. Because fungi (*Aspergillus* and *Penicillium*) produce more acid and can adapt to acidic environments, they are extremely effective in P-solubilization and outperform bacteria (Li et al., 2016; Mendes et al., 2014; Zhang et al., 2018; Zhao et al., 2020).

In other instances, P solubilization is also performed by the action of an enzyme called alkaline phosphatase. Phosphate-solubilizing microorganisms can dissolve soil P into soluble and plant-available orthophosphate forms (mostly PO_4^{3-} , HPO_4^{2-} , and H_2PO_4^-) by releasing phosphatase enzymes and organic acids, lowering soil pH, and increasing chelation activities with additional P adsorption sites (Billah et al., 2019). Many microbes are known to secrete acidic metabolites that change the pH by chelation of metal ions and liberate fixed or insoluble phosphorus into bioavailable form to plants (Yadav and Dadarwal, 1997). The pH in the present investigation ranged from 3.4 to 5, and it declined from the starting pH 7. The pH was relatively higher (5) in *A. japonicus* where soluble-P concentration is very low and lower pH (3.4) was recorded in *A. niger* where soluble-P concentration was higher (Table 2). According to Narsian and Patel (1997), the inoculated fungi secrete acidic metabolites which in turn decrease the pH of the medium (Narsian and Patel, 1997). Gupta et al. (2010) found that pH reduced up to 3.92 and 4.03 from the initial pH by *Aspergillus sp.* from phyllosphere of Bhitarkanika mangrove which is in line with the result of present study.

4. CONCLUSIONS

In conclusion, though reports on AMF colonization and phosphate solubilizers from the marine angiospermic plant seagrass are meager, the present study reports for the first time on the occurrence of AMF spores and PSF from the

sediments of seagrass *T. hemprichii*. Mycorrhizal spores isolated from the sediments may belong to the genus *Glomus*, and phosphate-solubilizing fungi belong to the genus *Aspergillus*. Phosphorus cycling in seagrass and marine sediments is largely dependent on fungi, and their capacity to increase phosphorus availability enhances seagrass productivity and offers long-term solutions for managing nutrients in coastal ecosystems.

MANDATORY DISCLOSURE ON USE OF ARTIFICIAL INTELLIGENCE

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AUTHOR CONTRIBUTION

Arumugam Radjasegarin did research concept and design, writing of the article, and the final approval of the article.

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CONFLICT OF INTEREST

The authors declare that there is no conflict of interest.

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REFERENCES

- Adeleke, R., Nwangburuka, C., & Oboirien, B., 2017. Origins, roles and fate of organic acids in soils: A review. *South African Journal of Botany*. 1,393–406. <https://doi.org/10.1016/j.sajb.2016.09.002>
- Ahmed, N., Li, J., Li, Y., Deng, L., Deng, L., Chachar, M., et al. 2025. Symbiotic synergy: How arbuscular mycorrhizal fungi enhance nutrient uptake, stress tolerance, and soil health through molecular mechanisms and hormonal regulation. *IMA Fungus*. 16. <https://doi.org/10.3897/ima fungus.16.144989>
- Aliasgharzadeh, N., et al., 2001. Occurrence of arbuscular mycorrhizal fungi in saline soils of the Tabriz Plain of Iran in relation to some physical and chemical properties of soil. *Mycorrhiza* 11, 119–122. <https://doi.org/10.1007/s005720100113>
- Arid Land Research and Management. 11(2), 177–185. Begum, N., Qin, C., Ahanger, M., Raza, S., Khan, M., Ashraf, M., Ahmed, N., & Zhang, L. 2019. Role of arbuscular mycorrhizal fungi in plant growth regulation: Implications in abiotic stress tolerance. *Frontiers in Plant Science*. 10. <https://doi.org/10.3389/fpls.2019.01068>
- Bargaz, A., Lyamlouli, K., Chtouki, M., Zeroual, Y., & Dhiba, D., 2018. Soil microbial resources for improving fertilizers efficiency in an integrated plant nutrient management system. *Frontiers in Microbiology*. 31, 1606–1615. <https://doi.org/10.3389/fmicb.2018.01606>
- Barrow, J.R., Havstad, K.M. & McCaslin, B.D. 1997. Fungal root endophytes in fourwing saltbush, *Atriplex canescens*, on arid rangelands of southwestern USA.
- Billah, M., Khan, M., Bano, A., Hassan, T.U., Munir, A., & Gurmani, A.R. 2019. Phosphorus and phosphate solubilizing bacteria: Keys for sustainable agriculture. *Geomicrobiol Journal*. 36, 904–916. <https://doi.org/10.1080/01490451.2019.1654043>
- Bowen, G.D. 1987. *Ecophysiology of VA Mycorrhizal Plants* In: The biology and physiology of infection and its development (Ed.: Safir, G.R.) CRC Press, Boca Raton, Florida, 27–57.
- Brodersen, K., Koren, K., Mosshammer, M., Ralph, P., Köhl, M., & Santner, J. 2017. Seagrass-mediated phosphorus and iron solubilization in tropical sediments. *Environmental Science & Technology*. 51(24), 14155–14163. <https://doi.org/10.1021/acs.est.7b03878>
- Brown, A.M., & Bledsoe, C. 1996. Spatial and temporal dynamics of mycorrhizas in *Jaumea carnosa*, a tidal saltmarsh halophyte. *Journal of Ecology*. 84, 703–715. <https://doi.org/10.2307/2261333>
- Brundrett, M.C., Piche, Y., & Peterson, R.L. 1984. A new method for observing the morphology of vesicular-arbuscular mycorrhizae. *Canadian Journal of Botany*. 62, 2128–34. <https://doi.org/10.1139/b84-290>
- Carvalho, L.M., Correia, P.M., Martins-Loução, A. 2004. Arbuscular mycorrhizal fungal propagules in a salt marsh. *Mycorrhiza*. 14, 165–170. <https://doi.org/10.1007/s00572-003-0247-4>
- Chung, H., Park, M., Madhaiyan, M., Seshadri, S., Song, J., Cho, H., et al. 2005. Isolation and characterization of phosphate solubilizing bacteria from the rhizosphere of crop plants of Korea. *Soil Biology and Biochemistry*. 37(10), 1970–1974. <https://doi.org/10.1016/j.soilbio.2005.02.025>
- Das, D., Paries, M., Hobecker, K., Gigl, M., Dawid, C., Lam, H., et al. 2022. Phosphate starvation response transcription factors enable arbuscular mycorrhiza symbiosis. *Nature Communications*. 13. <https://doi.org/10.1038/s41467-022-27976-8>
- Diagne, N., Ngom, M., Djighaly, P., Fall, D., Hoher, V., & Svistoonoff, S. 2020. Roles of arbuscular mycorrhizal fungi on plant growth and performance: Importance in biotic and abiotic stressed regulation. *Diversity*. 12(10), 370. <https://doi.org/10.3390/d12100370>
- Ettinger, C., Arroyo, J., & Stajich, J. 2025. Assessing the evolutionary trajectory of arbuscular mycorrhizal conserved genes in seagrasses and aquatic close relatives. *bioRxiv*. 2025.01.23.634575. <https://doi.org/10.1101/2025.01.23.634575>
- Fortes, MD. 2013. A review: Biodiversity, distribution and conservation of Philippine seagrasses. *Philippine Journal of Science*. 142 (3), 95–111.

- Fraser, M.W., Gleeson, D.B., Grierson, P.F., Laverock, B., & Kendrick, G.A. 2018. Metagenomic evidence of microbial community responsiveness to phosphorus and salinity gradients in seagrass sediments. *Frontiers in Microbiology*. 9:1703. <https://doi.org/10.3389/fmicb.2018.01703>
- Fusconi, A., & Mucciarelli, M. 2018. How important is arbuscular mycorrhizal colonization in wetland and aquatic habitats? *Environmental and Experimental Botany*. 155(7). <https://doi.org/10.1016/j.envexpbot.2018.06.016>
- Gaur, A.C., & Sachar, S., 1980. Effect of rock phosphate on phosphate solubilization by *Aspergillus awamori*. *Current Science*. 49, 553–554.
- Genre, A., Lanfranco, L., Perotto, S. & Bonfante, P. 2020. Unique and common traits in mycorrhizal symbioses. *Nature Reviews Microbiology*, 18(11), 649–660. <https://doi.org/10.1038/s41579-020-0402-3>
- Gerdemann, J.W., & Nicholson, T.H. 1963. Spores of mycorrhizal endogone species extracted by wet sieving and decanting. *Transactions of the British Mycological Society*. 46, 235–244. [https://doi.org/10.1016/S0007-1536\(63\)80079-0](https://doi.org/10.1016/S0007-1536(63)80079-0)
- Ghosh, U., Subhashini, P., Dilipan, E., Raja, S., Thangaradjou, T., & Kannan, L. 2012. Isolation and characterization of phosphate-solubilizing bacteria from seagrass rhizosphere soil. *Journal of Ocean University of China*. 11, 86–92. <https://doi.org/10.1007/s11802-012-1844-7>
- Glaser, B., & Lehr, V.I., 2019. Biochar effects on phosphorus availability in agricultural soils: A meta-analysis. *Scientific Reports*. 27, 1–9. <https://doi.org/10.1038/s41598-019-45693-z>
- Gross, A., Lin, Y., Weber, P.K., Pett-Ridge, J., & Silver, W.L. 2020. The role of soil redox conditions in microbial phosphorus cycling in humid tropical forests. *Ecology*. 101 e02928. <https://doi.org/10.1002/ecy.2928>
- Gupta, N., Das, S., & Basak, U.C. 2010. TCP and rock phosphate solubilization by mangrove fungi grown under different pH and temperature in liquid culture. *International Journal of Agricultural Technology*. 6(3), 421–428.
- Hirrel, M.C., 1981. The effect of sodium and chloride salts on the germination of *Gigaspora margarita*. *Mycologia*. 73, 10–617. <https://doi.org/10.2307/3759487>
- Hirrel, M.C., Mehravaran, H., & Gerdemann, J.W. 1978. Vesicular-arbuscular mycorrhiza in the Chenopodiaceae and Cruciferae: Do they occur? *Canadian Journal of Botany*. 56, 2813–2817. <https://doi.org/10.1139/b78-336>
- Islam, M.K., Sano, A., Majumder, M.S., Hossain, M.A., & Sakagami, J.I. 2019. Isolation and molecular characterization of phosphate solubilizing filamentous fungi from subtropical soils in Okinawa. *Applied Ecology and Environmental Research*. 1, 9145–9157. https://doi.org/10.15666/aer/1704_91459157
- Joseph, S., & Jisha, M.S., 2009. Buffering reduces phosphate solubilizing ability of selected strains of bacteria. *World Journal of Agricultural Sciences*. 5(1), 135–137.
- Jumawan, J., Bitalas, M.B., Ramos, J.J.C., Garcia, A.R.P., Landero, R.S., Cordero, J.A., et al. 2015. Seagrass diversity and structure along the coastal area in Paligue, Hagonoy, Davao del Sur, Philippines. *AES Bioflux*. 7(3), 351–356.
- Kalamulla, R., Karunarathna, S., Tibpromma, S., Galappaththi, M., Suwannarach, N., Stephenson, S., et al. 2022. Arbuscular mycorrhizal fungi in sustainable agriculture. *Sustainability*. 14(19), 12250 <https://doi.org/10.3390/su141912250>
- Kaur, C., Selvakumar, G., & Ganeshamurthy, A.N. 2019. Acid tolerant microbial inoculants: A requisite for successful crop production in acidic soils. In: *Phyto and rhizo remediation*. Singapore: Springer, 9, 235–247. https://doi.org/10.1007/978-981-32-9664-0_10
- Khalique, A., Perveen, S., Alamer, K., Haq, M., Rafique, Z., Alsudays, I., et al. 2022. Arbuscular mycorrhizal fungi symbiosis to enhance plant–soil interaction. *Sustainability*. 14(13), 7840. <https://doi.org/10.3390/su14137840>
- Khan, A.G., & Belik, M., 1995. *Mycorrhiza*. In: Occurrence and ecological significance of mycorrhizal symbiosis in aquatic plants (Eds.:Varma, A. and Hock, B.). Springer Verlag, Berlin, 627–666. https://doi.org/10.1007/978-3-662-08897-5_27
- Khan, A.A., Jilani, G., Akhtar, M.S., Naqvi, S.M.S. & Rasheed, M. 2009. Phosphorus solubilizing bacteria: occurrence, mechanisms and their role in crop production. *Journal of Agricultural and Biological Research*. 1(1), 48–58.
- Kim, C.K., & Weber, D.J. 1985. Distribution of VA mycorrhiza on halophytes on inland salt playas. *Plant and Soil*. 83, 207–214.
- Kohout, P., Šýkorová, Z., Čtvrtilíková, M., Rydlová, J., Suda, J., Vohník, M., et al. 2012. Surprising spectra of root-associated fungi in submerged aquatic plants. *FEMS Microbiology Ecology*. 80 1, 216–35. <https://doi.org/10.1111/j.1574-6941.2011.01291.x>
- Kuyper, T., & Jansa, J. 2023. Arbuscular mycorrhiza: Advances and retreats in our understanding of the ecological functioning of the mother of all root symbioses. *Plant and Soil*. 489, 41–88. <https://doi.org/10.1007/s11104-023-06045-z>
- Landwehr, M., Hildebrandt, U., Wilde, P., Nawrath, K., Tóth, T., Biró, B. et al. 2002. The arbuscular mycorrhizal fungus *Glomus geosporum* in European saline, sodic and gypsum soils. *Mycorrhiza*. 12(4), 199–211. <https://doi.org/10.1007/s00572-002-0172-y>
- Le Tacon, F., Skinner, F.A., & Barbara, M. 1983. Spore germination and hyphal growth of a vesicular–arbuscular mycorrhizal fungus, *Glomus mosseae* (Gerdemann and Trappe), under decreased oxygen and increased carbon dioxide concentrations. *Canadian Journal of Microbiology*. 29, 1280–1285.
- Li, F., Wang, Z., Dai, J., Li, Q., Wang, X., Xue, C., et al. 2015. Fate of nitrogen from green manure, straw, and fertilizer applied to wheat under different summer fallow management strategies in dryland. *Biology and Fertility of Soils*. 51(7), 769–780. <https://doi.org/10.1007/s00374-015-1023-2>
- Li, Z., Bai, T., Dai, L., Wang, F., Tao, J., Meng, S., et al. 2016. A study of organic acid production in contrasts between two phosphate solubilizing fungi: *Penicillium oxalicum* and *Aspergillus niger*. *Scientific Reports*. 6. <https://doi.org/10.1038/srep25313>
- Liang, J.L., Liu, J., Jia, P., Yang, T.T., Zeng, Q.W., Zhang, S.C., et al. 2020. Novel phosphate-solubilizing bacteria enhance soil phosphorus cycling following ecological restoration of land degraded by mining. *Soil biology*. 14, 1600–1613. <https://doi.org/10.1038/s41396-020-0632-4>
- Liu, X., Yuan, Z., Liu, X., Zhang, Y., Hua, H., & Jiang, S., 2020. Historic trends and future prospects of waste generation and recycling in China's phosphorus cycle. *Environmental Science Technology*. 54, 5131–5139. <https://doi.org/10.1021/acs.est.9b05120>
- Long, M., McGlathery, K., Zieman, J., & Berg, P. 2008. The role of organic acid exudates in liberating phosphorus from seagrass-vegetated carbonate sediments. *Limnology and Oceanography*. 53. <https://doi.org/10.4319/lo.2008.53.6.2616>
- Lu, G.Y., Song, X.X., Yu, Z.M., & Cao, X.H. 2017. Application of PAC-modified kaolin to mitigate *Prorocentrum donghaiense*: Effects on cell removal and phosphorus cycling in a laboratory setting. *Journal of Applied Phycology*. 29, 917–928. <https://doi.org/10.1007/s10811-016-0992-3>

- Marins, J., & Carrenho, R. 2017. Arbuscular mycorrhizal fungi and dark septate fungi in plants associated with aquatic environments. *Acta Botanica Brasilica*. 31, 295–308. <https://doi.org/10.1590/0102-33062016abb0296>
- Martin, F., & Van Der Heijden, M. 2024. The mycorrhizal symbiosis: Research frontiers in genomics, ecology, and agricultural application. *The New Phytologist*. <https://doi.org/10.1111/nph.19541>
- McMahon, K.D., & Read, E.K. 2013. Microbial contributions to phosphorus cycling in eutrophic lakes and wastewater. *Annual Review of Microbiology*. 67, 199–219. <https://doi.org/10.1146/annurev-micro-092412-155713>
- Mendes, G., Freitas, A., Pereira, O., Silva, I., Vassilev, N., & Costa, M. 2014. Mechanisms of phosphate solubilization by fungal isolates when exposed to different P sources. *Annals of Microbiology*. 64, 239–249. <https://doi.org/10.1007/s13213-013-0656-3>
- Miller, S.P., & Bever, J.D. 1999. Distribution of arbuscular mycorrhizal fungi in stands of the wetland grass *Panicum hemitomon* long a wide hydrologic gradient. *Oecologia*. 119, 586–592. <https://doi.org/10.1007/s004420050823>
- Nanjundappa, A., Bagyaraj, D., Saxena, A., Kumar, M., & Chakdar, H. 2019. Interaction between arbuscular mycorrhizal fungi and *Bacillus* spp. in soil enhancing growth of crop plants. *Fungal Biology and Biotechnology*. 6. <https://doi.org/10.1186/s40694-019-0086-5>
- Narsian, V., & Patel, H.H. 1997. Salt tolerance and phosphate solubilizing activity of *Aspergillus aculeatus*. *Indian Journal of Microbiology*. 37, 43–44. [https://doi.org/10.1016/S0038-0717\(99\)00184-4](https://doi.org/10.1016/S0038-0717(99)00184-4)
- Nielsen, S.L., Thingstrup, I., & Wigand, C. 1999. Apparent lack of vesicular arbuscular mycorrhiza (VAM) in the seagrass *Zostera marina* L. and *Thalassia testudinum* Banks ex König. *Aquatic Botany*. 63, 261–266. [https://doi.org/10.1016/S0304-3770\(98\)00123-5](https://doi.org/10.1016/S0304-3770(98)00123-5)
- Onodera, S., Okuda, N., Ban, S.H., Saito, M., Paytan, A., & Iwata, T. 2020. Phosphorus cycling in watersheds: From limnology to environmental science. *Limnology*. 21, 327–328. <https://doi.org/10.1007/s10201-020-00631-1>
- Phillips, J.M., & Hayman DA. 1970. Improved procedures for clearing roots and staining parasitic and vesicular arbuscular mycorrhizal fungi for rapid assessment of infection. *Transactions of the British Mycological Society*. 55, 158–161. [https://doi.org/10.1016/S0007-1536\(70\)80110-3](https://doi.org/10.1016/S0007-1536(70)80110-3)
- Pomeroy, L.R., Smith, E.E., & Grant, C.M. 1965. The exchange of phosphate between estuarine water and sediments. *Limnology and Oceanography*. 10, 167–172. <https://doi.org/10.4319/lo.1965.10.2.0167>
- Promod, K., & Dhevendaran, K. 1987. Studies on phosphobacteria in Cochin backwater. *Journal of Marine Biology Association of India*. 29, 297–305.
- Ram, H., Malik, S.S., Dhaliwal, S.S., Kumar, B., & Singh, Y. 2015. Growth and productivity of wheat affected by phosphorus-solubilizing fungi and phosphorus levels. *Plant Soil Environment*. 61(3), 122–126. <https://doi.org/10.17221/982/2014-PSE>
- Reddy, M.S., Kumar, S., Babita, K., Reddy, & M.S., 2002. Bio solubilisation of poorly soluble rock-phosphate by *Aspergillus tubingensis* and *Aspergillus niger*. *Bioresource Technology* 84, 187–189. [https://doi.org/10.1016/S0960-8524\(02\)00040-8](https://doi.org/10.1016/S0960-8524(02)00040-8)
- Redondo, A.F.S., Dagoc, K.M.F., Ignacio, M.T.T., Sanchez R.R.G., & Tampus A.D. 2017. Seagrass mapping and assessment using remote sensing in the Municipality of Kauswagan, Lanao del Norte, Philippines. *Journal of Biodiversity Environmental Science*. 11(4), 74–88.
- Reynolds, P.L., Duffy, E., & Knowlton, N. 2016. Seagrass and seagrass beds. *Smithsonian institution*, 1–16.
- Richardson, A.E., Hadobas, P.A., Hayes, J.E., O'Hara, C.P., & Simpson, R.J., 2001. Utilization of phosphorus by pasture plants supplied with myo-inositol hexa phosphate is enhanced by the presence of soil micro-organisms. *Plant and Soil* 229, 47–56. <https://doi.org/10.1023/A:1004871704173>
- Rodriguez, H., Fraga, R., Gonzalez, T., Bashan, Y., 2006. Genetics of phosphate solubilization and its potential applications for improving plant growth-promoting bacteria. *Plant and Soil*. 287, 15–21. https://doi.org/10.1007/978-1-4020-5765-6_2
- Saranya, K., Sundaramanickam, A., Manupoori, S., & Kanth, S.V. 2022. Screening of multi-faceted phosphate-solubilising bacterium from seagrass meadow and their plant growth promotion under saline stress condition. *Microbiological Research*. 261, 127080. <https://doi.org/10.1016/j.micres.2022.127080>
- Shi, J., Wang, X., & Wang, E. 2022. Mycorrhizal symbiosis in plant growth and stress adaptation: From genes to ecosystems. *Annual Review of Plant Biology*. 74, 569–607. <https://doi.org/10.1146/annurev-arplant-061722-090342>
- Shukla, S., Didwania, N., & Choudhary, R. 2025. Arbuscular mycorrhizal fungi (AMF): A pathway to sustainable soil health, carbon sequestration, and greenhouse gas mitigation. *Journal of the Saudi Society of Agricultural Sciences*. 24(4), 22. <https://doi.org/10.1007/s44447-025-00023-w>
- Silva Filho, G.N., & Vidor, C. 2001. Phosphate solubilizing activity of microorganisms in the presence of nitrogen, iron, calcium and potassium. *Pesquisa Agropecuaria Brasileira*. 36, 1495–1508. <https://doi.org/10.1590/S0100-204X2001001200007>
- Singh, H., 2011. Effect of inoculation with phosphate solubilizing fungus on growth and nutrient uptake of wheat and maize plants fertilized with rock phosphate in alkaline soils. *European Journal of Soil Biology* 47(1), 30–34. <https://doi.org/10.1016/j.ejsobi.2010.10.005>
- Sivakumar, N. 2013. Effect of edaphic factors and seasonal variation on spore density and root colonization of arbuscular mycorrhizal fungi in sugarcane fields. *Annals of Microbiology*. 63, 151–160. <https://doi.org/10.1007/s13213-012-0455-2>
- Strullu-Derrien, C., Seloosse, M., Kenrick, P., & Martin, F. 2018. The origin and evolution of mycorrhizal symbioses: From palaeomycology to phylogenomics. *The New Phytologist*. 220(4), 1012–1030. <https://doi.org/10.1111/nph.15076>
- Subba Rao, N.S. 1988. Biofertilizers. In: *Agriculture*. Oxford and IBH Publishing, New Delhi.
- Ugarelli, K., Chakrabarti, S., Laas, P., & Stingl, U. 2017. The seagrass holobiont and its microbiome. *Microorganisms*. <https://doi.org/10.3390/microorganisms5040081>
- Umer, M., Anwar, N., Mubeen, M., Li, Y., Ali, A., Alshaharni, M., et al. 2025. Roles of arbuscular mycorrhizal fungi in plant growth and disease management for sustainable agriculture. *Frontiers in Microbiology*. 16. <https://doi.org/10.3389/fmicb.2025.1616273>
- Van Duin, W.E., Rozema, J., & Ernst, W.H.O. 1990. Seasonal and spatial variation in the occurrence of vesicular-arbuscular (VA) mycorrhiza in salt marsh plants. *Agriculture, Ecosystems & Environment*. 29, 107–110. [https://doi.org/10.1016/0167-8809\(90\)90263-D](https://doi.org/10.1016/0167-8809(90)90263-D)
- Vazquez, P., et al., 2000. Phosphate-solubilizing microorganisms associated with the rhizosphere of mangroves in a semiarid coastal lagoon. *Biology and Fertility of Soils*. 30, 460–468. <https://doi.org/10.1007/s003740050024>
- Vinson, N.S., Ante, S.C., Roxas, R.J.F.S., Salvio, S.M.C., Rabe, S.L.C., Torres, M.A.J., et al. 2016. Correlation between water quality and

- seagrass distribution along intertidal zone in Sarangani Province, Philippines. *Journal of Biodiversity Environmental Science*. 8(5), 2220–6663.
- Wahab, A., Muhammad, M., Munir, A., Abdi, G., Zaman, W., Ayaz, A., et al. 2023. Role of Arbuscular Mycorrhizal Fungi in Regulating Growth, Enhancing Productivity, and Potentially Influencing Ecosystems under Abiotic and Biotic Stresses. *Plants*, 12. <https://doi.org/10.3390/plants12173102>
- Wang, X., Wang, C., Sui, J., Liu, Z., Li, Q., Ji, C., et al. 2018. Isolation and characterization of phosphofungi, and screening of their plant growth-promoting activities. *AMB Express*. 8(1), 63. <https://doi.org/10.1186/s13568-018-0593-4>
- Xu, Z., Lv, Y., Fang, M., Liu, J., Zeng, H., & Ban, Y. 2021. Diverse and abundant arbuscular mycorrhizal fungi in ecological floating beds used to treat eutrophic water. *Applied Microbiology and Biotechnology*. 105, 6959–6975. <https://doi.org/10.1007/s00253-021-11470-0>
- Yadav, K.S., & Dadarwal, K.R. 1997. *Biotechnological approaches in soil microorganisms for sustainable crop production*. In: Phosphate solubilization and mobilization through soil microorganisms (Ed.: Dadarwal, K.R.). Scientific publishers, P. O. Box 91, Jodhpur, India. pp. 293–305.
- Yu, M., Wang, Q., Tao, W., Liu, G., Liu, W., Wang, L., et al. 2020. Interactions between arbuscular mycorrhizal fungi and soil properties jointly influence plant C, N, and P stoichiometry in West Lake, Hangzhou. *RSC Advances*. 10, 39943–39953. <https://doi.org/10.1039/d0ra08185j>
- Yuan, H.Z., Pan, W., Ren, L.J., Liu, E.F., & Shen, J. 2015. Species and biogeochemical cycles of organic phosphorus in sediments from a river with different aquatic plants located in Huaihe river watershed, China. *International Journal of Phytoremediation*. 17(1–6), 215–221. <https://doi.org/10.1080/15226514.2013.876969>
- Zaidi, A., & Khan, M.S., 2005. Interactive effect of rhizotrophic microorganisms on growth, yield and nutrient uptake of wheat. *Journal of Plant Nutrition*. 28, 2079–2092. <https://doi.org/10.1080/01904160500320897>
- Zhang, C., Van Der Heijden, M., Dodds, B., Nguyen, T., Spooren, J., Held, A., et al. 2023. A tripartite bacterial-fungal-plant symbiosis in the mycorrhiza-shaped microbiome drives plant growth and mycorrhization. *Microbiome*. 12. <https://doi.org/10.1186/s40168-023-01726-4>
- Zhang, H., Zhou, M., Zai, X., Zhao, F., & Qin, P. 2020. Spatio-temporal dynamics of arbuscular mycorrhizal fungi and soil organic carbon in coastal saline soil of China. *Scientific Reports*. 10. <https://doi.org/10.1038/s41598-020-66976-w>
- Zhang, Y., Chen, F., Wu, X., Luan, F., Zhang, L., Fang, X., et al. 2018. Isolation and characterization of two phosphate-solubilizing fungi from rhizosphere soil of moso bamboo and their functional capacities when exposed to different phosphorus sources and pH environments. *PLoS ONE*. 13. <https://doi.org/10.1371/journal.pone.0199625>
- Zhao, M., Wang, H., Wang, S., Han, Q., & Shi, Y. 2020. Phosphorus forms in the sediment of seagrass meadows affected mainly by fungi rather than bacteria: A preliminary study based on ³¹P-NMR and high-throughput sequencing. *Oceanological and Hydrobiological Studies*. 49, 408–420. <https://doi.org/10.1515/ohs-2020-0036>