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Metabolic characterization of phosphate solubilizing microorganisms and their role in improving soil phosphate solubility, yield of upland rice (*Oryza sativa* L.), and phosphorus fertilizers efficiency

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Phosphate solubilizing microbes (PSM) can improve soil P availability by P dissolution. These microbes can make substances that regulate plant growth, which promotes plant growth. The present study aimed to characterize PSM and determine how PSM application affected P solubilization, soil phosphatase activity, and upland rice yield. The greenhouse experiment used a factorial randomized block design (RBD) with two factors and three replications. The first factor was PSM isolates, which came in four different forms: without microbes, with microbes (*Burkholderia* sp.), with fungus (*Penicillium* sp.), and with a combination of microbes (*Burkholderia* sp. and *Penicillium* sp.). The PSM isolates were characterized to analyze the production of organic acids, phosphatase enzymes, and phytohormones. The second factor was the superphosphate fertilizer dose, which has four levels: 0, 50, 75, and 100 kg P ha^{-1}. According to the PSM characterization, it produced organic acids such as lactate acid, oxalate acid, citric acid, and acetate acid, as well as phytohormones (IAA) and the enzyme phosphatase. The pot experiment results show that the PSM inoculation raised the available P and soil phosphatase, P content of the plant, decreased soil organic P, and increased upland rice production. For improving available P, phosphatase activity, P content of the plant, and upland rice yields, mixed inoculants of phosphate-solubilizing bacteria and fungi performed better. The availability of soil P, the activity of the enzyme phosphatase, and the upland rice yields were all improved by applying P fertilizer at 75 kg P ha^{-1}. This study showed that PSM as a biofertilizer reduced the dosage of inorganic fertilizers by up to 25%.

KEYWORDS

available P, organic acid, phosphatase, organic P, P fertilizer

Introduction

One of the macronutrients crucial for plant growth is phosphorus (P). However, several barriers prevent plants from accessing P in the soil, particularly in marginal soil. The primary issue with phosphorus is that it is present in high soil concentrations yet inaccessible to plants. In this instance, it heavily depends on the soil's qualities, properties, and management (Balemi and Negisho, 2012; Xu et al., 2020). In agricultural soils, high P fixation by Al and Fe hydroxides is frequently a problem (Penn and Camberato, 2019). The key factors that contributed to the lack of P in most soil are the low soil P availability, low soil P total, low fixation of soluble P, and the fact that most of the P in soil is still in organic form and not available to plants (Shen et al., 2011).

It is required to develop the usage of microbes that contribute to the transformation of P nutrients in the soil and can be utilized as biofertilizers, such as phosphate solubilizing microbes, to increase plant development and fertilization effectiveness (Kalayu, 2019). Recently, the genus *Burkholderia* has become necessary as phosphate solubilizing microbes (Moreno-Conn et al., 2021) and the genus *Penicillium* (Reyes et al., 2001; Countinho and Felix, 2012). The phosphate solubilizing microbes (PSM) can remove phosphorus (P) from bonds with aluminum, iron, calcium, and magnesium (Al, Fe, Ca, and Mg), allowing it to dissolve P that is unavailable to plants and make it available to them (Alori et al., 2017). Sharma et al. (2013) stated that PSM could solubilize and mineralize P from inorganic and organic pools of total soil P. This is because, in the soil, organic acids produced by bacteria can create stable complexes with P-binding cations (Menezes-Blackburn et al., 2016).

In addition to being able to release fixed P, the phosphate-solubilizing microbes have various benefits for promoting plant growth, including the ability to create phosphatase enzymes (Behera et al., 2017; Fitriatin et al., 2020). According to Stevenson (1986), between 15 and 80% of soil's phosphorus (P) is contained in its organic form. P availability may come from soils with a high organic P concentration (Khosa et al., 2021). Since plants cannot directly utilize the inorganic form of P, it must first be converted into a soluble (organic) P through a mineralization process helped by soil enzymes (Quiquampoix and Mousain, 2003; Tian et al., 2021).

The phosphate solubilizing microbes as plant growth-promoting rhizobacteria PGPR play an essential role in increasing plant growth and yield (Kalam et al., 2020; Basu et al., 2021; Hamid et al., 2021; Nasab et al., 2021) and can withstand the adverse effects arising from various biotic and abiotic stresses (Kour et al., 2019; Bhat et al., 2022; Gowtham et al., 2022; Shah et al., 2022; Verma et al., 2022). Kusale et al. (2021a,b) isolated *Klebsiella variicola* from the wheat rhizosphere, producing phytohormone, organic acid, phytase, salt ameliorating, and antioxidant metabolites. They found this bacterium as a potential bioinoculant for salinity stress management. Another potential for PGPR can inhibit plant diseases. Suriani et al. (2020) reported that the significant reduction of blast disease due to applying a mixture of piper leaves extracts and PGPR improved the growth and yield of rice.

The importance of phosphate-solubilizing microbes in increasing nutrient availability and food yield has been demonstrated in numerous studies. Common bean productivity and nutritional availability increased due to phosphate-solubilizing bacteria, promoting biological activity (Bamagoos et al., 2021). Pereira et al. (2020) applied phosphate-solubilizing bacteria as plant growth-promoting bacteria (PGPB) *Azospirillum brasilense*, *Bacillus subtilis*, and *Pseudomonas fluorescens* increased maize production by up to 34% and increased plant P uptake. To improve the soil P nutrient content and maximize the P fertilization, it is necessary to investigate the characteristics of PSM and their ability to increase P solubility in the soil through P organic mineralization into P inorganic and fixed P dissolving.

Materials and methods

Soil sample collection

Burkholderia sp. and *Penicillium* sp. were isolated from the rice rhizosphere. Ten grams of rhizospheric soil samples (10 cm depth) were collected from Jatinangor District, Sumedang Regency, West Java Province, Indonesia $(6^{0}54'56,4''S)$ and $(107^{0}46'16,9''E)$. Soil samples as a source of isolates of phosphate solubilizing microbes were stored in zip lock bags and transferred to the laboratory.

Isolation of P solubilizing microbes

Isolation of PSM was carried out by a serial dilution plate method using Pikovskaya media (10 g glucose, 5 g $Ca_3(PO_4)_2$, 0.2 NaCl, 0.5 g $(NH_4)SO_4$, 0.1 g $MgSO_4 \cdot 7H_2O$, 0.5 g yeast extract, 0.2 g KCl, 0.002 g $FeSO_4 \cdot 7H_2O$, 0.002 g $MnSO_4 \cdot H2O$, 15 g agar, in 1 L distilled water, pH 7) (Nautiyal, 1999). One gram soil sample was dissolved into 9 ml of sterilized distilled water in test tubes and mixed. The serial soil dilutions were made for 10^{-4}, 10^{-5}, 10^{-6}, and 10^{-7}. Furthermore, 0.5 ml of each dilution was drawn using a micropipette and placed on to plate with Pikovskaya media, and spread using a sterile L-shaped spreader. The plates were then inoculated for 2–5 days at room temperature. The clear zone indicated the ability of the isolate to dissolve phosphate in Pikovskaya media, which contains insoluble phosphate (Tricalcium phosphate). The characteristic morphology of *Burkholderia* sp. were small in diameter (about 1 mm) and white or pale yellow with well-defined margins. *Burkholderia* sp. are rod-shaped, motile, free-living, and Gram-negative bacteria. While *Penicillium* sp. are filamentous fungi that have branched conidiospores.

Estimation of organic acid production and phosphatase activity

Organic acid was measured using HPLC (Photodiode Array Detector, Singapore Product Waters 2998) (Sarker and Al-Rashid, 2013). The mobile phase used was 5.0 mM L^{-1} H_2SO_4 in ultrapure water (HPLC grade) at a flow rate of 0.6 ml per minute. 10 μl sample was injected with a run time of 40 min for each sample. Standard solutions were injected to obtain the retention time for each compound.

Phosphatase enzyme activity was determined according to Eivazi and Tabatabai method (Margesin, 1996). The substrate was added with p-nitrophenyl to form the p-nitrophenol compound through enzyme activity. Consecutively, it was stained by sodium hydroxide solution, which can be detected by a 400 nm spectrophotometer (Shimadzu Corp, Tokyo, Japan), indicating phosphate enzyme activity.

Screening and estimation of IAA

The synthesis of phytohormones (IAA) was determined by the colorimetric method of Gordon and Weber (Sarker and Al-Rashid, 2013) using Salkowski's reagent. Salkowski reagent is a mixture of 35% perchloric acid ($HClO_4$) and 0.5 M ferric chloride ($FeCl_3$), which pink color developed by positive reaction indicates IAA production. This method is mainly used for detecting IAA from microbes.

Greenhouse studies

The pot experiment was conducted at an elevation of ~782 meters above sea level in the greenhouse of the Agriculture Faculty at Universitas Padjadjaran in West Java, Indonesia. Ultisol from Jatinangor was employed and taken at a depth of 0 to 20 cm. The soil pH was 5.11, soil P availability was moderate (16.9 mg kg^{-1}), its C-org level was moderate (2.86%), and its CEC level was high (38.5 cmol kg^{-1}). C-org. Using the Walkley and Black method, the Bray method was used to determine P availability, and CEC was determined using the 1N ammonium acetate at pH 7 (van Reeuwijk, 2012).

A factorial randomized block design (RBD) with two factors and three replications was used for the experimental setup. The first factor was PSM isolates, which were divided into four levels: those without microbes, those with *Burkholderia* sp., those with *Penicillium* sp., and those with a combination of *Burkholderia* sp. and *Penicillium* sp. The second factor was the superphosphate fertilizer dose, which has four levels: 0, 50, 75, and 100 kg P ha^{-1}. This dose was used to determine the efficient dose range caused by the application of PSM.

A mixture of soil (10 kg per pot with the size of 40 cm x 50 cm) and cow dung (50 g) was incubated for 2 weeks. When two plants were planted per pot, and P fertilizer was applied. In accordance with the specified dosage, P fertilizer was provided, and PSM isolate was conducted with a density of 10^6 CFU ml^{-1} and was inoculated to 10 ml pot^{-1}.

According to the Eivazi and Tabatabai approach, soil phosphatase, P availability, soil organic P utilizing extraction method, and P content of plant were the observed responses (Kjeldahl method). Total P in the plant can be extracted by wet ashing method using a mixture of concentrated acids HNO_3 and $HClO_4$. The level of the P element in the extract was measured using a spectrophotometer (Soil Research Institute, 2005).

Statistical analysis

Data was collected for an analysis of variance (ANOVA), F-Test was done to show the significant effects of tested treatments on observed variables. Duncan Multiple Range Test (DMRT) at $P < 0.05$ was used to compare treatment means.

Results and discussion

Biochemical characteristics of PSM

The synthesis of organic acids, phosphatase activity, and concentration of P-dissolved in Pikovskaya media indicated the phosphate solubilizing capacity of the isolates (Supplementary Table 1). Analysis of the organic acids production revealed that both isolates, *Burkholderia* sp. and

Penicillium sp. produced organic acids, including lactate acid, oxalate acid, citric acid, and acetate acid. Lactic acid was produced in more amounts compared to other organic acids. In comparison, glutamic acid was produced in the least amount. The capacity of these bacteria to dissolve phosphate will differ depending on their ability to produce organic acids (Sharma et al., 2016; Serna-Posso et al., 2017). Osmolovskaya et al. (2018) claimed that each organic acid has a different capacity to chelate metal ions. Two factors, including the stability constant of complex organic acids with metal ions and the structure of the hydroxyl and carboxyl molecules in the primary carbon chain, affect this variance. Yang et al. (2022) reported that the capacity of phosphate-solubilizing fungi to produce organic acids and a decrease in the pH of the medium is closely related to the ability of phosphate solubilizing to produce organic acids.

Burkholderia sp. produced more organic acids than *Penicillium* sp. As a result, it had a better capacity to dissolve P than *Penicillium* sp. It also showed higher phosphatase enzymes and more production of IAA. Bacteria generally exhibit higher Psolubilization than fungi. The synergism action of *Burkholderia* sp. and *Penicillium* sp. can increase the production of organic acids and, thus, more P solubilization. Previous studies have shown that the production of organic acids by the co-culture (bacteria and fungi) was more significant than the sum of organic acid production by the individual cultures (Rodrigues and Nahas, 2012).

Phosphatase activity and soil P

Analysis of soil phosphatase showed a rise carried on by PSM inoculation. Compared to the other treatments, mixed inoculations of *Burkholderia* sp. and *Penicillium* sp. usually had a stronger tendency to increase soil phosphatase. This investigation demonstrated that giving a mixed bacteria and fungi inoculant significantly impacted soil phosphatase more than the microbe alone.

Based on the phosphatase data from Supplementary Table 2, it could be seen that *Burkholderia* sp. isolate increased phosphatase activity by 142.7% compared to the control. Additionally, the phosphatase activity was increased by 147.9% when *Burkholderia* sp. isolate and *Penicillium* sp. were combined, which was significantly more significant than the control. The synergy between *Burkholderia* species and *Penicillium* species, which produced more phosphatase enzymes, was thought to be the origin of this phenomenon.

Under low pH or high acidity conditions, acid phosphatase activity will work more actively (Tagad and Sabharwa, 2018). Phosphatase activity will increase along with an increase in organic P. This is due to the PSM activity, which hydrolyzes the organic P in the soil. High phosphatase activity most likely occurred due to PSM hydrolyzing P organic from organic P in the soil. Phosphatase activity will also work with the amount of P organic (Ma et al., 2021).

Burkholderia sp. and *Penicillium* sp. were inoculated combined, increasing the amount of accessible P in the soil by 8.5% (Supplementary Table 2). PSM can produce organic acids that combine to form complex chemicals, which causes this behavior. This complex compound production will reduce P fixation, increasing the amount of accessible P (Rashid et al., 2016).

The results of this experiment revealed that applying 75 kg P_2O_5 ha^{-1} enhanced P availability in soil by 26.7% during the vegetative phase and by 20.7% when using 100 kg P_2O_5 ha^{-1}. Additionally, when the amount of P fertilizer in the soil solution rises, P is absorbed into free elements like Al and Fe (Penn and Camberato, 2019). P availability increased more by applying 75 kg P_2O_5 ha^{-1} than by using 100 kg P_2O_5 ha^{-1}. Fe minerals fixation is thought to be the reason for the low P transfer to soil. As a result, residual fertilization cannot be optimally absorbed by plants if fertilization dosage is increased.

According to the experiment, mixed inoculation of *Burkholderia* sp. and *Penicillium* sp. could improve P availability in the soil more than inoculation of *Burkholderia* sp. This ensures that fungi, rather than bacteria, may survive in soil with low pH levels as Ultisol.

Following inoculation with a phosphate-solubilizing bacteria, the organic soil P concentration was dropped (Supplementary Table 2). The fact that phosphatase-producing bacteria are present and have caused a decrease in the amount of organic soil P showed that organic P was being mineralized. According to de Oliveira Rita et al. (2013), the reduction in the organic soil P content indicates that P organic is mineralized.

The experiment's outcome demonstrated that a mixture of *Burkholderia* sp. and *Penicillium* sp. solubilized the least amount of organic soil P alone. But mixing these phosphate-solubilizing bacteria and fungi results in a faster mineralization rate than using a single isolate of either bacteria or fungi. Based on the results of this experiment, it can be inferred that a combination of *Burkholderia* sp. and *Penicillium* sp. increased the mineralization of P in organic soil. The finding supported it that treatment of combined inoculation of *Burkholderia* sp. and *Penicillium* sp. caused the maximum activity of soil phosphatase. According to the experiment results, the combined inoculation of *Burkholderia* sp. and *Penicillium* sp. decreased the soil organic P content and increased the soil P availability.

The P content of plant and yield of upland rice

The application of *Burkholderia* sp., *Penicillium* sp., and combined inoculant (*Burkholderia* sp. and *Penicillium* sp.) each considerably raised the P content of the plant, according to the observation at the end of the vegetative period (Supplementary Table 3). This is probably due to the usage of PSM, which can reduce the dose of phosphorus fertilizers. The inoculant of *Burkholderia* sp. and *Penicillium* sp. was applied, increasing the P content of the plant by 27.3%. The P content of the plant increased after an increase in P level. This is due to the fact that fungi can survive in highly harsh soil conditions and that they also maximize plant P uptake. *Burkholderia* sp. inoculant application, however, raised the P content in the plant by 18.2% at the end of the vegetative period.

Supplementary Table 3 shows that applying P fertilizer at doses of 75 and 100 kg P_2O_5 ha^{-1} significantly increased the P content of plants. This effect happens because plants respond to fertilization at the end of the vegetative period. The P fertilization at a dosage of 75% of the recommended dosage increased the concentration of plant P by 12.5%, while fertilization at 100% increased P fertilization by 16.7%. The presence of organic acids created by the upland rice root system is thought to be the reason for the P plant's high content, which is at 100% of the recommended dosage.

The results showed that PSM isolate and P fertilizer did not interact to alter upland rice output (milled dry grain). The combined inoculant of *Burkholderia* sp. and *Penicillium* sp. increased milled dry grain by 41.1%, even if the result did not show any interaction (Supplementary Table 3). It varies directly to how much PSM mixed inoculant is applied to the soil P availability parameter. *Burkholderia* sp. and *Penicillium* sp. inoculant each boost upland rice output by 33% and 21%, respectively (Supplementary Table 3). Even though *Burkholderia* sp. and *Penicillium* sp. separately improved yield, it was still lower than applying a combination inoculant of both types.

IAA produced by PSM can cause increased rice yields. Supplementary Table 1 shows that *Burkholderia* sp. produced higher IAA than *Penicillium* sp. In line with that, upland rice yield was higher in treatment *Burkholderia* sp. compared to rice yields in treatment *Penicillium* sp. *Penicillium* sp. and *Burkholderia* sp. will interact to fulfill each other requirements for food, especially P. Because *Penicillium* sp. and *Burkholderia* sp. work synergistically, phosphatase enzyme is released throughout the mineralization and immobilization processes, converting P organic to P inorganic. Therefore, until the end of the generative phase, the growth of any of them is ideal for plant growth.

Additionally, the ability of *Burkholderia* and *Penicillium* species to emit organic acids acts as a factor that can raise the P element produced as a result of Fe fixation. The synergy helps provide P for upland rice until harvest time, particularly in filling its grains, which eventually results in a rise in the yield of milled dry grains. According to Hutagaol et al. (2021), the application of phosphate-solubilizing fungi (PSF) improved the growth and production of rice compared to the control (no application of PSF). With its high phosphate-solubilizing capacity, *Penicillium guanacastense* could be used as a biofertilizer in forestry and agriculture (Qiao et al., 2019). The application of *Burkholderia sp.* in a particular soil type may help in plant nutrient uptake by solubilizing added and support their survival in extreme conditions by other qualities that promote plant growth (Baghel et al., 2020). Vafa et al. (2021) reported applying a combination of phosphate-solubilizing bacteria and N-fixing bacteria (*Azotobacter* sp. and *Azospirillum* sp.) mycorrhizal fungus, and seaweed extract improves growth parameters and grain yield in wheat.

Upland rice production was raised by 17.9% after P fertilizer application with a dose of 75 kg P_2O_5 ha^{-1}. Upland rice yield was not increased by increasing the P dose over 75 kg P_2O_5 ha^{-1} but decreased by 11% with a 100 kg P_2O_5 ha^{-1}. The response of the plants to fertilizer decreases with increasing soil nutrient levels (Li et al., 2019). P fertilizer in excessive quantities will impact soil micronutrient deficiencies (Zn, Fe, Bo, and Mn), making minerals unstable and competing with root activity to absorb nutrients.

Although there was no interaction between PSM and P fertilizer in terms of upland rice yield, excessive P content inhibits the role of PSM in phosphorus transformation. According to Liu et al. (2021), bacterial activity in P transformation increases in conditions of P deprivation. Behera et al. (2017) reached a similar conclusion. Their study revealed that a high P concentration in the medium decreased bacterial activity.

Conclusions

According to this study, phosphate-solubilizing microbes increased soil phosphatase activity, phosphorus availability, phosphorus concentration, and upland rice yield. This PSM inoculation can enhance P organic mineralization by lowering the soil P organic content. The effects of raising P available content, soil phosphatase activity, organic P mineralization, P content of the plant, and upland rice production are better when *Burkholderia* sp. and *Penicillium* sp. mixed inoculant are used. Applying phosphate fertilizer at 75% of the recommended rate positively affects soil phosphatase activity, phosphate availability, soil P organic soil, and upland rice production. Additionally, PSM can be developed as a biofertilizer to increase phosphorus fertilization efficiency.

Data availability statement

The original contributions presented in the study are included in the article/Supplementary material, further inquiries can be directed to the corresponding author.

Author contributions

BNF conducted experimental verification and wrote the original draft of the manuscript. OM contributed to the research idea, designing the study, and editing the manuscript. DH provision of laboratory facilities for the study, analyzed the data, and editing of the manuscript. TAA and MP writing-review and editing, formal analysis, and revision. TAA fund acquisition.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fsufs.2022.1032708/full#supplementary-material

References

Alori, E. T., Glick, B. R., and Babalola, O. O. (2017). Microbial phosphorus solubilization and its potential for use in sustainable agriculture. *Front. Microbiol.* 8, 971. doi: 10.3389/fmicb.2017.00971

Baghel, T., Thakur, J. K., Yadav, S. S., Manna, M. C., Mandal, A., Shirale, A. O., et al. (2020). Phosphorus and potassium solubilization from rock minerals by endophytic *Burkholderia* sp. Strain FDN2-1 in soil and shift in the diversity of bacterial endophytes of corn root tissue with crop growth stage. *Geomicrobiol. J.* 37, 550–563. doi: 10.1080/01490451.2020.1734691

Balemi, T., and Negisho, K. (2012). Management of soil phosphorus and plant adaptation mechanisms to phosphorus stress for sustainable crop production: a review. *J. Soil Sci. Plant Nutr.* 12, 547–561. doi: 10.4067/S0718-95162012005000015

Bamagoos, A. A., Alharby, H. F., Belal, E. E., Khalaf, A. E. A., Abdelfattah, M. A., Rady, M. M., et al. (2021). Phosphate-solubilizing bacteria as a panacea to alleviate stress effects of high soil $CaCO_3$ content in *Phaseolus vulgaris* with special reference to P-releasing enzymes. *Sustainability* 13, 1–22. doi: 10.3390/su13137063

Basu, A., Prasad, P., Das, S. N., Kalam, S., Sayyed, R. Z., Reddy, M. S., et al. (2021). Plant growth promoting rhizobacteria (PGPR) as green bioinoculants: recent developments, constraints, and prospects. *Sustainability* 13, 1140. doi: 10.3390/su13031140

Behera, B. C., Yadav, H., Singh, S. K., Mishra, R. R., Sethi, B. K., Dutta, S. K., et al. (2017). Phosphate solubilization and acid phosphatase activity of *Serratia* sp. isolated from mangrove soil of Mahanadi river delta, Odisha, India. *J. Genet. Eng. Biotechnol.* 15, 169–178. doi: 10.1016/j.jgeb.2017.01.003

Bhat, B. A., Tariq, L. S., Nissar, S., Islam, S. T., Islam, S., Mangral, Z., et al. (2022). The role of plant-associated rhizobacteria in plant growth, biocontrol, and abiotic stress management. *J. Appl. Microbiol.* 00, 1–25. doi: 10.1111/jam.15796

Countinho, F., and Felix, W. (2012). Solubilization of phosphates in vitro by *Aspergillus* spp. and Penicillium spp. *Ecol. Eng.* 42, 85–89. doi: 10.1016/j.ecoleng.2012.02.002

de Oliveira Rita, J. C., Gama-Rodrigues, A. C., Gama-Rodrigues, E. F., Zaia, F. C., and Nunes, D. A. D. (2013). Mineralization of organic phosphorus in soil size fractions under different vegetation covers in the north of Rio de Janeiro. *R. Bras. Ci. Solo.* 37, 1207–1215. doi: 10.1590/S0100-06832013000500010

Fitriatin, B. N., Fauziah, D., Fitriani, F. N., Ningtyas, D. D., Suryatmana, P., Hindersah, R., et al. (2020). Biochemical activity and bioassay on maize seedling of selected indigenous phosphate-solubilizing bacteria isolated from the acid soil ecosystem. *Open Agric.* 5, 300–304. doi: 10.1515/opag-2020-0036

Gowtham, H. G., Singh, S. B., Shilpa, N., Aiyaz, M., Nataraj, K., Udayashankar, A. C., et al. (2022). Insight into recent progress and perspectives in the improvement of antioxidant machinery upon PGPR augmentation in plants under drought stress: a review *Antioxidants* 11, 1763. doi: 10.3390/antiox11091763

Hamid, B., Zaman, M., Farooq, S., Fatima, S., Sayyed, R. Z., Baba, Z. A., et al. (2021). Bacterial plant biostimulants: a sustainable way towards improving growth, productivity, and health of crops. *Sustainability* 13, 2856. doi: 10.3390/su13052856

Hutagaol, D., Ani, N., and Lubis, A. (2021). Application of phosphate solubilizing fungi indegenous paddy soil increased P availability, rice growth and production. *Budapest Int. Res. Exact Sci. (BirEx) J.* 3, 178–187. doi: 10.33258/birex.v3i3.2094

Kalam, S., Basu, A., Ahmad, I., Sayyed R. Z., Enshasy, H. E., Dailin, D. J., et al. (2020). Recent understanding of soil acidobacteria and their ecological significance: a critical review. *Front. Microbiol.* 11, 580024. doi: 10.3389/fmicb.2020.580024

Kalayu, G. (2019). Phosphate solubilizing microbes: promising approach as biofertilizers. *Int. J. Agron.* 1, 1–7. doi: 10.1155/2019/4917256

Khosa, S. A., Ernile, K. O., Khan, K. S., and Akmal, M. (2021). Phosphorus mineralization in response to organic and inorganic amendment in a semi-arid pasture soil. *Eur. J. Soil Sci.* 10, 26–31 doi: 10.18393/ejss.801099

Kour, D., Rana, K. L., Yadav, A. N., Yadav, N., Kumar, V., Kumar, A., et al. (2019). "Drought tolerant phosphorus solubilizing microbes: biodiversity and biotechnological applications for alleviation of drought stress in plant," in *Plant Growth Promoting Rhizobacteria for sustainable stress Management Vol 1 Abiotic Stress Management Sayyed*, eds Arora and Reddy (Singapore: Springer), 255–308. doi: 10.1007/978-981-13-6536-2_13

Kusale, S. P., Attar, Y. C., Sayyed, R. Z., Enshasy, H. E., Hanapi, Z., Ilyas, N., et al. (2021b). Inoculation of *Klebsiella variicola* Alleviated slat stress salinity and improved growth and nutrients in wheat and maize. *Agronomy* 8, 11050927. doi: 10.3390/agronomy11050927

Kusale, S. P., Attar, Y. C., Sayyed, R. Z., Malek, R. A., Ilyas, N., Suriani, N. L., et al. (2021a). Production of plant beneficial and antioxidants metabolites by *Klebsiella variicola* under salinity stress. *Molecules* 26, 1894. doi: 10.3390/molecules26071894

Li, Z., Zhang, R., Xia, S., Wang, L., Liu, C., Zhang, R., et al. (2019). Interactions between N, P and K fertilizers affect the environment and the yield and quality of satsumas. *Glob. Ecol. Conserv*. 19, e006632. doi: 10.1016/j.gecco.2019.e00663

Liu, Q., Wang, X., Zhou, J., Yu, X., Liu, M., Li, Y., et al. (2021). Phosphorus deficiency promoted hydrolysis of organophosphate esters in plants: mechanisms and transformation pathways. *Environ. Sci. Technol.* 55, 9895–9904. doi: 10.1021/acs.est.1c02396

Ma, X., Li, H., Zhang, J., and Shen, J. (2021). Spatiotemporal pattern of acid phosphatase activity in soils cultivated with maize sensing tophosphorus-rich patches. *Front. Plant Sci.* 12, 650436. doi: 10.3389/fpls.2021.650436

Margesin, R. (1996). "Acid and alkaline phosphomonoesterase activity with the subtrate p-nitrophenyl phosphate," in *Methods in Soil Biology*, eds F. Schinner, R. Ohlinger, E. Kandeler, and R. Margesin (Berlin Heidelberg: Springer-Verlag), 213-217.

Menezes-Blackburn, D., Paredes, C., Zhang, H., Giles, C. D., Darch, T., Stutter, M., et al. (2016). Organic acids regulation of chemical–microbial phosphorus transformations in soils. *Environ. Sci. Technol.* 50, 11521–11531. doi: 10.1021/acs.est.6b03017

Moreno-Conn, L. M., López-Casallas, M., and Barrera,. F. M. C. (2021). Phosphate solubilization by Burkholderia species isolated from Oxisols from the Colombian high plains. *Cienc. Tecnol. Agropecuaria*. 22, e1897. doi: 10.21930/rcta.vol22_num2_art:1897

Nasab, B. F., Sayyed, R. Z., Ahmad, R. P., and Rahmani, F. (2021). "Biopriming and nanopriming: green revolution wings to increase plant yield, growth, and development under stress condition and forward dimensions," in *Antioxidants in Plant-Microbe Interaction,* eds HarikeshBahadur Singh, Anukool Vaishnav, and R.Z.Sayyed (Singapore: Springer), 623–655. doi: 10.1007/978-981-16-1350-0_29

Nautiyal, C. S. (1999). An efficient microbiological growth medium for screening phosphate solubilizing microorganisms. *FEMS Microbiol. Lett.* 170, 265–270. doi: 10.1111/j.1574-6968.1999.tb13383.x

Osmolovskaya, N., Dung, V. V., and Kuchaeva, L. (2018). The role of organic acids in heavy metal tolerance in plants. *Biol. Commun.* 63, 1–8. doi: 10.21638/spbu03.2018.103

Penn, C. J., and Camberato, J. J. (2019). A critical review on soil chemical processes that control how soil ph affects phosphorus availability to plants. *Agriculture*. 9, 120. Available online at: https://www.mdpi.com/journal/agriculture doi: 10.3390/agriculture9060120

Pereira, N. C. M., Galindo, F. S., Gazola, R. P. D., Dupas, E., Rosa, P. A. L., Mortinho, E. S., et al. (2020). Corn yield and phosphorus use efficiency response to phosphorus rates associated with plant growth promoting bacteria. *Front. Environ. Sci.* 8, 2–12. doi: 10.3389/fenvs.2020.00040

Qiao, H., Sun, X. R., Wu, X. Q., Li, G. L., Wang, Z., Li, D. W., et al. (2019). The phosphate-solubilizing ability of *Penicillium guanacastense* and its effects on the growth of *Pinus massoniana* in phosphate-limiting conditions. *Biol. Open* 8, bio046797. doi: 10.1242/bio.046797

Quiquampoix, H., and Mousain, D. (2003). *Enzymatic Hydrolysis of Organic Phosphorus In Organic Phosphorus In The Environment*. Wallingford: CABI Publishing. doi: 10.1079/9780851998220.0089

Rashid, M. I., Mujawar, L. H., Shahzade, T., Almeelbi, T., Ismail, I. M., and Oves, M. (2016). Bacteria and fungi can contribute to nutrient bioavailability and aggregate formation in degraded soils. *Microbiol. Res.* 183, 26–41. doi: 10.1016/j.micres.2015.11.007

Reyes, I., Baziramakenga, R., Bernier, L., and Antoun, H. (2001). Solubilization of phosphate rocks and minerals by a wild-type strain and two UV-induced mutants of *Penicillium rugulosum*. *Soil Biol. Biochem.* 33, 1741–1747. doi: 10.1016/S0038-0717(01)00099-2

Rodrigues, R. B., and Nahas, E. (2012). Synergistic action of both *Aspergillus niger* and *Burkholderia cepacea* in co-culture increases phosphate solubilization in the growth medium. *FEMS Microbiol. Lett.* 332, 84–90. doi: 10.1111/j.1574-6968.2012.02580.x

Sarker, A., and Al-Rashid, J. (2013). *Analytical protocol for determination of Indole 3 acetic acid (IAA) production by Plant Growth Promoting Bacteria (PGPB).* Technical report of Quantification of IAA by microbes. 1–2.

Serna-Posso, E. J., Prager, M. S., and Cisneros-Rojas, A. D. (2017). Organic acids production by rhizosphere microbes isolated from a typic melanudands and its effects on the inorganic phosphates solubilization. *Acta Agronómica*. 66, 241–247. doi: 10.15446/acag.v66n2.56148

Shah, S., Wang, D., Shah, F., Alharby, H., Bamagoos, A. A., Almjrashi, A., et al. (2022). comprehensive impacts of climate change on rice production and adaptive strategies in China. *Front. Microbiol.* 13, 926059. doi: 10.3389/fmicb.2022.926059

Sharma, S., Sayyed, R., Sonawane, M., Trivedi, M., and Thivakaran, G. (2016). *Neurospora* sp SR8, a novel phosphate solubiliser from rhizosphere of soil of Sorghum in Kachh, Gujarat. *Indian J. Exp. Biol.* 54, 644–649.

Sharma, S. B., Sayyed, R. Z., Trivedi, M. H., and Gobi, T. (2013). Phosphate solubilizing microbes: sustainable approach for managing phosphorus deficiency in agricultural soils, *Springer Plus* 2, 587. doi: 10.1186/2193-1801-2-587

Shen, J., Yuan, L., Zhang, J., Li, H., Bai, Z., Chen, X., et al. (2011). Phosphorus dynamics: from soil to plant. *Plant Physiol.* 156, 997–1005. doi: 10.1104/pp.111.175232

Soil Research Institute (2005). *Technical Guidelines for Chemical Analysis of Soil, Plants, Water and Fertilizers*. Agricultural Research and Development Agency, Ministry of Agriculture.

Stevenson, F. J. (1986). *Cycles of Soil Carbon, Nitrogen, Phosphorus, Sulfur, Micronutrient*. New York, NY; Chichester; Weinheim; Brisbane, QLD; Toronto, ON; Singapore: A Wiley-Inetrscience Publication John Wiley and Sons.

Suriani, N. L., Suprapta, D., Novizar, N., Parwanayoni, N. I., Darmadi, A., Dewi, D., et al. (2020). A mixture of piper leaves extracts and rhizobacteria for sustainable plant growth promotion and biocontrol of blast pathogen of organic Bali rice. *Sustainability* 12, 8490. doi: 10.3390/su12208490

Tagad, C. K., and Sabharwa, S. G. (2018). Purification and characterization of acid phosphatase from *Macrotyloma uiflorum* seeds. *J. Food Sci. Technol.* 55, 313–320. doi: 10.1007/s13197-017-2941-9

Tian, J., Ge, F., Zhang, D., Deng, S., and Liu, X. (2021). Roles of phosphate solubilizing microbes from managing soil phosphorus deficiency to mediating biogeochemical p cycle. *Biology*. 10, 158. doi: 10.3390/biology10020158

Vafa, N., Sohrabi, Y., Sayyed, R. Z., Suriani, N. L., and Datta, R. (2021). Effects of combinations of Rhizobacteria, mycorrhizae, and seaweeds on growth and yields in wheat cultivars under the influence of supplementary irrigation. *Plants* 10, 811. doi: 10.3390/plants10040811

van Reeuwijk, L. P. (2012). *Procedures for Soil Analysis. International Soil Reference and Information Centre (ISRIC)/ Food and Agriculture Organization of The United Nations (FAO). 6th Edn*. Wageningen. The Netherlands.

Verma, A., Shameem, N., Jatav, H. S., Sathyanarayana, E., Parray, J. A., Poczai, P., et al. (2022). Fungal endophytes to combat biotic and abiotic stresses for climate-smart and sustainable agriculture. *Front. Plant Sci.* 13, 953836. doi: 10.3389/fpls.2022.953836

Xu, X. L., Mao, X. L., Van Zwieten, L., Niazi, N. K., Lu, K. P., Bolan, N. S., et al. (2020). Wetting-drying cycles during a rice-wheat crop rotation rapidly (im)mobilize recalcitrant soil phosphorus. *J. Soils and Sediments* 20, 3921–3930. doi: 10.1007/s11368-020-02712-1

Yang, T., Li, L., Wang, B., Tian, J., Shi, F., Zhang, S. (2022). Isolation, mutagenesis, and organic acid secretion of a highly efficient phosphate-solubilizing fungus. *Front. Microbiol.* 13, 793122. doi: 10.3389/fmicb.2022.793122