REVIEW ARTICLE

Genetic and ecological inheritance of plant growth-promoting rhizobacteria

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Abstract

Background The utilization of beneficial (Rhizo) bacteria, as an alternative to traditional fertilizers, has emerged as an eco-friendly strategy for ameliorating sustainable agricultural production. This approach aims to reduce the use of agrochemicals and minimize environmental pollution.

Scope This review provides an updated insight into the ecological impact of plant growth-promoting rhizobacteria (PGPR), focusing on the resident microbiome and its potential transferability to the next generation of plants.

Conclusion In this context, PGPR are assumed to alter the rhizosphere microbiome by outcompeting the existing taxa through nutrient deprivation, acidification of the environment, metabolites production, and consequently, increasing the copiotrophic taxa. Such modifications can maximize the beneficial interactions of plant-PGPR by increasing the bioavailability of nutrients and handling diverse signaling pathways. The effects of interactions within the PGPR-root system can adjust the composition of root exudates and influence the release of bioactive molecules by the root, especially under stress conditions, which can act as signals to reactivate and recruit the beneficial microbes in the rhizosphere and endosphere in favor of the plants. Such changes in microbiome structure can occur gradually over time, even if the survival rate of PGPR in soil and their re-colonization efficiency inside plant tissue are limited. The aforementioned modifications in the rhizosphere and plant microbiome have the potential to increase the survival chances of the progeny plants growing under the same stress conditions. Establishing a comprehensive and robust knowledge framework that addresses all of these issues is critical for significantly advancing the field of microbe-plant interactions and for developing reliable applications of PGPR.

Introduction

Nowadays, the demand for agricultural products has surged to meet the needs of the growing human population. Meeting this demand requires either expanding the area under cultivation or increasing production per unit area. The first strategy, involving land-use change and intensive management practices, has not been effective. The conversion of natural landforms into agricultural land has turned out to be a gamble and has led to land degradation (Cerdà et al. 2010;

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Yaghoubi et al. 2019a, 2020). The second solution led to the widespread use of synthetic inputs (e.g., fertilizers, pesticides, and herbicides) to improve crop yields. As a result, chemicals have become the dominant source of pollution in agriculture (Meena et al. 2017; Yaghoubi et al. 2018). In addition, the increased global demand for agrochemicals has driven up their prices, causing economic issues (Nishimoto 2019). These issues call for a rethink of technologies aimed at increasing crop production and emphasize the need for alternative strategies such as the use of beneficial natural processes and bio-based products. One of the most advanced alternatives is the use of rhizobacteria as Plant Growth-Promoting Rhizobacteria (PGPR). These free-living and root-colonizing bacteria are classified according to their mode of action, namely: (i) biofertilization (increasing the availability of nutrients to plants); (ii) hormonal stimulants or phytostimulators (stimulating plant growth through the secretion or production of certain hormones); (iii) bioremediation (biodegrading toxic organic compounds and chemical contaminants in soils and having the potential to enhance phytoremediation); and (iv) biological pesticides and herbicides (controlling weeds, insects and plant pathogens by producing certain antibiotics or metabolic antiviral compounds) (Joutey et al. 2013; Yaghoubi et al. 2019b; Bakhshandeh et al. 2020; Manoj et al. 2020). Recent examples of identified PGPR and their function as agents of biofertilization, phytostimulation, bioremediation and bioprotection, are summarized in Table 1.

While numerous studies have investigated the effects of PGPR, several questions remain unanswered. These relate to PGPR-induced changes in the plant microbiome and their potential heritability to the next generation of plants, as well as their effects on agro-ecosystems functions beyond the host plants and the legacies left in the host communities. Despite their importance, these issues have often been ignored. In this regard, a keyword search of "biostimulant AND bacteria" in Web of Science (webofscience.com) revealed 254 papers on the PGPR-based biostimulants in the last decade (2014–2023). Among them, only 10 articles discussed the microbiome alterations in plants and/or rhizosphere, followed by 4 articles showing the effects of biostimulants on ecosystems, with only one addressing the legacy effect of biostimulants. Therefore, the present article aims to review and discuss the most relevant findings on the ecological and genetic impacts of PGPR. The focus was on impacts at the level of the host plants/rhizosphere microbiomes, the next generation of stimulated plants and agro-ecosystems.

The ecological impact of PGPR on the resident community

Plant endosphere and rhizosphere microbiome assembly

PGPR, like other invasive species, may have unexpected significance for the ecosystem and legacy impacts via niche construction, where the effects of PGPR can extend beyond the host plants toward ecosystem functions and even outlast the persistence of the PGPR (Callahan et al. 2014; Moore et al. 2022). One of these effects can be the modification of the resident microbiome (Table 2). Plants possess a so-called microbiome, which comprises the collective of microorganisms living on and within the plant, including those associated with flowers (anthosphere), fruits (carposphere), stems (caulosphere), leaves (phylloplane), root surface (rhizoplane), and within plant tissues (endosphere), as well in the soil under the direct influence of the root system (rhizosphere), and germinating seeds (spermosphere) (Shade et al. 2017). Microbiomes composition can be affected by different environmental and plant growth conditions (Chouhan et al. 2021; Mukherjee et al. 2022), but can, in turn, affect plant production and tolerance to environmental stress (Lau and Lennon 2012; Sugiyama et al. 2013). Nevertheless, much uncertainty still exists about the activation and recruitment of the microbiome in biostimulated plants, especially under biotic and abiotic stress conditions. Although the effect of PGPR in modifying the rhizosphere and plant microbial communities has been shown to be one of the main modes of action of PGPR to benefit plants under field conditions (Kusstatscher et al. 2020), the emergence or increase in the relative abundance of some microorganisms can also pose a threat to plant and human health. Understanding the specific drivers in plant microbiome assembly in response to biostimulants, and whether the responses are host- or environment-mediated, is crucial for developing the reliable application of beneficial bacteria in sustainable agriculture (Yaghoubi et al. 2022; Bandopadhyay et al. 2023).

Table 1 Beneficial effects of PGPR in improving plant-based agro-ecosystem functions

PGPR species	Experiment condition	Summary of results	Reference
- *Acinetobacter beijerinckii* - *Pseudomonas fluorescens*	Field	Improving the utilization of carbon sources for alfalfa plant growth.	Tang et al. 2023
- *Pantoea agglomerans* - *Rahnella aquatilis* - *Pseudomonas orientalis*	Field	Increasing the grain yield, K use efficiency and K uptake in straw and grain in rice plants, as well as reducing the use of K chemical fertilizers.	Yaghoubi et al. 2018a, 2019b
- *Herbaspirillum* sp. - *Burkholderia* sp. - *Pseudacidovorax* sp. - *Azospirillum* sp.	Field	Significantly increasing plant growth, NPK uptake and grain yield in rice plants, as well as reducing the use of nitrogen fertilizers.	de Souza et al. 2013
- *Bacillus* sp.	Field	Enhancing number of bolls per plant and boll weight, P availability and yield in cotton plants.	Qureshi et al. 2012
- *Pseudomonas fluorescens*	Field	Inoculation showed a significant increase in number of tillers per wheat plant, grain yield, and straw yield, compared to un-inoculated plants.	Shaharoona et al. 2008
-*Bacillus megaterium* -*Enterobacter* sp. -*Arthrobacter chlorophenolicus*	Field and pot	Significantly increasing plant height, grain yield and straw yield of wheat plants under pot and field conditions.	Kumar et al. 2014
- *Bacillus* sp. - *Enterobacter gergoviae*	Field and pot	Increasing rice grain yield in pot and field experiments.	Rajapaksha et al. 2011
- *Actinobacterium* sp.	Pot	Boosting the level of antioxidant molecules and rapeseed plant biomass under elevated CO_2 conditions.	Hagagy and AbdElgawad 2023
- *Saccharomonospora* sp.	Pot	Improving biomass production and plant tolerance to chromium toxicity.	Albqmi et al. 2023
-*Nocardiopsis* sp.	Pot	Boosting the antioxidants content and health-promoting activities of cabbage sprouts.	AbdElgawad et al. 2023
- *Bacillus velezensis*	Pot	Alleviating the inhibitory effect of salt on lettuce growth through improving reactive oxygen scavenging and osmotic adjustment.	Bai et al. 2023
- *Actinobacterium* sp.	Pot	Improving soybean plant toleration and adaptation against galaxolide contamination.	Halawani and Aloufi 2023
- *Acinetobacter pittii* - *Acinetobacter oleivorans* - *Acinetobacter calcoaceticus* - *Comamonas testosteroni*	Pot	Improving the metabolic and nutrient status of durum wheat grains under non-stress, drought and salinity conditions.	Yaghoubi et al. 2022
- *Achromobacter xylosoxidans*	Pot	Improving maize growth and productivity under drought stress.	Danish et al. 2020
- *Bacillus* sp.	Pot	Ameliorating salt stress and enhancing plant growth under salt stress by inducing maize plant responses such as activation of defense enzymes and regulation of chlorophyll, proline, and soluble sugar contents.	Misra and Chauhan 2020
- *Pseudomonas libanensis*	Pot	Enhancing phytoremediation of metal-polluted saline soils and decreasing the metal uptake by sunflower plants.	Ma et al. 2019

Table 1 (continued)

PGPR species	Experiment condition	Summary of results	Reference
- *Artherobacter woluwensis* - *Microbacter iumoxydans* - *Artherobacter aurescen*, - *Bacillus megaterium* - *Bacillus aryabhattai*	Pot	Maintaining osmotic balance and regulating salt tolerance in soybean plants.	Khan et al. 2019
- *Bacillus amyloliquefaciens*	Hydroponic system	PGPR reprograms rice plant metabolism for deficiency-induced stress amelioration, by inducing metabolic and physiological parameters.	Bisht et al. 2019
- *Aneurinibacillus aneurinilyticus* - *Paenibacillus* sp.	Pot	Alleviating the negative effects of salinity stress by activation of ACC deaminase in French bean seedlings. Increasing root and shoot length, root and shoot fresh weight, root and shoot biomass, and total chlorophyll content in seedlings subjected to salinity stress.	Gupta and Pandey 2019

In this regard, some recent studies have reported significant changes in the microbial community structure of the rhizosphere and endosphere in response to the PGPR inoculation under both controlled environments and real field conditions (Table 2). Although the mechanisms underlying these effects are not well understood yet, three hypotheses have been defined, including resource competition, direct antagonism and synergism (Mawarda et al. 2020). Once introduced, PGPR inoculants may become stable in the soil and potentially outcompete certain taxa by using existing resources, by acidifying the environment (Zhang et al. 2009), or by producing siderophores and having greater access to the soil iron reservoir (Wandersman and Delepelaire 2004; Mawarda et al. 2020). In addition, Castro-Sowinski et al. (2007) proposed the secretion of antibiotic compounds by PGPR (e.g., 2,4-diacetyl phloroglucinol, trifolitoxin and phenazine) as one of the main strategies of PGPR to influence rhizobacterial communities.

The genetic diversity of microbial communities may also be affected by microbial inoculums through interactions and horizontal gene transfer (HGT) (Mawarda et al. 2020). In this regard, Van Elsas et al. (1998) described the transfer of a mobilizable plasmid from *Pseudomonas fluorescens* to Gram-negative bacteria, mainly *Enterobacter* spp., in the rhizosphere of field-grown wheat. According to Xiong et al. 2017; the inoculation of *Bacillus amyloliquefaciens* increased the abundance of taxa with a potentially antagonistic effect on plant pathogens. The occurrence of genetic transformations within communities may be traced to areas of high microbial density (e.g., the rhizosphere) that support quick and pervasive horizontal gene transfer (Kent et al. 2020). This process provides further opportunities for bidirectional transfer with unforeseen consequences that may persist long after the original inoculant has disappeared (Moore et al. 2022). It is also important to consider the potential acquisition of DNA from the host communities by PGPR, as this can potentially affect PGPR traits, especially their function and persistence in an agro-ecosystem (Munck et al. 2020).

The recent interpretations overlook many indirect effects of PGPR on soil microbial communities, including implications for soil properties (e.g. nutrient availability, cation exchange capacity, pH) (Kusstatscher et al. 2020; Lopes et al. 2021), root morphology (Gomes et al. 2001), and plant root secretions (Yuan et al. 2015), which are themselves affected in some way by rhizobacteria and could stimulate microbial growth in the rhizosphere (see the following sub-section for a deep discussion of this topic). Furthermore, potential biases in rhizobacterial community structure could results from other factors such as plant age (Castro-Sowinski et al. 2007), developmental stage (Herschkovitz et al. 2005; Piromyou et al. 2011), and agricultural practices including tillage (Yaghoubi et al. 2020), crop rotation (Alvey et al. 2003), and wastewater

Table 2 The impacts of PGPR application on the composition of rhizosphere and plant endosphere microbial communities

PGPR	Host	Experimental condition	Summary of results	Reference
- *Acinetobacter beijerinckii* - *Pseudomonas fluorescens*	Alfalfa	Field	Improving the diversity and richness of the rhizosphere bacterial communities.	Tang et al. 2023
-*Azospirillum brasilense* - *Pseudomonas fluorescens*	Maize	Field	Modifying the physiology of the rhizosphere microbiomes in the reproductive stage.	Di Salvo et al. 2018a
- *Azospirillum brasilense*	Wheat	Field	Regulating the physiology and genetic structure of rhizosphere microbial communities	Di Salvo et al. 2018b
- *Pseudomonas brassicacearum* - *Burkholderia sordidicola*	Rapeseed	Field and pot	Reporting a correlation between the diversity of the seed microbiome and the colonization of beneficial bacteria.	Rybakova et al. 2017
- *Azospirillum brasilense*	Rice	Field	Increasing the genetic diversity of rhizosphere bacterial communities.	García de Salamone et al. 2010
- *Azospirillum lipoferum*	Maize	Field	Shifting in the composition of the indigenous rhizobacterial community.	Baudoin et al. 2009
- *Bacillus velezensis*	Lettuce	Pot	Regulating the rhizosphere bacterial community composition under salt stress.	Bai et al. 2023
- *Pseudomonas sivasensis*	Canola	Pot	Significant alterations in the diversity of the native rhizosphere microbiome by raising the abundance of beneficial bacteria.	Świątczak et al. 2023
- *Acinetobacter pittii* - *Acinetobacter oleivorans* - *Acinetobacter calcoaceticus* - *Comamonas testosteroni*	Durum wheat	Pot	Significant changes in the rhizosphere and root endophytic bacterial communities.	Yaghoubi et al. 2021
- *Bacillus amyloliquefaciens*	Cucumber	Pot	Reducing the rhizosphere bacterial diversity, despite not having a direct effect on the inhibited taxa in the rhizosphere.	Wang et al. 2021
- *Enterobacter* sp. - *Pseudomonas* sp.	Tomato	Pot	Modulating the rhizosphere microbiome functioning and improving microbial diversity.	Zuluaga et al. 2021
- *Paracoccus versutus* - *Aeromonas caviae*	Maidenhair fern	Pot	Sustaining microbial diversity in the rhizosphere under heavy metal stress	Marwa et al. 2020
- *Pseudomonas* sp. - *Burkholderia* sp.	Mustard greens	Pot	Bacterial communities in the rhizosphere had more complex and compact associations in the presence of PGPR.	Kong et al. 2019

Table 2 (continued)

PGPR	Host	Experimental condition	Summary of results	Reference
- Bacillus amyloliquefaciens	Cucumber	Pot	Suppressing disease by altering the structure and function of rhizosphere microbiome.	Han et al. 2019
- Burkholderia phytofirmans	Maize	Pot	Reporting minor changes in the rhizosphere and plant-associated microbial communities.	Touceda-González et al. 2015
- Bacillus aryabhattai *- Bacillus megaterium*	Mustard greens	Pot	Significant shifts in the rhizosphere microbial community of eight-week inoculated soil.	Jeong et al. 2013
- Bacillus subtilis	Tomato	Pot	Changes in rhizosphere microbial communities resulted in root-architectural alterations.	Felici et al. 2008

irrigation (Oved et al. 2001). Wei et al. (2019) considered some plant-associated changes in bacterial communities as a result of recruitment of specific bacteria via characteristic root exudates. This may also explain why the plant-dependent impact on bacterial community structure is more pronounced in the rhizosphere compared to the root endosphere (Edwards et al. 2015).

How does the interaction between root exudates and PGPR lead to distinct changes in the resident bacterial community?

Elucidating the chemical mechanisms by which plant-PGPR interactions result in the release of beneficial exudates may be critical to our understanding of how plant-microbes associations influence plant biological pathways and lead to proper responses to environmental challenges. One of the beneficial effects of PGPR can be attributed to the regulation of the release of root exudates, which are known for their strong impacts on biological processes in the rhizosphere (Castro-Sowinski et al. 2007). Root exudates are composed of diverse metabolites and easily degradable organic carbon and nitrogen compounds such as sugars, amino acids, organic acids, fatty acids, phytohormones, volatile organic compounds, hydrolytic enzymes, vitamins, phenolic and flavonoid compounds (Wang et al. 2022; Lopes et al. 2023). Recent findings on the assembly of bacterial communities

in the rhizosphere by niche-based (deterministic) processes, as opposed to the neutral (stochastic) processes in bulk soil (Wang et al. 2022), have heightened the necessity for revealing the role of these exudates in building the network of plant roots and their surrounding rhizosphere microorganisms.

It has been documented that PGPR can affect positively root-microbe interactions in the rhizosphere, either by providing nutritional support or by activating behavioral and physiological responses to the microorganisms (Canarini et al. 2019). One known potential of PGPR to exert these beneficial effects is chemotaxis, a key motility trait that allows PGPR to move towards the root surface, as the first phase of bacterial colonization (Yuan et al. 2015). Such chemotactic ability of PGPR, together with the potential to exude a variety of chemical compounds, can modify the release of carbon and nitrogen substrates into the rhizosphere that are qualitatively/quantitatively different and also differently metabolized by microorganisms (Baetz and Martinoia 2014; Sasse et al. 2018). It is well documented that PGPR can affect plant molecular and biochemical processes through the synthesis and exudation of many metabolites and organic compounds, including phytohormones (e.g., 3-indol acetic acid, gibberellins, cytokinins, etc.), enzymes (e.g., chitinases, cellulases, proteases, chitinase, and glucanases), volatile organic compounds, vitamins (e.g., pantothenic acid, thiamine, riboflavin, pyrroloquinoline quinone, and biotin), antibiotics,

1-aminocyclopropane-1-carboxylate deaminase, enzymatic and non-enzymatic antioxidants (e.g., hydratases, hydrolases, dioxygenases, dehydrogenases and aldolases) (Yaghoubi et al. 2024).

In contrast, the positive effects of root exudates, mainly phenolic compounds, on the colonization of roots by beneficial microorganisms and the increased abundance of certain PGPR have already been proved, as such bioactive molecules are considered the first line of roots-PGPR communications in the rhizosphere (Badri et al. 2009; Yuan et al. 2015). Table 3 summarizes some recent findings on the effects of root exudates on plant-bacteria associations. Passive transport is the main mechanism for secreting most low molecular weight organic compounds and non-polar molecules across membranes without requiring energy, which depends on concentration gradients between the extracellular and intracellular environments (Chaparro et al. 2014). In contrast, ATP-binding cassette (ABC) transporters, as a large superfamily of membrane proteins, have been proposed to play a major role in transporting diverse complex compounds and polar molecules across the cellular membrane, either extracellularly over the plasma membrane or intracellularly into the vacuoles (Zhou et al. 2016). The functions of ABC transporters can be closely related to the transfer of secreted substrates in PGPR-root relationships in the rhizosphere (Badri et al. 2009; Zhou et al. 2016). It has been reported that the changes in exopolysaccharides and lipid-packing in the cell surface of some PGPR (e.g., *Bacillus cereus*) in response to the shifts in the composition of root exudates, resulted in higher efficiency of bacterial colonization (Dutta et al. 2013).

Moreover, the signaling function of these exudates can be a possible explanation for the recruitment of beneficial microbes in the rhizosphere in favor of plants, especially under stress conditions (Rolfe et al. 2019; Arif et al. 2020; Bandopadhyay et al. 2023). A well-known example of PGPR recruitment by the roots was observed when low molecular weight organic acids (e.g., malic acid, citric acid, and fumaric acid) secreted by roots served as source of carbon substrate and signaling molecules (Yuan et al. 2015; Zhou et al. 2022; Zhang et al. 2023). Increased recruitment of some PGPR into the rhizosphere in response to specific exudate compounds is consistent with the previous finding of higher activity of auxin-producing PGPR (e.g., *Pseudomonas fluorescens*)

when plants secreted L-tryptophan, a precursor of auxin synthesis, into the rhizosphere (Kamilova et al. 2006b). However, these findings must be interpreted with caution, as changes in the structure of the existing rhizosphere microbial communities due to interactions between root exudates and soil properties (e.g., pH, water potential, and nutrient availability) (Peiffer et al. 2013), plant species and genotype (Chen and Liu 2024) and plant developmental stage (Yuan et al. 2015) should not be overlooked.

In PGPR-inoculated soils, the increased persistence and accumulation of organic matter have been linked to the release of biosynthesized metabolites and phytohormones (e.g., auxins, cytokinins, gibberellins) caused by the interactions of PGPR with the resident microbiome (Hellequin et al. 2019) and root exudates (Grover et al. 2021). This, in turn, can lead to high relative abundances of copiotrophic taxa in the soil, as the main decomposers of soil organic matter, and consequently, can maximize the microbial carbon use efficiency (Yaghoubi et al. 2019a, 2020). In addition to released metabolites, endophytes have also been found in the rhizosphere of rice (Hardoim et al. 2012) and maize (Johnston-Monje and Raizada 2011) under field and pot experiments, indicating the colonization of specific functional endophytes (e.g., *Burkholderia gladioli*) in the rhizosphere under stress (e.g., nutrient deficiency) (Shao et al. 2021). Figure 1 provides an overview of the interactions between PGPR and root exudates.

Which area experiences more changes, endosphere or rhizosphere?

Research on biostimulation of wheat plants with beneficial bacteria has shown that structural modifications in bacterial communities are more pronounced in the endosphere than in the rhizosphere. This suggests that the endosphere is more influenced by biofertilization (Yaghoubi et al. 2021). It has been speculated that rhizosphere bacterial communities are less susceptible to perturbations induced by non-indigenous microorganisms. This is because they are exposed to soil fluctuations and diverse environmental conditions, and consequently may have acquired innate abilities to maintain their microbiome composition against changes in the surrounding environment. This resilience is likely to be greater than that of endophytes (Björklöf et al. 2003;

Table 3 Effects of interactions among root exudates and plant-PGPR associations

Metabolites	Plant	Experimental condition	Summary of results	Reference
Aspartic acid and fructose	Rice	Field	Suggesting a positive interaction among root exudates, plants and root-colonizing bacteria.	Reshma and Dileep 2024
Indole-3-acetic acid and abscisic acid	Maize	Field	Confirming the effects of phytohormones exuded by roots on plant–microbiome interactions in the rhizosphere.	Lopes et al. 2023
Organic acids	Maize	Field	Higher levels of root organic acid anions significantly increased the abundance of several genera of actinobacteria in the rhizosphere, which in turn, improved P solubilization in soil and P uptake by plants.	Zhang et al. 2023
Phenolic acids, alkaloids, benzoquinones, cinnamic acid, naphthoquinone, lignin, terpenoids, flavones, coumarin, naphthalene family, and amino acids	*Aconitum pendulum, Ajuga lupulina, Artemisia dubia, Artemisia nanschanica, Euphorbia fischeriana, Ligularia virgaurea, Morina kokonorica, Oxytropis ochrocephala, Pedicularis kansuensis, Sphallerocarpus gracilis, Kobresia pygmaea* and *Elymus nutans*	Grasslands	Root exudates directly influenced the soil microorganisms' composition and diversity, which its effect was more pronounced in the rhizosphere than in bulk soil, mainly because of the higher levels of nutrient content and microbial C metabolism activity.	Wang et al. 2022
Glutaric acid, 3-hydroxybutyric acid and 4-methylcatechol	*Leymus chinensis*	Field	Modulating root exudate components by plants is considered a mechanism to promote microbial diversity and recruit potentially beneficial microorganisms (e, g., members of the genera *Haliangium, Nitrospira* and *Mortierella*).	Lin et al. 2022
Amino acids, organic acids, and sugars	Sweet clover	Field	The structure of rhizosphere microbial communities was changed in response to the root exudations.	Zhou et al. 2022
Organic acids (acetic acid, oxalic acid, succinic acid and tartaric acid)	Wheat	Field	Shifts in the microbial community structure in the rhizosphere, mainly through recruiting beneficial microbes under high nitrogen levels of soil.	Chen et al. 2019
Flavones (e.g., apigenin and luteolin)	Maize	Field and phytochamber	Suggesting that root-derived flavonoids improve nitrogen acquisition and plant growth, mainly through stimulating the enrichment of bacteria of the taxa Oxalobacteraceae in the rhizosphere.	Yu et al. 2021

Table 3 (continued)

Metabolites	Plant	Experimental condition	Summary of results	Reference
Organic acids, phenylpropanoids, and benzenoids.	Ryegrass	Pot	Shifts in root exudate compounds significantly changed the abundance of rhizosphere and endophytic bacteria.	Cao et al. 2024
Taxifolin	Tomato	Pot	Stimulating tomato plants to recruit plant-beneficial bacteria (e, g, *Bacillus* sp.) in response to a flavonoid compound, taxifolin, exudated from the roots.	Zhou et al. 2023
Coumarins	Arabidopsis	Pot	Suggesting that the modified bacterial root microbiota in response to secreted coumarins can be considered an integral mediator of plant adaptation to iron-limiting soils.	Harbort et al. 2020
Threonine, glyoxylic oxime acid, serine, pentanoic acid, glucopyranoside, tartaric acid, and pyrrolidinone	Groundnut	Pot	*Confirming the effects of PGPRs (Bacillus sonorensis and Pseudomonas aeruginosa) on the* variations in root exudates	Ankati and Podile 2019
L-malic acid	Tomato	Pot	Stimulating biofilm formation ex planta of *Bacillus subtilis*	Chen et al. 2012
Organic acids and sugars	Tomato	Pot	Inoculation of plants with *Pseudomonas fluorescens* resulted in shifts in the composition of root exudates, mainly by increasing the content of citric acid and decreasing succinic acid and total sugars.	Kamilova et al. 2006a
Isoflavones	Soybean	In vitro	Showing the various definitions for a chemical signal of root exudates, in which isoflavones had a synergistic effect on both beneficial (*Bradyrhizobium japonicum*) and pathogenic (*Phytophthora sojae*) microbes.	Morris et al. 1998

Fig. 1 Scheme of the interactions between PGPR and root exudates, signals that reactivate and recruit beneficial microbes in the rhizosphere and endosphere
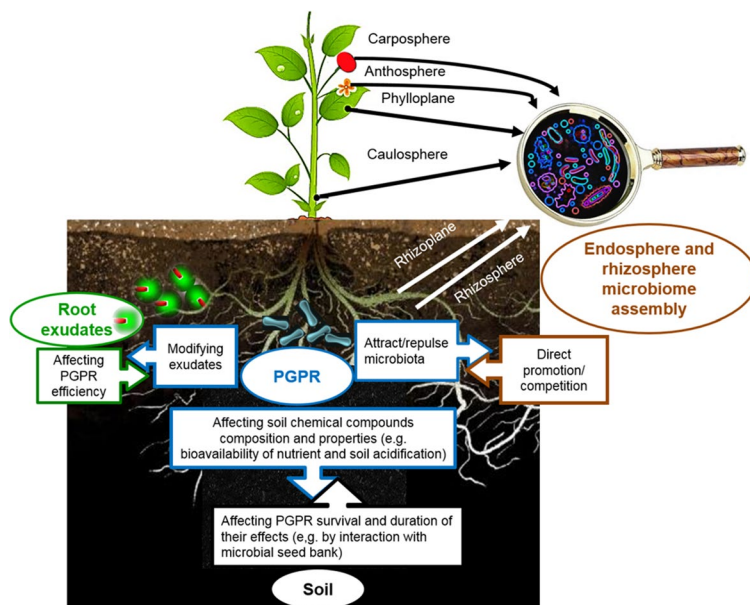
Orozco-Mosqueda et al. 2020; Lopes et al. 2021; Yaghoubi et al. 2021). Although the modifications in soil properties (e.g. soil pH, porosity, water holding capacity, etc.) are mediated by beneficial microbes (Moore et al. 2022), the efficiency and customization of microbiome engineering are primarily affected by soil and environmental conditions, as well as by plant species, genotype, growth stage, and growth conditions (Arif et al. 2020). Accordingly, a previous field experiment has shown that changes in the rhizosphere microbiome are deeply associated with the plant nitrogen uptake (Bell et al. 2015), with the latter serving as a tool to modify the composition and function of the rhizosphere microbiome and improve the plant fitness. While previous studies have demonstrated that higher levels of readily metabolizable root exudates result in greater changes and diversity in the rhizosphere bacterial communities compared to those in the bulk soils (Castro-Sowinski et al. 2007), it is noteworthy that rhizobacterial communities exhibit a lower responsiveness to change compared to those residing in the endosphere. It can be concluded that major changes in bacterial communities in response to the PGPR inoculation are in the order of endosphere > rhizosphere > bulk soil. A possible explanation can be related to the limited niche overlap between PGPR and resident bacteria in the soil as compared to the endosphere, where spatial partitioning and nutrient versatility are definitely important

factors contributing to this specified overlap, even if the resident bacteria and the applied PGPR are phylogenetically close (Castro-Sowinski et al. 2007). Plant endophytic colonization is limited to specific bacterial species, and even a minor change in the rhizosphere bacterial community can significantly shift the endosphere microbiome, with general perspectives stating that the soil-root interface acts as a selective barrier to assemble the endosphere community composition (Zhang et al. 2020). Furthermore, stronger changes in endosphere microbial communities may reveal a major plant-mediated strategy: plant phenotypic and genotypic responses to PGPR provide a modified habitat via regulated root architecture under field conditions (Chen et al. 2019).

Survival of PGPR and the durability of their effects in the environment

Regardless of the mechanisms involved in shifting the soil microbiome, it remains unclear whether the impact of PGPR inoculants are long-lasting or rapidly disappearing (Mawarda et al. 2020). However, understanding such tripartite PGPR-plant-rhizosphere interactions and their effects over time on PGPR survival may be beneficial as knowledge becomes available. For example, a field experiment by Yin et al. (2013) and a pot study by Wang et al. (2018) reported resilience of several months after inoculation. In a

field trial, Johansen and Olsson (2005) found that the effect of *Pseudomonas fluorescens* inoculation on the structure of the resident microbiome lasted up to six days after inoculation. Similarly, inoculation of soils with *Escherichia coli* in a laboratory-scale experiment showed the persistence of bacteria in soil for less than 28 days (Mallon et al. 2018). The period of persistence of PGPR in the soil has been related to the ability of these beneficial bacteria in niche construction, such as the efficiency of root colonization or biofilm formation, as well as sporulation ability under abiotic stress (Moore et al. 2022). Interestingly, it has been proved that even if the survival rate of PGPR in soil and re-colonization efficiency inside plant tissue is limited, the bacterial community structures in the rhizosphere and endosphere will gradually be influenced by PGPR inoculation (Yaghoubi et al. 2021). A possible explanation could be that diverse bacterial taxa engage in symbiotic interactions (Faust and Raes 2012), mainly in competition with others for resources (Gralka et al. 2020) and by targeting the inoculant necromass as a nutrient source (Płociniczak et al. 2020). The evidence for such mechanisms could be the higher abundance of some specific taxa in microbial communities, especially those bacterial genera belonging to *Arthrobacter*, *Actinoplanes*, and *Pseudomonas.* These genera are known for their nutritional versatility, using a variety of substrates (e.g. as nucleic acids) for their oxidative metabolism (Comi and Cantoni 2011; Płociniczak et al. 2020; Yaghoubi et al. 2021). Furthermore, roots are able to use associated microbes as a source of nutritive compounds, especially organic phosphorus in the form of bacterial DNA (Paungfoo-Lonhienne et al. 2010) and leave an indirect impact on associated microbial communities. However, it is not clear whether plants prefer specific microbes as nutrient sources (Arif et al. 2020).

Despite the short survival/durability of PGPR in soil, the improvement of plant growth and production by PGPR-treatment supports the idea that there are two diverse possible mechanisms induced by PGPR, including the high-density cell-dependent type and the regulation of microbial community-dependent type (Kang et al. 2013; Yaghoubi et al. 2021). The first strategy is a well-known classical standpoint concerning the necessity of establishing and supporting a necessary population density of PGPR in the soil to maintain their effectiveness in stimulating the plant at a satisfactory level (Kang et al. 2013). The second strategy is the regulation of soil microbial community structures, which may result from competition for space, resources, and other biotic and abiotic limiting factors (Georgiou et al. 2017).

Despite the aforementioned information, there is currently no reliable evidence to speculate that the legacy effects of PGPR on the host plants and agro-ecosystems can be manifested in the neighboring ecosystems. Moore et al. (2022) suggested that the horizontal transfer of PGPR genes to resident taxa, together with changes and temporal dynamics of resident microbiomes, can significantly affect resident functional groups and biotic and abiotic interaction networks, even in herbivore and pollinator communities. For instance, PGPR have been shown to enhance the release of volatile organic compounds (VOC), and to improve the quality and quantity of nectar and pollen (Moore et al. 2022). Additionally, PGPR have been observed to extend the length of the growing season of crops (Panke-Buisse et al. 2015). These benefits can be the reasons to attract pollinators (Liu and Brettell et al. 2019) and bird populations that feed on pollinator insects and crop seeds/fruits (Moore et al. 2022). Indeed, it has been proved that the low molecular weight (< 300 Dalton), high vapor pressure, and low boiling point allow some VOCs synthesized by PGPR to volatilize and act as signaling molecules over short and long distances (Santoro et al. 2015; Fincheira and Quiroz 2018), thus interacting with plants and other living (micro) organisms in the environment (Tahir et al. 2017). Moreover, Mohanty et al. (2021) reported a decline in herbivorous activity by invertebrates in response to VOCs released by PGPR, which could be correlated with greater activation of the jasmonic acid immune signaling pathway in PGPR-treated plants, confirming the induced systemic plant defenses against herbivores (Hol et al. 2013).

Heritability to the next generation of plants

Microbiome transmission pathways to the progeny of plants

Since the microbial element of the mother plants can be inherited by the next generation of plants through the healthful seeds, the interactions between PGPR

and plant (seed) microbiome can be critical to affect the seed germination process as well as plant production and survival, especially in the field-grown plants under biotic and abiotic stress (Mitter et al. 2017; Arif et al. 2020). The seed microbiome, as the initial inoculum for the plant microbiome, guides the plant to establish resistance to stress and can be a powerful biomarker for breeding and microbiome engineering approaches (Rybakova et al. 2017). Despite this, little progress has been made to clarify whether the bacteria that colonize the PGPR-treated (inoculated) seed during its development are those that will be established in the next generation of plants. Therefore, it seems necessary to provide additional information on the effects of the seed microbiome on seedling emergence and plant tolerance in order to develop microbial-based solutions for improving seed vigor and plant tolerance to stress. The following basic questions are raised here, especially in relation to stressed plants: will the plant (seed) microbiome of the next generation be acquired by horizontal transfer from the surrounding habitat and/or by vertical transfer from the PGPR-treated parent? Will the stress conditions alter the microbial communities in the plants, resulting in altered microbiome structure of the next generation of plants? If so, will this enhance the ability of the next generation to respond to stress with greater resilience? Will exposure to stress in one generation adversely affect subsequent generations of the plant if not exposed to the same stress?

Until recently, three major pathways of microbiome transfer to the next generation of plants have been suggested, the first being the internal pathway through the xylem or non-vascular tissue of the parent plant, as a means of vertical transmission. The second pathway is known as the floral pathway through the stigma of the parent plant, which can be both horizontal and vertical transmissions depending on the selection exerted by the plant. The third one is the external pathway through seed inoculation/contamination with microbial inoculum, which is associated with horizontal transmission (Maude 1996; Shade et al. 2017). Verifying the effect of PGPR on the mode of microbiome transmission to the progeny plants and defining the transmission rates is technically problematic because many taxa of the progeny microbiome overlap with those in the rhizosphere, endosphere, and bulk soil (Hardoim et al. 2015; Muller et al. 2016). Investigating the plant microbiota through the

application of green fluorescent protein (GFP) labelling offers a promising avenue for elucidating the vertical transmission of microbiomes across successive plant generations (Ma et al. 2011). However, this method has important limitations, such as the need for genetic manipulation of microbial strains and the inaccessibility of tools for yet uncultivable and non-model microbes (Shade et al. 2017).

Ecological effects of PGPR on the progeny of plants

While there is no reliable evidence confirming the inheritance of the microbiome of PGPR-treated plants to the progeny, some beneficial effects of PGPR have been found in the next-generation plants, especially those grown under stress (Tiwari et al. 2022a, b). To assess the potential of PGPR-mediated intergenerational defense, Devi et al. (2023) found improved defense against a pathogen (*Bipolaris sorokiniana*) in the progeny of PGPR-treated wheat plants compared to the progeny of untreated plants. This confirms that the beneficial effects of PGPR are not restricted to the parent and can be inherited by subsequent generations. One possible explanation is that the customized seed microbiome establishes early contact with plant tissues, thus evading competition with pathogens and soil microorganisms (Mitter et al. 2017). Another plausible explanation is that stressed plants redirect nutrient allocation toward healthier seed development, rather than using it solely for growth and biomass production, resulting in seeds with increased nutritional compounds and inherent resistance to adverse conditions (Tiwari et al. 2022b). Moreover, the altered composition of the seed microbiome can also have a direct impact on seed features, affecting the seed dormancy through cytokinin synthesis under field conditions, and promoting a homogeneous germination rate in progeny (Goggin et al. 2015). The ability to influence seed dormancy is significant, because the dormant state can reduce the impact of the seed-associated microbiome on the assembly of the progeny microbiome (Lennon and Jones 2011). In fact, the beneficial microorganisms in seeds may not be able to survive for extended periods with limited resources (including water) and space prior to seed germination, which can prevent benefits to the next generation (Shade et al. 2017).

It cannot be overlooked that the parental habitat under diverse environmental conditions plays a role in

inducing transgenerational plasticity (Yakovlev et al. 2012) and may be helpful for the seedlings of progeny to pre-adapt to various stressors when exposed to the same environmental conditions (Galloway and Etterson 2007). Regardless of changes in the microbiome, recent studies have discussed the concept of inter-generational transmission of stress tolerance ability in PGPR-treated plants. These studies have reported the formation of immunological memories in stressed plants that can provide an individual gene pool with long-term persistence in subsequent plant genera-tions. Such a gene pool can stimulate faster practical responses to upcoming challenges (Mauch-Mani et al. 2017; Tiwari et al. 2022a). This plant adaptation strat-egy can also be independent of any DNA sequence alterations, known as a maternal effect or epigenetic effect, by forming transcriptional memory and inher-itable changes in the phenotype of stressed plants (Tiwari et al. 2022b).

Although there are some doubts about whether the progenies will be fully protected from stress, at least not to the same extent as the parents, epigenetic manipulation has been much scrutinized as an excel-lent evolutionary strategy in plants. This evolutionary approach enables the restoration of stress tolerance, potentially reducing reliance on agrochemicals, with-out altering the genetic makeup of the plants (Mauch-Mani et al. 2017; Tiwari et al. 2022b). All noted modifications in the mother plant phenotype, nutri-ent composition, and seed microbiome can initiate a transgenerational establishment through epigenetic modifications such as DNA methylation, histone post-translational transformations, histone variant creation, and chromatin structure remodeling (Shanker et al. 2020; Oberkofler et al. 2021). Such a creation of epi-genetic marks in plants can be associated with post-transcriptional gene-silencing processes in plant cells by small interfering RNAs, which in turn are linked to RNA-dependent DNA polymerases (Mauch-Mani et al. 2017). This plant adaptation process has been reported in the progenies of parents exposed to abi-otic (Shanker et al. 2020) and biotic stress (Kathiria et al. 2010). In addition to epigenetic events in plants, epigenetics can also occur in the microbiome, where DNA methylation in microorganisms not only pre-serves their DNA from self-cleavage by activating certain enzymes, but also affects gene regulation and represents genetic variability (Gopal and Gupta 2016). The findings in this field are subject to at least one limitation, as reported by Mauch-Mani et al. (2017), which suggest that epigenetic modifications are naturally very rapidly reversible, and therefore transgenerational immunity may be extinguished after a few stress-free generations, mainly to terminate the unnecessary costs of adaptation.

Concluding remarks and future perspectives

This review attempts to provide a new insight into the ecological consequences of PGPR, mainly on the res-ident microbiome and their possible heritability to the next generation of plants.

In this regard, PGPR can change the rhizosphere microbiome by outcompeting the existing taxa by consuming the resources, acidifying the environment, producing metabolites (e.g. siderophores and anti-biotics) and organic compounds, and consequently increasing the copiotrophic taxa. The interaction effects of the PGPR-root system can adjust the com-position of root exudates and influence the release of bioactive molecules and metabolites by the root, especially under stress conditions. These molecules can act as signals to attract/repulse the beneficial bac-teria in the rhizosphere and endosphere in favor of the plants. It also appears that the most relevant shifts in bacterial community structures in response to PGPR treatments occur in the endosphere, followed by the rhizosphere, and bulk soil, respectively. Such changes in microbiome structure can occur gradually, even if the survival rate of PGPR in soil and re-colonization efficiency in plant tissues are limited. The discussed modifications in the rhizosphere and plant microbi-ome can potentially boost the chances of survival of the progeny plants growing under the same stress con-ditions. A better understanding of the diverse interac-tions that occur at the systems level in the rhizosphere and endosphere, as a pool of plant-microbe signaling, can lead to biotechnological advances for potential applications of PGPR in sustainable agriculture under various environmental conditions.

Despite what has been discussed so far, more emphasis should be placed on employing emerging technologies to understand the persistence of applied PGPR over time, as well as their legacy effects on host plants and, at a larger scale, on agro-ecosystems and neighboring ecosystems. Thus, there is ample

room for further progress to guarantee the conjunction of the microbiome from parent to progeny. This can be achieved by targeting seed endophytes, root architecture, picking 'microbe-friendly' plants, and plant genome engineering to attract beneficial microorganisms.

Declarations

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