

ORIGINAL RESEARCH

Open Access



Synergistic biochar-*Bacillus* consortium enhances phosphorus availability, root architecture, and inflorescence development in greenhouse cherry tomato

Sainan Liu^{1,2}, Yongjia Shi^{1,2}, Aijia Zhang^{1,2}, Yuwei Huang^{1,2}, Dianyun Cao^{1,2*} and Yu Lan^{1,2*}

Abstract

Mobilizing legacy phosphorus (P) in greenhouse soils offers a strategy to alleviate P limitation and enhance crop productivity. This study applied biochar-*Bacillus* consortium as a bio-organic soil amendment. By altering the soil bacterial community, it improved P availability and plant P uptake, promoted root and inflorescence development, and ultimately increased cherry tomato yield. Specifically, soil application of biochar-*Bacillus* consortium (BM) significantly enhanced soil available phosphorus by 10.16%, microbial biomass phosphorus by 174.76%, and alkaline phosphatase activity by 68.52% in the rhizosphere relative to the control (CK). This enhancement in P bioavailability was significantly correlated with shifts in the soil bacterial community. Compared to treatments with biochar alone (B) or *Bacillus* liquid culture (M) alone, the enhanced P availability promoted plant P uptake and improved root architecture, as reflected by significant increases in root length, surface area, volume, and tip number. In addition, the improvement of inflorescence development was reflected in a substantial increase in the proportion of effective fruit branches, thereby contributing to a significant yield enhancement of 23.53%. Collectively, this work demonstrates that amending soils with a biochar-*Bacillus* consortium effectively enhances P bioavailability and cherry tomato productivity, thus emphasizing its potential for sustainable intensification in controlled agricultural systems.

Highlights

- A biochar-*Bacillus* consortium (BM) enhanced soil phosphorus (P) bioavailability.
- The BM treatment reduced the rhizosphere MBC:MBP ratio and restructured the soil bacterial community.
- The BM treatment enhanced root architecture and improved P acquisition in cherry tomato.
- The BM treatment improved cherry tomato yield by optimizing inflorescence architecture.

Keywords Microbial phosphorus mobilization, Biochar-microbe interaction, Inflorescence development, Root morphology, Protected cultivation

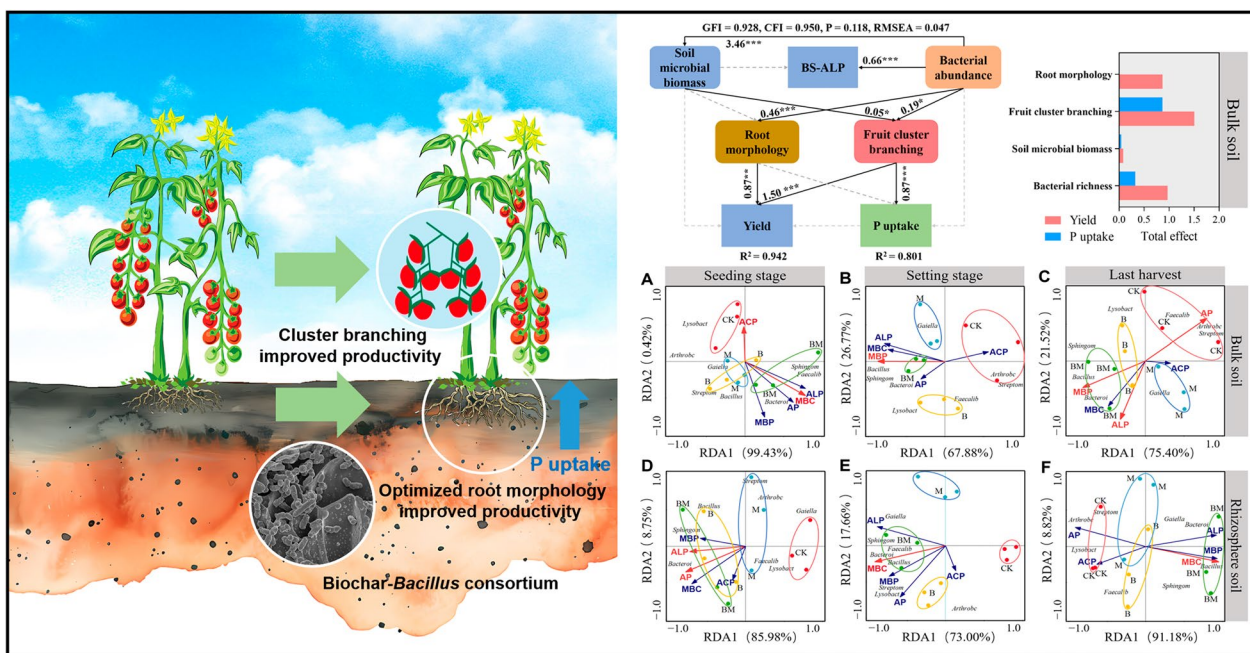
*Correspondence:

Dianyun Cao
dianyuncao@syau.edu.cn
Yu Lan
lanyu312228@syau.edu.cn

Full list of author information is available at the end of the article

© The Author(s) 2026. **Open Access** This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if changes were made. The images or other third party material in this article are included in the article's Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit <http://creativecommons.org/licenses/by/4.0/>.

Graphical Abstract



1 Introduction

Cherry tomato cultivation is a high-value agriculture enterprise under greenhouse conditions, owing to its substantial economic value and nutritional benefits (Silva et al. 2022; Li et al. 2019). Inflorescence architecture is the primary determinant of cherry tomato yield, motivating targeted selection of valid-branching varieties to maximize reproductive output (Sun et al. 2024). Current strategies for enhancing this trait, including conventional breeding and gene-editing approaches, however, face practical challenges to widespread adoption due to prolonged breeding cycles, regulatory uncertainties, and unresolved environmental concerns. Hence, bio-organic strategies that can directly optimize inflorescence development and enhance yield are urgently needed for sustainable protected cultivation of cherry tomato.

Phosphorus (P) is an essential macronutrient that coordinately regulates plant inflorescence development and root architecture (Harish et al. 2025; Cho et al. 2025). As a structural component of nucleic acids, phospholipids, and nucleoproteins, P deficiency critically impairs root development and flower bud differentiation in cherry tomatoes (Beltran-Medina et al. 2023). Optimized phosphate fertilization improves root architecture and system productivity in cereal

rotations (Harish et al. 2025), while molecular studies show that P availability controls flowering time through subcellular reprogramming (Cho et al. 2025). However, under greenhouse cultivation conditions, the majority of phosphorus undergoes complex soil biogeochemical processes including microbial immobilization, mineral precipitation, and surface adsorption reactions. These processes collectively reduce phosphorus bioavailability and promote its accumulation in agricultural soils (Dixon et al. 2024). Given the low utilization ratio of P fertilizers in soil, global P resource limitations, and the continued high input of phosphate fertilizers, it is necessary to explore methods to improve P acquisition from legacy P and to investigate the correlation between the tomato P uptake and inflorescence branching (Gao et al. 2019; Hui et al. 2014).

Biochar serves as a multifunctional soil amendment that improves soil properties, regulates nutrient cycling, and shapes beneficial microbial communities (Bolan et al. 2023). Its porous structure and surface functional groups make it an effective microbial carrier, protecting inoculated bacteria and enhancing their survival and activity (Batista et al. 2018; Tu et al. 2020; Azeem et al. 2021). These properties support bacterial colonization and immobilization on biochar surfaces, thereby establishing a synergistic biochar–microbe interaction that has been

shown to alter soil nutrient cycling (Parasar and Agarwala 2025). Beneficial microorganisms such as the phosphate-solubilizing bacteria (PSB) *Bacillus megaterium* and *Bacillus mucilaginosus* are known to enhance soil phosphorus bioavailability and plant phosphorus uptake (Leite et al. 2024). However, microbial inoculants like PSB often fail under field conditions due to environmental stresses, pathogen pressure, and competition with native soil microbes, especially in the absence of protective carriers (Ajeng et al. 2023). Consequently, a biochar-*Bacillus* consortium is expected to improve phosphorus uptake in cherry tomato. Yet, despite the acknowledged role of soil microbiomes in plant nutrition, how such a consortium specifically optimizes root morphology, phosphorus acquisition, and inflorescence branching to increase yield in cherry tomato remains poorly understood.

Building upon this background, the present study aimed to: (i) evaluate the efficacy of a biochar-*Bacillus* consortium in enhancing the root morphology, fruit-cluster branching, dry material accumulation, and yield of cherry tomato; (ii) assess the synergistic effects of the consortium on key soil parameters, including phosphorus bioavailability, microbial biomass, and phosphatase activity; and (iii) investigate associated shifts in soil microbial community structure in response to fertilization with pristine biochar, *Bacillus* suspension alone, or biochar inoculated with *Bacillus* (Hou et al. 2020). We hypothesized that biochar-*Bacillus* consortium would promote the solubilization of legacy soil phosphorus by modifying the microbial community structure, thereby enhancing phosphorus uptake and plant growth, with particular benefits for root architecture and inflorescence development in cherry tomato.

2 Materials and methods

2.1 Experiment materials

Cherry tomato (*Lycopersicon esculentum* var. *cerasiforme*) seedlings were purchased from Shenyang Qiushi Agricultural Technology Development Co., Ltd. Biochar was prepared from rice husks by pyrolysis at 600°C for 1 h. Its key properties are summarized in Table 1. Three phosphate-solubilizing *Bacillus* strains (*B. mucilaginosus* 19749, *B. subtilis* 19,743, and *B. megaterium* 1.0234) were obtained from China General Microbiological Culture Collection Center (CGMCC) for bacterial inoculation. Individual bacterial suspensions of each strain were prepared through liquid culture, followed by centrifugation and resuspension in sterile deionized water. The final suspensions were adjusted to a viable cell density of approximately 5×10^8 CFU mL⁻¹, with a spore yield of 60%. To prepare the biochar-*Bacillus* consortium (BM), the three bacterial suspensions were combined with biochar under sterile conditions at a volumetric-to-mass

Table 1 Chemical properties of soil and biochar

Chemical property	Soil	Biochar
Total C (%)	1.30	40.21
Total N (%)	0.16	0.49
Total P (g kg ⁻¹)	0.45	12.50
Available N (mg kg ⁻¹)	78.26	238.55
Available P (mg kg ⁻¹)	21.68	289.62
Available K (mg kg ⁻¹)	20.50	345.30
Organic carbon (%)	1.95	37.55
pH	7.96	8.85

ratio of 1:1:1:15 (suspension: biochar). The mixture was incubated with shaking at 28 °C for 4 h and subsequently vacuum-dried for 12 h. A *Bacillus* liquid inoculant (M), consisting of the three bacterial suspensions mixed at a 1:1:1 volumetric ratio, served as the *Bacillus*-only treatment; its total bacterial concentration was matched to that of the BM consortium.

2.2 Experiment design

A protected cultivation experiment was conducted at the Kalima Research Center of Shenyang Agricultural University, Shenyang, China (41°11'N and 122°23'E). The soil is classified as meadow soil, with its physical and chemical properties detailed in Table 1. The experiment included four treatments, each replicated three times in a randomized complete block design. Each experimental plot consisted of three rows (each 8.1 m long) with 0.6 m row spacing, containing 50 plants and covering an area of 17 m². The total experimental area within the greenhouse was 408 m². The treatments were designated as follows: (1) CK: a control with no amendment; (2) B: biochar applied at 12 t hm⁻¹; (3) BM: biochar-*Bacillus* consortium, with biochar applied at 12 t hm⁻² and *Bacillus* liquid culture at 4.2 L per plot; and (4) M: *Bacillus* liquid culture alone at the same dosage (4.2 L) as in the BM treatment. Cherry tomato seedlings were transplanted in mid-to-late March, and harvested in early July. Plants were managed using a single-stem training system, with five fruit clusters retained on the main stem.

2.3 Application of biochar-*Bacillus* consortium and liquid *Bacillus* culture

Based on the experimental design, biochar (B treatment) or biochar-*Bacillus* consortium (BM treatment) was evenly broadcast onto the plot surface and subsequently incorporated into the 0–20 cm soil layer using a rotavator. For the M treatment (*Bacillus* liquid culture only), 84 mL of the microbial suspension was applied per planting hole prior to transplanting. Each cherry tomato

seedling was then positioned in the hole to ensure full contact between the root system and the bacterial inoculant.

2.4 Cherry tomato plant sampling and measurements

At harvest, all cherry tomato plants within a randomly selected 2 m × 2 m (4 m²) area per plot were sampled. Fruit number and fresh weight were recorded to calculate the tomato yield per treatment (Wu et al. 2021). Above- and below-ground tissues (fruits, leaves, stems, and roots) were carefully separated, washed, and their fresh biomass determined. Root systems were scanned using an Epson 1680 scanner (Epson, Japan), and morphological parameters, including total length, volume, surface area, and tip numbers, were quantified with the WinRhizo image analysis system. All plant tissues were then oven-dried at 80 °C for 48 h to constant weight for dry-biomass determination. To assess reproductive architecture, sixteen plants per plot were systematically sampled along an “S” -shaped transect. The number of fruit-bearing lateral branches (branch fruit) was counted throughout the harvest period until five designated fruit clusters on the main stem had been collected. The proportion of branch fruit per plant was calculated using Eq. (1).

$$\text{Proportion of branch fruit (\%)} = \text{Number of branch fruit per cherry tomato plant} / 5 \times 100 \quad (1)$$

Total phosphorus concentration in shoot (fruits, stems, leaves) and root tissues were determined by molybdenum-blue colorimetry after sulfuric acid-hydrogen peroxide digestion of dried plant material (Wang et al. 2022).

Phosphorus uptake efficiency was subsequently calculated using Eqs. (2) and (3).

$$P \text{ uptake (Kg ha}^{-1}\text{)} = P \text{ content} \times \text{Biomass yield (kg ha}^{-1}\text{)} \times 1000 \quad (2)$$

$$P \text{ uptake efficiency (\%)} = P \text{ uptake (kg ha}^{-1}\text{)} / P \text{ fertilizer application rate (kg ha}^{-1}\text{)} \times 100 \quad (3)$$

2.5 Soil chemical and enzymatic analysis

Rhizosphere soil was sampled by taking loosely root-attached soil after gently shaking the roots. Soil samples from each plot were collected using a five-point sampling approach. Samples were air-dried and sieved (2 mm) for subsequent physicochemical analysis. Fresh soil samples were preserved at 4 °C for enzymatic assays, or at −80 °C for molecular analysis. Soil available phosphorus was analyzed following established protocols (Bao 2000). Microbial biomass carbon (MBC) and phosphorus (MBP) were quantified using chloroform-fumigation extraction

(Quadros et al. 2016). Phosphatase activities (alkaline and acid) were determined spectrophotometrically by quantifying *p*-nitrophenol release following enzymatic hydrolysis of *p*-nitrophenyl phosphate (PNPP) substrate in fresh soil incubations (Tumbure and Schmalenberger 2024).

2.6 Molecular microbiological analysis

The samples from rhizosphere soil and bulk soil were analyzed by 16S rDNA amplicon analysis. The total DNA was extracted from three duplicate subsamples using a OMEGA Soil DNA Kit. Based on previous comparisons, 16S rDNA amplicons targeting the V3-V4 hypervariable regions (515F/806R primers) were PCR-amplified and sequenced on the Illumina NovaSeq PE250 platform. Quality-filtered sequences were processed using USEARCH for chimera removal, followed by UPARSE clustering into OTUs at 97% similarity threshold (Edgar et al. 2011).

2.7 Statistical analyses

Treatment differences in soil physicochemical properties were analyzed by Duncan's test ($p < 0.05$). All statistical analyses of the physicochemical properties were performed using IBM SPSS Statistics 21. The GraphPad Prism 9.5 statistical program was used to graph the art-

work. Redundancy analysis (RDA) was conducted in Canoco 5.0 to assess associations between soil environmental properties and bacterial species characteristics. The latent variable path analyses of structural equation modeling (SEM) were performed using IBM Amos 23.

3 Results and discussions

3.1 Biochar-*Bacillus* consortium enhances root morphology

Root morphological parameters (total length, surface area, volume, and tip number) were quantified to assess the response to biochar-supported *Bacillus* inoculation. The biochar-*Bacillus* consortium (BM) elicited the most pronounced improvement in all measured root traits compared to the control (CK) (Fig. 1). While biochar alone (B) increased root length, surface area, and volume relative to CK, it did not significantly affect tip number.

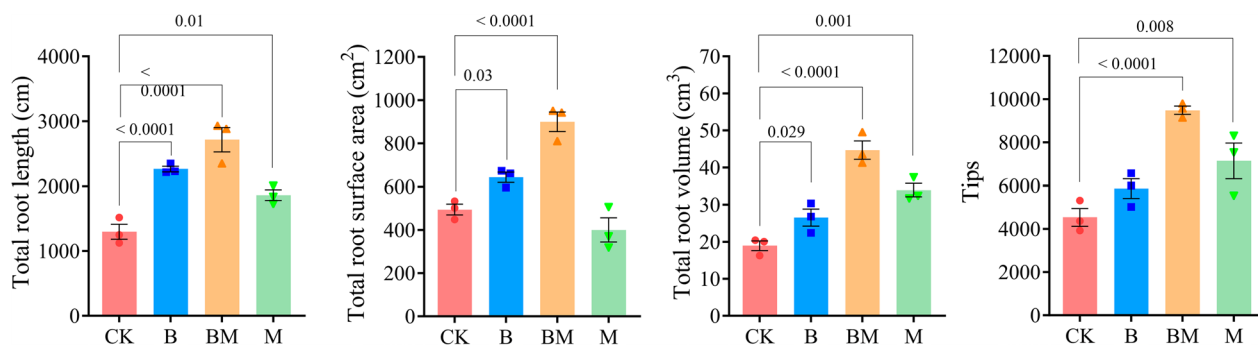


Fig. 1 Root morphological responses of cherry tomato to biochar-*Bacillus* consortium application. CK, conventional fertilization control; B, conventional fertilization with biochar; BM, conventional fertilization with biochar-*Bacillus* consortium; M, conventional fertilization with *Bacillus* liquid inoculant. Values marked with different numbers above bars indicate statistically significant differences ($p < 0.05$)

Inoculation with *Bacillus* alone (M) also enhanced root length, volume, and tip number relative to CK. The P values are marked on the bar chart (Fig. 1).

Crop nutrient acquisition and yield are closely linked to root morphological and architectural traits (Dziewit et al. 2024). Consistent with previous studies, the co-application of biochar-*Bacillus* (BM) significantly improved root morphological parameters compared to conventional fertilization (Liu et al. 2022; Jin et al. 2023; Canal et al. 2024). This enhancement can be explained by several interconnected mechanisms. First, inoculated *Bacillus* strains promote plant growth through multiple pathways, including phosphate solubilization, indole-3-acetic acid (IAA) synthesis, and siderophore production (Canal et al. 2024). Second, biochar amendment improves soil physical conditions by reducing bulk density and increasing water-holding capacity, thereby creating a more porous matrix for root proliferation (Wang et al. 2024). Third, biochar modulates rhizosphere nutrient availability—particularly phosphorus—by stimulating organic matter turnover and enriching phosphorus-cycling microbial taxa (Chang et al. 2025). Elevated phosphorus levels are known to support root system expansion. Moreover, biochar can upregulate plant genes involved in lignin biosynthesis, nutrient transport, and energy metabolism, which collectively enhance stress tolerance and preserve root architecture under suboptimal conditions (Yang et al. 2024). Together, these effects position biochar as a multifunctional carrier that sustains microbial activity and synergistically enhances root development in cherry tomato.

3.2 Enhancement of soil phosphorus availability and plant phosphorus uptake by the biochar-*Bacillus* consortium

Available phosphorus (AP) was measured in bulk and rhizosphere soils at the seedling, fruit-setting, and final-harvest stages to track dynamics across the growing

season. AP levels declined over time in both soil compartments under all treatments (Fig. 2A). Compared to CK, the BM treatment most strongly influenced AP: at the seedling stage, it increased AP by 15.18% in bulk soil and 10.16% in rhizosphere soil, whereas by the final harvest, AP was reduced by 10.65% (bulk) and 13.50% (rhizosphere). At fruit-setting, BM did not significantly alter bulk-soil AP but raised rhizosphere AP by 4.67%. In general, the available P level in the bulk soil decreased faster than that in the rhizosphere soil. In the B treatment, available P level showed a similar trend as that in BM. Overall, AP declined more rapidly in bulk than in rhizosphere soil.

Dry matter accumulation and phosphorus concentration in roots, stems, leaves, and fruits were determined, along with whole-plant phosphorus uptake efficiency. BM and B treatments significantly increased dry matter mass in stems, leaves, and roots relative to CK, whereas M did not differ significantly from CK (Fig. 2B). Whole plant dry weight under BM rose by 38.11%. Phosphorus content was significantly elevated by BM in all plant tissues, with the greatest accumulation occurring in stems and leaves (Fig. 2C). B and M treatments raised P content only in stems, leaves, and roots. Correspondingly, BM boosted overall phosphorus uptake efficiency by 19.99%, exceeding all other treatments; both B and M also significantly outperformed CK (Fig. 2D).

A major constraint on agricultural productivity is the limited capacity of crops to access legacy phosphorus stored in soil. In this study, the biochar-*Bacillus* consortium (BM) increased soil AP during the early growth stage of cherry tomato. This increase can be attributed partly to the direct phosphate contribution from biochar and to its porous structure, which reduces phosphorus fixation (Deng et al. 2024). Furthermore, the consortium likely stimulated the activity of phosphorus-solubilizing microorganisms (Hu et al. 2023). The decline in AP

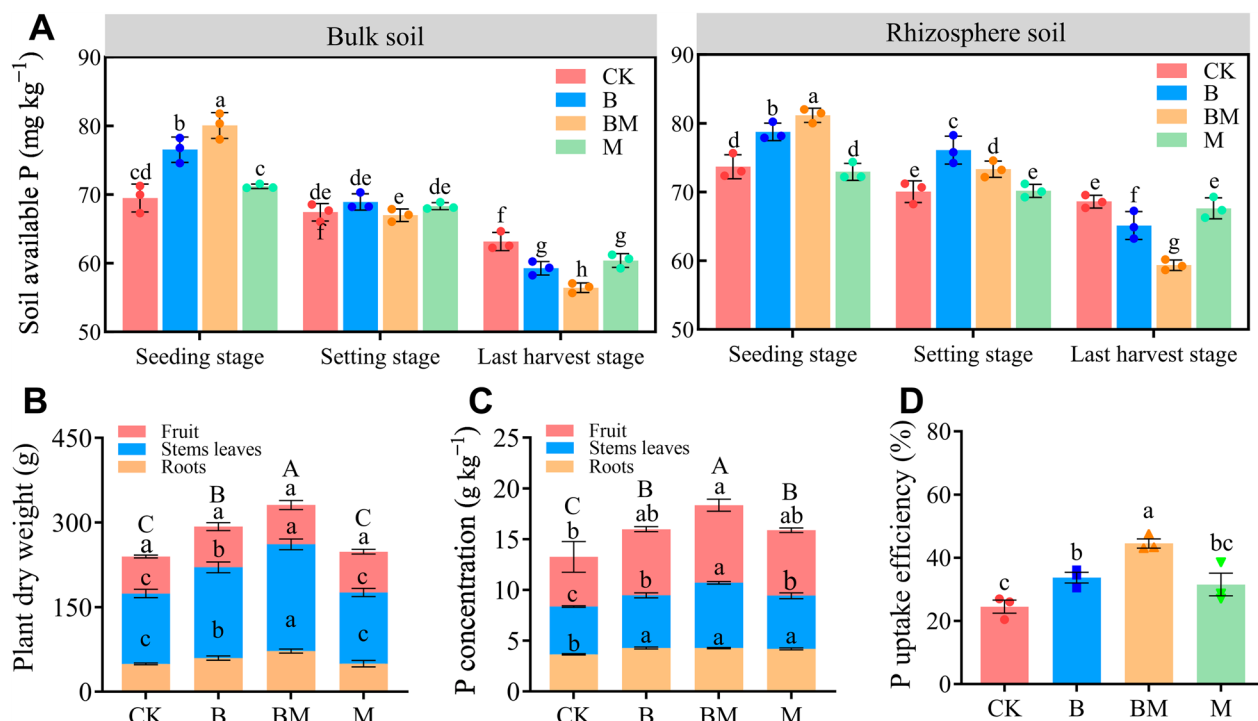


Fig. 2 Phosphorus uptake responses of cherry tomato to biochar-*Bacillus* consortium application. CK, conventional fertilization control; B, conventional fertilization with biochar; BM, conventional fertilization with biochar-*Bacillus* consortium; M, conventional fertilization with *Bacillus* liquid inoculant. Different letters above each bar indicate significant differences ($p < 0.05$)

observed at final harvest under BM treatment was consistent with enhanced plant phosphorus uptake. Previous studies have shown that suitable biochar types can simultaneously elevate soil phosphorus availability and plant phosphorus acquisition (Li et al. 2023), and that phosphate-solubilizing bacteria improve phosphorus uptake and yield by reshaping soil microbial communities (Gurdeep et al. 2015). We therefore propose that the biochar-*Bacillus* consortium enhances phosphorus availability and plant uptake primarily by stimulating the abundance and function of phosphorus-mobilizing microbiota, ultimately driving increases in crop yield.

3.3 Biochar-*Bacillus* consortium modulates soil microbial biomass stoichiometry and phosphatase-driven phosphorus mobilization

Soil microbial biomass carbon (MBC) and phosphorus (MBP) represent key reservoirs of soil nutrient cycling (Chen et al. 2019). As shown in Fig. 3A, D, MBC levels were consistently higher in rhizosphere than in bulk soil across treatments. The BM treatment produced the most pronounced increase in MBC, elevating bulk-soil MBC from 85.43 mg kg⁻¹ (CK) to 256.76 mg kg⁻¹ and rhizosphere MBC from 225.15 mg kg⁻¹ (CK) to 366.69 mg kg⁻¹ at final harvest (Fig. 3D). Similarly, BM significantly enhanced MBP in both soil compartments

relative to CK (Fig. 3B, E). In bulk soil, MBP rose from 10.45 mg kg⁻¹ (CK) to 24.29 mg kg⁻¹ under BM, while in the rhizosphere it increased from 9.39 mg kg⁻¹ (CK) to 25.8 mg kg⁻¹. The microbial biomass C:P ratio (MBC:MBP) declined in response to biochar-based amendments. In the rhizosphere, both B and BM treatments significantly reduced the ratio relative to CK (19.61), with values of 15.44 (B) and 14.42 (BM) (Fig. 3F). Notably, the MBC:MBP ratio was consistently higher in rhizosphere than in bulk soil across all treatments.

In this study, the biochar-*Bacillus* consortium elevated soil microbial biomass carbon (MBC) and phosphorus (MBP) while lowering the microbial C:P ratio in the rhizosphere. These shifts reflect a direct microbial response to altered phosphorus availability and indicate accelerated microbial phosphorus cycling. Biochar amendments provide slow-release nutrients that stimulate microbial growth and metabolism (Jiang et al. 2024). Moreover, the consortium improved soil micro-environments by increasing porosity (Fig. 1), stabilizing temperature and moisture conditions, and promoting root development—all of which favor microbial biomass accumulation (Zhang et al. 2023). Microbial biomass turnover, particularly MBP mineralization, represents a key pathway for replenishing bioavailable soil phosphorus (Li et al. 2024). A lower microbial C:P ratio is often

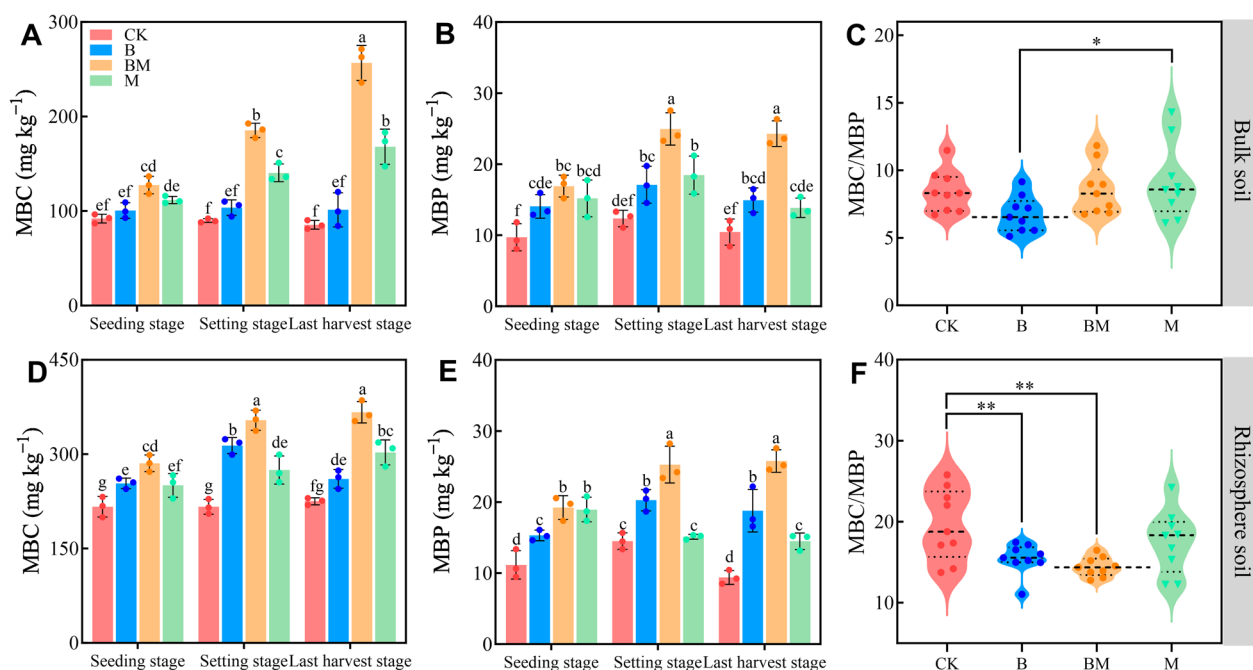


Fig. 3 Effects of biochar-*Bacillus* consortium on soil microbial biomass. **A, D** Microbial biomass carbon (MBC); **B, E** Microbial biomass phosphorus (MBP); **C, F** Microbial biomass C:P ratio (MBC: MBP). CK, conventional fertilization control; B, conventional fertilization with biochar; BM, conventional fertilization with biochar-*Bacillus* consortium; M, conventional fertilization with *Bacillus* liquid inoculant. Different letters above each bar indicate significant differences. * and ** indicate significant differences among treatments at $p < 0.05$ and $p < 0.01$. The violin plots show the median as “---”, and 25th and 75th percentiles as “...”

associated with higher phosphorus release during microbial turnover, as microbes tend to maintain stoichiometric homeostasis (Wang et al. 2019). Thus, we propose that the biochar-*Bacillus* consortium enhances rhizosphere phosphorus availability primarily by increasing MBP pools and promoting its mineralization, consistent with the observed rise in available phosphorus (Fig. 2A).

Soil alkaline (ALP) and acid (ACP) phosphatase activities, key indicators of fixed phosphorus mobilization, were analyzed. As shown in Fig. 4, both ALP and ACP activities were generally higher in rhizosphere than in bulk soil from the fruit-setting stage onward. Compared to CK, the BM treatment consistently increased ALP activity in both soil compartments across all growth stages. The highest ALP activity was recorded in BM-treated rhizosphere soil at harvest (151.15 nmol g⁻¹ h⁻¹), representing a 68.5% increase over CK (89.69 nmol g⁻¹ h⁻¹) (Fig. 4B). In contrast, ACP activity in bulk soil under BM was significantly lower than in CK and other treatments. For instance, at fruit-setting stage, ACP activity decreased from 25.92 nmol g⁻¹ h⁻¹ (CK) to 17.57 nmol g⁻¹ h⁻¹ (BM) (Fig. 4A). In the rhizosphere, BM reduced ACP activity only at final harvest, with a decrease of 5.79 nmol g⁻¹ h⁻¹ relative to CK (Fig. 4B). Notably, the combined activity of ACP+ALP under BM treatment significantly exceeded that of all

other treatments in both bulk and rhizosphere soils throughout the experiment.

The findings indicated that the biochar-*Bacillus* consortium significantly enhanced soil phosphatase activity, with a pronounced stimulation of ALP. Prior studies indicate ACP originates primarily from plant root exudates, whereas ALP is largely of microbial origin, particularly from phosphorus-solubilizing microorganisms (Spohn and Kuzyakov. 2013; Wan et al. 2025). The elevated ALP observed here likely reflects an expansion of phosphate-solubilizing microbial populations induced by the consortium. Notably, soil available phosphorus (AP) at final harvest was inversely correlated with ALP activity, consistent with reported feedback regulation in which ALP expression increases under low inorganic phosphorus availability (Chen et al. 2019). These findings support the inference that the biochar-*Bacillus* consortium stimulates phosphate-mobilizing microbiota, enhances fixed phosphorus mineralization, and thereby promotes plant phosphorus uptake. The decline in ACP activity may be attributed to two interrelated mechanisms. First, the increased ALP activity and improved phosphorus supply from the consortium likely reduced plant dependence on root-secreted ACP for phosphorus acquisition. This could trigger a reallocation of carbon resources away from ACP synthesis toward root growth or beneficial

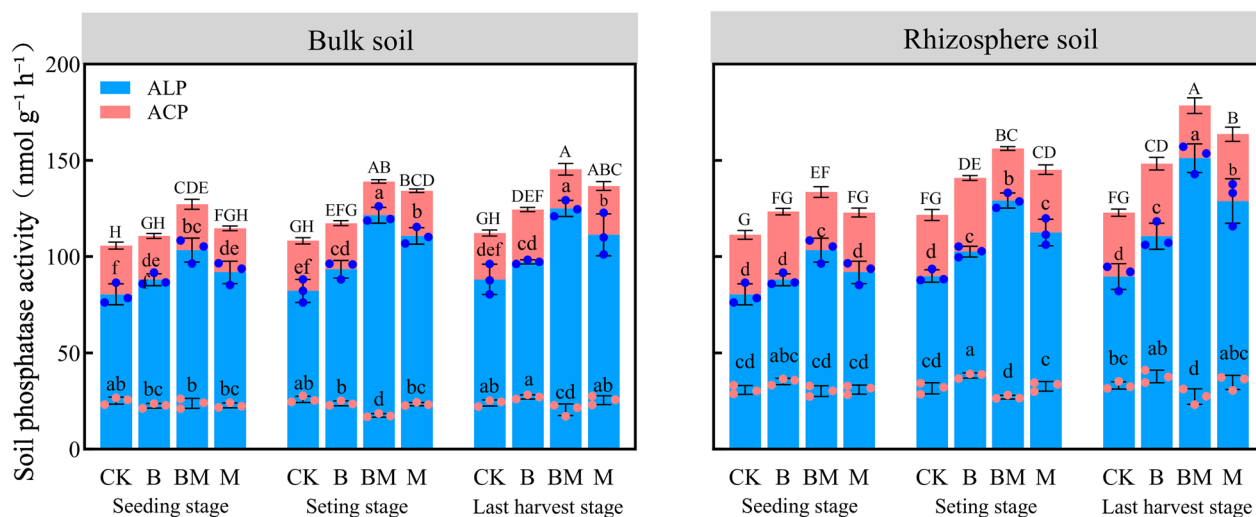


Fig. 4 Soil alkaline (ALP) and acid (ACP) phosphatase activities in response to biochar-*Bacillus* consortium application. CK, conventional fertilization control; B, conventional fertilization with biochar; BM, conventional fertilization with biochar-*Bacillus* consortium; M, conventional fertilization with *Bacillus* liquid inoculant. Different lowercase letters above each bar indicate significant differences for ALP and ACP activities, respectively, while different uppercase letters denote significant differences for the sum of ALP and ACP activities ($p < 0.05$)

microbial symbioses (Raven et al. 2018). Second, the consortium altered the rhizosphere microbial community, favoring taxa that thrive in alkaline-stabilized micro-environments but contribute little to ACP production. Together, these shifts explain the overall suppression of ACP activity in the treated soil.

3.4 Biochar-*Bacillus* consortium promotes beneficial restructuring of soil bacterial communities

The biochar-*Bacillus* consortium significantly enhanced the alpha diversity of the bulk soil microbial community at both the seeding and final harvest stages, but it exhibited no significant effect on the rhizosphere soil (Table S2). The eight most abundant genera across treatments were *Sphingomonas*, *Lysobacter*, *Faecalibacterium*, *Arthrobacter*, *Bacteroides*, *Gaiella*, *Bacillus*, and *Streptomyces*, whose total relative abundance shifted dynamically during the growing season (Fig. 5). BM treatment significantly elevated the relative abundance of *Bacillus* and *Sphingomonas* at setting and last harvest stages in both soil compartments. For instance, in bulk soil, BM increased *Bacillus* abundance by 152% and 181% relative to CK at the two stages, while in the rhizosphere the increases reached 300% and 145%, respectively (Fig. 5B, C, E, and F). Conversely, BM reduced *Faecalibacterium* abundance in bulk soil at both fruit-setting and final harvest stages, and in the rhizosphere only at final harvest, with declines of 24.56%, 81.99%, and 58.84% compared to CK, respectively (Fig. 5B, C, and F). Cluster analysis revealed that in the rhizosphere, bacterial communities under BM and B treatments grouped closely across

all three stages, while M separated more clearly at final harvest (Fig. 5D, E, and F). In bulk soil, BM and M clustered together at seeding and final harvest, whereas CK and B grouped separately from the inoculated treatments at final harvest (Fig. 5A, B, and C). The results suggests that the BM treatment shaped a beneficial root microbiome, as evidenced by an increase in soil bacterial alpha diversity and the enrichment of two key beneficial genera: *Bacillus*, which encompasses many species known to enhance phosphorus availability, and *Sphingomonas*, a plant-growth-promoting rhizobacterium (Asaf et al. 2020). The concomitant decline in *Faecalibacterium* suggests a community shift toward a more phosphorus-mobilizing and plant-beneficial microbial structure.

Redundancy analysis (RDA) revealed distinct clustering of microbial taxa associated with phosphorus-related biological functions, including ALP activity, MBC, and MBP, under different treatments (Fig. 6). At the seeding stage, MBC accounted for 47.1% of the bacterial community variation in bulk soil (Fig. 6A), while AP (37.1%) and ALP (14.4%) were the dominant explanatory variables in rhizosphere soil (Fig. 6D). Moreover, the bacterial community structure of CK in the rhizosphere soil separated clearly from other treatments along RDA1 (Fig. 6D), a pattern consistent with findings from a recent rice-soil incubation study (Keru et al. 2024). These results support the hypothesis that the observed shifts arise from the combined effect of direct phosphorus input from biochar and a consortium-driven restructuring of the microbial community, which functionally correlates with enhanced phosphatase activity and phosphorus solubilization.

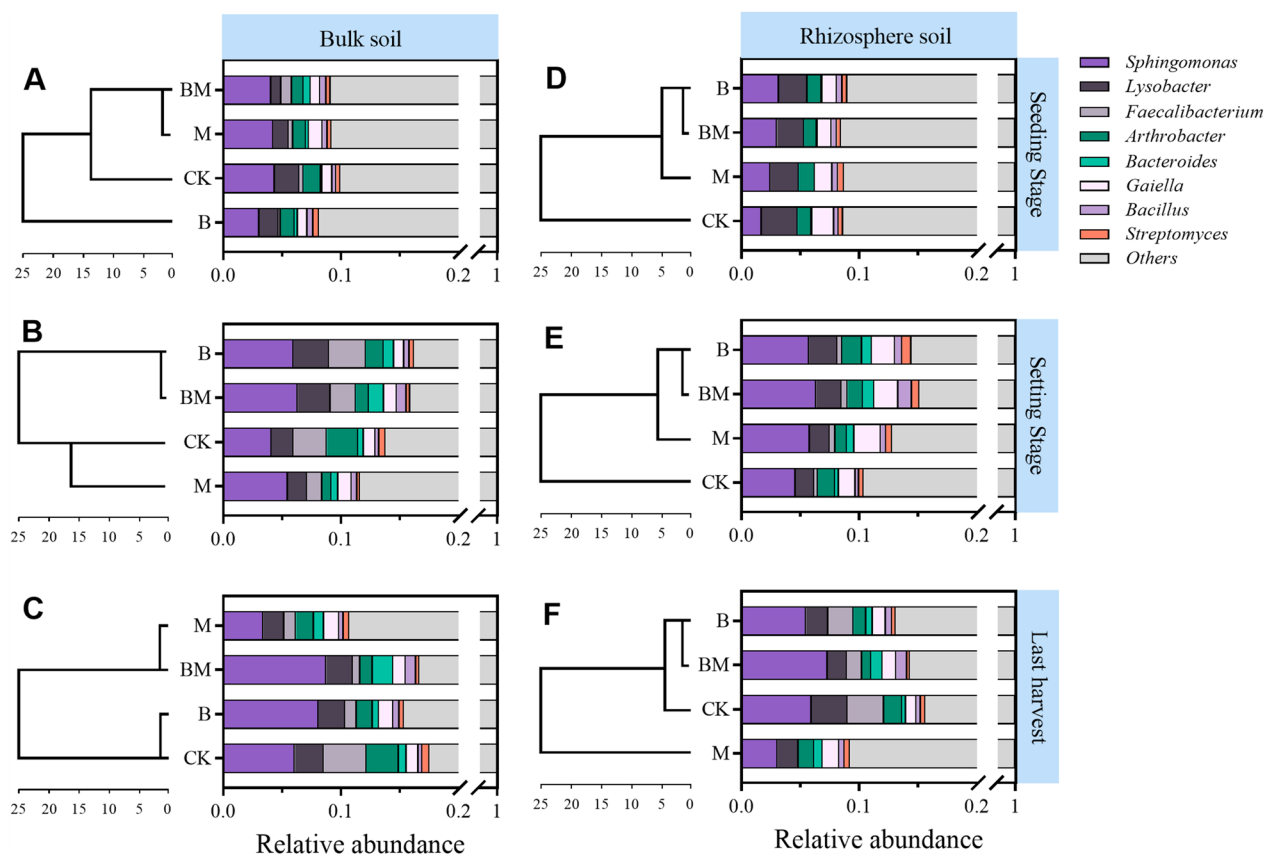


Fig. 5 Cluster analysis and relative abundance of dominant bacterial genus levels. CK, conventional fertilization control; B, conventional fertilization with biochar; BM, conventional fertilization with biochar-*Bacillus* consortium; M, conventional fertilization with *Bacillus* liquid inoculant

At the fruit-setting stage, RDA indicated that soil MBP (27.8%) in bulk soil (Fig. 6B) and MBC (42.5%) in rhizosphere soil were the dominant factors shaping bacterial communities (Fig. 6E). Specifically, MBP was positively correlated with the relative abundance of *Bacillus* and *Sphingomonas* in bulk soil, while MBC covaried strongly with *Bacillus* and *Bacteroides* in the rhizosphere (Fig. 6B, 6E). Moreover, bacterial communities in both bulk and rhizosphere soils under CK clustered distinctly apart from other treatments along RDA1 (Fig. 6D). By the final harvest stage, the key explanatory variables for bacterial composition shifted to AP (36.8%), ALP (15.0%), and MBP (12.8%) in bulk soil (Fig. 6C), and MBC (59.1%) in rhizosphere soil (Fig. 6F). Correspondingly, MBP showed a positive correlation with *Bacillus* and *Bacteroides* in bulk soil, and MBC was positively associated with *Bacillus* in the rhizosphere (Fig. 6C, F). At this stage, both CK and BM treatments formed distinct clusters, separating from other groups along RDA1 in both soil compartments (Fig. 6D). Given that microbial biomass phosphorus (MBP) represents a critical reservoir of labile soil phosphorus (Lidbury et al.2022), the observed

increases in bacterial alpha diversity and *Bacillus* abundance induced by the biochar-*Bacillus* consortium, which correlated positively with MBP and MBC, suggest a mechanistic link. The consortium not only altered microbial community structure but also lowered the microbial biomass C:P ratio. Together, these shifts indicate that the BM treatment enhances phosphorus availability by accelerating MBP turnover, thereby fostering a rhizosphere microenvironment more favorable for cherry tomato growth and phosphorus acquisition.

3.5 Biochar-*Bacillus* consortium promotes fruit-cluster branching and enhances yield in cherry tomato

The BM treatment reduced individual fruit weight by 7.11% but increased fruit number per plant by 24.75% relative to CK (Fig. 7; Table S1). To understand this shift, we analyzed the proportion of fruit clusters that developed branched inflorescences across treatments (Fig. 3). The BM treatment significantly increased the proportion of branched clusters compared to all other treatments, which corresponded with a marked yield improvement. On a per-hectare basis (converted from 667 m² plots),

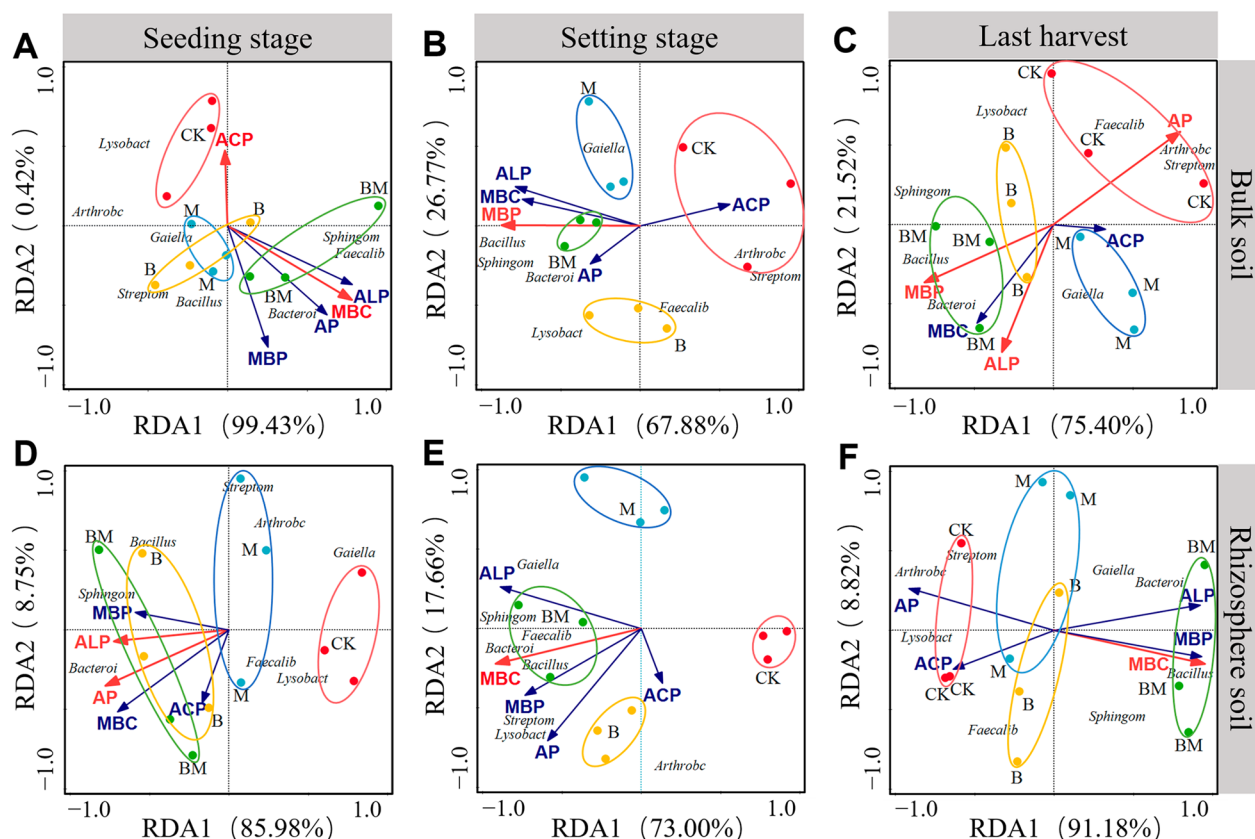


Fig. 6 Redundancy analysis (RDA) of the relationships among soil properties, the top ten significant genera, and bacterial community structure. CK, conventional fertilization control; B, conventional fertilization with biochar; BM, conventional fertilization with biochar-*Bacillus* consortium; M, conventional fertilization with *Bacillus* liquid inoculant. AP, Soil available phosphorus; MBC, Soil microbial biomass carbon; MBP denotes Soil microbial biomass phosphorus; ALP, Alkaline phosphatase activity; ACP, Acid phosphatase activity. Red arrows denote significant positive correlations ($p < 0.05$)

BM elevated yield by 23.53% over CK. Both B and M treatments also significantly boosted yield, with increases of 7.24% and 9.86%, respectively, relative to CK.

Structural equation modeling (SEM) revealed distinct pathways linking microbial communities, soil processes, and plant performance in bulk and rhizosphere soils. In bulk soil, microbial biomass (MBC and MBP), alkaline phosphatase (ALP) activity, and root morphological traits (length, surface area, volume, tip number) were significantly driven by the abundance of key bacterial genera (*Bacillus* and *Bacteroides*) identified via 16S rDNA sequencing. Fruit-cluster branching (measured as the proportion of branched clusters and individual fruit weight) was jointly mediated by soil microbial biomass and bacterial abundance. Furthermore, fruit-cluster branching exerted a significant positive effect on plant phosphorus uptake, while final yield was collectively regulated by root morphology and inflorescence architecture (Fig. 8A). In the rhizosphere soil, the microbial biomass was primarily determined by the bacterial abundance.

The microbial biomass has significant positive effect on the ALP, root morphology, and fruit cluster branching. In addition, the yield and P uptake were primarily determined by the fruit cluster branching (Fig. 8B).

These findings align with meta-analyses indicating that microbial inoculants enhance crop yield and quality through improved nutrient availability (Orozco-Mosqueda et al. 2021; Minchev et al. 2024). They also corroborate recent work showing that phosphorus availability optimizes floral development in ornamentals by modulating root architecture and phosphorus nutrition (Zhai et al. 2023). In the present study, the biochar-*Bacillus* consortium consistently enhanced phosphorus uptake, root architecture, inflorescence branching, and yield in cherry tomato. The consortium-driven improvement in soil phosphorus availability likely elevated plant phosphorus status and membrane phospholipid synthesis, which may promote the formation of productive fruit branches, a process that could further stimulate rhizosphere phosphorus activation. Inflorescence architecture

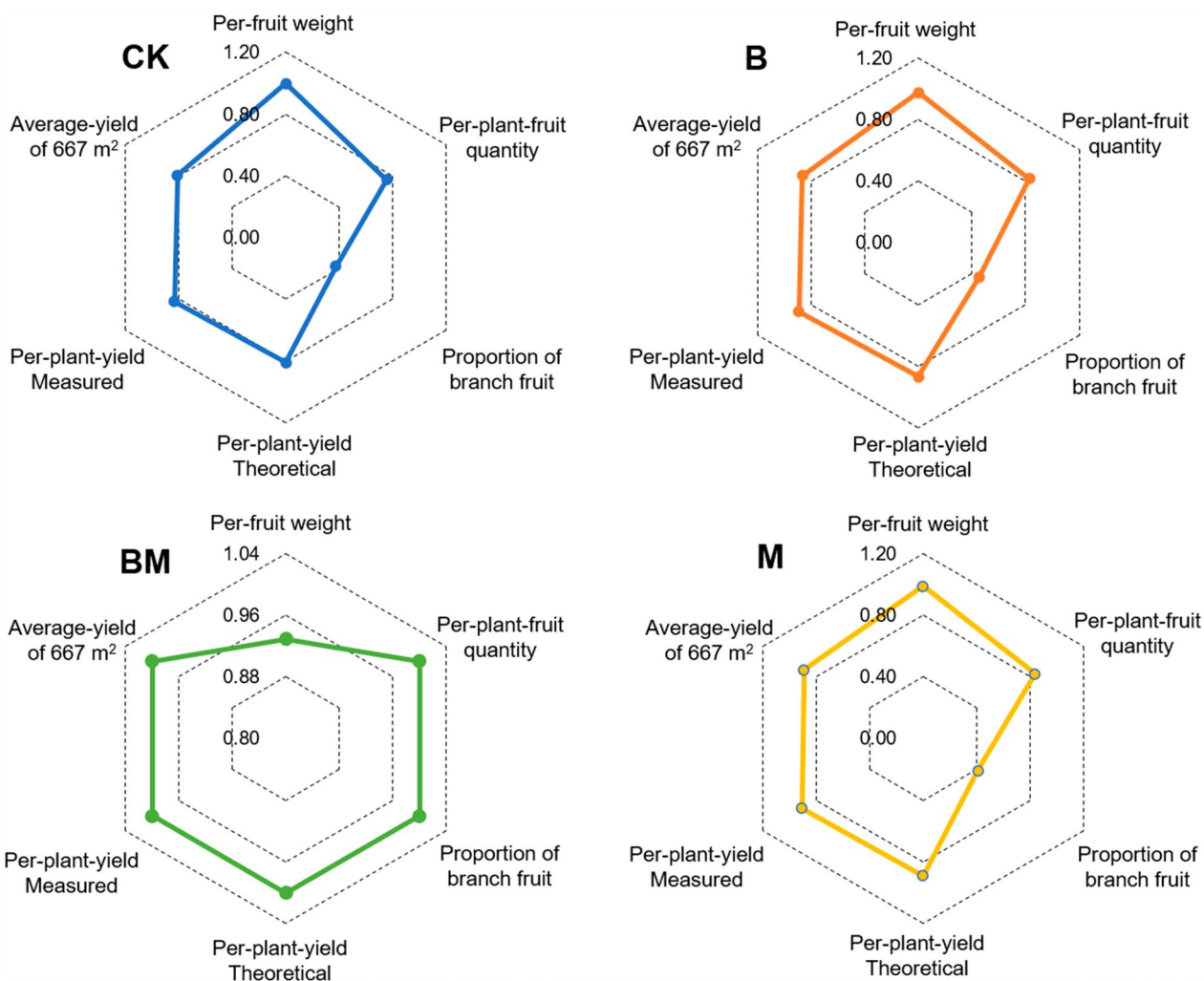


Fig. 7 Radar plots showed the effects of biochar-*Bacillus* consortium on panicle branching morphology and yield of cherry tomato. CK, denotes Conventional fertilization control; B, denotes Conventional fertilization combined with biochar; BM, denotes biochar-*Bacillus* consortium; M, denotes Conventional fertilization with *Bacillus*

in tomato is governed by meristem activity (Soyk et al. 2017), and although it is a polygenic trait, subtle modifications in meristem maturation can induce agronomically beneficial phenotypes (Sun et al. 2024). While this study demonstrates that consortium-mediated soil biological functions strongly promote fruit-cluster branching, the precise mechanisms through which meristem activity is modulated remain a central question for future investigation.

4 Conclusions

This study evaluated the effects of a biochar-*Bacillus* consortium (BM) on soil phosphorus bioavailability, microbial functions, root morphology, inflorescence architecture, phosphorus uptake, and yield in cherry tomato. The BM treatment significantly increased soil available phosphorus (AP), microbial biomass

carbon (MBC) and phosphorus (MBP), and alkaline phosphatase (ALP) activity, while lowering the microbial biomass C:P ratio. Concurrent shifts in bacterial community composition were observed at key growth stages, indicating that the consortium enriched taxa associated with MBP accumulation and turnover, thereby enhancing phosphorus mobilization in the rhizosphere. These soil biological improvements directly promoted plant phosphorus acquisition, which in turn stimulated root architectural development and increased the proportion of fruit-bearing lateral branches. Under protected cultivation, the BM treatment raised cherry tomato yield by 23.53% relative to the conventional control. Collectively, our findings reveal a synergistic soil-plant pathway through which biochar-microbe interactions enhance

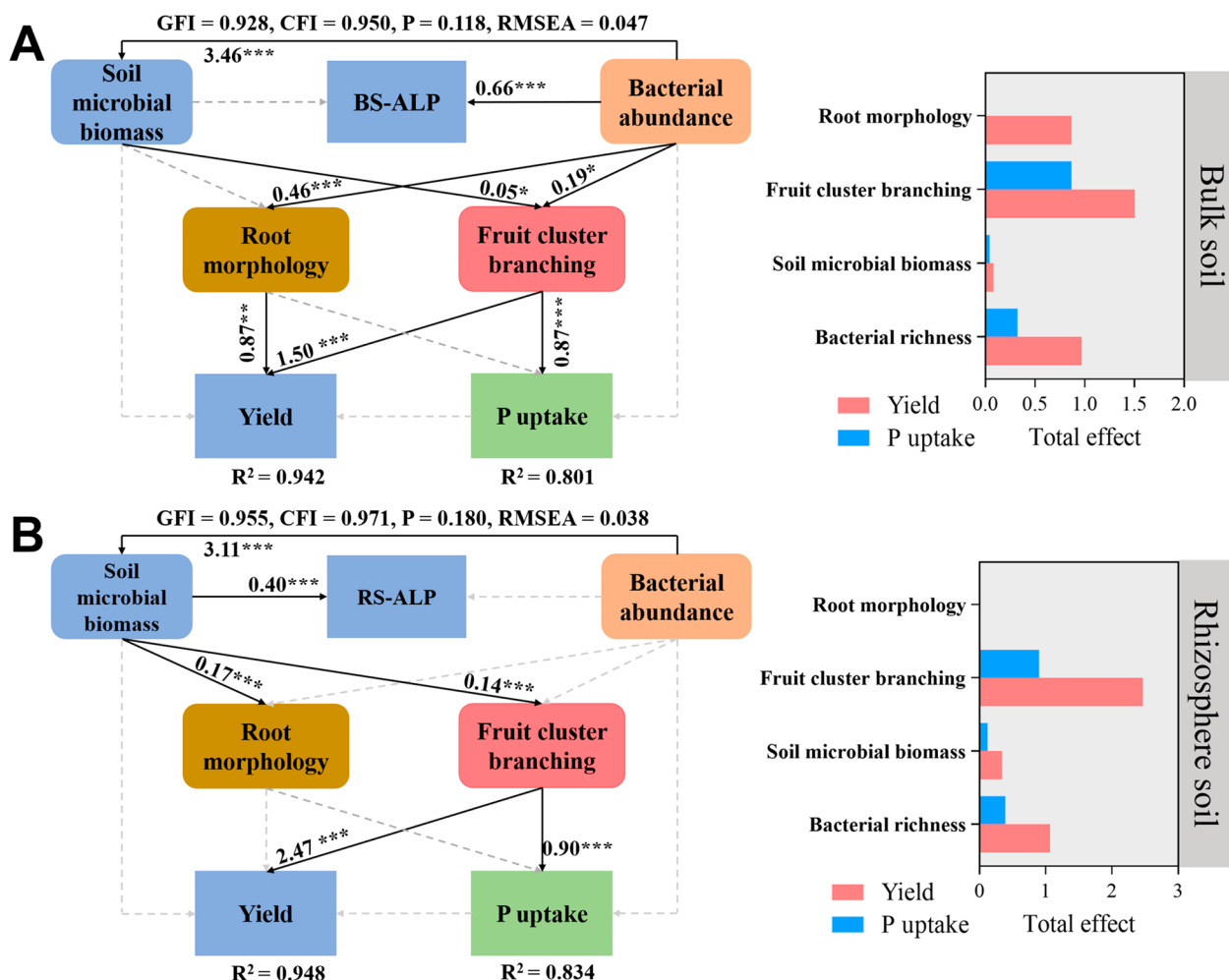


Fig. 8 Structural equation modeling (SEM) of soil–plant interactions in cherry tomato. Single-headed arrows represent the hypothesized direction of causation. Numbers next to single-headed arrows are standardized path coefficients, which indicate the effective size of the relationship. **p* < 0.05; ***p* < 0.01; ****p* < 0.001

crop productivity by concurrently optimizing phosphorus availability, root growth, and reproductive development.

Supplementary Information

The online version contains supplementary material available at <https://doi.org/10.1007/s42773-026-00586-z>.

Supplementary Material 1.

Acknowledgements

We appreciated the support from Natural Science Foundation of Liaoning (2024-MS-095), Liao Ning Revitalization Talents Program (XLYC2403038), National Natural Science Foundation of China (32402691).

Author contributions

Liu Sainan: designed and executed the research, analyzed results, and drafted the paper. Shi Yongjia: assisted for carried out partial tests. Zhang Aijia: carried out partial tests. Huang Yuwei: assisted on solving experimental problems. Cao

Dianyun: revised the manuscript as corresponding author. Lan Yu: revised the manuscript and supervised the study as corresponding author.

Funding

Natural Science Foundation of Liaoning (2024-MS-095), Liao Ning Revitalization Talents Program (XLYC2403038), National Natural Science Foundation of China (32402691).

Data availability

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

Declarations

Competing interests

The authors declare that they have no competing interests.

Author details

¹College of Agronomy, Shenyang Agricultural University, Shenyang, China. ²Key Laboratory of Biochar and Soil Improvement, Ministry of Agriculture and Rural Affairs, Shenyang 110161, China.

Received: 10 July 2025 Revised: 21 January 2026 Accepted: 28 January 2026

Published online: 01 March 2026

References

- Ajeng AA, Abdullah R, Ling TC (2023) Biochar-*Bacillus* consortium for a sustainable agriculture: physicochemical and soil stability analyses. *Biochar* 5(1):17
- Asaf S, Numan M, Khan AL, Al-Harrasi A (2020) *Sphingomonas*: from diversity and genomics to functional role in environmental sustainability and plant growth promotion. *J Hazard Mater* 389:122086
- Azeem M, Hassan TU, Tahir MI, Ali A, Zhang Z (2021) Tea leaves biochar as a carrier of *Bacillus cereus* improves the soil function and crop productivity. *Appl Soil Ecol* 157:103732
- Bao SD (2000) Method for soil agricultural chemistry. 3rd edn. Professional Committee of Agricultural Chemistry of Chinese Society for Soil Sciences. China Agriculture Press, Beijing
- Batista E, Juliana S, Matos T, Fornari MR, Ferreira TM, Bruno S, De FRA, Mangrich AS (2018) Effect of surface and porosity of biochar on water holding capacity aiming indirectly at preservation of the Amazon biome. *Entific Reports* 8(1):10677
- Beltran-Medina I, Romero-Perdomo F, Molano-Chavez L, Gutiérrez AY, Silva AMM, Estrada-Bonilla G (2023) Inoculation of phosphate-solubilizing bacteria improves soil phosphorus mobilization and maize productivity. *Nutr Cycl Agroecosyst* 126:21–34
- Bolan SD, Hou D, Wang L, Hale L, Egamberdieva D, Tammeorg P, Li R, Wang B, Xu J, Wang T, Sun H, Padhya LP, Wang H, Siddique KHM, Rinklebe J, Kirkham MB, Bolan N (2023) The potential of biochar as a microbial carrier for agricultural and environmental applications. *Sci Total Environ*. <https://doi.org/10.1016/j.scitotenv.2023.163968>
- Canal SB, Bozkurt MA, Ucar CP (2024) The effects of endophytic bacteria along with humic acid and biochar on phytoremediation of rapeseed (*Brassica napus* L.). *J Crop Health* 76:1615–1625
- Chang L, Ju TH, Liang K, Li YF (2025) Biochar-influenced solubilization and mineralization mechanisms of phosphorus in saline-sodic soils. *Soil Biol Biochem* 209:109890
- Chen X, Jiang N, Condon LM, Dunfield KE, Chen Z, Wang J, Chen L (2019) Impact of long-term phosphorus fertilizer inputs on bacterial *phoD* gene community in a maize field, Northeast China. *Sci Total Environ* 669:1011–1018
- Cho H, Choi I, Bouain N, Nawaz A, Zheng L, Shahzad Z, Brandizzi F, Rhee SY, Rouached H (2025) Phosphorus availability controls flowering time through subcellular reprogramming of bGLU25 and GRP7 in *Arabidopsis*. *Dev Cell* 10:005
- Deng L, Tu P, Ahmed N, Zhang G, Cen Y, Huang B, Deng L, Yuan H (2024) Biochar-based phosphate fertilizer improve phosphorus bioavailability, microbial functioning, and citrus seedling growth. *Sci Hortic*. <https://doi.org/10.1016/j.scienta.2024.113699>
- Dixon MM, Afkairin A, Davis JG, Chitwood-Brown J, Buchanan CM, Ippolito JA, Manter DK, Vivanco JM (2024) Tomato domestication rather than subsequent breeding events reduces microbial associations related to phosphorus recovery. *Sci Rep* 38:1–9
- Dziewit K, Amakorová P, Novák O, Szal B, Podgórska A (2024) Systemic strategies for cytokinin biosynthesis and catabolism in *Arabidopsis* roots and leaves under prolonged ammonium nutrition. *Plant Physiol Biochem*. <https://doi.org/10.1016/j.plaphy.2024.108858>
- Edgar RC, Haas BJ, Clemente JC, Quince C, Knight R (2011) UCHIME improves sensitivity and speed of chimera detection. *Bioinformatics* 27:2194–2200
- Gao L (2019). Current situation of cultivation techniques of facility vegetables and problems in production also its sustainable development strategies. IOP conference series. Earth and environmental science 252 5 52069.
- Gurdeep K, Reddy MS (2015) Effects of phosphate-solubilizing bacteria, rock phosphate and chemical fertilizers on maize-wheat cropping cycle and economics. *Pedosphere* 25(3):428–437
- Harish MN, Choudhary AK, Dass A, Singh VK, Rajanna GA, Bana RS, Paramesh V, Varatharajan T, Bhupenachandra I, Sadhukhan R, Kumar A, Sachin KS, Teli KG, Singh SRK, Sannagoudar MS, Muniyappa L, Prasad HPN (2025) Double zero-tilled bed-planting and optimized P-fertilization in maize-wheat rotation: An empirical investigation on root architecture, carbon-phosphorus dynamics, and soil carbon pools. *J Environ Manage* 392:126668
- Hou Q, Wang W, Yang Y, Hu J, Bian C, Jin L, Li G, Xiong X (2020) Rhizosphere microbial diversity and community dynamics during potato cultivation. *Eur J Soil Biol* 98:103176
- Hu W, Zhang Y, Xiangmin R, Fei J, Peng J, Luo G (2023) Coupling amendment of biochar and organic fertilizers increases maize yield and phosphorus uptake by regulating soil phosphatase activity and phosphorus-acquiring microbiota. *Agric Ecosyst Environ*. <https://doi.org/10.1016/j.agee.2023.108582>
- Hui H, Qian TT, Liu WJ, Jiang H, Yu HQ (2014) Biological and chemical phosphorus solubilization from pyrolytical biochar in aqueous solution. *Chemosphere* 113:175–181
- Jiang H, Yuan C, Wu Q, Heděnc P, Zhao Z, Yue K, Ni X, Wu F, Peng Y (2024) Effects of transforming multiple ecosystem types to tree plantations on soil microbial biomass carbon, nitrogen, phosphorus and their ratios in China. *Appl Soil Ecol* 193:105145
- Jin X, Rahman MK, Ma C, Zheng X, Wu F, Zhou X (2023) Silicon modification improves biochar's ability to mitigate cadmium toxicity in tomato by enhancing root colonization of plant-beneficial bacteria. *Ecotoxicol Environ Saf* 249:114407
- Keru Y, Zhaokun X, Xianzhi F, Jiawei M, Yongjun W, Dan L, Zhengqian Y (2024) Effects of biochar inoculation with *Bacillus megaterium* on rice soil phosphorus fraction transformation and bacterial community dynamics. *Rice Sci* 31:361–365
- Leite ADA, Cardoso AAS, Leite RA, Barrera AMV, Queiroz DDL, Viana TC, Oliveira-Longatti SM, Silva CA, Moreira FMS, Lehmann J, Melo LCA (2024) Phosphate-solubilizing bacteria increase maize phosphorus uptake from magnesium-enriched poultry manure biochar. *Biol Fertil Soils* 60:421–436
- Li J, Xu Y, Liu H (2019) Variations of soil quality from continuously planting greenhouses in North China. *Int J Agric Biol Eng* 12(1):139–145
- Li H, Ren R, Zhang H, Zhang G, He Q, Han Z, Meng S, Zhang Y, Zhang X (2023) Factors regulating interaction among inorganic nitrogen and phosphorus species, plant uptake, and relevant cycling genes in a weakly alkaline soil treated with biochar and inorganic fertilizer. *Sci Total Environ*. <https://doi.org/10.1016/j.scitotenv.2023.167280>
- Li M, He X, Zhang P, Wang R, Wang J, Zhang X, Yin H (2024) Close linkage between available and microbial biomass phosphorus in the rhizosphere of alpine coniferous forests along an altitudinal gradient. *Rhizosphere* 30:100904
- Lidbury IDEA, Scanlan DJ, Murphy ARJ, Christie-Oleza JA, Aguilo-Ferretjans MM, Hitchcock A, Daniell TJ (2022) A widely distributed phosphate-insensitive phosphatase presents a route for rapid organophosphorus remineralization in the biosphere. *PNAS* 119(5):e2118122119
- Liu SN, Du HT, Huang YW, Lan Y, Lu JK, Wang SY, Meng J (2022) Effects of biochar application and phosphorus-solubilizing bacteria on rice seedling growth and rhizosphere phosphorus availability under phosphorus stress. *Chin J Ecol* 41(8):1560–1569
- Minchev Z, Ramírez-Serrano B, Dejana L, Lee Díaz AS, Zitalpopoca-Hernandez G, Orine D, Saha H, Papantoniou D, García JM, González-Céspedes A, Garbeva P, Dam NM, Soler R, Giron D, Martínez-Medina A, Biere A, Hauser T, Meyling NV, Rasmann S, Pozo MJ (2024) Beneficial soil fungi enhance tomato crop productivity and resistance to the leaf-mining pest *Tuta absoluta* in agronomic conditions. *Agron for Sustain Dev* 44(6):55
- Orozco-Mosqueda MC, Flores A, Rojas-Sánchez B, Urtis-Flores CA, Morales-Cedeño LR, Valencia-Marin MF, Chávez-Avila S, Rojas-Solis D, Santoyo G (2021) Plant growth-promoting bacteria as bioinoculants: attributes and challenges for sustainable crop improvement. *Agron* 11:1–15
- Parasar BJ, Agarwala N (2025) Unravelling the role of biochar-microbe-soil tripartite interaction in regulating soil carbon and nitrogen budget: a panacea to soil sustainability. *Biochar* 7:37
- Quadros PDD, Zhalnina K, Davis-Richardson AG, Drew JC, Menezes FB, Camargo FADO, Triplett EW (2016) Coal mining practices reduce the microbial biomass, richness and diversity of soil. *Appl Soil Ecol* 98:195–203
- Raven JA, Lambers H, Smith SE, Westoby M (2018) Costs of acquiring phosphorus by vascular land plants: patterns and implications for plant coexistence. *New Phytol* 217(4):1420–1427
- Silva PC, Ferreira AFA, Araújo ES, Neto JVB, Costa AR, Fernandes LS, Martins AAS, Cândido RS, Jardim AMRF, Pandorfi H, Silva MV (2022) Cherry tomato crop management under irrigation levels: morphometric characteristics

- and their relationship with fruit production and quality. *Gesunde Pflanz* 75:1277–1288
- Soyk S, Lemmon ZH, Oved M, Fisher J, Liberatore KL, Park SJ, Goren A, Jiang K, Ramos A, Knaap E, Eck JV, Zamir D, Eshed Y, Lippman ZB (2017) Bypassing negative epistasis on yield in tomato imposed by a domestication gene. *Cell* 169:1142–1155
- Spohn M, Kuzyakov Y (2013) Distribution of microbial- and root-derived phosphatase activities in the rhizosphere depending on P availability and C allocation – coupling soil zymography with ¹⁴C imaging. *Soil Biol Biochem* 67:106–113
- Sun S, Liu Z, Wang X, Song J, Fang S, Kong J, Li R, Wang H, Cui X (2024) Genetic control of thermomorphogenesis in tomato inflorescences. *Nat Commun* 15(1):1472
- Tu C, Wei J, Guan F, Liu Y, Sun Y, Luo Y (2020) Biochar and bacteria inoculated biochar enhanced Cd and Cu immobilization and enzymatic activity in a polluted soil. *Environ Int*. <https://doi.org/10.1016/j.envint.2020.105576>
- Tumbure A, Schmalenberger A (2024) Struvites with comparable nitrogen and phosphorus composition have similar agronomic response but shape cherry tomato rhizosphere bacterial community structure differently. *Appl Soil Ecol*. <https://doi.org/10.1016/j.apsoil.2024.105276>
- Wan W, Yang Y, Grossart HP, Xiong X, He D (2025) Soil alkaline phosphatase-encoding bacteria relate closely to microbial biomass phosphorus in changing environments. *Environ Res* 282:122078
- Wang J, Wu Y, Zhou J, Bing H, Sun H, He Q, Li J, Wilcke W (2019) Soil microbes become a major pool of biological phosphorus during the early stage of soil development with little evidence of competition for phosphorus with plants. *Plant Soil* 446:259–274
- Wang L, Chen X, Tang Z (2022) Arbuscular mycorrhizal symbioses improved biomass allocation and reproductive investment of cherry tomato after root-knot nematodes infection. *Plant Soil* 482:513–527
- Wang Y, Zou L, Lou C, Geng X, Zhang S, Chen X, Zhang Y, Huang D, Liang A (2024) No-tillage with straw retention influenced maize root growth morphology by changing soil physical properties and aggregate structure in Northeast China: a ten-year field experiment. *Geoderma Reg*. <https://doi.org/10.1016/j.geodrs.2024.e00840>
- Wu WJ, Chen YJ, Li GY (2021). Mechanism of rice straw biochar on tomato yield and quality in cadmium polluted farmland. *Journal of Agricultural Environmental Sciences* 1–17.
- Yang L, Shen P, Liang H, Wu Q (2024) Biochar relieves the toxic effects of microplastics on the root-rhizosphere soil system by altering root expression profiles and microbial diversity and functions. *Ecotoxicol Environ Saf*. <https://doi.org/10.1016/j.ecoenv.2024.115935>
- Zhai Y, Hu X, Zhao X, Xu M, Li W, Guo S (2023) Phosphorous and arbuscular mycorrhizal fungi improve snapdragon flowering through regulating root architecture and phosphorus nutrition. *J Soil Sci Plant Nutr* 23:4279–4289
- Zhang X, Feng Q, Adamowski JF, Biswas A, Cao J, Liu W, Qin Y, Zhu M (2023) Conversion of grassland to abandoned land and afforested land alters soil bacterial and fungal communities on the Loess Plateau. *Appl Soil Ecol* 183:104758