ARTÍCULO ORIGINAL

Application of native phosphorus-solubilizing fungi in tomato under different doses of mineral fertilization

Aplicación de hongos solubilizadores de fósforo nativos en tomate bajo diferentes dosis de fertilización mineral

Aplicação de fungos solubilizadores de fósforo nativos em tomate sob diferentes doses de fertilização mineral

***Romero-Fernández, Ablraham de Jesús* [1]*; Mendoza-Villarreal, Rosalinda* [1]*; Perea-Vélez, Yazmín Stefani* [2]*; Díaz-Armendáriz, Abigail* [2]

[1] Universidad Autónoma Agraria Antonio Narro, Departamento de Horticultura, Calzada Antonio Narro No. 1923, Col. Buenavista, 25315, Saltillo, Coahuila, México

[2] Programa en Edafología, Colegio de Postgraduados, Campus Montecillo, Carretera México Texcoco km 36.5, 56230, Texcoco, Estado de México, México

abrahamrofer@gmail.com

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Abstract

The sustainable agricultural model proposes reducing the use of chemical fertilizers and promoting alternatives that preserve soil health, produce nutritious food, and contribute to climate change mitigation. In this context, the use of beneficial microorganisms, such as phosphate-solubilizing fungi, is considered a biological strategy to improve nutrient availability, distinguishing itself from chemical fertilizers by its origin and mode of action. This research aimed to evaluate the effect of inoculation with *Penicillium* sp. or *Aspergillus* sp. individually, and in combination with four doses of rock phosphate (100 %, 75 %, 50%, and 25 %) to improve tomato plants under greenhouse conditions. The fungal strains *Penicillium* sp. A56, *Aspergillus* sp. Mu42, and *Penicillium* sp. Mu73 were isolated from agricultural soils in the state of Coahuila. Plants without inoculation or fertilization with phosphate rock were used as controls. Four months after inoculation, the concentrations of P in leaves, root, and substrate were determined. Growth variables were also evaluated, including plant height, root length, stem diameter, fresh and dry weight, number of flowers, and clusters. The results indicated that the best response was obtained with 75% rock phosphate, followed by 50%, and finally 25% and 100%, which showed similar performance. *Penicillium* sp. Mu73+ 75 % rock phosphate (RP) presented, on average, 3.1 times more available phosphorus concentrations in the substrate, whereas *Aspergillus* sp. Mu42+ 50 % RP and *Aspergillus* sp. Mu42+ 75 % RP presented, on average, 6.2 and 8.1 times larger leaves and higher root phosphorus concentrations, respectively, than did the control and the treatments with different doses of rock phosphate. In addition to increasing the concentration of phosphorus, the fungi improved some of the growth variables of the tomato plants. On average, the height, stem diameter, fresh and dry weight, number of flowers, and number of bunches increased by 27 %, 15 %, 62 %, 43 %, 5 %, and 20 % respectively, compared with those of both the control treatment and the plants treated with different doses of rock phosphate. Inoculation with these fungi, which solubilize phosphate from organic sources and act as plant growth promoters should be considered a viable option to reduce production costs associated with chemical fertilization and increase the nutritional status of crops to ensure food for future generations.

Keywords: sustainable agriculture; plant–microorganisms relationship; organic fertilizers; nutrient solubilization

Resumen

El modelo agrícola sostenible propone reducir el uso de fertilizantes químicos y promover alternativas que preserven la salud del suelo, que produzcan alimentos nutritivos y contribuyan a mitigar el cambio climático. En este contexto, el uso de microorganismos benéficos, como los hongos solubilizadores de fosfato (PSF) se consideran una estrategia biológica para mejorar la disponibilidad de nutrientes, diferenciándose de los fertilizantes químicos por su origen y mecanismo de acción. Esta investigación tuvo como objetivo evaluar el efecto individual de la inoculación con *Penicillium* sp. o *Aspergillus* sp., y su combinación con cuatro dosis de roca fosfórica (100 %, 75 %, 50 % y 25 %) para mejorar las plantas de tomate en condiciones de invernadero. Las cepas utilizadas (*Penicillium* sp. A56, *Aspergillus* sp. Mu42 y *Penicillium* sp. Mu73) se aislaron de suelos agrícolas del estado de Coahuila. Como testigos se utilizaron plantas sin inoculación y fertilización con roca fosfórica. Cuatro meses después de la inoculación, se determinaron las concentraciones de P en hojas, raíces y sustrato. También se determinaron variables de crecimiento como altura, longitud de raíz, diámetro de tallo, peso fresco y seco, número de flores y racimos; el orden promedio de la mejor combinación de hongos y las diferentes concentraciones de roca fosfórica fue 75 %>50 %>25 %=100 %. *Penicillium* sp. Mu73+ 75 % presentó, en promedio, 3,1 veces mayores concentraciones de fósforo disponible en el sustrato, mientras que *Aspergillus* sp. Mu42+ 50 % y *Aspergillus* sp. Mu42+ 75 % presentaron, en promedio, concentraciones de fósforo en hojas y raíces 6,2 y 8,1 veces mayores, respectivamente, que el testigo y los tratamientos con diferentes dosis de roca fosfórica. Además de aumentar la concentración de fósforo, los hongos mejoraron algunas de las variables de crecimiento de las plantas de tomate. La altura, el diámetro del tallo, el peso fresco y seco, el número de flores y el número de racimos aumentaron en promedio un 27 %, 15 %, 62 %, 43 %, 5 % y 20 %, respectivamente, en comparación con los del tratamiento testigo y las plantas tratadas con diferentes dosis de roca fosfórica. La inoculación de estos hongos que solubilizan el fosfato de fuentes orgánicas y actúan como promotores del crecimiento de las plantas debe considerarse una opción viable para reducir los costos de producción asociados a la fertilización química y aumentar el estado nutricional de los cultivos para asegurar alimentos para las generaciones futuras.

Palabras clave: agricultura sustentable; relación planta-microorganismo; fertilizantes orgánicos; solubilización de nutrientes

Resumo

O modelo agrícola sustentável propõe reduzir o uso de fertilizantes químicos e promover alternativas que preservem a saúde do solo, que produzam alimentos nutritivos e contribuam para mitigar as mudanças climáticas. Nesse contexto, o uso de microrganismos benéficos, como os fungos solubilizadores de fosfato (PSF), é considerado uma estratégia biológica para melhorar a disponibilidade de nutrientes, diferenciando-se dos fertilizantes químicos por sua origem e mecanismo de ação. Esta pesquisa teve como objetivo avaliar o efeito individual da inoculação com *Penicillium* sp. ou *Aspergillus* sp., e sua combinação com quatro doses de rocha fosfática (100 %, 75 %, 50 % e 25 %) para melhorar plantas de tomate em condições de cultura em estufa. As cepas utilizadas (*Penicillium* sp. A56, *Aspergillus* sp. Mu42 e *Penicillium* sp. Mu73) foram isoladas de solos agrícolas do estado de Coahuila. Como controles negativos, foram utilizadas plantas sem inoculação e fertilização com rocha fosfática. Quatro meses após a inoculação, foram determinadas as concentrações de P nas folhas, raízes e substrato. Também foram determinadas variáveis de crescimento, como altura, comprimento da raiz, diâmetro do caule, peso fresco e seco, número de flores e cachos; a ordem média da melhor combinação de fungos e as diferentes concentrações de rocha fosfática foi 75 %>50 %>25 %=100 %. *Penicillium* sp. Mu73+ 75 % apresentou, em média, 3,1 vezes maiores concentrações de fósforo disponível no substrato, enquanto *Aspergillus* sp. Mu42+ 50 % e *Aspergillus* sp. Mu42+ 75 % apresentaram, em média, concentrações de fósforo nas folhas e raízes 6,2 e 8,1 vezes maiores, respectivamente, do que o controle absoluto e os tratamentos com diferentes doses de rocha fosfórica. Além de aumentar a concentração de fósforo, os fungos melhoraram algumas das variáveis de crescimento das plantas de tomate. A altura, diâmetro do caule, peso fresco e seco, número de flores e número de cachos aumentaram em média 27 %, 15 %, 62 %, 43 %, 5 % e 20 %, respectivamente, em comparação com aqueles do tratamento controle e as plantas tratadas com diferentes doses de rocha fosfática. A inoculação desses fungos que solubilizam o fosfato de fontes orgânicas e atuam como promotores do crescimento de plantas deve ser considerada uma opção viável para reduzir os custos de produção associados à fertilização química e aumentar o estado nutricional das culturas para garantir alimentos para as gerações futuras.

Palavras-chave: agricultura sustentável; relação planta–microrganismo; fertilizantes orgânicos; solubilização de nutrientes

Introduction

According to the Food and Agriculture Organization (FAO), tomatoes are the most widely cultivated and economically significant vegetable in the world. Most tomato crops are consumed fresh or processed, with these two sectors representing the primary destinations for tomato production. The main producing countries are China (23 %), India (7 %), the United States (7 %) and Turkey (6 %), which together account for 43 % of global tomato production (FAO, 2020). Regarding cropping system, 98 % of tomatoes are produced under conventional agricultural systems, and the rest under an organic farming scheme (Vázquez Huerta et al., 2014).

One of the characteristics of conventional agriculture is the intensive use of inputs such as synthetic fertilizers, pesticides, and herbicides to maximize crop yields (Hu et al., 2012). This system is based on standardized agricultural practices geared toward large-scale production and the chemical control of pests, diseases, and weeds. These practices include intensive mechanized tillage, planting high-yielding varieties, periodic application of agrochemicals, and the use of automated irrigation. Soil management relies on deep or conventional tillage, which turns over the soil profile to prepare the ground and control weeds, although it can cause loss of organic matter and erosion. Regarding crop residue management, plant residues are frequently removed or burned to leave the field "clean" for the next cycle, thus reducing the return of biomass to the soil and affecting its long-term fertility. For instance, one hectare of tomatoes requires approximately 300-400 kg of N-K, and 300 kg of P. Among these nutrients, phosphorus is considered the most limiting nutrient for agricultural production (Yang et al., 2011). The low availability of P in soils is due to its high reactivity and tendency to bind with iron, calcium, or aluminium ions, resulting in phosphate compounds with low solubility (Tapia and García, 2013). On the other hand, an overuse of synthetic chemical fertilizers causes soil degradation through salinity and increases production costs (Cárdenas-Navarro et al., 2004; Baweja et al., 2020; Hossain et al., 2022). In this context, in the last few years there has been an increased interest in the use of new technologies, such as biotechnology, to counteract the negative impacts of poor agricultural practices (such as the overuse of chemical fertilizers, pesticide mismanagement, monocropping, over-tilling or deforestation, poor water management or use of contaminated water sources) and allow increasing yields under a sustainable production scheme (Gómez-Tovar et al., 2005; Ervin et al., 2010; Barrows et al., 2014). Phosphate-solubilizing fungi (PSF) can transform organic and inorganic phosphates into soluble forms by breaking the bonds formed by phosphorus and metal ions (Fe, Ca, and Al) (Restrepo-Franco et al., 2015). In addition, the use of native strains of fungi in biological inoculants increases the likelihood of effectiveness in the field, since they are adapted to local soil conditions (Armenta-Bojórquez et al., 2010).

The application of rock phosphate (RP) can be ecologically viable since it constitutes a resource of interest as an organic source of P for agriculture (Raigemborn et al., 2010). Despite its low soluble P content, it is an affordable and sustainable alternative when applied directly to microorganisms capable of solubilizing P, such as phosphate-solubilizing fungi (Gyaneshwar et al., 2002). Previous studies have demonstrated that RP in combination with phosphorus-solubilizing fungi in crops such as tomato (Sibi, 2011), cucumber (García-López et al., 2016), rice (Borges Chagas et al., 2015), beans (Elías et al., 2016), oats (Lima-Rivera et al., 2016), coffee (Cisneros and Menjivar, 2016), sorghum (Steiner et al., 2016) and rice (Turan et al., 2023) improves agronomic variables and quality of the crop. Therefore, using RP in combination with native PSF is an option to reduce the inappropriate and excessive use of chemical fertilizers that affect soil health and contribute to greenhouse gas emissions (Sahandi et al., 2019). Moreover, the fungal genera *Aspergillus* and *Penicillium* perform various ecological functions such as phosphate solubilization, production of plant growth-promoting metabolites, and decomposition of organic matter (Adedayo and Babalola, 2023; Khan et al., 2010), although some species can exhibit phytopathogenic activity, such as the production of mycotoxins and the development of opportunistic diseases (Sweeney and Dobson, 1998). Therefore, this work aimed to evaluate the effect of individual inoculation of tomato plants with *Penicillium* sp. or *Aspergillus* sp., in combination with four RP doses (100 %, 75 %, 50 %, and 25 %), under greenhouse conditions, in order to identify the most effective fungal strain and recommend the optimal RP concentration to increase the nutritional status of P (substrate-plant) and its agronomic variables.

Materials and Methods

Preparation of the inoculum of phosphorus-solubilizing fungi (PSF)

The fungi strains *Penicillium* sp. A56, *Aspergillus* sp. Mu42, and *Penicillium* sp. Mu73 were isolated from agricultural soils of the state of Coahuila (Romero-Fernández et al., 2019). The strains were chosen for their high capacity to solubilize $Ca_3(PO_4)_2$ in solid and liquid media. PSF were propagated in solid potato dextrose agar culture medium in 90×110 mm Petri dishes incubated at 25 °C for 15 days in the dark. After that, a spore suspension of each of the strains was made with sterile distilled water, and with the help of a Neubauer chamber under a compound microscope, a spore count was performed to reach a concentration of $1x10^8$ CFU mL^{-1} (Steiner et al., 2016). The strains had been previously tested by Arias Mota et al. (2019).

Inoculation of tomato plants and fertilization with RP

Tomato (*Solanum lycopersicon* L.) seeds were disinfected with 3% commercial hypochlorite for 5 min and sown in a germination tray. One month after sowing, the plants were transplanted into 10 L pots containing a mixture of peat moss and perlite at a 1:1 ratio (v/v). The peat was sterilized by autoclaving in three consecutive 60-min cycles each, at 120°C. Each PSF strain was individually inoculated ($1x10^8$ CFU mL^{-1}) at the transplant, and the inoculants were applied directly to the substrate, the root system of the plant. Similarly, RP was applied directly to the substrate before transplanting, at concentrations of 100%, 75%, 50% and 25% (Torres and De Pragier, 2014).

Greenhouse trial

The trial was conducted with a completely randomized design with 17 treatments and 5 replicates of each treatment for a total of 85 experimental units. These were a) control (without fungi or RP); b) four RP concentrations (100 %, 75 %, 50 %, and 25 %); c) Individual inoculation of the three fungi *Penicillium* sp. Mu73, *Aspergillus* sp. Mu42 and *Penicillium* sp. A56; and d) the four combinations with the four RP concentrations. The experiment was maintained for 4 months in a greenhouse at Universidad Autónoma Agraria Antonio Narro , Saltillo, Coahuila, Mexico. Irrigation was provided with a drip system, and 25 mL of Hewitt nutrient solution without phosphorus (Hewitt, 1969) was added weekly to each of the treatments. At the end of the experiment, the plants were harvested to measure height, root length, stem diameter, fresh and dry weight, number of flowers, and number of clusters. Additionally, the P concentration in leaves, root, and substrate was measured.

P concentration in the substrate and in aerial parts and roots of tomato plants

The concentration of available P in substrate samples from each of the treatments was quantified via the ascorbic acid reduction method (Bray and Kurtz, 1945). Colorimetric reactions were measured with a spectrometer at 882 nm. For leaf analysis, samples were taken from the third pair of leaves, in the direction of the four cardinal points, from the outside to the inside of the fruiting branch. Leaves longer than 5 cm were considered as the first pair (Pulgarín, 2007). The roots were washed with abundant tap water to eliminate substrate residues, and then both leaves and roots were placed in an oven at 60 °C until reaching a constant weight. Subsequently, 0.25 g of dry leaf or root material was individually calcined in an oven at 500 °C for 2 h (Mckean, 1993). The resulting ashes were dissolved in 25 mL of 0.3 M HCl in test tubes, and the extracts were filtered through Whatman 42 filter paper. The total P concentration of each sample was subsequently analyzed via the molybdenum blue method (Murphy and Riley, 1962), and the absorbance was measured at 660 nm.

Growth variables

Plant height (cm) was measured from the root crown to the shoot apical meristem. Stem diameter (mm) was determined with an electronic Vernier caliper. Root length (cm) was evaluated from the root crown to the apical meristem. Fresh weight (g) was obtained directly with an analytical balance, and dry weight (g) was determined after drying the samples at 60 °C in an oven until a constant weight was reached. The number of flowers and clusters was counted manually.

Statistical analysis

The data were analyzed with the R statistical package (version 4.0). The normal distribution of the results was corroborated with the Shapiro–Wilk test ($p \leq 0.05$), and the homogeneity of variance was confirmed with Bartlett's test ($p \leq 0.05$). When the data did not have statistical normality, the nonparametric Kruskal–Wallis test was performed; one-tailed Tukey mean comparison tests were also performed ($p \leq 0.05$). Spearman correlation analysis ($r \leq 0.7$) was performed to determine the relationships among the variables.

Results and Discussion

Tomato plant growth variable

The fertilization with RP and PSF improved tomato plant growth (Table 1). Plant height ranged from 58.0 to 70.8 cm when different doses of RP were applied, while with PSF and RP combinations, plant height ranged from 78.0 to 106.6 cm (Table 1). In treatments combining PSF with different doses of RP, the average development of stem diameter was 1.1 times higher than in both the control treatment and the different doses of RP used individually (Table 1). The increase in stem diameter in plants treated with different doses of organic fertilization in combination with PSF could be related to a nutritional status favored by fungal symbiosis and stimulation with phytohormones (Acurio Vásconez and España Imbaquingo, 2017), although these effects were not measured in the present experiment. According to Lagunes-Fortiz et al. (2021), the increase in plant stem diameter is a highly important parameter because it contains the conduits that transport water and nutrients to the different organs of the plant. It also influences the resistance of a plant to bending due to external factors in the field, such as wind or rain. Tomatoes exhibit erect growth, so optimal thickening of the stem favors the development of all the structural organs of the plant. Plant height, stem diameter, and fresh weight of tomato plants treated with *Penicillium* sp. A56+ 25 % RP were higher than those of the other treatments, in agreement with previous researchers who found increased height of tomato under greenhouse conditions (Sibi, 2011; Elías et al., 2016; Bononi et al., 2020). Root length ranged from 28.8 to 32.6 cm with different doses of RP and in the control treatment, while length ranged from 20.2 to 31.0 cm when microbial inoculums were combined with different doses of RP. In contrast, plants from the control treatment (no fertilization with RP and no inoculation with PSF) and those fertilized with 75 % of RP showed the greatest root length compared to the other treatments (Table 1). The highest dry weight was observed for the *Penicillium* sp. Mu73+ 50 % RP treatment, and the *Aspergillus* sp. Mu42+ 50 % RP treatment presented the highest number of flowers and clusters of all other treatments (Table 1). These results agree with other studies where RP combined with PSF inoculation increased the plant growth (Sibi, 2011; Elías et al., 2016; Bononi et al., 2020).

Table 1. Growth variables of tomato plants four months after inoculation with *Penicillium* and *Aspergillus* under different doses of rock phosphate.

Treatment	Height (cm)	Root length (cm)	Stem diameter (mm)	Fresh weight (g)	Dry weight (g)	Number of flowers	Number of bunches
Control	58.0 g	32.6 a	7.2 g	77.6 n	17.0 i	11.4 i	3.0 e
PR 25 %	58.6 g	30.2 bc	7.5 gf	102.6 l	23.2 g	14.0 hi	3.0 e
PR 50 %	61.2 g	28.8 bcd	7.3 fg	85.0 m	19.8 hi	13.4 hi	3.0 e
PR 100 %	64.0 g	31.0 b	7.6 efg	133.8 k	23.2 g	19.0 g	3.2 de
PR 75 %	70.8 f	32.4 a	7.7 efg	132.8 k	22.6 gh	16.0 gh	3.0 e
Mu42+25	77.8 e	20.8 h	9.1 b	148.0 j	36.7 d	24.0 f	3.4 cde
Mu73+25	78.0 e	22.6 fgh	8.1 def	234.8 h	29.1 e	27.8 e	3.4 cde
Mu73+75	79.4 e	22.2 gh	8.9 bc	274.4 f	44.9 c	28.6 de	3.4 cde
Mu42+100	79.8 e	24.6 efg	8.3 cde	247.2 g	40.4 bc	30.2 cde	4.0 bcd
Mu73+100	81.0 de	27.2 cde	8.6 bcd	252.6 g	44.9 c	26.8 ef	3.2 de
A56+75	82.4 de	25.2 efg	8.3 cde	208.4 i	25.6 fg	31.6 bcd	3.8 b
Mu73+50	82.6 de	25.6 ef	8.1 def	274.8 f	48.0 a	33.6 b	4.0 bcd
A56+50	86.2 cd	26.8 de	9.2 b	325.4 d	25.5 fg	26.8 ef	3.4 cde
Mu42+50	86.4 cd	24.4 efg	8.9 bc	289.0 e	47.2 b	35.8 a	5.2 a
Mu42+75	89.4 c	23.0 fgh	9.2 ab	333.2 c	41.7 b	27.8 e	3.4 cde
A56+100	98.4 b	31.0 b	9.3 ab	398.2 b	37.6 cd	32.2 bc	4.2 cb
A56+25	106.6 a	20.2 h	9.7 a	406.4 a	26.6 ef	34.8 b	4.6 b

Values are average, n=5. RP= rock phosphate. Identical letters between columns show that there are no significant differences between treatments (Tukey, α=0.05). PR 25 %: rock phosphate 25 %; PR 50 %: rock phosphate 50 %; PR 75 %: rock phosphate 75 %; PR 100 %: rock phosphate 100 %; Mu73+ 25: *Penicillium* sp. Mu73 + rock phosphate 25 %; Mu73+ 50: *Penicillium* sp. Mu73 + rock phosphate 50 %; Mu73+ 75: *Penicillium* sp. Mu73 + rock phosphate 75 %; Mu73+ 100: *Penicillium* sp. Mu73 + rock phosphate 100 %; Mu42+ 25: *Aspergillus* sp. Mu42 + rock phosphate 25 %; Mu42+ 50: *Aspergillus* sp. Mu42 + rock phosphate 50 %; Mu42+ 75: *Aspergillus* sp. Mu42 + rock phosphate 75 % ; Mu42+ 100: *Aspergillus* sp. Mu42 + rock phosphate 100 %; A56+ 25: *Penicillium* sp. A56 + rock phosphate 25 %; A56+ 50: *Penicillium* sp. A56 + rock phosphate 50 %; A56+ 75: *Penicillium* sp. A56 + rock phosphate 75 %; A56+ 100: *Penicillium* sp. A56 + rock phosphate 100 %.

These results suggest that both control plants and those treated with different doses of RP exhibited nutrient stress associated with limited P availability. Given that this macronutrient plays a fundamental role in the internal transport of nutrients and in root system growth, adequate root extension is essential to optimize nutrient uptake. In contrast, short root length in plants inoculated with PSF was due to greater nutrient availability in the roots of tomato plants, which explains why elongation was not necessary: the plants absorbed P directly (Barea et al., 2008). Compared with the absolute control, fresh weight of plants treated with *Aspergillus* sp. Mu42+ 100 % RP increased by 80.9 %. The dry weight of tomato plants in the *Penicillium* sp. Mu73+ 50 % RP treatment was 65.5% higher than that in the control treatment. Compared with the control treatment and with different doses of RP, the inoculation of PSF combined with different RP doses improved the fresh and dry weights of tomato plants by 62 % and 43 %, respectively (Table 1). Fungi modify plant physiology, including the water absorption capacity of the plants, resulting in greater fresh biomass without losing the structures that give them rigidity when they are dried (Bänziger et al., 1997). The highest number of flowers (35) and bunches (5) occurred in plants treated with *Aspergillus* sp. Mu42+ 50 % RP. The number of flowers and bunches increased by an average of 50 % and 21 %, respectively, when PSF and RP were applied together compared with the control treatment and when RP was applied individually. The variable number of flowers and the number of bunches are among the main components that can be considered indicators of tomato yield (Ramírez-Vargas and Nienhuis, 2012), so their measurement is highly important. Some studies agree with this proposal; for example, Lores et al. (2023) evaluated different types of bunches/plants in two commercial tomato hybrids under greenhouse conditions, and found that as the number of bunches/plants increased, total and commercial production increased. Similarly, Mueller and Wamser (2009) evaluated bunches/plants and reported an increase in total production as a function of the number of bunches per plant.

Available P in the substrate of tomato plants

The concentration of available P in the substrate differed among the treatments evaluated (Figure 1). The concentration of available P in the substrate of all the treatments inoculated with fungi was on average 3.5 and 31.6 times higher than that in treatments with only RP and control (Figure 1). The highest concentration of available P in the substrate was observed in the *Penicillium* sp. Mu73+ 75 % RP (40.2 mg kg^{-1}) treatment, followed by the *Penicillium* sp. Mu73+ 25 % RP (22.7 mg kg^{-1}) and *Aspergillus* sp. Mu42+ 50 % RP (21.5 mg kg^{-1}) treatments (Figure 1).

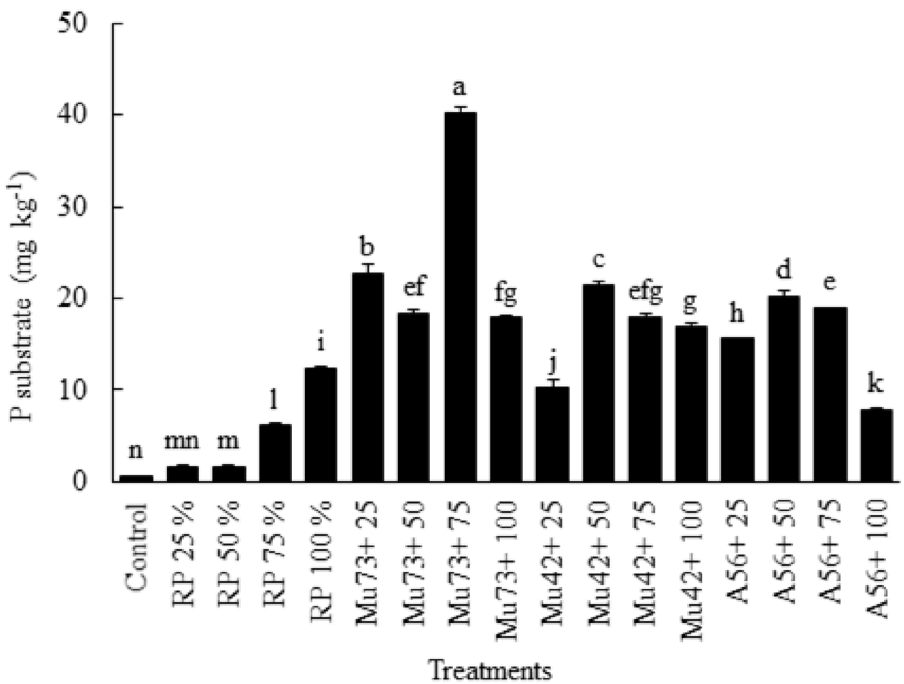

Figure 1. Available phosphorus in the substrate of tomato plants inoculated individually with two strains of *Penicillium* sp. and one of *Aspergillus* sp. under different doses of rock phosphate. Identical letters mean that there are no significant differences between the treatments evaluated. PR 25 %: rock phosphate 25 %; PR 50 %: rock phosphate 50 %; PR 75 %: rock phosphate 75 %; PR 100 %: rock phosphate 100 %; Mu73+ 25: *Penicillium* sp. Mu73 + rock phosphate 25 %; Mu73+ 50: *Penicillium* sp. Mu73 + rock phosphate 50 %; Mu73+ 75: *Penicillium* sp. Mu73 + rock phosphate 75 %; Mu73+ 100: *Penicillium* sp. Mu73 + rock phosphate 100 %; Mu42+ 25: *Aspergillus* sp. Mu42 + rock phosphate 25 %; Mu42+ 50: *Aspergillus* sp. Mu42 + rock phosphate 50 %; Mu42+ 75: *Aspergillus* sp. Mu42 + rock phosphate 75 %; Mu42+ 100: *Aspergillus* sp. Mu42 + rock phosphate 100 %; A56+ 25: *Penicillium* sp. A56 + rock phosphate 25 %; A56+ 50: *Penicillium* sp. A56 + rock phosphate 50 %; A56+ 75: *Penicillium* sp. A56 + rock phosphate 75 %; A56+ 100: *Penicillium* sp. A56 + rock phosphate 100 %.

Other studies have shown how fungi in conjunction with RP increase the available P concentration in the substrate. For example, Sibi (2011) reported that the concentration of available P in the substrate increased 2.6- and 2.4-fold when *Aspergillus awamori* and *Trichoderma viride* were inoculated individually on tomato plants with 5 % RP compared with the control treatment 90 days after inoculation. Velázquez et al. (2017) reported a 1.3-fold increase in available P in the substrate of lettuce plants inoculated with *Penicillium thomii* and RP of sedimentary origin at 60 days of evaluation. Recently, Turan et al. (2023) reported that, during 50 days of evaluation, the concentration of available phosphate in the substrate increased 3.0-fold in canola plants inoculated with *Penicillium oxalicum* and RP as an insoluble P source compared with that in the treatment without inoculation. The authors mentioned above concluded that the application of RP in agriculture can be technologically feasible when combined with solubilizing fungi, given their ability to promote P solubilization in plants in some soils. Additionally, in the present study, the results of the P available in the substrate suggest favorable effects of the fungi *Aspergillus* sp. and *Penicillium* sp. on the use of organic P sources for plants, such as RP. This evidence highlights the possibility of reducing or substituting synthetic phosphate fertilizers with organic P sources which, combined with PSF strains, achieve a higher concentration of soluble P at a lower cost and without damaging the environment. Therefore, further studies should be pursued on these strains and other inorganic P sources to compare solubilization efficiency and economic costs.

Total P in the aerial parts of tomato plants

Leaf P concentration differed among the treatments evaluated (Figure 2). In the control and RP treatments, leaf P concentration ranged from 1.0 to 6.8 mg kg^{-1}, while it ranged from 8.5 to 17.1 mg kg^{-1} in treatments with PSF in combination with RP. The highest P concentrations in leaves were found in the *Aspergillus* sp. Mu42+ 75 % RP (17.1 mg kg^{-1}), *Penicillium* sp. A56+ 50 % RP (15.3 mg kg^{-1}), and *Aspergillus* sp. Mu42+ 50 % RP (13.8 mg kg^{-1}) treatments. These results coincide with those reported by Figueroa-Cares et al. (2018), who observed low P concentrations in the leaves of tomato plants in both the control treatment and those fertilized with 25 % RP, 50 % RP, and 75 % RP. In contrast, plants fertilized with 100 % RP showed normal P concentrations, while in all plants inoculated with PSF, the foliar P content was high (3.5–7.5 mg kg-1). These results suggest that at low doses of mineral fertilization (75 % and 50 %), the use of phosphate-solubilizing fungi is more effective since it provides favorable conditions to achieve solubilization processes in the production of organic acids or in biological mineralization processes (Begonia et al., 2004). Other studies on the combination of PSF and RP have also reported increases in leaf P concentrations compared with those in the treatments with no such combination. For example, García-López et al. (2015) reported that P concentration in leaves of cucumber plants inoculated with *Trichoderma asperellum* increased by 35 % 26 days after inoculation. Moreover, Elías et al. (2016) reported that leaf P concentration in bean plants inoculated with *Aspergillus* sp. and *Penicillium* sp increased by 25 % and 21 % 80 days after inoculation.

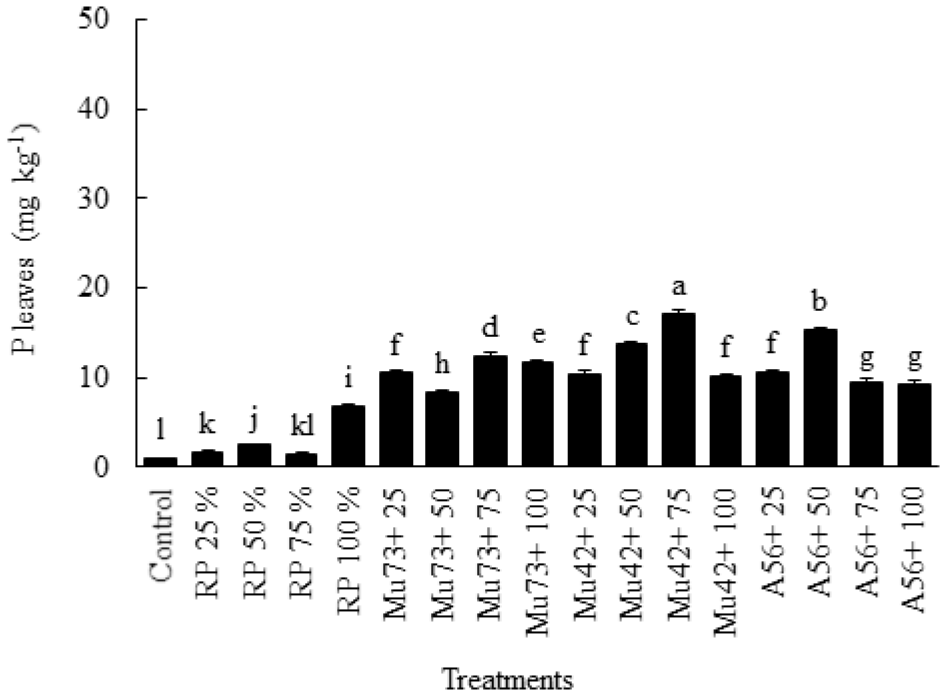

Figure 2. Foliar phosphorus concentration of tomato plants inoculated individually with two strains of *Penicillium* sp. and one of *Aspergillus* sp. with different doses of rock phosphate. Identical letters indicate that there are no significant differences between the treatments evaluated (Tukey, α=0.05), n=5 ± standard deviation. PR 25 %: rock phosphate 25 %; PR 50 %: rock phosphate 50 %; PR 75 %: rock phosphate 75 %; PR 100 %: rock phosphate 100 %; Mu73+ 25: *Penicillium* sp. Mu73 + rock phosphate 25 %; Mu73+ 50: *Penicillium* sp. Mu73 + rock phosphate 50 %; Mu73+ 75: *Penicillium* sp. Mu73 + rock phosphate 75 %; Mu73+ 100: *Penicillium* sp. Mu73 + rock phosphate 100 %; Mu42+ 25: *Aspergillus* sp. Mu42 + rock phosphate 25 %; Mu42+ 50: *Aspergillus* sp. Mu42 + rock phosphate 50 %; Mu42+ 75: *Aspergillus* sp. Mu42 + rock phosphate 75 %; Mu42+ 100: *Aspergillus* sp. Mu42 + rock phosphate 100 %; A56+ 25: *Penicillium* sp. A56 + rock phosphate 25 %; A56+ 50: *Penicillium* sp. A56 + rock phosphate 50 %; A56+ 75: *Penicillium* sp. A56 + rock phosphate 75 %; A56+ 100: *Penicillium* sp. A56 + rock phosphate 100 %.

Bononi et al. (2020) reported a P uptake efficiency of up to 141 % in soybean plants inoculated with *Trichoderma* sp. at the seventh week of evaluation compared with non-inoculated plants. The authors explain that RP, being an insoluble phosphate, induces greater secretion of phosphatases, which facilitates the release of P to the plant, fostering its growth and productivity. However, the participation of this enzyme needs to be verified with the fungi under study. On the other hand, RP releases phosphorus to the soil more slowly than chemical sources such as triple superphosphate, which results in low yields in the first years (Ptáček, 2016). In this sense, our results suggest that the joint application of PSF and RP is of great importance for agriculture because the aerial part of the plant obtains nutritional benefits from an economical source of phosphorus. In addition, RP persists in the soil longer than triple superphosphate, so application of P will not be necessary in subsequent tomato production cycles (Bononi et al., 2020). Therefore, studies should be conducted to evaluate the residual effect of RP under field conditions on crops of interest. In addition, encouraging producers to use these native fungi as an alternative for fungal inoculums in conjunction with RP is a promising strategy to increase environmental awareness, reduce production costs, conserve and recover soils, and maintain biodiversity.

Phosphorus available in the roots of tomato plants

PSF increased P concentration not only in the substrate and aerial parts but also in the roots. The P concentration in the roots ranged from 4.4 to 7.5 mg kg^{-1} in the control treatment and in those with RP alone, whereas that of the fungal treatments ranged from 8.6 to 45.7 mg kg^{-1} (Figure 3). The average concentration in the treatments inoculated with fungi was 3.8 times higher than that in the control treatment and those inoculated with RP alone (Figure 3). Compared with the control, plants inoculated with *Aspergillus* sp. Mu42+ 50 % RP presented the highest 90.3 % increase in total root P concentration (Figure 3). Souchie et al. (2005) reported that the P concentration in roots of maize plants treated with *P. oxalicum* increased by 55 % compared with that of the control after five months. Many factors can interfere with the efficiency of PSF, such as the mode of preparation of the inoculant, the form of application to the soil or substrate, and the location where it is applied (García-López et al., 2015). The agronomic and economic efficiency of RP can be equivalent to that of soluble phosphate fertilizers in some circumstances, but specific conditions must be considered when making this decision (García-López et al., 2016).

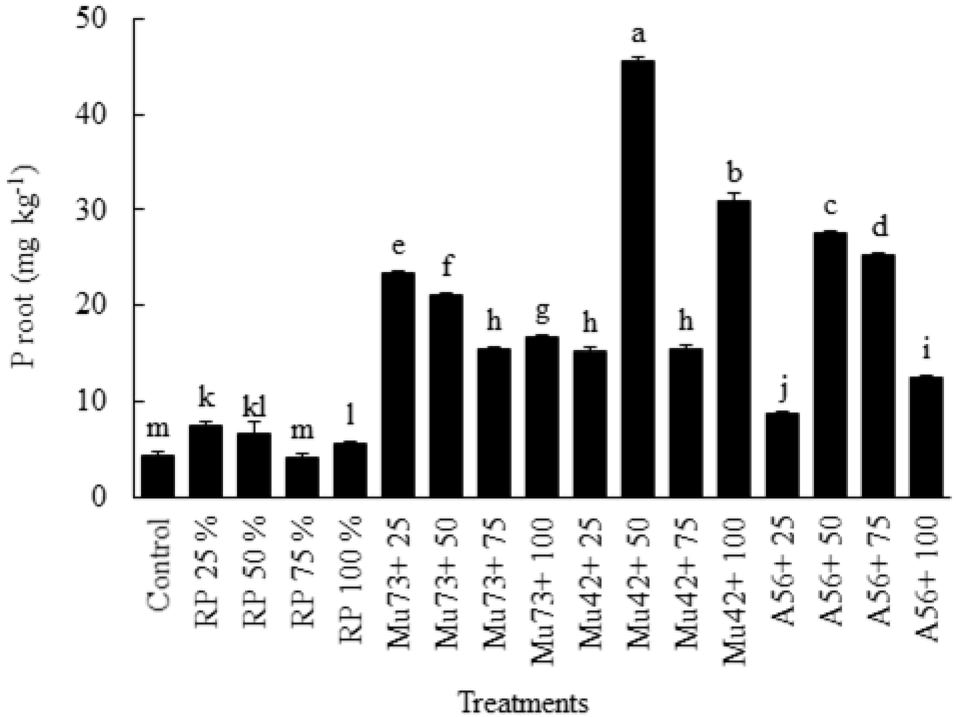

Figure 3. Phosphorus concentration in the root of tomato plants inoculated individually with two strains of *Penicillium* sp. and one of *Aspergillus* sp. with different doses of rock phosphate. Identical letters indicate that there are no significant differences between the treatments evaluated (Tukey, α=0.05), n=5 ± standard deviation. PR 25 %: rock phosphate 25 %; PR 50 %: rock phosphate 50 %; PR 75 %: rock phosphate 75 %; PR 100 %: rock phosphate 100 %; Mu73+ 25*:* *Penicillium* sp. Mu73 + rock phosphate 25 %; Mu73+ 50: *Penicillium* sp. Mu73 + rock phosphate 50 %; Mu73+ 75: *Penicillium* sp. Mu73 + rock phosphate 75 %; Mu73+ 100: *Penicillium* sp. Mu73 + rock phosphate 100 %; Mu42+ 25: *Aspergillus* sp. Mu42 + rock phosphate 25 %; Mu42+ 50: *Aspergillus* sp. Mu42 + rock phosphate 50 %; Mu42+ 75: *Aspergillus* sp. Mu42 + rock phosphate 75 %; Mu42+ 100: *Aspergillus* sp. Mu42 + rock phosphate 100 %; A56+ 25: *Penicillium* sp. A56 + rock phosphate 25 %; A56+ 50: *Penicillium* sp. A56 + rock phosphate 50 %; A56+ 75: *Penicillium* sp. A56 + rock phosphate 75 %; A56+ 100: *Penicillium* sp. A56 + rock phosphate 100 %.

Relationships between growth variables and phosphorous concentration

After 4 months of evaluation in the greenhouse, correlations were observed between P concentration (in substrate, leaves, or root) and the agronomic variables of the plants (Table 2). Interestingly, there are no studies on the correlations between P concentration and agronomic variables in tomato plants inoculated with PSF in combination with different doses of RP under greenhouse conditions. Therefore, the results were compared with studies on other plants of agricultural interest. The concentration of P in the substrate was positively correlated with the number of flowers (r= 0.7). Previous studies attributed this correlation to the ability of P to increase fruiting potential by increasing the intensity and level of flower set per bunch (Rodríguez Araujo et al., 2010). Leaf P concentration was positively correlated to the P concentration in the substrate (r= 0.7) because of the efficient translocation of P from the soil to the aerial part of the plant. It was also correlated with height (r= 0.7), stem diameter (r= 0.8), fresh weight (r= 0.8), dry weight (r=0.7), and number of flowers (r= 0.8). Fungi use different routes to solubilize organic nutrient sources such as P, making them available for plant nutrition.

Table 2. Relationship between the concentration of available-absorbed phosphorus and growth variables of tomato plants four months after inoculation with *Penicillium* and *Aspergillus* with different doses of rock phosphate.

Variable	Substrate phosphorus	Leaves phosphorus	Root phosphorus
Height	-	0.7	-
Stem diameter	-	0.8	-
Root length	-	-0.7	-
Fresh weight	-	0.8	-
Dry weight	-	0.7	0.7
Number of flowers	0.7	0.8	0.7
Number of clusters	-	-	-
Substrate phosphorus	-	0.7	-
Flower phosphorus	-	-	-
Root phosphorus	-	-	-

N=5. - = no correlation.

Thus, PSF promotes greater height, stem diameter, root length, plant quality, yield, and production of various crops of agronomic and social interest that are present in basic food baskets (Whitelaw, 1999; Singh and Reddy, 2011; Patil et al., 2012). P concentration in leaves was also negatively correlated to root length (r= -0.7). It is inferred that the increase in leaf P resulted in the absence of root growth as reported by González et al. (2020). In roots, P concentration was positively correlated to the number of flowers, number of clusters, and dry weight (r= 0.7) of the plants. Adequate P absorption by the roots sustains the development of healthy and strong plants, which positively affects flowering, increases bunch production, and even accelerates fruit ripening (Lores et al., 2023).

Conclusions

The results of the present study showed that the inoculation of PSF in combination with different concentrations of RP increased the availability and absorption of P and consequently improved the growth variables of tomato plants under greenhouse conditions. In this sense, plants inoculated with PSF and the different doses of RP showed an average increase of P concentration of 76 % in the substrate, 76 % in foliage, and 73 % in roots compared to plants in the control treatment and with RP alone. Compared with control plants and those treated with different doses of RP, plants in the PSF treatment increased on average by 1.4, 1.1, 2.6, 1.7, 2.0, and 1.2 times the height, stem diameter, fresh weight, dry weight, number of flowers, and number of bunches, respectively.

Our results corroborate the high phosphate solubilizing capacity of *Penicillium* and *Aspergillus* species. The findings of this research have important implications for growers, who may take advantage of the use of soil fungi with plant growth-promoting qualities in combination with a mineral source of phosphate. In this sense, different trends were observed: the combination of *Penicillium* sp. M73 with 75 % and 50 % RP increased the availability of P in the substrate and the dry weight of tomato plants. In contrast, compared with the other treatments evaluated, *Aspergillus* sp. Mu 42 combined with 75 % and 50 % RP doses increased leaves and root P uptake, as well as the number of flowers and bunches. Therefore, the use of these inoculums is an ecologically acceptable alternative that can gradually reduce or completely replace chemical fertilizer applications by increasing the efficiency and utilization of soil nutrients. In addition, the reintroduction of native fungi helps to reestablish the microbiological balance of the soil. The use of solubilizing microorganisms can be optimized with appropriate combinations of strains, environmental conditions, and plant genotypes. Therefore, further research should be undertaken to define the optimal conditions for inoculant activity in the field. These include interactions between different fungal species and native soil bacteria or other inoculants, such as the widely used mycorrhizal fungi. Studies under field conditions should be conducted to define dosages and improve the understanding of responses to inoculation under different climatic and soil conditions. Long-term demonstration plot experiments should be established to understand inoculant behavior and impacts on soil microbiological health, including rotation and/or interaction with other crops. Additional efforts should be made to develop better fungal inoculants to expand and consolidate the supply in the tomato production market. Commercial inoculums that allow adaptation to climate change increase tomato productivity, quality, and yield to safeguard the food security of producers and consumers.

Author contribution

AJRF: investigation, data curation, formal analysis, visualization, writing original draft; RMV: conceptualization, supervision, funding acquisition; YSPV: validation, writing-review, and editing; ADA: validation, visualization, writing-review, and editing.

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Data and materials availability

All data generated or analyzed during this study are included in this published article.

Consent for publication

All authors agreed and approved the manuscript for publication.

Conflict of interest

All the authors declare that they have no conflicts of interest.

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