ENGINEERING Agriculture

Engineering Journals

COMMENTS

2026 / Volume 13 / Issue 5 / 26731

Beyond phosphate solubilization: root exudates orchestrate bacterial phosphorus mining

Zhihui WEN*, Lin ZHANG*, Fusuo ZHANG (✉)

State Key Laboratory of Nutrient Use and Management, College of Resources and Environmental Sciences, Key Laboratory of Plant–Soil Interactions (Ministry of Education), China Agricultural University, Beijing 100193, China.

*These authors contribute equally to the work

Received August 30, 2026;
Accepted August 30, 2026.

Correspondence: zhangfs@cau.edu.cn

This is a non-peer reviewed article

© The Author(s) 2026. Published by Higher Education Press. This is an open access article under the CC BY license (http://creativecommons.org/licenses/by/4.0)

Phosphorus is essential for plant growth, yet much of the P in soil remains inaccessible because of strong chemical fixation and the slow turnover of organic P. Plants have evolved diverse adaptive strategies to cope with P limitation, including beneficial associations with root-associated microorganisms. In more than two-thirds of terrestrial plant species, arbuscular mycorrhizal fungi play a central role in P acquisition by extending soil exploration beyond the root depletion zone[1]. However, it remains largely unclear whether non-mycorrhizal plants can similarly outsource P mining to microbial partners and, if so, how such cooperation is established. A recent study in *Cell* by Wang et al.[2] provides an elegant answer to this question. Under P deficiency, *Arabidopsis thaliana* recruits compatible bacteria to the rhizoplane through malate exudation and supplies metabolites that fuel bacterial P mobilization. This microbial mobilization enables roots to acquire otherwise inaccessible P, thereby improving plant P nutrition and growth. Beyond identifying an alternative P-acquisition strategy in a non-mycorrhizal plant, the study positions root exudates as organizers of a mutually beneficial plant-bacterium partnership through which plant carbon investment yields a nutritional return. Together, these findings advance a system-level view of plant nutrient acquisition as an emergent outcome of functional integration across the plant–microbiome–soil continuum.

Bacterial phosphate-solubilizing capacity alone does not predict host benefit

Wang et al.[2] screened 130 cultured bacterial strains isolated from *Arabidopsis* roots. When hydroxyapatite was supplied as the sole P source, 26 strains (20%) alleviated plant P-starvation responses and promoted plant growth. These strains spanned two phyla, 13 families and 15 genera, indicating that the capacity to improve plant P nutrition was distributed across diverse bacterial lineages rather than restricted to a single taxonomic group.

Surprisingly, the extent of plant growth promotion was unrelated to the phosphate-solubilizing capacity of these strains under free-living culture conditions. Some strains with weak phosphate-solubilizing activity strongly promoted plant growth, whereas many strong solubilizers conferred little or no benefit. These findings challenge the long-standing assumption that phosphate-solubilizing capacity measured *in vitro* predicts a strain's ability to improve plant P nutrition. That is, a strain that solubilizes P efficiently in culture is not necessarily an effective partner for the plant, as releasing phosphate from hydroxyapatite alone does not ensure its availability for root uptake. This disconnect raises a more fundamental question: what enables a bacterium to translate its phosphate-solubilizing potential into a nutritional benefit for the host?

One metabolite, three coordinated functions

To address this question, Wang et al.[2] conducted a detailed analysis of *Acinetobacter guillouiae* R1280, one of the bacterial strains that promoted *Arabidopsis* growth under P deficiency. Their results showed that root-derived malate coordinated three distinct but complementary functions in this specific plant–bacterium interaction. First, malate served as a chemotactic signal that attracted R1280 toward the differentiated root zone, consistent with earlier evidence that malate exuded by roots can recruit beneficial bacteria[3]. Second, malate, together with root-derived glutamate and γ-aminobutyric acid, supplied carbon substrates that supported bacterial proliferation and metabolic activity. Third, malate promoted R1280 colonization of the rhizoplane, thereby positioning bacterial P mobilization close to the root uptake surface. Collectively, these findings establish malate exudation as a central organizer of the *Arabidopsis*–R1280 interaction, linking P-deficiency-induced activation of the plant STOP1–ALMT1 pathway to bacterial recruitment, metabolic provisioning and spatial positioning.

Recruitment alone, however, was insufficient to confer a nutritional benefit on the host. Following rhizoplane colonization, R1280 underwent extensive transcriptional and metabolic reprogramming relative to its free-living state. These changes encompassed enhanced energy generation and carbon and nitrogen metabolism, together with increased expression of genes mediating P mobilization and acquisition, including *gcd*, which contributes to gluconate-mediated inorganic P solubilization; *phoD*, which encodes an alkaline phosphatase involved in organic P mineralization; and *pstS*, which contributes to high-affinity bacterial phosphate uptake. Disruption of these genes weakened P mobilization and reduced plant growth promotion, demonstrating that host benefit depended on the metabolic activity of R1280 rather than its presence on the rhizoplane alone.

For bacterially mobilized phosphate to benefit the host, the plant also required an effective uptake system. Impairing PHF1-dependent trafficking of plant PHT1 transporters limited the ability of *Arabidopsis* to acquire phosphate mobilized by R1280. Together, these findings illustrate a tightly integrated functional chain through which a plant-bacterium association can improve host P nutrition: plant-derived metabolites recruit and fuel compatible bacterial partners, bacterial metabolism mobilizes otherwise inaccessible P within reach of roots, and root transporters capture part of the released phosphate.

Mutual benefit depends on compatibility, proximity and time

The benefit of malate exudation depended on the presence of a compatible bacterial partner. Although carboxylates are widely recognized for their capacity to mobilize soil P directly through acidification, ligand exchange or metal complexation[4], root-derived malate mobilized little phosphate from hydroxyapatite under sterile conditions. In the absence of bacteria, *stop1* and *almt1* mutants showed slightly less growth inhibition than wild-type plants under P deficiency, suggesting that the carbon cost of malate exudation was not offset by improved P nutrition. In the presence of R1280, however, this pattern was reversed: malate supported bacterial recruitment and activity, converting the plant's carbon expenditure into enhanced P acquisition and growth. In this system, malate exudation therefore benefited the plant only when a compatible bacterial partner used the exuded carbon to support P mobilization.

The benefit conferred by the partnership was strongly constrained by spatial proximity. R1280 proliferated and mobilized phosphate predominantly on the root surface, whereas little bacterial growth or soluble phosphate accumulation was detected in the surrounding medium. Separating the roots from R1280 with an agar barrier only 1 mm thick markedly reduced plant growth promotion. These findings indicated that P mobilization benefited the host only when it occurred sufficiently close to the root surface for the released phosphate to be captured by root P transporters. The rhizoplane therefore functioned not merely as the location of the interaction but as an integral component of the mechanism itself. This spatial pattern highlights the microscale organization of plant–microbe interactions and suggests that effective nutrient exchange can be concentrated at root–microbe interfaces rather than distributed uniformly throughout the rhizosphere[5].

The outcome of the interaction also changed over time. During the early stages of colonization, R1280 intensified rather than alleviated the plant phosphate-starvation response, consistent with initial competition between the bacterium and the plant for scarce phosphate. Only after reaching the root surface, proliferating and undergoing metabolic reprogramming did R1280 mobilize sufficient phosphate to offset this initial

competition and shift the interaction toward mutual benefit. Therefore, mutual benefit in the *Arabidopsis*–R1280 association emerged from partner compatibility, spatial proximity and the temporal progression of the interaction, rather than from an intrinsic property of the bacterium. More generally, the same bacterial partner can be beneficial, neutral or even detrimental, depending on the balance between the nutritional gains from microbial P mobilization and the costs of carbon investment and nutrient competition. Such context dependence may help explain why microbial inoculants that perform well under controlled conditions often show inconsistent effects on plant nutrition in more complex environments[6,7].

Carbon-for-nutrient exchange: from conceptual advance to field translation

Carbon-for-nutrient exchange is well established in mycorrhizal symbioses, where it forms the functional basis of mutual benefit. Plants allocate carbon to fungal partners, thereby supporting hyphal growth and nutrient acquisition beyond the root depletion zone. In return, the fungi transfer a portion of the acquired nutrients to the host[8–10]. By demonstrating that a non-mycorrhizal plant can establish such an exchange directly with a bacterial partner, Wang et al.[2] extended this principle beyond classical mycorrhizal symbioses. In the *Arabidopsis*–R1280 system, malate exudation constituted the plant's carbon investment, whereas bacterial P mobilization and subsequent root P uptake converted that investment into a nutritional return. Although mycorrhizal and plant–bacterium partnerships differ in partner identity and spatial organization, both couple plant carbon investment to microbial activities that enhance access to limiting nutrients. Carbon-for-nutrient exchange therefore represents a unifying principle shared by mycorrhizal and direct plant–bacterium pathways of nutrient acquisition.

This shared exchange logic aligns with the Rhizobiont framework, which conceptualizes the plant together with its root system, rhizosphere, hyphosphere, bulk soil and associated microorganisms as a functionally integrated nutrient-acquisition system[11]. The *Arabidopsis*–R1280 interaction provides a mechanistic example of how such a system operates. Root-derived malate recruited R1280 to the rhizoplane and supplied carbon to sustain its activity, thereby positioning bacterial P mobilization within reach of root uptake and closing the loop between carbon investment and nutrient return. Through this spatial and functional coordination, root exudation integrated bacterial function into plant nutrient acquisition at the system level. To establish how broadly this mode of coordination applies, future studies should assess whether similar carbon-for-nutrient exchanges occur across diverse plant species, microbial partners and soil environments. They should also quantify the nutritional returns on plant carbon investment and determine how soil conditions and resident microbial communities promote or constrain exchange stability.

Microbe-based strategies are increasingly recognized as an important route to improving crop nutrient-use efficiency and reducing mineral fertilizer inputs[12,13]. The study contributes to this effort by offering a design principle for agricultural translation rather than a ready-made microbial solution. Effective translation requires matching microbial functions with host traits and with the spatial and temporal context of nutrient uptake. Microbial screening should therefore move beyond assessments of P-mobilizing activity *in vitro* to identify strains that respond to crop-derived metabolites, colonize relevant root microsites, and deliver measurable nutritional benefits under realistic soil conditions. Complementary breeding efforts could target root-exudation traits that favor compatible microbial partners and nutrient-uptake traits that enhance the capture of mobilized nutrients. Successful field deployment will also depend on inoculant formulation, placement, and timing to ensure that microbial activity occurs within reach of absorptive roots and coincides with crop nutrient demand. Rather than seeking universally beneficial microorganisms, the challenge is to develop plant–microbe–soil systems in which microbial functions, host traits, and environmental conditions are effectively aligned. Achieving this goal will require testing such combinations across crop genotypes, soil types, and management regimes to determine whether they consistently improve nutrient-use efficiency while sustaining microbial colonization and function.

Acknowledgements

We thank Dr. Ian Riley and Dr. Jiayin Pang for their valuable comments and assistance with language editing on an earlier version of this manuscript. This work was supported by the National Natural Science Foundation of China (32130094) and the Fundamental and Interdisciplinary Disciplines Breakthrough Plan of the Ministry of Education of China (JYB2025XDXM702).

REFERENCES

1. Smith S E, Read D J. *Mycorrhizal Symbiosis*. 3rd ed. London: *Academic Press*, 2008
2. Wang Y J, Gao C L, Liu F, Liu Y H, Zhou Z Y, Wang Q, Zhang F X, Cheng H Y, Jiang X W, Wang W, Wang B L, Tang Y J, Zhou F, Wang G D, Wang Y P, Yang W C, Schulze-Lefert P, Liu D, Bai Y, Zhou J M. Mutually beneficial interactions between bacteria and *Arabidopsis* promote phosphorus nutrition and growth. *Cell*, 2026 [Published Online] doi: 10.1016/j.cell.2026.07.048
3. Rudrappa T, Czymmek K J, Paré P W, Bais H P. Root-secreted malic acid recruits beneficial soil bacteria. *Plant Physiology*, 2008, **148**(3): 1547–1556
4. Li L, Li S M, Sun J H, Zhou L L, Bao X G, Zhang H G, Zhang F S. Diversity enhances agricultural productivity *via* rhizosphere phosphorus facilitation on phosphorus-deficient soils. *Proceedings of the National Academy of Sciences of the United States of America*, 2007, **104**(27): 11192–11196
5. Hinsinger P, Bengough A G, Vetterlein D, Young I M. Rhizosphere: biophysics, biogeochemistry and ecological relevance. *Plant and Soil*, 2009, **321**(1): 117–152
6. Castrillo G, Teixeira P J P L, Paredes S H, Law T F, de Lorenzo L, Feltcher M E, Finkel O M, Breakfield N W, Mieczkowski P, Jones C D, Paz-Ares J, Dangl J L. Root microbiota drive direct integration of phosphate stress and immunity. *Nature*, 2017, **543**(7646): 513–518
7. Finkel O M, Salas-González I, Castrillo G, Spaepen S, Law T F, Teixeira P J P L, Jones C D, Dangl J L. The effects of soil phosphorus content on plant microbiota are driven by the plant phosphate starvation response. *PLoS Biology*, 2019, **17**(11): e3000534
8. Duan S L, Feng G, Limpens E, Bonfante P, Xie X N, Zhang L. Cross-Kingdom nutrient exchange in the plant–arbuscular mycorrhizal fungus–bacterium continuum. *Nature Reviews Microbiology*, 2024, **22**(12): 773–790
9. Wen Z H, Pang J Y, Shen J B. Integrating root exudation into belowground carbon economics. *Trends in Plant Science*, 2026, **31**(6): 771–786
10. Duan S L, Huo Y J, Tian Y X, Yan W H, George T S, Huang C D, Feng G, Zhang L. The interplay of direct and mycorrhizal pathways for plants to efficiently acquire phosphorus from soil. *Frontiers of Agricultural Science and Engineering*, 2025, **12**(1): 47–56
11. Shen J B, Bai Y, Wei Z, Chu C C, Yuan L X, Zhang L, Cui Z L, Cong W F, Zhang F S. Rhizobiont: an interdisciplinary innovation and perspective for harmonizing resources, environment, and food security. *Acta Pedologica Sinica*, 2021, **58**(4): 805–813 (in Chinese)
12. Xu H R, Liu W D, He Y H, Zou D, Zhou J H, Zhang J Y, Bai Y. Plant-root microbiota interactions in nutrient utilization. *Frontiers of Agricultural Science and Engineering*, 2025, **12**(1): 16–26
13. Wang L Y, Liao D, Rengel Z, Shen J B. Soil–plant–microbe interactions in the rhizosphere: incremental amplification induced by localized fertilization. *Frontiers of Agricultural Science and Engineering*, 2025, **12**(1): 57–68