Trends in Horticulture 2024, 7(2), 4980.
https://doi.org/10.24294/th.v7i2.4980

Article

Rhizospheric bacteria: Potent source of phytohormones and phytostimulants for horticultural plants in agronomy

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CITATION

Chauhan JV, Gohel SD. Rhizospheric bacteria: Potent source of phytohormones and phytostimulants for horticultural plants in agronomy. Trends in Horticulture. 2024; 7(2): 4980. https://doi.org/10.24294/th.v7i2.4980

ARTICLE INFO

Received: 4 March 2024
Accepted: 8 April 2024
Available online: 14 May 2024

Abstract: Horticultural crops are rich in constituents such as proteins, carbohydrates, vitamins, and minerals important for human health. Under biotic and abiotic stress conditions, rhizospheric bacteria are powerful sources of phytohormones such as indole acetic acid (IAA), gibberellic acid (GA), abscisic acid (ABA) and Plant growth regulators including cytokines, ammonia, nitrogen, siderophores, phosphate, and extra cellular enzymes. These phytohormones help horticultural crops grow both directly and indirectly. In recent agricultural practices, the massive use of chemical fertilizers causes a major loss of agricultural land that can be resolved by using the potent plant growth-promoting rhizospheric bacteria that protect the agricultural and horticultural crops from the adverse effect of phytopathogens and increase crop quality and yield. This review highlights the role of multifunctional rhizospheric bacteria in the growth promotion of horticultural crops in greenhouse conditions and agricultural fields. The relevance of plant growth hormones in horticultural crops highlighted in the current study is crucial for sustainable agriculture.

Keywords: rhizospheric bacteria; Plant growth regulators; horticultural plants; phytohormones; abiotic stress

1. Introduction

The rhizospheric bacteria are present in the soil and have a variety of physiological and metabolic characteristics that are also utilized for the synthesis of secondary metabolites [1]. The rhizosphere, or area around the plant's root, is home to plant growth-stimulating microorganisms. Rhizobacteria with the label "plant growth-promoting" stimulate and accelerate the growth of plants in a variety of ways. Hiltner [2] used the term "rhizosphere" for the first time and referred to the area around the root as a zone of utmost microbial activity.

The microbial community attached to the root is called root colonizer. Some bacterial genera included in the PGPR are *Arthrobacter*, *Bacillus*, *Burkholderia*, *Enterobacter*, *Klebsiella*, *Pseudomonas* and other microbial communities [3]. Several research data highlight the role of diverse bacteria that stimulate the growth and production of vegetable crops and research is still being done to understand the potential of PGP microbes [4,5]. Moreover, various plant growth-promoting bacteria including *Arthrobacter*, *Pseudomonas*, and *Bacillus* were associated with horticultural crops including tomatoes and potatoes [6,7]. The cytokines and auxins play an important role in the shoot and root development of apple, mango, kiwi, and avocado fruit plants [8,9]. Additionally, cytokinins protect plants against pests and phytopathogens to enhance the yield and quality of horticultural crops [10]. The flowering and fruit development of temperate fruit crops such as peach, cherry, pear, and strawberry, and vegetables such as celery, carrot, tomato, and cotton plants were regulated by the gibberellin [11].

According to Spaepen et al. [12], one of the key ways in which numerous rhizobacteria support plant development is by the generation of hormones that enhance the growth of plants. The hormones that enhance the growth of plants play a crucial role in controlling plant growth and development since they are signal molecules that function as chemical messengers. Organic substances known as phytohormones affect the biochemical, physiological, and morphological processes in plants at very low concentrations [13]. PGPR produces many phytohormones like auxin (IAA), gibberellins, cytokines, abscisic acid, and ethylene. Plant growth regulators (PGRs) are another name for the hormones generated by PGPR [14,15].

In recent years due to the extensive use of chemical fertilizers, the horticultural crops/products consumed by people in regular diets including fruits, spices, vegetables, as well as medicinal and aromatic plants have led to low productivity, food poisoning, and less income as compared to investment [16–18]. The production of siderophore, ammonia, indole acetic acid, extracellular enzymes [19–21], and other PGPs by rhizospheric bacteria increases the nutritional value and output of horticulture crops. Thus, this review updates the excellent information regarding the role of rhizospheric bacteria in sustainable agricultural methods for the improvement of agronomic crops through the production of various macronutrients and phytohormones.

2. Phytohormones produced by plant growth-promoting bacteria

2.1. Auxin

Auxin is a phytohormone and is also called a secondary metabolite produced by PGPR. Auxin aids in the growth and development of the plant. The procedure of cellular division also needs auxin [22]. Auxin has an impact on the shoot and root meristem sizes. According to Retzer et al. [23] and Ruzza et al. [24], auxin is necessary for gravitropism, phototropism, and shadow avoidance of roots and shoots. The phytohormones have a direct or indirect relationship with numerous physiological processes in plants. The auxin is synthesized by rhizobia which enhances plant growth by the formation of more nodules [25].

The non-pathogenic strain of rhizobacteria, such as Enterobacter sp., produced a high concentration of auxin [26]. The higher auxin content frequently indicates the presence of root-colonizing PGPR that promotes plant root growth [27–29]. The growth of roots can be enhanced by PGPR by loosening cell walls due to the colonization of the PGPs [30]. The rhizobacteria can stimulate root growth because of their capacity to synthesize indole acetic acid (IAA) [31]. In a recent study, *Bacillus* sp. isolated from sediment samples promoted the root and shoot of different varieties of *Solanum lycopersicum* L. by the production of IAA [32]. Similarly, an increase in the length of the plant and the number of leaves by 50% was observed in vegetables including cabbage, cauliflower and brinjal by application of indole acetic acid [33]. Actinobacterial strains TSm39 and KhEc 12 isolated from the rhizospheric soil of plants *Suaeda maritima* L. and *Euphorbia caducifolia* L. respectively produced indole acetic acid and enhanced plant growth [34,35]. Moreover, the role of auxin in plant growth-promoting traits was studied in different horticultural crops including root, shoot, and leaf development in apple (*Malus Domestica*), cucumber (*Cucumis sativus* L.), and grapevine (*Vitis vinifera* L.) respectively [36,37]. Additionally, the flowering and fruit development in strawberries, hazelnut, and cotton plants, vegetative growth in grapevine, shape, and weight of tomato fruit was regulated by the auxin biosynthesis [38–41].

Concerning bacterial IAA production, PGPR promotes the expansion of roots. As an illustration, IAA is produced by *Azospirillum* promoted rooting [42]. PGPR produces IAA, promotes colonization of bacteria around the root, enhances the plant tuber, improves plant mineral uptake, and affects the release of root exudation [42,43]. The total impact of boosting plant development cannot be achieved by IAA biosynthesis alone. In addition to the IAA synthesis, several other systems, such as phytohormone production and diazotrophy, cooperate to promote plant growth [44]. IAA synthesis by rhizobacteria can also regulate root growth. The optimum level of IAA produced by PGPR increases root growth but the overproduction of IAA by PGPR with the endogenously produced plant IAA decreases the root growth.

2.2. Cytokines

One of the classes of phytohormones is cytokines, which regulate plant growth. Both microorganisms and plants can produce cytokines. Cyanobacteria, *Agrobacterium tumefaciens*, *Pseudomonas savastanoi*, *Rhodococcus fuscians*, and slime mold *Discoideum*, as well as plant pathogenic bacteria, generate cytokines. Auxin and cytokinin levels in balance control plant organogenesis and root architecture. According to Vacheron et al. [45], some PGPRs synthesize both auxin and cytokinin hormones. All known cytokinins were separated by immunoaffinity chromatography and then finally identified by gas chromatography and mass spectrometry in the growth media of *Paenibacillus*, *Polymyxa* [46]. The *Pseudomonas* and other microbes with different crops under osmotic stress (25% PEG) conditions are capable of producing cytokines. In the past, cytokinins were generated by 70 rhizobacterial species, including *Pseudomonas putida*, *Stenotraphomonas maltophilia*, and *Pseudomonas stutzeri*, which were identified from the coleus rhizosphere [47].

In some plant-microbe interactions, the generation of microbial cytokinin is required in addition to plant cytokinin for the microbial stimulation of plant development. The leaf area of lettuce and wheat was previously raised by *Bacillus subtilis* with significant cytokinin synthesis in the rhizosphere [48]. Furthermore, cytokinin promoted shoot cell division and lengthening, and decreased root growth but did not reduce the accumulation of root biomass [49–51]. If cytokine-producing bacteria are delivered to the shoot, their introduction into the rhizosphere might not necessarily prevent root growth. According to Ilangumaran and Smith [52], the function of bacterial cytokinins in salt stress resistance is mainly unknown. Rhizobacterial cytokinin production led to an increase in leaf area and cytokinin-induced higher stomatal opening may have accelerated the loss of soil moisture [53]. Shoot ABA concentrations of lettuce increased by 2.1-fold after being inoculated with cytokinin-producing B. subtilis strains into well-watered plants [54].

The concentration of foliar cytokinin, which prevents leaf growth, was reduced by both salinity and drought [48,55]. By reserving water for use during reproductive development, the cytokinin-producing *B. subtilis* strain was introduced into lettuce plants' rhizospheres, which increased the cytokinin levels of both well-watered and drought-stricken plants [49]. Alfalfa plants inoculated with cytokinin-producing transgenic *Sinorhizobium* strains could withstand drought stress better [56]. The synthesis of cytokinin by PGPR encouraged plant growth by increasing output under both normal and stressful situations. Application of cytokinin during the fruit development stage of the litchi (*Litchi chinensis* Sonn.) plant decreased the water loss during the post-harvest stage, reduced the deterioration of the litchi, and enhanced the shelf life of the fruit [57]. Additionally, the cytokinin-producing *Pseudomonas fluorescens* G20-18 protected the Arabidopsis plant against the phytopathogenic bacteria *P. syringae* [58]. Cytokinin promotes leaf size and stops soil water evaporation. According to O'Brien and Benkava [59] and Grobkinsky et al. [58] the cytokinins also control chlorophyll production and chloroplast biogenesis, as well as the emergence of plant tolerance to biotic and abiotic stress. Plant cytokinin concentration can be influenced by PGPR. Many PGPR strains can produce cytokinin, which can increase host plant shoot growth and fruit formation [60–64].

2.3. Gibberellins

Gibberellins play a role in the growth and creation of reproductive organs as well as the ripening of fruits and the viability of seeds [65]. At high temperatures, gibberellins promote seed germination [66]. Guo et al. [67] and Wang et al. [68] stated that exogenous or microbial gibberellin could promote the development of xylem and shoots while suppressing root growth. A recent analysis found that gibberellins improve horticulture crop growth by controlling key agronomically significant traits such as plant stature, axillary meristem expansion, compound leaf development, flowering period, and parthenocarpy [69]. Furthermore, the DELLA repressor of gibberellin-induced genes, a component of the gibberellin signaling system, has a detrimental effect and is the primary cause of the suppression of plant development under stress [70,71]. The quantity of endogenous gibberellins in plants is impacted by PGPR. Gibberellins can be produced by some PGPR strains [72]. The host plant's branch length was raised by the inoculation of the PGPR strains *Bacillus cereus* and *Promicromonospora* sp. which produced gibberellins [73,74]. The exogenous gibberellins play an important role in the storage of vegetables under low temperatures. The gibberellic acid delays the yellowing of the broccoli, regulates the sugar content in potatoes, affects the morphology and nutritional value of the garlic, and sprouting of the toona plant under chilling stress [75–79].

To promote shoot growth in mutant rice plants lacking gibberellin synthesis, PGPR *Leifsonia soli* and *Enterococcus faecium* produced gibberellins. These strains increase the amount of bacterial gibberellins to make up the absence of plant gibberellins [73,80]. The number of gibberellins in the plant rose after the inoculation of gibberellin-producing PGPR strains of *Promicromonospora* sp. and *Bacillus amyloliquefaciens*, including those that were lacking in the culture media of these strains [73,81]. According to recent research, gibberellins are essential for improving seed germination, vigor index, and seedling length in a variety of vegetable plants, including tomato, eggplant, pea, okra, potato, and lettuce plants [33].

2.4. Abscisic acid (ABA)

Various PGPR strains can synthesize ABA among the various microorganisms that produce ABA. [82,83]. Salt tolerance is the most important parameter of bacteria and by turning on the stress-resistance genes, PGPR and plants produce ABA in response to abiotic stresses such as drought, cold, and salt [84]. When sugarcane roots are inoculated with *Gluconacetobacter diazotrophicus*, this boosts the plant tolerance to drought because ABA-dependent signaling genes of the shoot are more active than they are in uninoculated plants [85].

According to Shakirova et al. [86], ABA prevents plants from being dehydrated by promoting the expression of dehydrins. ABA is produced in the rhizosphere by a variety of root-associated bacteria. The plastids of plants are used to produce ABA [87,88]. According to Forchetti et al. [89], ABA is reportedly produced by rhizospheric and endophytic bacteria such as *Achromobacter*, *Bacillus*, and *Pseudomonas*. Without interacting with plants, certain marine Streptomyces also synthesize ABA and several phytohormones [90]. According to a recent study that considered the new information that came from model agricultural plant structures, the ABA increased the productivity of several cereal crops under drought stress. Moreover, the role of ABA in enhancing yield parameters including the number of tillers and grains of cereal crops such as rice and barley under salinity stress was studied [91]. A more recent study indicated that ABA with polyamines regulates photosynthesis and stomatal movement in strawberries under drought stress [92]. The different phytohormones produced by rhizospheric microbes and their response under stress conditions are depicted in **Table 1**.

Table 1. Plant growth hormones are produced by various rhizospheric microorganisms.

Hormones produced by PGPR	Name of PGPR	Associated plant	Response	Type of stress	Reference
Auxin (IAA)	*Bacillus* sp. NCTB5I, *Brevundimonas* sp. CHTB and *Pseudomonas* sp. CHTB 5B	*Glycine max* L. (Soyabean)	Increased the root length, shoot length and total biomass of plant	Drought	[93]
	Bacillus sp.	*Gossypium hirsutum* L. (Cotton)	Increased % seed germination, root and shoot length and total biomass of plant	Salt	[94]
	Rhizobium sp.	*Acacia cyanophylla* L. (Blue leaved wattle)	Increased dry biomass and shoot length	Salt	[95]
	Pseudomonas extremorientalis	*Silybum marianum* L. (milk thistle)	Increased the root length, shoot length and total biomass of plant	Salt	[96]
	Bacillus licheniformis	*Arachis hypogaea* L. (groundnut)	Increased biomass, and total plant length in stress condition	Salt	[97]

Table 1. (*Continued*).

Hormones produced by PGPR	Name of PGPR	Associated plant	Response	Type of stress	Reference
Auxin (IAA)	*Azospirillum*	*Lactuca sativa* L. (lettuce)	Increased biomass of the plant and enhanced N and P uptake in plant tissue under stress conditions	Salt	[98]
	Bacillus safensis Strain FN13 and *Cinnamomum camphora.*	*Brassica juncea* L. (Indian mustard)	PGPR strains protected canola plant against the inhibitory effect of cadmium	Heavy metal	[99,100]
	Arthrobacter sp. and *Bacillus* sp.	*Capsicum annuum* L. (pepper)	Reduced upregulation or even down regulation of the stress inducible genes over control plants	Osmotic stress (4.5% TEG)	[101]
	Burkholderia phytofirmans	*Vitis vinifera* L. (Grape vine)	Effectively increased antioxidant and color pigments, and catalase activity in plants under heat stress	Temperature	[102]
Gibberellins	*Priestia aryabhattai* strain KW05 and *Pseudomonas frederiksbergensis* strain KW07	*Brassica oleracea* L. (Broccoli)	Increased seed germination, fresh weight and shoot length	Salinity	[103]
	Azospirillum sp. and *Azotobacter* sp.	*Nigella sativa* L. (Black seed**)**	Increased the chlorophyll and relative water content	Salinity	[104]
	Enterococcus faecium	*Cucumis melo* L. (yellow melon)	Increased in shoot and root lengths, plant fresh weight, and chlorophyll content	Salinity	[105]
	Sphingomonas sp. LK11	*Solanum lycopersicum* L. (Tomato)	Modulated the oxidative stress and lipid peroxidation	Salinity	[106]
	Bacillus velezensis strain ZM39	*Juglans regia* L. (English walnut)	Enhanced root and shoot length, leaf area and chlorophyll content	Drought	[107]
	Pseudomonas putida H-2-3	*Glycine max* L. (Soyabean)	Enhanced salicylic acid and chlorophyll content	Salinity and drought	[108]
Gibberellins Cytokinin	*Phoma glomerata* LWL2 and *Penicillium* sp. LWL3	*Oryza sativa* L. (Rice)	Increased the root length, shoot length and assimilation of essential nutrients	Salinity and drought	[109]
	Azospirillum brasilense RA-17	*Triticum aestivum* L. (Wheat)	Increased proline and hormonal content in wheat kernel	-	[110]
	Bacillus subtilis	*Triticum durum* L. (Wheat)	Promote the plant growth by Increasing ion homeostasis	Drought	[111]
	Pseudomonas fluorescens G20-18	*Solanum lycopersicum* L. (Tomato)	Increases root and leaf growth and development	Drought	[112]
	Citrococcus zhacaiensis	*Glycine max* L. (Soyabean)	Enhanced the water holding capacity, biomass and yield	Drought	[113]
Abscisic acid	*Azotobacter chroococcum*	*Zea mays* L. (Maize)	Improved stomatal closure and water absorption efficiency	Salt	[114]
	Bacillus amyloliquefaciens RWL-1	*Oryza sativa* L. (Rice)	Regulated the plant growth by production of essential amino acids	Salt	[115]

Table 1. (*Continued*).

Hormones produced by PGPR	Name of PGPR	Associated plant	Response	Type of stress	Reference
Abscisic acid	*Pseudomonas fluorescens*	*Vitis vinifera* L. (Grape vine)	Increased length of shoot and root, area of leaves and resistance to drought	Drought	[116]
	Variovorax paradoxus	*Pisum sativum* L. (Pea)	Increased root and shoot biomass and stomatal conductance	Drought	[117]
	Rhodococcus sp. P1Y	*Solanum lycopersicum* L. (Tomato)	Increased leaf biomass	Osmotic stress	[118]

3. Conclusion

This review reflects the role of rhizospheric bacteria in horticulture by the production of various phytohormones including indole acetic acid (IAA), cytokinins, gibberellins, and abscisic acid. With the growing population and climate change, it is essential to be concerned about the food and nutritional security of the different fruits, vegetables, and cereal plants in abiotic stress. Therefore, a significant role of phytohormones in the abiotic stress tolerance of horticultural plants is evaluated in the present study. Moreover, the roles of different phytohormones in the promotion of plant growth parameters including root and shoot length, numbers of leaves and rhizoids, and development of fruits and vegetables were described. Furthermore, novel interdisciplinary approaches are discussed in the present study that dissect the actions of the different phytohormones in increasing yield, nutrients, and disease resistance in horticultural plants.

Author contributions: Writing—original draft preparation, formal analysis, and editing, JVC; conceptualization, review and editing, funding acquisition, SDG. All authors have read and agreed to the published version of the manuscript.

Funding: The authors acknowledge the support from DST-SERB (Department of Science and Technology-Science and Engineering Research Board) New Delhi, India (Sanction order no. ECR/2016/000928 Dated: 20.03.2017) for financial support. The authors also acknowledge the Department of Biosciences, Saurashtra University, Rajkot for providing financial support and infrastructure facilities.

Conflict of interest: The authors declare no conflict of interest.

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