Effects of Different Application Methods of Phosphate-Solubilizing Microbial Fertilizer on Root Growth and Phosphorus Nutrition in Masson Pine Families: Postprint

Authors: Pang Li, Li Jiaxin, Tian Yonglin, Qiao Zhiwei, Wang Yunpeng, Zhang Minghao

Date: 2022-12-01T00:00:00+00:00

Abstract

To investigate the effects of localized application of phosphorus-solubilizing bacteria (PSB) fertilizer on phosphorus nutrition of Masson pine (*Pinus massoniana*) under low phosphorus stress, a pot inoculation experiment with localized and uniform application of PSB fertilizer was conducted. Using WinRHIZO Pro STD1600+ root image analysis software, H_2SO_4-H_2O_2 digestion, and molybdenum-antimony colorimetric method, the responses of root morphological parameters and seedling phosphorus uptake of different Masson pine families to different PSB fertilizer application methods were studied. The results showed that: (1) Both localized and uniform application of PSB fertilizer significantly affected Masson pine growth, while localized application significantly increased main growth indicators including seedling height, ground diameter, root-to-shoot ratio, and dry mass of roots and whole plants compared with uniform application. (2) Localized application of PSB fertilizer significantly increased root length, root surface area, root volume, and root tip number of seedlings, whereas uniform application showed increases in root parameters but the differences were not significant; localized application increased fine root length with $0 < D \leq 0.5$ mm by nearly 2-fold compared with uniform application. The difference in root growth between the two treatments was related to the heterogeneous distribution of soil phosphorus caused by localized PSB fertilizer application. (3) Compared with uniform application of PSB fertilizer, localized application significantly increased phosphorus uptake in roots, stems, leaves, and whole seedlings. Correlation analysis indicated that seedling phosphorus uptake was significantly positively correlated with root morphological parameters and root length with $D \leq 1.0$ mm. This suggests that localized PSB fertilizer application promotes phosphorus uptake in seedlings by inducing root growth.

(4) Different Masson pine families showed varied responses to PSB fertilizer application. Family No. 22, derived from low-phosphorus-tolerant provenance, was more sensitive to localized PSB fertilizer application, with all growth indicators significantly higher than those of families No. 10 and No. 50. In summary, under low phosphorus conditions, localized application of PSB fertilizer had more significant effects on Masson pine seedling growth and phosphorus uptake than uniform application. These research results can provide reference and guidance for the management of Masson pine plantations on phosphorus-deficient sites.

Full Text

Effects of Different Application Modes of Phosphorus-Solubilizing Bacterial Fertilizer on Seedling Root Growth and Phosphorus Nutrition of *Pinus massoniana* Families

Pang Li[1], Li Jiaxin[1], Tian Yonglin[1], Qiao Zhiwei[2], Wang Yunpeng[3], Zhang Minghao[1]

[1]College of Agriculture, Anshun College, Anshun 561000, Guizhou, China
[2]College of Resources and Environmental Engineering, Anshun College, Anshun 561000, Guizhou, China
[3]Research Institute of Subtropical Forestry, Chinese Academy of Forestry, Zhejiang Provincial Key Laboratory of Tree Breeding, Masson Pine Engineering Technology Research Center of National Forestry and Grassland Administration, Hangzhou 311400, China

Abstract: To investigate the effects of zonal application of phosphorus-solubilizing bacterial (PSB) fertilizer on phosphorus nutrition of *Pinus massoniana* under low-phosphorus stress, we conducted a pot inoculation experiment with localized and uniform PSB fertilizer application. Using WinRHIZO Pro STD1600+ root image analysis software, H_2SO_4-H_2O_2 digestion, and molybdenum-antimony anti-colorimetric methods, we examined the responses of root morphological parameters and phosphorus uptake in different *P. massoniana* families to different PSB fertilizer application modes. The results showed: (1) Both localized and uniform PSB fertilizer application significantly affected *P. massoniana* growth, with localized application significantly increasing main growth indices including seedling height, basal diameter, root-to-shoot ratio, and dry mass of roots and whole plants compared to uniform application. (2) Localized PSB fertilizer application significantly increased root length, surface area, volume, and tip number, whereas uniform application produced non-significant increases in these parameters. Localized application increased fine root length ($0 < D \leq 0.5$ mm) by nearly twofold compared to uniform application. These differences in root growth between the two treatments were related to the heterogeneous phosphorus distribution created by localized PSB fertilizer application. (3) Compared with uniform application, localized application significantly increased phosphorus uptake in roots, stems, leaves, and whole plants. Correlation analysis indicated that seedling phosphorus uptake was significantly positively correlated with root morphological parameters and root length for D ≤ 1.0 mm roots, suggesting that localized PSB fertilizer application promotes phosphorus uptake by inducing root growth. (4) Different *P. massoniana* families showed varied responses to PSB fertilizer application. Family No. 22, derived from low-phosphorus-tolerant provenances, was most sensitive to localized PSB fertilizer application, with all growth indices significantly higher than those of families No. 10 and No. 50. In conclusion, under low-phosphorus conditions, localized PSB fertilizer application has more significant effects on *P. massoniana* seedling growth and phosphorus uptake than uniform application. These findings provide reference and guidance for managing *P. massoniana* plantations on phosphorus-deficient sites.

Keywords: PSB fertilizer; *Pinus massoniana* family; low-phosphorus environment; root growth; phosphorus absorption

Introduction

Pinus massoniana is one of the most important and widely distributed fast-growing timber species in subtropical China. According to the ninth national forest inventory, the planted area of *P. massoniana* forests in China has reached 8.04 million hectares, supporting numerous industries including papermaking, wood processing, and forest chemical engineering. However, southern China is dominated by acidic soils where over 90% of phosphorus is adsorbed and fixed, resulting in low available phosphorus content. Compared with other fast-growing timber species, *P. massoniana* is more sensitive to soil phosphorus deficiency, making phosphorus the primary factor limiting productivity in *P. massoniana* plantations.

Phosphorus-solubilizing bacterial (PSB) fertilizer is a microbial fertilizer whose phosphorus-solubilizing microorganisms can convert fixed soil phosphorus into available forms through acid dissolution and/or enzymatic hydrolysis for plant absorption and utilization. Studies have shown that phosphorus-solubilizing microorganisms isolated from rhizosphere soils can increase soil available phosphorus content by dissolving various phosphorus forms and accelerating phosphorus fraction transformation. PSB fertilizer application not only improves soil physicochemical properties and available phosphorus content but also promotes plant root growth and development, increases plant phosphorus absorption, and consequently enhances plant growth and phosphorus nutrition. For instance, inoculating *P. massoniana* seedlings with *Burkholderia sp.* WJ27 significantly increased primary root length, seedling height, and phosphorus content. Similarly, inoculation with two efficient phosphorus-solubilizing fungi, *Penicillium guanacastense* JP-NJ2 and *P. pinophilum* JPNJ4, demonstrated beneficial growth-promoting effects on *P. massoniana* seedling height and basal diameter.

Understanding the growth-promoting effects of phosphorus-solubilizing bacteria and their influencing factors is crucial for rational development and widespread application of PSB fertilizer. Numerous studies have shown that plant responses to uniform versus localized nutrient supply differ significantly. However, most pot and field experiments mix PSB fertilizer with substrate or soil uniformly or apply it directly to the sowing layer, leaving unclear how the heterogeneous phosphorus distribution created by zonal PSB fertilizer application affects plant growth, development, and phosphorus absorption. Given that bio-fertilizers have become an important component of China' s fertilizer industry, understanding plant responses to different application modes is essential for their widespread application. Therefore, this study used WinRHIZO Pro STD1600+ root image analysis software to investigate responses of root morphological parameters and phosphorus uptake in different *P. massoniana* families to uniform and localized PSB fertilizer application, aiming to provide guidance for using microbial PSB fertilizer to improve *P. massoniana* seedling growth and phosphorus nutrition and enhance plantation productivity.

Materials and Methods

1.1 Experimental Materials

We selected three superior full-sib families from the second-generation breeding population of *P. massoniana*: No. 10 [7750 (Hunan) × 1126 (Guangxi)], No. 22 [6627 (Jiangxi) × 5907 (Zhejiang)], and No. 50 [6610 (Jiangxi) × 3412 (Anhui)]. Plastic pots with upper inner diameter of 24 cm, lower inner diameter of 15 cm, and height of 16 cm were used as containers. The substrate consisted of infertile acidic yellow soil from central Guizhou Province, with organic matter content of 6.42 $g \cdot kg^{-1}$, total N and total P contents of (0.38 ± 0.10) $g \cdot kg^{-1}$ and (0.31 ± 0.06) $g \cdot kg^{-1}$ respectively, hydrolyzable N, available P, and available K contents of (25.2 ± 2.20) $mg \cdot kg^{-1}$, (0.81 ± 0.15) $mg \cdot kg^{-1}$, and (43.7 ± 5.50) $mg \cdot kg^{-1}$ respectively, and pH of (4.85 ± 0.12). The PSB fertilizer was prepared by mixing bacterial broth of *Pseudomonas fluorescens* and two *Pseudomonas* strains (high-density fermentation in a mixed culture) with organic nutrient soil at a 1:9 ratio in a blender, containing $\geq 0.5 \times 10^7$ $cfu \cdot g^{-1}$ viable bacteria and $\geq 50\%$ organic matter.

1.2 Experimental Design

Three treatments were established: localized PSB fertilizer application (localized), uniform PSB fertilizer application (uniform), and no PSB fertilizer (control). For the localized treatment, each pot was divided into A and B sides separated by a fixed PVC partition (12 cm height) to prevent nutrient exchange between sides [Figure 1: see original paper]. PSB fertilizer mixed with substrate (same amount as uniform treatment) was applied to side A, while side B received only an equal amount of substrate without fertilizer. The uniform treatment involved mixing PSB fertilizer with substrate at a 1:5 ratio before pot application. The control treatment used sterilized PSB fertilizer mixed with substrate. All pots were topped with a 3 cm layer of clean river sand as a sowing layer.

Pinus massoniana seeds were soaked in 0.4% potassium permanganate solution for 20 minutes, rinsed several times with distilled water, and placed in petri dishes with sterilized moist filter paper until germination at 25°C in an artificial climate chamber. Germinated seeds were sown in the center of the sowing layer (2–3 seeds per pot), and after emergence, one uniform seedling per pot was retained. The experiment used a completely randomized block design with single-plant plots and five blocks (to minimize environmental effects), yielding five replicates per treatment per family. Sowing occurred in early May 2020, with the vigorous growth period from June to August, and harvest completed in mid-November after one growth cycle. The experiment was conducted in a greenhouse at Anshun College, with soil moisture maintained at 50–80% throughout the trial to ensure normal water requirements.

1.3 Measurements

1.3.1 Seedling Growth Indices and Phosphorus Content Determination Seedling height and basal diameter were measured using a steel tape and vernier caliper, respectively. Harvested seedlings were separated into roots, stems, and leaves, killed at 105°C for 30 minutes, then oven-dried at 60°C to constant weight to obtain dry mass of each component. Appropriate amounts of dried samples were digested using H_2SO_4-H_2O_2 method, and phosphorus content in different organs was determined by molybdenum-antimony anti-colorimetric method (NY/T 2017-2011).

Root morphological parameters including root length, diameter, surface area, volume, and tip number were obtained by scanning root systems and analyzing images with WinRHIZO Pro STD1600+ (Regent Instruments Inc., Canada).

1.4 Statistical Analysis

Root-to-shoot ratio = underground dry weight / aboveground dry weight
Organ phosphorus uptake (mg) = organ phosphorus content ($mg \cdot g^{-1}$) × organ dry mass (g)
Whole-plant phosphorus content ($mg \cdot g^{-1}$) = (root P content × root dry mass + stem P content × stem dry mass + leaf P content × leaf dry mass) / (root dry mass + stem dry mass + leaf dry mass)
Whole-plant phosphorus uptake ($mg \cdot plant^{-1}$) = whole-plant phosphorus content ($mg \cdot g^{-1}$) × whole-plant dry mass ($g \cdot plant^{-1}$)

Data processing and chart preparation were performed using Microsoft Office Excel 2003. Multi-factor ANOVA and correlation analysis were conducted using IBM SPSS Statistics 19.0, with Duncan' s multiple range test ($\alpha = 0.05$) for mean comparisons.

Results

2.1 Effects of Different PSB Fertilizer Treatments on *P. massoniana* Seedling Growth

As shown in , PSB fertilizer application significantly affected *P. massoniana* seedling growth ($P < 0.001$). Compared with the control, localized application significantly increased seedling height, basal diameter, root dry mass, root-to-shoot ratio, and whole-plant dry mass by 19.5%, 38.5%, 76.9%, 20.5%, and 54.4%, respectively. Uniform application increased seedling height, root dry mass, and whole-plant dry mass by 11.4%, 38.5%, and 34.9%, respectively. Compared with uniform application, localized application significantly increased seedling height, basal diameter, root dry mass, root-to-shoot ratio, and whole-plant dry mass by 7.3%, 29.9%, 27.8%, 16.4%, and 14.4%, respectively, indicating that localized PSB fertilizer application significantly enhanced basal diameter and root-to-shoot ratio.

Different *P. massoniana* families exhibited varied responses to PSB fertilizer application [Figure 2: see original paper]. Under localized application, all growth indices of the three families increased significantly compared with the control, with family No. 22 showing the greatest increases: seedling height (30.1%), basal diameter (50.0%), root dry mass (142.8%), root-to-shoot ratio (30.3%), and whole-plant dry mass (100%). Under uniform application, family No. 22 also showed the greatest increases in seedling height (19.1%), basal diameter (16.7%), root dry mass (85.7%), and whole-plant dry mass (72.4%). Families No. 10 and No. 50 showed significant increases in seedling height and whole-plant dry mass, while root-to-shoot ratios increased but not significantly compared with the control. These results indicate that family No. 22 was most sensitive to PSB fertilizer application.

2.2 Root Morphological Characteristics and Root Length Responses to PSB Fertilizer

As shown in , PSB fertilizer application significantly increased root length, surface area, volume, and tip number. Compared with the control, localized application increased these parameters by 21.4%, 19.7%, 20.0%, and 37.9%, respectively, while uniform application increased them by 10.6%, 9.8%, 4.3%, and 14.2%, respectively.

The PSB fertilizer × family interaction significantly affected root length, surface area, and tip number [Figure 3: see original paper]. Compared with the control, family No. 22 under localized and uniform applications showed increases of 42.3% and 30.6% in root length, 30.2% and 23.7% in surface area, 34.7% and 20.0% in volume, and 47.4% and 19.8% in tip number, respectively. Family No. 10 under localized treatment showed clear increases of 18.3%, 16.9%, 15.4%, and 24.0% in these respective traits. Family No. 50 under localized treatment showed increases of 13.2%, 11.3%, and 23.6% in surface area, volume, and tip number, respectively. These results demonstrate that family No. 22 was sensitive to PSB fertilizer application, with both localized and uniform treatments significantly inducing root growth.

PSB fertilizer application enhanced the development of roots with diameters of $0 < D \leq 0.5$ mm and $0.5 \text{ mm} < D \leq 1.0$ mm [Figure 4: see original paper]. Compared with the control, root length in the $0 < D \leq 0.5$ mm diameter class increased by 61.5% and 22.9% under localized and uniform treatments, respectively, while root length in the $0.5 \text{ mm} < D \leq 1.0$ mm class increased by 17.7% and 10.4%, respectively. Root length increases were not significant for diameter classes of $1.0 \text{ mm} < D \leq 2.0$ mm and $D > 2.0$ mm. Notably, localized application significantly promoted the development of $0 < D \leq 0.5$ mm roots compared with uniform application.

2.3 Effects of Different PSB Fertilizer Treatments on Phosphorus Uptake

As shown in , PSB fertilizer application significantly affected phosphorus uptake in all organs and whole plants. Localized and uniform applications increased root phosphorus uptake by 109.9% and 46.1%, stem phosphorus uptake by 51.7% and 36.2%, leaf phosphorus uptake by 68.8% and 49.6%, and whole-plant phosphorus uptake by 71.5% and 45.2%, respectively, compared with the control. Under localized application, the magnitude of increase in phosphorus uptake followed the order: root > leaf > stem, whereas under uniform application, the order was: leaf > root > stem.

PSB fertilizer application significantly increased phosphorus uptake in different organs and whole plants across all three families [Figure 5: see original paper]. Under localized and uniform applications, family No. 22 showed the greatest increases in root and whole-plant phosphorus uptake (163.4% and 83.6% for roots; 114.2% and 76.1% for whole plants). Family No. 10 showed the second-greatest increases in root and whole-plant phosphorus uptake. Under localized application, families No. 22 and No. 10 showed substantial increases in leaf phosphorus uptake (120.5% and 74.9%, respectively), while families No. 50 and No. 22 showed large increases in stem phosphorus uptake (81.2% and 80.3%, respectively).

2.4 Correlations Between Main Growth Indices and Phosphorus Uptake

As shown in , root morphological parameters including root length, surface area, and volume were significantly positively correlated with seedling phosphorus uptake under PSB fertilizer treatments. Root length for diameter classes of $0 < D \leq 0.5$ mm and $0.5 \text{ mm} < D \leq 1.0$ mm showed extremely significant positive correlations with phosphorus uptake. Root phosphorus uptake was significantly positively correlated with seedling height, basal diameter, root-to-shoot ratio, whole-plant dry mass, and whole-plant phosphorus uptake.

Discussion

Microbial fertilizers improve soil conditions and increase nutrient supply through microbial life activities, thereby enhancing plant nutrition and growth. Phosphorus-solubilizing bacterial fertilizer is a type of microbial fertilizer that can degrade insoluble soil phosphorus into plant-available forms, increasing plant phosphorus nutrition. Previous research demonstrated that inoculating eucalyptus seedlings with phosphorus-solubilizing bacteria promoted growth. Our results similarly show that different PSB fertilizer application modes significantly affected *P. massoniana* seedling growth and phosphorus uptake. Localized application significantly increased main growth indices including seedling height, basal diameter, root-to-shoot ratio, and dry mass of roots and whole plants compared with uniform application. Localized application also promoted phosphorus uptake in roots, stems, leaves, and whole plants, with the greatest increase observed in root phosphorus uptake.

Root-to-shoot ratio reflects plant response strategies to environmental conditions and represents the allocation of photosynthetic products between aboveground and belowground parts. Our finding of increased root-to-shoot ratio indicates that localized PSB fertilizer application significantly induced root development in *P. massoniana* seedlings under low-phosphorus conditions. This aligns with research showing that inoculation with phosphorus-solubilizing *Pseudomonas sp.* significantly increased root dry weight in white clover.

Plant roots exhibit strong plasticity, with morphology and function significantly influenced by soil nutrient levels and distribution. Studies have shown that phosphorus-solubilizing bacteria inoculation increases soil phosphorus availability, thereby improving root morphology. Our research on *P. massoniana* demonstrates that PSB fertilizer application significantly increased root length, surface area, volume, and tip number, with localized application showing more pronounced promotion of root growth than uniform application. These results likely relate to the heterogeneous nutrient distribution created by localized PSB fertilizer application. Research indicates that under heterogeneous nutrient conditions, plants increase root proliferation to acquire nutrients from rich patches and promote aboveground growth. Adequate nutrient supply in rich patches can accelerate root elongation.

Furthermore, phosphorus-solubilizing bacteria inoculation significantly affects root development across different diameter classes. Studies have shown that phosphorus-solubilizing bacterial agents significantly increased the proportion of watermelon root length in the 0–0.5 mm diameter range, and bio-fertilizer application significantly improved fine root ($D \leq 2$ mm) surface area, volume, and biomass in *Cyclocarya paliurus*. Our results demonstrate that both uniform and localized PSB fertilizer applications promoted growth of *P. massoniana* fine roots ($D \leq 1.0$ mm), with localized application increasing $0 < D \leq 0.5$ mm fine root length by nearly twofold compared with uniform application. Fine roots are the primary sites for soil nutrient absorption and exhibit strong physiological plasticity under different soil nutrient conditions, directly affecting nutrient acquisition and utilization. Research suggests that fine root proliferation (D $\leq$ 1.5 mm) and improved nitrogen-phosphorus absorption efficiency may be important mechanisms for phosphorus-efficient *P. massoniana* to cope with low-phosphorus environments. Our findings show significant positive correlations between root morphological parameters, D $\leq$ 1.0 mm root length, and seedling phosphorus uptake, representing an important reason for the significantly greater phosphorus uptake under localized versus uniform PSB fertilizer application.

Significant genetic variation exists among tree families in foraging behavior and nutrient acquisition under heterogeneous nutrient distribution. Our study revealed significant differences among three *P. massoniana* families in growth and phosphorus uptake responses to PSB fertilizer application. Family No. 22, with low-phosphorus-tolerant provenances (female parent 6627 from Jiangxi and male parent 5907 from Zhejiang), showed significantly higher growth indices under localized application than families No. 10 and No. 50, likely due to significant induction of root proliferation by localized PSB fertilizer application.

In conclusion, *P. massoniana* seedlings show significantly different responses to PSB fertilizer application modes under low-phosphorus conditions, with localized application demonstrating more pronounced growth promotion than uniform application. Localized application significantly increased root-to-shoot ratio, promoted root growth, and induced proliferation of fine roots (D $\leq$ 1.0 mm). Differences in root growth represent an important reason for the higher phosphorus uptake and main growth indices under localized versus uniform PSB fertilizer application. Additionally, due to different genetic backgrounds, *P. massoniana* families exhibited varied performance, with family No. 22 (low-phosphorus-tolerant background) being most sensitive to PSB fertilizer application and showing significantly higher growth indices under localized treatment. These results may also relate to interactions between phosphorus-solubilizing bacteria and roots in the rhizosphere, warranting further research on effects of PSB fertilizer application on organic acid exudation and soil microbial communities in different *P. massoniana* families.

References

ADNANE B, WISSAL E, SAID K, et al., 2021. Benefits of phosphate solubilizing bacteria on belowground crop performance for improved crop acquisition of phosphorus[J]. *Microbiol Res*, 252: 126842.

BERGKEMPER F, SCHLER A, ENGEL M, et al., 2016. Phosphorus depletion in forest soils shapes bacterial communities towards phosphorus recycling systems[J]. *Environ Microbiol*, 18(6): 1988-2000.

FAN YM, LI W, WEN ZM, et al., 2021. Responses of grassland community biomass and root-shoot ratio to nitrogen addition in different restoration years on the Loess Plateau[J]. *Acta Ecol Sin*, 41(24): 9824-9835.

FRANSEN B, KROON HD, 2001. Long-term disadvantages of selective root placement: Root proliferation and shoot biomass of two perennial grass species in a 2-year experiment[J]. *J Eco*, 89: 711-722.

GAO CH, WANG G, DONG YZ, et al., 2003. Effect of phosphorus bacteria in the pot and the field[J]. *J Shanxi Agric Sci*, (3): 40-43.

HAYAT R, ALI S, AMARA U, et al., 2010. Soil beneficial bacteria and their role in plant growth promotion: a review[J]. *Ann Microbiol*, 60(4): 579-598.

HE D, WAN W, 2022. Distribution of culturable phosphate-solubilizing bacteria in soil aggregates and their potential for phosphorus acquisition[J]. *Microbiol Spec*: e00290-22.

HE Y, LIAO H, YAN XL, 2003. Localized supply of phosphorus induces root morphological and architectural changes of rice in split and stratified soil cultures[J]. *Plant and Soil*, 248: 247-256.

HUANG PF, LIU JA, JIN AX, et al., 2012. Isolation and screening, identification of phosphorus-solubilizing bacteria in rhizosphere soil of *Pinus massoniana* and its phosphate-degradation capacity[J]. *Chin Agric Sci Bull*, 28(19): 12-16.

KUMAR R, SHASTRI B, 2017. Role of phosphate-solubilizing microorganisms in sustainable agricultural development[J]. *Agron Environ Sust*, 2(13): 271-303.

LI CH, ZHANG YM, FENG LQ, et al., 2016. Research summary of local root fertilization and water-fertilizer coupling technology[J]. *Gansu Agric Sci Technol*, (7): 61-66.

LI HB, MA QH, LI HG, et al., 2014. Root morphological responses to localized nutrient supply differ among crop species with contrasting root traits[J]. *Plant Soil*, 376: 151-163.

LI HP, GAN YN, HAN QQ, et al., 2022. Isolation of phosphate solubilizing bacteria from soil of spruce forest in the Qilian Mountains and their growth promotion effects in white clover[J]. *Acta Agr Sin*, 30(4): 879-888.

LI QL, LI AB, HUANG ZY, et al., 2022. Application of phosphorus solubilizing microorganisms in forest soil ecological restoration[J]. *World For Res*, 35(1): 15-20.

LIU HK, CHEN X, ZHANG MZ, et al., 2020. Anatomical characteristics of fine roots of 11 tree species in the hilly foothills areas in central Shandong Province and their drought resistance strategies[J]. *Sci Silv Sin*, 56(7): 185-193.

LIU YH, LI XH, SHENG KY, et al., 2022. Effects of phosphate-solubilizing bacteria *Burkholderia* ZP-4 and *Klebsiella* ZP-2 on soil phosphorus fraction and bacterial diversity[J]. *Chin J Soil Sci*, 53(2): 472-481.

LÜ J, PAN HX, YU C, 2020. Screening, identification and phosphate-solubilizing characteristics of phosphate-solubilizing *Paraburkholderia sp.* from *Pinus massoniana* rhizosphere soil[J]. *Biotechnol Bull*, 36(9): 147-156.

LÜ J, YU C, 2020. Screening and identification of an effect phosphate-soluble *Burkholderia sp.* and its growth-promoting effect on *Pinus massoniana* seedlings[J]. *J Appl Ecol*, 31(9): 2923-2934.

MOMMER L, VAN RUIJVEN J, JANSEN C, et al., 2012. Interactive effects of nutrient heterogeneity and competition: Implications for root foraging theory[J]. *Funct Ecol*, 26: 66-73.

PURWANINGSIH S, SUTISNA E, NUGROHO AA, 2022. Characterization, diversity, and effectiveness phosphate solubilizing bacteria from the soil and rhizosphere on the growth of *Glycine max* L. in greenhouse[J]. *Earth Environ Sci*, 976(1).

QIAO H, WU XQ, WEI W, 2016. Effects of two phosphate-solubilizing *Penicillium* strains on microbial community structure and their growth-promoting in masson pine rhizosphere[J]. *J Nanjing For Univ(Nat Sci Ed)*, 40(6): 109-116.

SONG P, ZHANG R, ZHOU ZC, et al., 2017. Effects of localized nitrogen supply treatments on growth and root parameters in *Pinus massoniana* families under phosphorus deficiency[J]. *Chin J Plant Ecol*, 41(6): 622-631.

SONG P, ZHANG R, ZHANG Y, et al., 2016. Effects of simulated nitrogen deposition on fine root morphology, nitrogen and phosphorus efficiency of *Pinus massoniana* clones under phosphorus deficiency[J]. *Chin J Plant Ecol*, 40(11): 1136-1144.

WANG ZG, HU YL, XU WH, et al., 2015. Separation and identification of a phosphorus solubilizing bacteria and its promoting effect on watermelon root[J]. *Acta Agric Zhejiang*, 27(5): 798-803.

WU WL, HONG JP, MENG HS, et al., 2016. Effects of continuous application of phosphorus bacterial fertilizer on soil alkaline phosphatase activity and Hedley phosphorus forms in the reclaimed soil[J]. *Soil Fert Chin*, (4): 59-64.

XU ZH, WANG ZK, CHEN ZY, et al., 2021. Biofertilizer applications affected root architecture and root morphology of *Cyclocarya paliurus*[J]. *Soil Fert Chin*, (4): 258-266.

YAN XL, HU WJ, MA YH, et al., 2020. Nitrogen uptake preference of *Cunninghamia lanceolata*, *Pinus massoniana*, and *Schima superba* under heterogeneous nitrogen supply environment and their root foraging strategies[J]. *Sci Silv Sin*, 56(2): 1-11.

YU XL, 2011. Screening of high-effect phosphate-soluble microorganisms in eucalyptus soil and that effect on the growth of eucalyptus[D]. Fuzhou: Fujian Agriculture and Forestry University.

ZHANG DB, WANG XH, ZHOU SC, et al., 2019. Response of masson pine container seedlings from different families to substrate proportion and control released fertilizer[J]. *J Zhejiang For Univ*, 36(5): 1044-1050.

ZHANG FS, CUI ZL, WANG JQ, et al., 2007. Current status of soil and plant nutrient management in China and improvement strategies[J]. *Chin Bull Bot*, 24(6): 687-694.

ZHANG H, FORDER BG, 2000. Regulation of Arabidopsis root development by nitrate availability[J]. *J Exp Bot*, 51: 51-59.

ZHANG Y, ZHOU ZC, JIN GQ, et al., 2010. Genetic distances of parents of *Pinus massoniana* and relationship between growth traits and heterosis of progeny[J]. *J Nanjing For Univ*, 34(1): 9-14.

ZHANG Y, ZHOU ZC, YANG Q, 2013. Genetic variations in root morphology and phosphorus efficiency of *Pinus massoniana* under heterogeneous and homogeneous low phosphorus conditions[J]. *Plant Soil*, 364: 93-104.

ZHENG QY, XIE YT, BIAN HY, et al., 2022. Effects of phosphate solubilizing bio-fertilizer on phosphorus fractions and fertility of red soil[J]. *J Jiangxi Agric Univ*, 44(1): 233-244.

ZHANG YC, LIU FZ, WANG HB, 2020. Research progress on plant-growth-promoting mechanisms of phosphate-solubilizing rhizosphere microbes[J]. *Soil Fert Chin*, (2): 1-9.

ZHOU ZC, XIE YR, JIN GQ, et al., 2005. Study on phosphorus efficiency of different provenances of *Pinus massoniana*[J]. *Sci Silv Sin*, 41(4): 25-30.

Note: Figure translations are in progress. See original paper for figures.