

Harnessing the Power of PGPR: Unraveling the Molecular Interactions Between Beneficial Bacteria and Crop Roots

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Abstract Plant growth-promoting rhizobacteria (PGPR) have emerged as a promising eco-friendly alternative to chemical fertilizers and pesticides, offering significant benefits for sustainable agriculture. This systematic review delves into the intricate molecular interactions between PGPR and crop roots, highlighting their potential to enhance plant growth and health. PGPR, such as fluorescent *Pseudomonas* spp., *Bacillus cereus*, and multispecies inoculants, have been shown to improve crop yields by various mechanisms, including nitrogen fixation, phosphate solubilization, siderophore production, and the synthesis of phytohormones. These bacteria also play a crucial role in disease suppression by competing with pathogens for nutrients, producing antimicrobial compounds, and inducing systemic resistance in plants. The review further explores the role of root exudates and bacterial secretions in modulating these interactions, emphasizing the importance of specific genes and metabolites in the process. Recent advancements in metatranscriptomics and gene expression profiling have provided deeper insights into the molecular mechanisms underlying these beneficial interactions, paving the way for more effective application of PGPR in agriculture. By understanding these complex interactions, we can develop innovative strategies to harness the full potential of PGPR, ultimately contributing to sustainable crop production and environmental conservation.

Keywords Plant growth-promoting rhizobacteria (PGPR); Crop roots; Molecular interactions; Sustainable agriculture; Nitrogen fixation; Phosphate solubilization; Disease suppression; Root exudates; Metatranscriptomics

Plant Growth-Promoting Rhizobacteria (PGPR) are a diverse group of bacteria that colonize plant roots and enhance plant growth through various mechanisms. These mechanisms include nutrient solubilization, phytohormone production, and biological nitrogen fixation, among others (Lugtenberg and Kamilova, 2009; Bhattacharyya and Jha, 2011; Nagargade et al., 2018). The significance of PGPR lies in their potential to replace chemical fertilizers and pesticides, thereby promoting sustainable agricultural practices (Bhattacharyya and Jha, 2011; Pérez-Montaña et al., 2014; Sinha et al., 2021). Understanding the molecular interactions between PGPR and crop roots is crucial for optimizing their application and maximizing their benefits in agriculture (Benizri et al., 2001; Oleńska et al., 2020).

PGPR are beneficial bacteria found in the rhizosphere, the region of soil surrounding plant roots. They promote plant growth directly by enhancing nutrient availability and indirectly by protecting plants from pathogens (Lugtenberg and Kamilova, 2009; Singh et al., 2013; Nagargade et al., 2018). The ability of PGPR to improve plant health and yield makes them a valuable tool in sustainable agriculture (Bhattacharyya and Jha, 2011; Pérez-Montaña et al., 2014; Sinha et al., 2021).

The molecular interactions between PGPR and crop roots are complex and involve various signaling pathways and biochemical processes. These interactions are essential for the successful colonization of plant roots by PGPR and the subsequent promotion of plant growth (Benizri et al., 2001; Lugtenberg and Kamilova, 2009). A deeper understanding of these molecular mechanisms can lead to the development of more effective PGPR-based biofertilizers and biocontrol agents (Nagargade et al., 2018; Oleńska et al., 2020).

The purpose of this review is to highlight the importance of PGPR in sustainable agriculture, identify key molecular mechanisms involved in PGPR-crop root interactions, and discuss potential applications and future directions. By systematically reviewing the current knowledge on PGPR and their interactions with crop roots, this paper aims to provide a comprehensive understanding of their role in sustainable agriculture and identify areas for future research and development.

1 Molecular Mechanisms of PGPR-Root Interactions

1.1 Signal molecules and receptors

Root exudates play a crucial role in attracting plant growth-promoting rhizobacteria (PGPR) to the rhizosphere. These exudates consist of a variety of organic compounds, including sugars, amino acids, and secondary metabolites, which serve as chemical signals to beneficial microbes. For instance, the study by (Yi et al., 2018) highlights the importance of root exudates in modulating the transcriptomic response of *Bacillus mycoides* to potato root exudates, indicating that these exudates are pivotal in establishing beneficial plant-microbe interactions. Similarly (Palma et al., 2020), discusses how root exudates influence the expression of bacterial genes involved in microbe-plant interactions, further emphasizing their role in attracting and selecting specific microbial populations.

Specific signal molecules such as flavonoids and strigolactones are key players in the communication between plants and PGPR. Flavonoids, for example, have been shown to be involved in the biosynthetic pathways that regulate plant-microbe interactions (Thomas et al., 2019). These molecules not only attract beneficial bacteria but also modulate their behavior to enhance colonization and symbiosis. Strigolactones, another class of signal molecules, are known to play a role in the establishment of symbiotic relationships with mycorrhizal fungi and potentially with PGPR as well (Baysal and Silme, 2019).

PGPR possess specific receptors that recognize and respond to plant-derived signals. These receptors enable the bacteria to detect and move towards the root exudates, facilitating colonization. The study by (Wheatley and Poole, 2018) reviews the molecular mechanisms governing bacterial attachment to roots, highlighting the role of specific receptors in recognizing plant signals. Additionally (Mark et al., 2005), identifies genes in *Pseudomonas aeruginosa* that are regulated in response to root exudates, suggesting the presence of specialized receptors that mediate these interactions.

1.2 Colonization and biofilm formation

The initial attachment of PGPR to root surfaces is a critical step in the colonization process. This attachment is often mediated by bacterial surface structures such as pili and flagella, which facilitate close contact with the root epidermis (Wheatley and Poole, 2018). The biphasic mechanism of root attachment, as described in (Wheatley and Poole, 2018), involves an initial reversible phase followed by a more stable, irreversible attachment, ensuring effective colonization.

Biofilm formation is a significant aspect of PGPR colonization, providing a protective environment for the bacteria and enhancing their ability to persist in the rhizosphere. Biofilms facilitate nutrient exchange and protect the bacteria from environmental stresses and antimicrobial compounds. The study by (Yi et al., 2018) underscores the importance of biofilm formation in the context of plant-microbe interactions, as it allows for sustained colonization and interaction with the host plant.

Several factors influence the effectiveness of PGPR colonization, including the composition of root exudates, soil conditions, and the presence of other microbial communities. For instance (Somenahally, 2017), discusses how soil conditions such as moisture stress and pH can impact root-microbe interactions, thereby affecting colonization efficiency. Additionally, the presence of deleterious microorganisms in the rhizosphere can compete with PGPR for resources, influencing their colonization success (Schippers et al., 1987).

1.3 Modulation of root architecture

PGPR can significantly influence root development and architecture, promoting root growth and branching. This modulation is often mediated by the production of plant hormones and other growth-promoting substances. For example (Thomas et al., 2019), identifies differentially expressed genes in rice roots during interactions with *Azospirillum brasilense*, many of which are involved in hormone signaling pathways that regulate root development.

PGPR influence root architecture through the production and modulation of plant hormones such as auxins, cytokinins, and gibberellins. Auxins, in particular, play a crucial role in root elongation and branching. The study by (Thomas et al., 2019) highlights the involvement of hormone signaling pathways in the interaction between rice roots and *Azospirillum brasilense*, indicating that PGPR can alter the hormonal balance within the plant to promote root growth.

PGPR also interact with plant stress hormones such as ethylene and abscisic acid (ABA) to enhance plant stress tolerance. For instance (Pineda et al., 2010), reviews the role of beneficial soil-borne microbes in helping plants cope with biotic and abiotic stresses, including the modulation of stress hormone levels. By influencing the levels of ethylene and ABA, PGPR can help plants better manage stress conditions, thereby improving overall plant health and productivity.

2 Functional Benefits of PGPR in Crop Growth

2.1 Nutrient acquisition

Plant Growth-Promoting Rhizobacteria (PGPR) play a crucial role in enhancing nutrient availability to crops through various mechanisms such as nitrogen fixation, phosphate solubilization, and potassium solubilization. For instance, PGPR like *Azospirillum*, *Azotobacter*, and *Klebsiella* are known for their nitrogen-fixing capabilities, which convert atmospheric nitrogen into a form that plants can readily absorb and utilize (Hayat et al., 2012; Kuan et al., 2016; Mohanty et al., 2021). Additionally, phosphate-solubilizing bacteria such as *Bacillus megaterium* and *Pseudomonas* species release organic acids that convert insoluble phosphates into soluble forms, making phosphorus more accessible to plants (Wu et al., 2012; Tang et al., 2020; Mohanty et al., 2021).

PGPR facilitate nutrient uptake by altering plant hormone levels, which enhances root surface area and morphology, thereby increasing nutrient absorption. For example, the production of indole acetic acid (IAA) by PGPR stimulates root elongation and branching, leading to a larger root surface area for nutrient uptake (Bhattacharyya and Jha, 2011; Ankati and Podile, 2019; Mohanty et al., 2021). Furthermore, PGPR can produce siderophores that chelate iron from the soil, making it more available to plants (Bhattacharyya and Jha, 2011; Hayat et al., 2012). The synergistic interaction between earthworms and PGPR has also been shown to significantly increase the availability of nitrogen, phosphorus, and potassium in the soil, further enhancing nutrient uptake (Wu et al., 2012).

2.2 Stress tolerance

PGPR contribute to plant tolerance against various abiotic stresses such as drought, salinity, and heavy metals. For instance, PGPR like *Bacillus* and *Pseudomonas* species produce exopolysaccharides that help in soil aggregation and water retention, thereby aiding plants in drought conditions (Hayat et al., 2012; Mohanty et al., 2021). Additionally, PGPR can produce ACC deaminase, which lowers ethylene levels in plants under stress, thus promoting root growth and stress tolerance (Bhattacharyya and Jha, 2011; Hayat et al., 2012).

The molecular pathways involved in PGPR-mediated stress mitigation include the production of antioxidants, osmolytes, and stress-related proteins. For example, PGPR can induce the production of osmoprotectants like proline and trehalose in plants, which help in maintaining cellular osmotic balance under stress conditions (Hayat et al., 2012; Vejan et al., 2019). Moreover, PGPR can activate plant defense pathways by inducing the expression of stress-responsive genes, thereby enhancing the plant's ability to withstand adverse environmental conditions (Bhattacharyya and Jha, 2011; Hayat et al., 2012).

2.3 Disease suppression

PGPR exhibit biocontrol mechanisms that suppress phytopathogens through the production of antimicrobial compounds, competition for nutrients and niches, and induction of systemic resistance in plants. For instance, PGPR like *Pseudomonas* and *Bacillus* species produce antibiotics, siderophores, and lytic enzymes that inhibit the growth of pathogenic microbes (Bhattacharyya and Jha, 2011; Hayat et al., 2012; Mohanty et al., 2021).

PGPR produce a variety of antimicrobial compounds such as hydrogen cyanide, phenazines, and pyrrolnitrin, which directly inhibit the growth of phytopathogens (Bhattacharyya and Jha, 2011; Hayat et al., 2012; Mohanty et al., 2021). These compounds disrupt the cell membranes of pathogens, interfere with their metabolic processes, and ultimately lead to their death.

PGPR can induce systemic resistance in plants, making them more resilient to pathogen attacks. This is achieved through the activation of plant defense mechanisms, including the production of pathogenesis-related proteins and secondary metabolites (Bhattacharyya and Jha, 2011; Hayat et al., 2012). For example, the production of volatile organic compounds (VOCs) by PGPR can trigger systemic resistance in plants, enhancing their overall immunity against a wide range of pathogens (Bhattacharyya and Jha, 2011; Hayat et al., 2012).

In summary, PGPR offer multifaceted benefits in crop growth by enhancing nutrient acquisition, improving stress tolerance, and suppressing diseases through various biochemical and molecular mechanisms. These attributes make PGPR a valuable tool in sustainable agriculture, reducing the reliance on chemical fertilizers and pesticides while promoting healthier and more resilient crops.

3 Genomic and Proteomic Insights

3.1 Genomic studies

Recent advancements in sequencing technologies have significantly enhanced our understanding of the genomic landscape of Plant Growth-Promoting Rhizobacteria (PGPR). High-throughput sequencing methods, such as next-generation sequencing (NGS), have enabled comprehensive genomic analyses, facilitating the identification of key genes and regulatory networks involved in PGPR-plant interactions. These technologies have allowed researchers to sequence entire genomes of various PGPR strains, providing insights into their genetic makeup and potential functional capabilities (Verma et al., 2018).

Genomic studies have identified several key genes that play crucial roles in the interaction between PGPR and plants. These genes are involved in various processes such as nitrogen fixation, production of phytohormones, and synthesis of antimicrobial compounds. For instance, genes responsible for the production of indole-3-acetic acid (IAA), a plant hormone that promotes root elongation, have been identified in multiple PGPR strains (Ambrosini and Passaglia, 2017). Additionally, genes encoding for enzymes involved in phosphate solubilization and siderophore production, which enhance nutrient availability to plants, have also been characterized (Verma et al., 2018). The expression of these genes is often regulated in response to plant signals, highlighting the dynamic nature of PGPR-plant interactions.

3.2 Proteomic studies

Proteomic analyses have revealed a diverse array of proteins and enzymes secreted by PGPR that contribute to plant growth promotion and stress resistance. For example, the proteomic study of *Paenibacillus polymyxa* E681 interacting with *Arabidopsis thaliana* identified 41 differentially expressed proteins, including those involved in amino acid metabolism, antioxidant activity, and defense responses (Kwon et al., 2016). These proteins play vital roles in enhancing plant growth and providing resistance against environmental stresses.

The functional roles of PGPR proteins in promoting plant growth are multifaceted. Proteins involved in nitrogen fixation, such as nitrogenase, facilitate the conversion of atmospheric nitrogen into a form that plants can readily assimilate (Ambrosini and Passaglia, 2017). Enzymes like ACC deaminase lower plant ethylene levels, which can otherwise inhibit root growth under stress conditions (Ambrosini and Passaglia, 2017). Additionally, proteins

involved in the synthesis of antimicrobial compounds help in suppressing plant pathogens, thereby protecting the plants and promoting healthier growth (Verma et al., 2018). The upregulation of defense-related proteins in plants treated with PGPR, as observed in proteomic studies, further underscores the role of these proteins in enhancing plant resilience against biotic and abiotic stresses (Kwon et al., 2016; Dhawi, 2020).

In summary, genomic and proteomic studies have provided valuable insights into the molecular mechanisms underlying PGPR-plant interactions. The identification of key genes and proteins involved in these interactions paves the way for the development of more effective PGPR-based biofertilizers and biocontrol agents, contributing to sustainable agricultural practices.

4 Applications and Future Directions

4.1 Agricultural practices

The integration of Plant Growth-Promoting Rhizobacteria (PGPR) into crop management practices has shown significant promise in enhancing crop productivity and sustainability. PGPR can be applied through various methods such as seed inoculation, soil application, and fertigation. These methods have been demonstrated to improve nutrient availability, enhance root growth, and increase crop yields (Lopes et al., 2021; Mohanty et al., 2021; Stoll et al., 2021). For instance, the use of *Bacillus velezensis* strain BBC047 in nurseries and post-transplantation stages has significantly improved the growth and productivity of horticultural crops like basil, cabbage, tomato, and bell pepper (Stoll et al., 2021). Additionally, the combination of biochar with PGPR inoculants has been shown to enhance soil fertility and crop yield, particularly in acidic sandy soils (Kari et al., 2021).

The formulation and application methods for PGPR inoculants are critical for their effectiveness. Successful PGPR formulations should possess high rhizosphere competence, extensive competitive saprophytic ability, and ease of mass production (Mohanty et al., 2021). Seed coating, soil application, and root inoculation are common methods used to apply PGPR. However, challenges such as inconsistent results due to varying soil conditions and environmental factors need to be addressed (Lopes et al., 2021). Innovative approaches like immobilizing PGPR on biochar surfaces have shown promise in enhancing the effectiveness of PGPR inoculants (Kari et al., 2021). Moreover, the timing of PGPR application is crucial, with early-stage applications in nurseries being more effective than late-stage applications (Stoll et al., 2021).

4.2 Biotechnological advances

Genetic engineering of PGPR offers the potential to enhance their efficacy in promoting plant growth and stress tolerance. Advances in molecular biology and genetic engineering have enabled the development of PGPR strains with improved traits such as enhanced nutrient solubilization, hormone production, and stress tolerance (Oleńska et al., 2020; Mellidou and Karamanoli, 2022). For example, genetically engineered PGPR strains can produce higher levels of phytohormones like indole acetic acid (IAA) and ethylene, which are crucial for plant growth and stress response (Oleńska et al., 2020; Mohanty et al., 2021). Additionally, the identification and manipulation of genes associated with induced systemic resistance (ISR) can further enhance the biocontrol capabilities of PGPR (Meena et al., 2020).

The development of synthetic microbial consortia involves combining multiple PGPR strains to create a synergistic effect that enhances plant growth and health. These consortia can be tailored to specific crops and environmental conditions, providing a more robust and effective solution compared to single-strain inoculants (Li et al., 2020). For instance, a consortium of *Providencia rettgeri*, *Advenella incenata*, *Acinetobacter calcoaceticus*, and *Serratia plymuthica* has been shown to improve the growth and soil properties of various crops (Li et al., 2020). The use of synthetic microbial consortia can also help in overcoming the limitations of individual PGPR strains by providing a broader spectrum of beneficial traits (Li et al., 2020; Kong and Liu, 2022).

4.3 Challenges and future research

Despite the promising potential of PGPR, several challenges hinder their widespread application. Inconsistent results due to varying soil conditions, environmental factors, and the complex interactions within the rhizosphere are major obstacles (Lopes et al., 2021). Additionally, the survival and persistence of PGPR in the soil environment are critical factors that influence their effectiveness (Kong and Liu, 2022). Technical issues related to the formulation and application methods, such as seed coating, also need to be addressed to ensure the successful integration of PGPR into conventional agricultural practices (Stoll et al., 2021).

Future research should focus on understanding the ecological and evolutionary interactions between plants and their microbiomes to develop innovative approaches for PGPR application (Mellidou and Karamanoli, 2022). The integration of -omic technologies, such as genomics, proteomics, and metabolomics, can provide a holistic understanding of PGPR-plant interactions and help in the development of more effective PGPR strains (Mellidou and Karamanoli, 2022). Additionally, research should aim to identify and manipulate key genes associated with PGPR-mediated stress tolerance and disease resistance (Meena et al., 2020). Exploring the potential of synthetic microbial consortia and optimizing their formulation and application methods can also enhance the effectiveness of PGPR in diverse agricultural settings (Li et al., 2020). Finally, addressing the environmental and economic challenges associated with PGPR commercialization will be crucial for their successful adoption in sustainable agriculture (John et al., 2020; Meena et al., 2020).

5 Concluding Remarks

Plant Growth-Promoting Rhizobacteria (PGPR) engage in intricate molecular interactions with crop roots, significantly influencing plant health and development. These beneficial bacteria colonize the rhizosphere and root tissues, where they enhance nutrient availability, modulate phytohormone levels, and improve stress tolerance. PGPR can fix atmospheric nitrogen, solubilize phosphates, and produce siderophores, which facilitate nutrient uptake by plants. Additionally, they produce various bioactive compounds, including phytohormones and enzymes, which regulate plant growth and stress responses. These interactions are mediated through complex signaling pathways and gene expression changes, leading to improved root architecture and function.

The benefits of PGPR are multifaceted, encompassing both direct and indirect mechanisms that promote plant growth and health. Direct benefits include enhanced nutrient acquisition, improved root development, and increased production of growth-promoting hormones. Indirectly, PGPR protect plants from pathogens through competition for nutrients, production of antimicrobial compounds, and induction of systemic resistance. Furthermore, PGPR contribute to soil health by improving soil structure and fertility, making them valuable biofertilizers.

PGPR play a crucial role in achieving sustainable agricultural goals by reducing the reliance on synthetic fertilizers and pesticides. Their ability to enhance nutrient use efficiency and promote plant resilience to environmental stresses makes them an eco-friendly alternative to chemical inputs. The use of PGPR aligns with sustainable farming practices, promoting biodiversity and reducing the environmental footprint of agriculture.

The application of PGPR has significant implications for food security and environmental health. By improving crop yields and resilience, PGPR can contribute to stable food production in the face of climate change and other challenges. Moreover, their role in bioremediation and soil health maintenance supports environmental sustainability, reducing pollution and enhancing ecosystem services. The integration of PGPR into agricultural systems offers a promising pathway to secure food supplies while protecting natural resources and promoting environmental health.

In conclusion, harnessing the power of PGPR through a deeper understanding of their molecular interactions with crop roots can lead to innovative and sustainable agricultural practices. The multifaceted benefits of PGPR, from nutrient acquisition to stress tolerance and pathogen resistance, underscore their potential to revolutionize crop production and contribute to global food security and environmental sustainability.

Conflict of Interest Disclosure

The authors affirm that this research was conducted without any commercial or financial relationships that could be construed as a potential conflict of interest.

References

- Ambrosini A., and Passaglia L.M.P., 2017, Plant growth-promoting bacteria (PGPB): isolation and screening of PGP activities, *Current Protocols in Plant Biology*, 2(3): 190-209.
<https://doi.org/10.1002/pb.20054>
PMid:31725969
- Ankati S., and Podile A.R., 2019, Metabolites in the root exudates of groundnut change during interaction with plant growth promoting rhizobacteria in a strain-specific manner, *Journal of plant Physiology*, 243: 153057.
<https://doi.org/10.1016/j.jplph.2019.153057>
PMid:31675630
- Baysal Ö., and Silme R., 2019, The beneficial influence of microbial interactions on plant diseases and plant growth promoting effect, In: Varma A., Choudhary D. (eds), *Mycorrhizosphere and Pedogenesis*, Springer, Singapore, pp.151-166.
https://doi.org/10.1007/978-981-13-6480-8_9
- Benizri E., Baudoin E., and Guckert A., 2001, Root colonization by inoculated plant growth-promoting rhizobacteria, *Biocontrol Science and Technology*, 11(5): 557-574.
<https://doi.org/10.1080/09583150120076120>
- Bhattacharyya P.N., and Jha D.K., 2011, Plant growth-promoting rhizobacteria (PGPR): emergence in agriculture, *World Journal of Microbiology and Biotechnology*, 28: 1327-1350.
<https://doi.org/10.1007/s11274-011-0979-9>
PMid:22805914
- Dhawi F., 2020, Plant growth promoting rhizobacteria (PGPR) regulated phyto and microbial beneficial protein interactions, *Open Life Sciences*, 15(1): 68-78.
<https://doi.org/10.1515/biol-2020-0008>
- Hayat R., Ahmed I., and Sheirdil R.A., 2012, An overview of plant growth promoting rhizobacteria (PGPR) for sustainable agriculture, In: Ashraf M., Öztürk M., Ahmad M., Aksoy A. (eds), *Crop Production for Agricultural Improvement*, Springer, Dordrecht, pp.557-579.
https://doi.org/10.1007/978-94-007-4116-4_22
- John C.J., Kumar S., and Ge M., 2020, Probiotic prospects of PGPR for green and sustainable agriculture, *Archives of Phytopathology and Plant Protection*, 53(19-20): 899-914.
<https://doi.org/10.1080/03235408.2020.1805901>
- Kari A., Nagymáté Z., Romsics C., Vajna B., Tóth E., Lazanyi-Kovács R., Rizó B., Kutasi J., Bernhardt B., Farkas É., and Márialigeti K., 2021, Evaluating the combined effect of biochar and PGPR inoculants on the bacterial community in acidic sandy soil, *Applied Soil Ecology*, 160: 103856.
<https://doi.org/10.1016/j.apsoil.2020.103856>
- Kong Z.Y., and Liu H.G., 2022, Modification of rhizosphere microbial communities: a possible mechanism of plant growth promoting rhizobacteria enhancing plant growth and fitness, *Frontiers in Plant Science*, 13: 920813.
<https://doi.org/10.3389/fpls.2022.920813>
PMid:35720594 PMCID:PMC9198353
- Kuan K.B., Othman R., Rahim K.A., and Shamsuddin Z.H., 2016, Plant growth-promoting rhizobacteria inoculation to enhance vegetative growth, nitrogen fixation and nitrogen remobilisation of maize under greenhouse conditions, *PLoS ONE*, 11(3): e0152478.
<https://doi.org/10.1371/journal.pone.0152478>
PMid:27011317 PMCID:PMC4807084
- Kwon Y.S., Lee D.Y., Rakwal R., Baek S.B., Lee J.H., Kwak Y.S., Seo J.S., Chung W.S., Bae D.W., and Kim S.G., 2016, Proteomic analyses of the interaction between the plant-growth promoting rhizobacterium *Paenibacillus polymyxa* E681 and *Arabidopsis thaliana*, *PROTEOMICS*, 16(1): 122-135.
<https://doi.org/10.1002/pmic.201500196>
PMid:26460066
- Li H.Y., Qiu Y.Z., Yao T., Ma Y.C., Zhang H.R., and Yang X.L., 2020, Effects of PGPR microbial inoculants on the growth and soil properties of *Avena sativa*, *Medicago sativa*, and *Cucumis sativus* seedlings, *Soil & Tillage Research*, 199: 104577.
<https://doi.org/10.1016/j.still.2020.104577>
- Lopes M.J.S., Dias-Filho M.B., and Gurgel E.S.C., 2021, Successful plant growth-promoting microbes: inoculation methods and abiotic factors, *Frontiers in Sustainable Food Systems*, 5: 606454.
<https://doi.org/10.3389/fsufs.2021.606454>

- Lugtenberg B., and Kamilova F., 2009, Plant-growth-promoting rhizobacteria, *Annual Review of Microbiology*, 63: 541-56.
<https://doi.org/10.1146/annurev.micro.62.081307.162918>
PMid:19575558
- Mark G.L., Dow J.M., Kiely P.D., Higgins H., Haynes J., Baysse C., Abbas A., Foley T., Franks A., Morrissey J., and O'Gara F., 2005, Transcriptome profiling of bacterial responses to root exudates identifies genes involved in microbe-plant interactions, *Proceedings of the National Academy of Sciences of the United States of America*, 102(48): 17454-17459.
<https://doi.org/10.1073/pnas.0506407102>
PMid:16301542 PMCID:PMC1297666
- Meena M., Swapnil P., Divyanshu K., Kumar S., Harish, Tripathi Y.N., Zehra A., Marwal A., and Upadhyay R.S., 2020, PGPR-mediated induction of systemic resistance and physiochemical alterations in plants against the pathogens: Current perspectives, *Journal of Basic Microbiology*, 60(10): 828-861.
<https://doi.org/10.1002/jobm.202000370>
PMid:32815221
- Mellidou I., and Karamanoli K., 2022, Unlocking PGPR-mediated abiotic stress tolerance: what lies beneath, *Frontiers in Sustainable Food Systems*, 6: 832896.
<https://doi.org/10.3389/fsufs.2022.832896>
- Mohanty P., Singh P.K., Chakraborty D., Mishra S., and Pattnaik R., 2021, Insight into the role of PGPR in sustainable agriculture and environment, *Frontiers in Sustainable Food Systems*, 5: 667150.
<https://doi.org/10.3389/fsufs.2021.667150>
- Nagargade M., Tyagi V., and Singh M.K., 2018, Plant growth-promoting rhizobacteria: a biological approach toward the production of sustainable agriculture, In: Meena V. (eds), *Role of Rhizospheric Microbes in Soil*, Springer, Singapore, pp.205-223.
https://doi.org/10.1007/978-981-10-8402-7_8
- Oleńska E., Małek W., Wójcik M., Świącicka I., Thijs S., and Vangronsveld J., 2020, Beneficial features of plant growth-promoting rhizobacteria for improving plant growth and health in challenging conditions: A methodical review, *The Science of the Total Environment*, 743: 140682.
<https://doi.org/10.1016/j.scitotenv.2020.140682>
PMid:32758827
- Palma M.D., Scotti R., D'Agostino N., Zaccardelli M., and Tucci M., 2022, Phyto-friendly soil bacteria and fungi provide beneficial outcomes in the host plant by differently modulating its responses through (in) direct mechanisms, *Plants*, 11(20): 2672.
<https://doi.org/10.3390/plants11202672>
PMid:36297696 PMCID:PMC9612229
- Pérez-Montaño F., Alias-Villegas C., Bellogín R.A., del Cerro P., Espuny M.P., Jiménez-Guerrero I., López-Baena F.J., Ollero F.J., and Cubo T., 2014, Plant growth promotion in cereal and leguminous agricultural important plants: from microorganism capacities to crop production, *Microbiological Research*, 169(5-6): 325-336.
<https://doi.org/10.1016/j.micres.2013.09.011>
PMid:24144612
- Pineda A., Zheng S.J., van Loon J.A., Pieterse C.M.J., and Dicke M., 2010, Helping plants to deal with insects: the role of beneficial soil-borne microbes, *Trends in Plant Science*, 15(9): 507-514.
<https://doi.org/10.1016/j.tplants.2010.05.007>
PMid:20542720
- Schippers B., Bakker A.W., and Bakker P.A.H.M., 1987, Interactions of deleterious and beneficial rhizosphere microorganisms and the effect of cropping practices, *Annual Review of Phytopathology*, 25: 339-358.
<https://doi.org/10.1146/annurev.py.25.090187.002011>
- Singh J.S., 2013, Plant growth promoting rhizobacteria, *Resonance*, 18: 275-281.
<https://doi.org/10.1007/s12045-013-0038-y>
- Sinha D., Mukherjee S., and Mahapatran D., 2021, Multifaceted potential of plant growth promoting rhizobacteria (PGPR): an overview, In: Malik J.A. (ed), *Handbook of Research on Microbial Remediation and Microbial Biotechnology for Sustainable Soil*, IGI Global, pp.205-268.
<https://doi.org/10.4018/978-1-7998-7062-3.ch008>
- Somenahally A., 2017, Root-microbe interactions in response to soil conditions, In: Field D.J., Morgan C.L.S., McBratney A.B. (eds), *Global Soil Security, Progress in Soil Science*, Springer, Cham, pp.137-144.
https://doi.org/10.1007/978-3-319-43394-3_12
- Stoll A., Salvatierra-Martínez R., González M., Cisternas J., Rodríguez A., Vega-Gálvez A., and Bravo J., 2021, Importance of crop phenological stages for the efficient use of PGPR inoculants, *Scientific Reports*, 11: 19548.
<https://doi.org/10.1038/s41598-021-98914-9>
PMid:34599247 PMCID:PMC8486824
- Tang A., Haruna A.O., Majid N.M.A., and Jalloh M.B., 2020, Effects of selected functional bacteria on maize growth and nutrient use efficiency, *Microorganisms*, 8(6): 854.
<https://doi.org/10.3390/microorganisms8060854>
PMid:32517011 PMCID:PMC7356773

- Thomas J., Kim H.R., Rahmatallah Y., Wiggins G., Yang Q.Q., Singh R., Glazko G., and Mukherjee A., 2019, RNA-seq reveals differentially expressed genes in rice (*Oryza sativa*) roots during interactions with plant-growth promoting bacteria, *Azospirillum brasilense*. *PLoS ONE*, 14(5): e0217309.
<https://doi.org/10.1371/journal.pone.0217309>
PMid:31120967 PMCID:PMC6532919
- Vejan P., Abdullah R., Khadiran T., Ismail S., and Boyce A.N., 2016, Role of plant growth promoting rhizobacteria in agricultural sustainability-a review, *Molecules*, 21(5): 573.
<https://doi.org/10.3390/molecules21050573>
PMid:27136521 PMCID:PMC6273255
- Verma R.K., Sachan M., Vishwakarma K., Upadhyay N., Mishra R.K., Tripathi D.K., and Sharma S., 2018, Role of PGPR in sustainable agriculture: molecular approach toward disease suppression and growth promotion, In: Meena V. (eds), *Role of Rhizospheric Microbes in Soil*, Springer, Singapore, pp.259-290.
https://doi.org/10.1007/978-981-13-0044-8_9
PMCID:PMC5946563
- Wheatley R.M., and Poole P.S., 2018, Mechanisms of bacterial attachment to roots, *FEMS Microbiology Reviews*, 42(4): 448-461.
<https://doi.org/10.1093/femsre/fuy014>
PMid:29672765
- Wu F.Y., Wan J.H.C., Wu S.C., and Wong M.H., 2012, Effects of earthworms and plant growth-promoting rhizobacteria (PGPR) on availability of nitrogen, phosphorus, and potassium in soil, *Journal of Plant Nutrition and Soil Science*, 175: 423-433.
<https://doi.org/10.1002/jpln.201100022>
- Yi Y.L., Li Z.B., and Kuipers O.P., 2018, Plant-microbe interaction: transcriptional response of *Bacillus mycoides* to potato root exudates, *Journal of Visualized Experiments*, 137: e57606.
<https://doi.org/10.3791/57606-v>

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