Opinion paper

Triggering root system plasticity in a changing environment with bacterial bioinoculants – Focus on plant P nutrition

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Abstract

To improve the sustainability of agricultural systems, an efficient use of resources such as phosphorus (P) nutrients is necessary. To reach this goal, the development of more resilient crop varieties able to cope with heterogeneous soil conditions in space and time is a promising strategy. Plants face many stresses in their natural environment and can respond to them by adjusting their phenotype (phenotypic plasticity). Integrating plastic root system traits into breeding strategies may help reach acceptable yields in low-input systems by enhancing water and nutrient uptake, thus reducing resource inputs in conventional farming systems. Bacterial bioinoculants, also considered to be a class of biostimulants, have shown great potential to increase the nutrient use efficiency of plants through diverse strategies including the modulation of root system plasticity. However, the study of plant plasticity can be challenging, particularly regarding the root system. This paper aims to encourage the integration of bioinoculants into the study of root system plasticity in response to P deficiency. We first focus on the plasticity of root architectural traits in a P-limiting context and on how bioinoculants can modulate root system plasticity and

enhance P use efficiency. Then, important methodological points of attention to consider for the study of root system plasticity are highlighted.

Keywords
root system, P use efficiency, bacterial biostimulants, phenotypic plasticity

Declarations

Funding

This research was supported by internal research funds from the University of Liège (Belgium). BMD is supported by a grant from the German Research Foundation (project 470604360).

Conflicts of interest/Competing interests

The authors declare there are no conflicts of interest to disclose.

Availability of data and materials

Not applicable.

Code availability

Not applicable.

Acknowledgements

This research was supported by internal research funds from the University of Liège (Belgium). BMD acknowledges funding from the German Research Foundation (project 470604360). The authors are thankful to Marcus Griffiths (Donald Danforth Plant Science Center, St. Louis, Missouri, USA) and Maria C. Hernandez-Soriano (John Innes Centre, Norwich, UK) for commenting earlier versions of the manuscript.

Abbreviations

ACC 1-aminocyclopropane-1-carboxylic acid
AMF arbuscular mycorrhizal fungi
IAA indole-3-acetic acid
MAMP microbe-associated molecular pattern
P phosphorus
PGPR plant growth-promoting rhizobacteria
PSB phosphate-solubilizing bacteria
PSM phosphate-solubilizing microorganisms
PUE phosphorus-use efficiency

Introduction

In the context of global change, crop production systems are evolving towards strategies that promote the sustainable management of soil resources. This is particularly important for plant P nutrition, in view of the poor availability of P resources to crops in arable soils (Simpson et al. 2011) and uncertainties regarding the limited mineral P reserves that can be used to produce mineral fertilizers in an economically viable way (Cordell et al. 2009).

In order to develop strategies that allow better exploitation of soil resources in variable growing conditions, research on plant root systems and their high plasticity is becoming increasingly important (Bardhan et al. 2021; Lobet et al. 2019). The plant genotype influences the physical, chemical and biological properties of the rhizosphere (i.e., the root vicinity, 'soil influenced by roots' as originally defined by Hiltner (1904)) through root growth and rhizodeposition. The rhizosphere could therefore be considered as an 'extended phenotype' (result of the effects of plant genes outside the organism; defined by Dawkins (1982)) and a determinant for plant fitness (de la Fuente Cantó et al. 2020).

Rhizospheric traits, considering the root-soil-microorganisms tripartite interaction, are not yet integrated into breeding programmes (de la Fuente Cantó et al. 2020; Trivedi et al. 2020). However, they are determinants of improved P-acquisition efficiency, one of the highlighted strategies to obtain P-efficient genotypes (Cong et al. 2020). The interaction of plants with their microbiome and beneficial rhizospheric microorganisms is gaining more interest (Compant et al. 2019; Wei and Jousset 2017) and should be seen as a way to obtain new phenotypes with increased fitness (Trivedi et al. 2020). The use of 'microbial biostimulants' may help to reduce the input required to achieve an acceptable yield by increasing the bioavailability of nutrients in the soil and/or improving the plant nutrient use efficiency (Box 1) (du Jardin 2015). Bacteria are known to affect plant P nutrition through various mechanisms including improvement of P availability and modulation of plant growth (Pii et al. 2015), and constitute the focus of this paper.

The study of the impact of bacterial inoculants on plant plasticity in a P-limiting context deserves consideration. In this paper, we first focus on the plasticity of plant root systems, the traits of interest in P nutrition and the role of bacterial biostimulants in triggering root system plasticity. Then, the article focuses on growing conditions and methods of plasticity analysis that could be considered and eventually implemented in research.

Root system plasticity

The interest of plasticity for breeding programmes

For decades, breeding programmes have selected high-yielding varieties under constant optimal or targeted stress conditions. This strategy has resulted in reduced plasticity (Box 2) in crop species compared to wild ones (1.8-fold difference, among 11 species and a diversity of traits) (Des Marais et al. 2013). Cultivated genotypes, exhibiting more stable traits, may have greater susceptibility to varying or suboptimal conditions compared to more flexible wild-type genotypes (Dalal et al. 2017). Past selection also likely led to smaller root systems, enabling a reduction of the competition between crop root systems and consequently yield increases (Fradgley et al. 2020). However, in the current context, the need for crop cultivars that have sufficient productivity in low-input systems and reduced input requirements in high-input systems is emphasized (Lynch and Brown 2012). Phenotypic plasticity is an important component of plant root systems that needs to be further considered in order to achieve acceptable yields under varying conditions (Lobet et al. 2019; Reynolds et al. 2021). Root architectural plasticity was shown to be related to yield stability in response to drought and low phosphorus stress (Sandhu et al. 2016). It is also relevant for plant performance in the context of plant intra- and interspecific interactions (Yu et al. 2020; Zhang et al. 2020). Therefore, plant breeding strategies should seek 'robust' cultivars performing optimally in a broad range of suboptimal conditions.

Root system plasticity for enhanced P-use efficiency (PUE)

Root traits can be linked to their functional utility, i.e., resource acquisition or utilization (York et al. 2013), which

are components of P-use efficiency (PUE) (du Jardin 2020). Resource acquisition may be further explored by classifying the traits into two categories according to the foraging strategy: exploration of new soil domains and exploitation of the existing domains (York et al. 2013). A root strategy to enhance P acquisition comprises better exploration of soil P-rich domains and exploitation of these domains through P solubilization and uptake (Lynch 2019). Among the trait categories defined by McCormack et al. (2017), root dynamics, root system architecture, physiology, morphology, anatomy and microbial associations present interesting P-responsive traits (Fig. 1). Examples of the influence of the P context on root traits are given in Table 1. Due to the poor mobility of P, it can be argued that traits favouring soil exploration are probably of first importance in low input systems by enabling P interception by roots and locating plant exudates as well as microbial interactions in P-rich domains (Lynch 2019).

Bacterial inoculants and modulation of root system plasticity

Modulation of root system development by beneficial bacteria

The influence of rhizospheric microorganisms on root traits that are determinant for the plant PUE is described in Table 1. Numerous bacterial strains produce phytohormones, including auxins and cytokinins, as well as secondary metabolites that affect the auxin/cytokinin ratio and the ethylene level *in planta*. The auxin/cytokinin ratio is an important regulator of root system development (Vacheron et al. 2013). The stimulation of root development and branching by bacterial auxins increases the available root surface and the carbon supply for colonization by bacteria (Talboys et al. 2014). Bacteria-produced cyclodipeptides were shown to impact the root system architecture of *A. thaliana* through modulating auxin-responsive gene expression in roots (Ortiz-Castro et al. 2019). Volatile organic compounds emitted by rhizobacteria were also found to alter root system morphology in different plant species (Delaplace et al. 2015; Sharifi and Ryu 2018). Most beneficial rhizobacteria produce the enzyme 1-aminocyclopropane-1-carboxylic acid (ACC) deaminase, which degrades the precursor of ethylene ACC in plants. By lowering the ethylene level in plants, the bacterial ACC deaminase impacts the root system architecture (Vacheron et al. 2013) as ethylene level in plants modulate the formation and elongation of lateral roots as well as root hairs (Neumann 2016). The modulation of plant growth rate and phenology by bacteria (Delaplace et al. 2015; Poupin et al. 2013; Zaheer et al. 2019) also impacts the root system development and plant nutrition (Vacheron et al. 2013). Stimulating root growth rate can improve soil exploration through increased root surface area, which can lead to increased acquisition of soil resources (Poupin et al. 2013). Ion uptake kinetics were shown to be modulated by bacteria-released auxin. Despite increased root production, expression of P transporters per unit root surface was reduced in inoculated plants under low P conditions, which resulted in lower P uptake per unit of root surface area (Talboys et al. 2014). These examples show how beneficial bacteria modulate root traits and trigger the plant responses to P limitation. The role of bacteria in the timing of the triggering of plant P responses is a point that could be investigated.

Beneficial bacteria also improve plant growth by impacting plant nutrition. This can be achieved by increasing nutrient availability in the root vicinity (P solubilization and mineralization) or enhancing the plant's nutrient acquisition processes (rhizosphere acidification, changes in root exudation) (Vacheron et al. 2013). There is little evidence to suggest that phosphate-solubilizing microorganisms (PSM; bacteria and fungi, arbuscular mycorrhizal fungi excluded) solubilize sufficient P to meet plants' needs under field conditions. PSM can however show positive effects on the plant's response to P-limiting conditions through other mechanisms that impact root system development. The turnover of P in microbial biomass is more likely to provide P to plants over a long time

(Raymond et al. 2020) yet the recently discovered plant-fungus symbiosis referred to as 'feremycorrhiza' (non-root-colonizing fungi benefitting plant growth through rhizosphere modification and nutrients mobilization) offers promise for more efficient P solubilization (Kariman et al. 2020). Although mycorrhizal fungi are outside the scope of this paper, they make an important contribution to plant P nutrition by solubilizing P and enhancing soil exploration through their hyphae (Chippano et al. 2021; Richardson et al. 2011).

Bacterial biostimulants

As the root system exhibits plasticity in response to its biotic environment, modulation of the plant microbiome is of great interest to optimize plant production systems (Compant et al. 2019). Modulation of the plant microbiome can be achieved by inoculation of single strains or consortia as well as by agricultural management and plant selection (Compant et al. 2019; Hartman et al. 2018). The development of single strain inoculants usually starts with the screening of strain collections for beneficial functions like P solubilization, N fixation, plant hormones and ACC deaminase production. Promising strains are then tested in (semi-)controlled conditions and finally in the field. Using this bottom-up approach, many performant strains in the lab fail to reproduce this success in the field (Compant et al. 2019). Limited success of inoculants in the field and low reproducibility can be explained by competition between well-adapted microorganisms of the receiving environment and the introduced bacteria. The extent to which such priority effects and their associated mechanisms (niche pre-emption and niche modification) modulate the assembly of soil microbial communities and determine the success of plant inoculation in the field certainly deserves more attention in future research (Debray et al. 2022; Fukami 2015). The ability of the strain to colonize the targeted plant species and to exhibit the desired function in the environment is also important (Compant et al. 2019). The establishment of a lasting relationship between the host and the inoculated bacteria will depend on the ability of the bacteria to persist in the environment, to colonize the host and to be metabolically active (Charron-Lamoureux et al. 2020). Short exposure of plants to bacterial biostimulants might also result in positive outcomes through a priming effect (Cordovez et al. 2018). The assessment of bacterial population dynamics can be challenging, but it is essential to determine how to efficiently use bacterial inoculants in various environmental conditions. The presence of desired taxa and reactions can be assessed by using high-resolution tools (e.g. in situ sensors and omics analyses) measuring diagnostic molecules (e.g. exudates and volatiles) or microorganisms (Trivedi et al. 2020, supplementary information). Quantitative PCR can be used with specific primers to assess inoculant survival in the rhizosphere (Renoud et al. 2022), while next-generation sequencing techniques allow an in-depth characterization of the root-associated microbial diversity (Azarbad et al. 2022; Renoud et al. 2022). Soil-plant-bacteria interactions are complex and the beneficial properties of the strains may be specific to plant species and soil properties. Therefore, isolating and characterizing native bacterial strains living in the rhizosphere of plants growing in a target environment constitutes an alternative to the use of non-native consortia to obtain competitive strains which are well adapted to local biotic and abiotic conditions (Majeed et al. 2015; Santoro et al. 2015; Zahid et al. 2015).

By inoculating bacterial consortia, different mechanisms and desired traits can be combined. Strains with the same mode of action but tolerating different environmental conditions can also be co-inoculated (Compant et al. 2019). Based on plant-bacteria binary-association assays, Herrera Paredes et al. (2018) found that functional stacking within a bacterial consortium gives information on the effects of the consortium on the plant phenotypic response. The expression of phosphate starvation responsive genes and immune system-related genes was modulated by the bacterial synthetic communities and the effects of the bacteria were dependent on the nutritional status of the plant

(Herrera Paredes et al. 2018). The construction of synthetic microbial communities (through culture and screening for beneficial traits or synthetic biology) and their use to increase plant fitness and productivity can now be translated into practice but have not yet been integrated into crop breeding (Trivedi et al. 2020).

These elements suggest that desired combinations of plant traits can be reached by microbial-induced shifts of phenotype. Plant breeding could modify both genomic information and plant-associated microbiota to obtain new phenotypes (Wei and Jousset 2017). However, transmission of the plant microbiome and of microbiome-directed traits to the next generation is challenging (Wei and Jousset 2017). An inheritable assemblage of plant and microbes could be achieved by inoculating flowers with specific microbes that will then be vertically transmitted to the next plant generation (Mitter et al. 2017) and will play an important role in determining the structure of the root-associated microbiota, particularly at the early stages of plant development (Yang et al. 2017). Shao et al. (2021) observed that the assembly of the rhizosphere microbiome in maize is dominated by the soil microbiome but the seeds contained beneficial bacteria that promote phosphate acquisition of the plants when parents were cultivated in nutrient-deficient soil. The seed microbiome may serve as a functional compensation reservoir in the assembly of the root microbiome.

Studying root system plasticity

Challenges of root system phenotyping

Plant phenotyping can be challenging, especially when focusing on the root system which is not easily accessible. Considering that soil is a complex and heterogeneous matrix where many interactions occur, it is useful to work with simplified systems to improve our understanding of rhizosphere processes (Baudson et al. 2021; Rich and Watt 2013). However, the transposability of results from the lab to the field depends on the realism of the growing conditions used to perform the experiments. Arguments for a reversed lab-to-field pipeline arise as discrepancies between lab and field studies are often reported, as well as poor predictability of the outcome of field studies from greenhouse studies (Schmidt and Gaudin 2018).

Field-grown plants deliver valuable information about the root system architecture in real conditions but root phenotyping in the field is more challenging than under controlled conditions, and the environmental variability associated with field experiments makes it harder to identify the mechanisms underlying plasticity (Freschet et al. (2021) provides an extensive guide to field phenotyping methods). Therefore, the identification of seedling root traits that can be associated with mature root traits or performance of field-grown plants is a determinant for breeding programme strategies (Salungyu et al. 2020; Watt et al. 2013).

High-throughput phenotyping techniques generate a large volume of data that is needed to advance breeding and selection. However, the processing and analysis of this data is often a major bottleneck in root phenotyping studies, which is one of the reasons why machine learning approaches have gained popularity in recent years. For instance, deep learning now allows the fast and accurate segmentation of roots embedded in soil (Han et al. 2021; Smith et al. 2022), which is a prerequisite to quantify root plasticity under realistic conditions. The development of high performance and free image analysis software tools has greatly facilitated the standardization and increased speed of image analysis tasks, which is an important step towards integrating root phenotyping into plant breeding programmes. Examples of such root image analysis tools include RootPainter for image segmentation using deep learning (Smith et al. 2022), RhizoVision Explorer for the automated analysis of root crowns and scanned root images (Seethepalli et al. 2020, 2021), or Root-o-Mat for the analysis and mapping of enzyme activity at the soil-

root interface (Tegtmeier et al. 2021). Machine learning algorithms such as random forests have also proved useful in helping to identify important traits (Atkinson et al. 2017). The characterization of root physiological processes such as enzyme exudation and rhizosphere acidification has been facilitated by the development of 2D imaging techniques such as zymography and planar optodes (Blossfeld 2013; Ma et al. 2021). Although root exudation is a particularly challenging process to quantify in situ (Oburger and Jones 2018), leaf manganese concentration has been shown to be an interesting proxy for the exudation of carboxylates (Lambers et al. 2021). All the afore-mentioned phenotyping techniques can be implemented into co-cultivation systems to study the effects of bacteria on root system plasticity.

Studying the genetic control of plasticity and plant-bacteria interactions

The genetic control of root system plasticity is still poorly understood. The plasticity of a specific trait being a quantitative trait by itself, quantifying the plasticity as a trait would enable the identification of the genes involved in this plasticity (Laitinen and Nikoloski 2019). Using recombinant inbred lines, intraspecific variability in the plastic response of root traits was highlighted (Zhu et al. 2010) and plasticity-related regions in the context of P nutrition have already been reported (Zhu et al. 2005b, 2005a).

Regarding plant-bacteria interactions, the factors and mechanisms underlying recognition and interaction in plant symbiosis with rhizobia have been thoroughly investigated (Trivedi et al. 2020). The establishment of beneficial plant-bacteria interactions requires the modulation of plant immune responses by the bacteria. The plant immune system can recognize microbe-associated molecular patterns (MAMPs, such as flagellin, lipopolysaccharides, chitin) (Trivedi et al. 2020). Some beneficial plant-associated bacteria are able to escape the plant immune response to achieve an efficient plant-microbe symbiosis by avoiding receptor recognition through modification of the MAMP epitope, inhibition of the synthesis of MAMP-containing molecules or alteration of the bacterial cell wall composition (Hacquard et al. 2017). Microorganisms can also overcome plant defences by secreting effector proteins mimicking plant proteins, a strategy to elude MAMP-triggered immunity (Trivedi et al. 2020). On another side, the transcription factor PHR1 (PHOSPHATE STARVATION RESPONSE 1) is the major regulator of the phosphate starvation response and contributes to transcriptional regulation of the plant immune system, contributing to the assembly of the root microbiome (Castrillo et al. 2017). The signalling of the phytohormones salicylic acid, jasmonic acid and ethylene is essential in the defensive response action and in shaping the structure of microbial communities (Hacquard et al. 2017; Vishwakarma et al. 2020). In a review paper, Sharifi and Ryu (2018) discussed how bacterial volatile compounds might be perceived by plants, possibly sharing regulatory systems with green leaf volatiles. Indole produced by bacteria impacted indole-3-acetic acid (IAA) and jasmonate signalling in plants (Erb 2018). Tzipilevich et al. (2021) highlighted the role of bacterial auxin in bacterial survival and colonization of the root system through a feedback loop between bacteria and the plant immune system. The use of plant genotypes that are unable to detect bacterial signals would be of great interest to assess the impact of bacterial modulation of plasticity on plant performance.

Can modulation of root plasticity confer enhanced PUE and plant performance or fitness?

From an agronomic point of view, plasticity and performance (yield or biomass production per unit surface area) under stressful conditions should be considered together. The responsiveness to environmental constraints should not jeopardize the economic profitability of the crop (see the cost of plasticity, Box 2). The plasticity related to PUE should also be studied in order to assess the extent to which the response has a functional utility and confers an advantage regarding P stress (Hammond et al. 2009; Neto et al. 2016). This would make it possible to quantify

the benefits of the application of bioinoculants. Bacterial inoculants and traits conferring improved PUE may then be further explored and considered in breeding programmes (Hammond et al. 2009; Neto et al. 2016).

Considering the relationship between the variability of a trait and the yield (or a proxy) gives an insight into the impact of variation in the trait on plant performance (Neto et al. 2016). This can be achieved in an integrative manner by mapping the fitness landscape of specific root phenotypes, i.e., depicting the crop performance against a multi-dimensional set of external and internal factors (for instance, contrasting nutrient supplies or co-occurring stresses, trait plasticity and interaction with other traits). This approach becomes increasingly difficult as the cropping system becomes more complex (from high-input monoculture systems to low-input stressing environments) (Lynch and Brown 2012) and no examples of mapping of the fitness landscape in the context of biostimulant treatments under varying P conditions were reported at this time. This is a major challenge in the field of root phenomics.

Conclusion

Plants have developed adaptive strategies to cope with nutritional stresses including plasticity of the root system, enhancing soil exploration and exploitation. Bacterial inoculants are being considered in strategies for more sustainable crop production, notably due to their ability to modulate root system development at early stages. The inoculation of plants with bacterial biostimulants, as single strains or consortia, is a promising way to reach robust, P-responsive phenotypes. The plant microbiota could therefore be considered in crop breeding, together with the plant genome, to obtain new phenotypes. It is noteworthy that many challenges exist to study the root system plasticity in response to nutritional stress and inoculation with beneficial microorganisms, but important progress has been made in developing root system phenotyping techniques that could be implemented into co-cultivation systems. Key elements for the integration of bacterial inoculants into root phenotyping studies are given in Box 3, along with an example of experimental setup to study explorative root traits. The ability of bacteria to induce plasticity in traits that are important for the plant PUE is depicted by many examples. However, the impact of the bacteria-induced plasticity on plant PUE and performance should be quantified to be implemented into breeding programmes. The role of beneficial bacteria in the timing of the triggering of plant responses to P limitation and shift in plant phenology that could modulate the fitness landscape also deserves to be investigated.

Figure captions

Fig. 1 Root system traits enhancing P use efficiency. Root traits were classified according to McCormack et al. 2017

Table captions

Table 1 Influence of P starvation and microbial context on root system traits enhancing PUE, classified according to their foraging strategy

Box 1: Biostimulants

A plant biostimulant is defined in Regulation (EU) 2019/1009 of the European Parliament and of the Council of 5 June 2019 based on claims that it is '*a fertilizing product the function of which is to stimulate plant nutrition*

processes independently of the product's nutrient content with the sole aim of improving one or more of the following characteristics of the plant or the plant rhizosphere: nutrient use efficiency, tolerance to abiotic stress, quality traits or availability of confined nutrients in the soil or the rhizosphere' (EU 2019). Biostimulant products are composed of substances or microorganisms: humic and fulvic acids, protein hydrolysates, seaweed and plant extracts, biopolymers (e.g., chitosan), inorganic compounds (e.g., aluminium, cobalt, sodium, selenium and silicon), beneficial fungi and bacteria (i.e., microbial biostimulants, bioinoculants) (reviewed by du Jardin 2015). Biostimulants aim to affect the plant's physiology rather than supplying nutrients or protecting the plants against pathogens or pests. They should be considered in the context of 'high-output low-input' agriculture (du Jardin 2015, 2020).

Box 2: Phenotypic plasticity

Plants respond to variations in environmental conditions by modifying their phenotype (Nicotra et al. 2010). This response capacity is called phenotypic plasticity and can take place at different levels such as physiology, anatomy and morphology. The plastic response of plants to varying environmental conditions may eventually result in enhanced plant survival and fitness (Lobet et al. 2019). However, under favourable environmental conditions, the costs for the construction and maintenance of sensory and regulatory mechanisms underlying plasticity can have a negative impact on plant performance (Dalal et al. 2017; Schneider and Lynch 2020). The cost of plasticity is defined as '*the reduction in the fitness of a genotype due to its phenotypic plasticity, as compared to fixed patterns of development that maintain homeostasis under stable conditions*' (Dalal et al. 2017). Phenotypic plasticity may also be maladaptive when environmental conditions fluctuate and there is a time lag between environmental cues and the expression of the plastic response (Schneider and Lynch 2020).

Trade-offs among plastic responses exist under multiple stress conditions and may impair the plant's fitness as well. P has low mobility in soils and is present mainly in the topsoil due to the deposition of plant organic matter. In comparison with P, mobile resources like nitrate and water have a more vertical distribution in soils as they can quickly move to deeper soil layers. Therefore, favouring traits that enable P acquisition may reduce the efficiency of plants in taking up nitrate and water (Lynch 2011). In case of multiple edaphic stresses, identifying a single phenotype that performs optimally across contrasting environments is unlikely (Rangarajan et al. 2018). However, suites of traits benefitting the acquisition of several nutrients (e.g., N, S, K, B and P) were identified and could be considered to obtain root ideotypes suitable for multiple environmental conditions (White et al. 2013).

Trade-offs were also identified among functional traits related to P-uptake strategies (Fig. 1). Root diameter is positively correlated to the release of P-mobilizing exudates in the rhizosphere and colonization by arbuscular mycorrhizal fungi, but negatively correlated to root branching intensity and specific root length in herbaceous plant species (Wen et al. 2019). Han et al. (2022) recently provided a different picture by showing that the greatest root phosphatase activity in forest tree species was found in "do-it-yourself" species with a high specific root length and low mycorrhizal colonization rates.

Box 3: Key points for the integration of bioinoculants into root phenotyping studies

Given the lack of reproducibility that is often observed between laboratory and field studies when screening for bacterial strains promoting plant growth under P-limited conditions, the ability of bacterial inoculants to modulate root system traits and plasticity and improve plant fitness should ideally be tested under field or semi-controlled conditions (e.g., using outdoor mesocosms or rhizoboxes filled with field-collected soil) (Dal Cortivo et al. 2018; Durand et al. 2016). As environmental conditions are highly variable in space and time, such trials should ideally be repeated in different locations and different years to draw robust conclusions. The number of strains (either alone or in combination) that is possible to test in the field being limited, the strains and/or consortia should be selected based on criteria such as ability to maintain and grow in the rhizosphere and P-mobilizing traits. The use of native strains is an interesting approach to modulate the natural microbial community and its functioning because these strains are well adapted to local environmental conditions. The traits of interest should be clearly defined *a priori* as they will condition the choice of the growing system and sampling technique. Compared to lab studies, field trials allow plants to reach more advanced developmental stages, but the range of easily measurable traits is often more limited than under more controlled conditions. Following field trials, in-depth mechanistic studies of how selected bacterial strains affect plant traits, PUE and fitness can be carried out under more controlled conditions such as in the lab, in a greenhouse or in an ecotron, provided that environmental conditions are carefully chosen to mimic situations experienced by plants and their associated microbes in the field.

In table 1, a lack of data on the impact of bacterial inoculants on root growth angle was highlighted. Here we provide an example of an experimental approach that could be used to study the effects of bacterial inoculants on parameters that affect soil exploration by roots of a single crop under deficient P conditions, including root growth angles of main root axes and their plasticity. Field trials with coated seeds (either inoculated or not) should ideally be conducted in different locations (e.g., environmental gradient) and repeated in different years to measure plant performance (e.g. yield and yield stability) and root traits for which plasticity needs to be quantified. Root crown phenotyping methods (e.g., shovelomics) can be used to measure the growth angles of main root axes for crops such as maize, soybean and wheat (Fradgley et al. 2020; Seethepalli et al. 2020; Trachsel et al. 2011). Root growth angles and root growth rates can also be estimated in the field using root observation windows (i.e., rhizoboxes) (Alonso-Crespo et al. 2022; Freschet et al. 2021), and minirhizotrons can be used to provide additional information such as root length density and distribution in the soil (Freschet et al. 2021). Soil coring techniques can be used to collect roots to measure additional traits related to root anatomy, morphology and physiology shown in Figure 1 (Freschet et al. 2021).

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