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REVIEW

Plant growth-promoting rhizobacteria used in South Korea

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Abstract Many bacteria found in the rhizosphere provide contribution for the host plant's growth and protection that are known as plant growth-promoting rhizobacteria (PGPR). Plant–microbe interactions in the rhizosphere are important factors in determining the health of plants. Research for commercialization of these PGPR as an alternative to the use of chemical fertilizers for a more environmentally friendly treatment is continuously being improved. In this review, we discuss the essential traits that rhizobacteria must possess for them to be considered PGPR and report the bacterial species that exhibit these essential plant growth-promoting activities and which are approved for use by the South Korean regulations.

Keywords Biocontrol · Ethylene synthesis · Nitrogen fixation · Phosphate solubilization · Phytohormones · Plant growth-promoting rhizobacteria (PGPR) in South Korea · Siderophore

Introduction

One of the great challenges currently under consideration is to developing environmentally wide-ranging and sustainable crop production methods. Crop production must be increased to provide food for the increasing population. Although the use of chemical fertilizers is a viable option, there are health risks associated when their improper use and these agents can cause environmental destruction. Plant biotechnology has provided insight and aided the development of new crops to overcome complications caused by abiotic stresses (soil salinization and sodification, drought, soil pH, and temperature) and biotic factors such as pathogenicity by other living organisms, including bacteria, viruses, fungi, and parasites [1, 2].

In plant–microbe interactions, which have been widely examined, the host plant and bacteria present along the rhizosphere exhibit intimate interactions. These interactions promote host plant growth and pathogen suppression. The rhizosphere is a well-characterized ecological niche affected by root exudates [3]. Bacteria with direct and indirect positive effects on the growth and health of the plant are known as plant growth-promoting rhizobacteria (PGPR). In this review, we describe various important properties required by bacterial species to be considered PGPR and report various bacterial species exhibiting PGP qualities in South Korea.

Phytohormone production

Most distinguished phytohormones are consisted of cytokinins, auxins, gibberellins, ethylene, and abscisic acid, and PGPR show potential for the production of these hormones. These phytohormones can facilitate processes such as plant cell enlargement, division, and extension of symbiotic and non-symbiotic roots [1, 4, 5]. Furthermore, plant-associated bacteria may influence the hormonal balance of a plant.

Indole acetic acid (IAA), also known as auxin, governs different stages of plant growth and development, namely cell division, cell elongation, and tissue differentiation, and assists in apical dominance. IAA produced by rhizobacteria affects the root system through the increase of weight and

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size, the number of branches, and the surface area in contact with the soil.

Similarly, plant responses to cytokinin application include enhanced cell division, enhanced root development, enhanced root hair formation, inhibited root elongation, shoot initiation, and other physiological responses. Gibberellins, in contrast, are a group of phytohormones that affects developmental strategies in higher plants and include stem elongation, seed germination, flowering, and fruit setting [6, 7].

Ethylene synthesis inhibition

Ethylene is another growth regulator that affects physiological processes in plants. It is related primarily to the plant's growth and defense systems which are triggered by stress responses. Factors such as light, temperature, salinity, pathogen attacks, and nutritional status alter ethylene levels. Moreover, ethylene also facilitates additional processes not related to stress such as ripening, root elongation, and seed development. As ethylene levels decrease, root system growth increases, as described above. Degradation of 1-aminocyclopropane-1-carboxylic acid (ACC), a direct precursor of ethylene, creates a concentration gradient that favors its exudation. Maintaining a balance between the ethylene and auxin is important since the two are related growth regulators, some effects attributed to auxin-producing bacteria result from ACC degradation [1, 8].

Free nitrogen fixation

Nitrogen is a key component in the synthesis of cellular enzymes, proteins, chlorophyll, DNA, and RNA, and, as a result, it is important in plant growth. Bacterial strains capable of nitrogen fixation are divided into two categories: root/legume-associated symbiotic bacteria and free nitrogen-fixing bacteria. The former specifically infect the roots to produce nodules, while the latter are non-specific and can form symbiotic relationships with other plants and organisms [1, 9].

Phosphate solubilization

Phosphorus is the second most important mineral nutrient after nitrogen limiting plant growth. Although soils contain a high concentration of total phosphorus, the amount available for plant uptake is limited because P is in an insoluble form. Bacteria present in the rhizosphere can solubilize phosphate through different mechanisms. The most common method of solubilizing phosphorus is by secreting organic acids that act as chelators. Solubilization of P in the rhizosphere is the most common mode of action that increases the availability of nutrients for host plant uptake [10].

Production of siderophore

Another essential plant nutrient is iron. Iron serves as a cofactor for numerous enzymes that are important in physiological processes such as photosynthesis, nitrogen fixation, and respiration. Similar to phosphorus, iron is abundant in the soil but is not available for plant uptake because Fe^{3+} predominates and reacts to form insoluble hydroxides. In a similar manner to solubilizing phosphates, bacteria present in the rhizosphere release organic compounds for chelation. A different strategy involves absorbing the iron-organic compound complex, where the iron is reduced in the plant and directly assimilated [11].

Enzyme synthesis that hydrolyzes fungal cell walls

PGPR may be applicable in agriculture for the biocontrol of plant pathogens. Production of cell wall-degrading enzymes plays a very important role in controlling pathogens. Cell wall-degrading enzymes including chitinase, β-1,3-glucanase, cellulase, and protease that are secreted by PGPR directly inhibit the hyphal growth of fungal pathogens through the degradation of their cell which may be an alternative method for replacing chemical fungicides [2, 10, 12].

PGPR species in South Korea

South Korea is one of the top countries leading research and development for biotechnology. Development of PGPR is one focus of this field. The South Korean government approved the use of 108 total species of bacteria, yeast, and fungi as fertilizers and some species as feeds. However, there was some misunderstanding because of changes in taxonomy and some isolates were found to be the same species. In the present study, only 51 bacterial species have been identified to have strains included in the Korean Agricultural Culture Collection (KACC). Among these, 40 were found to have PGP activities in previous studies (Table 1), while the 11 species require further examination. Additional research is needed to evaluate the PGP characteristics of these 11 species (Table 2).

Conclusion

The PGP activities of rhizosphere bacteria show great promise for applications in sustainable and ecofriendly agriculture. PGPR not only promote growth by providing nutrients but are also useful as biocontrol agents to protect

Table 1 Regulated bacterial species in South Korea and their different PGP characteristics based on references with their respective KACC strain

Species	KACC number	PGPR functions											References
		Phytohormones				Nitrogen fixation	Siderophore	Biocontrol			Phosphate solubilization	Ethylene Inhibition	
		IAA	ABA	Cytokinin	GA			Anti-fungal	Anti-microbial	Insecticidal			
Acinetobacter calcoaceticus	11541					○[b]	○						[13]
Acetobacter peroxydans	NA					○							[14]
Alcaligenes defragrans	NA					○							[15]
Azospirillum brasilense	13364						○	○					[16]
Bacillus amyloliquefaciens	12067	○				○	○	○			○		[17]; This study
Bacillus licheniformis	10476		○		○	○		○			○		[18, 19]; This study
Bacillus macerans	11233					○					○		[20]; This study
Bacillus megaterium	10482		○								○	○	[21]
Bacillus mojavensis	NA							○					[22]
Bacillus natto	NA												NA
Bacillus polymyxa	10485					○	○				○		[20]; This study
Bacillus pumilus	10917		○		○			○			○		[18, 19, 23]; This study
Bacillus subtilis	10854					○	○	○			○		[24]; This study
Bacillus vallismortis	12149							○					[25]
Bacillus velezensis	14004					○		○			○		[26]; This study
Brevibacillus brevis	10857							○					[27]
Brevibacillus formosus	10902							○					[28]
Brevibacterium ammoniagenes (*Corynebacterium ammoniagenes*)[a]	NA												NA
Brevibacterium otitidis	NA								○				[29]
Brevibacterium linens	14346								○				[30]
Burkholderia cepacia	10190	○						○					[2, 31]
Burkholderia pyrrocinia	NA							○					[32]
Cellulomonas fimi	20534							○					[33]
Cellulomonas turbata Oerskovia turbata	15267								○				[34]
Klebsiella mobilis (*Enterobacter aerogenes*)	13732							○					[35]

Table 1 continued

Species	KACC number	PGPR functions											References
		Phytohormones				Nitrogen fixation	Siderophore	Biocontrol			Phosphate solubilization	Ethylene Inhibition	
		IAA	ABA	Cytokinin	GA			Anti-fungal	Anti-microbial	Insecticidal			
Lactobacillus acidophilus	12419	○							○				[36, 37]
Lactobacillus casei	12413	○											[37, 39]
Lactobacillus rhamnosus	11953								○				[39]
Lactobacillus confuse (*Weissella confuse*)	11841							○					[38]
Lactobacillus delbrueckii	13439							○					[40]
Lactobacillus fermentum	11441							○					[41]
Lactobacillus paracasei	12361							○					[42]
Lactobacillus plantarum	11451							○					[43]
Lactococcus lactis	13438							○					[44]
Lysinibacillus fusiformis	10903		○										[18]
Lysobacter antibioticus	11383								○				[45]
Microbacterium aurum	15219							○					[46]
Nocardiopsis dassonvillei	16782								○				[47]
Paenibacillus azoreducens	NA												NA
Paenibacillus lentimorbus	NA							○					[48]
Pediococcus cerevisiae (*Pediococcus acidilactici*)	12307								○				[49]
Photorhabdus luminescens	12254									○			[50]
Pseudomonas fluorescens	10327			○									[51]
Pseudomonas jessenii	NA												NA
Pseudomonas maltophilia (*Stenotrophomonas maltophilia*)	11358							○					[52]
Pseudomonas nitroreducens	15288	○				○							[30, 53]
Pseudomonas panipatensis	NA										○		[54]
Pseudomonas putida (*Pseudomonas mildenbergii*)	10266	○											[55]
Rhodobacter capsulate (*Rhodopseudomonas capsulata*) (*Rhodobacter capsulatus*)	15298					○							[56]
Rhodobacter sphaeroides (*Rhodopseudomonas sphaeroides*)	15299					○							[57]
Rhodopseudomonas viridis (*Blastochloris viridis*)	NA												NA
Rhodobacter rubrum	NA												NA

Table 1 continued

Species	KACC number	PGPR functions											References
		Phytohormones				Nitrogen fixation	Siderophore	Biocontrol			Phosphate solubilization	Ethylene Inhibition	
		IAA	ABA	Cytokinin	GA			Anti-fungal	Anti-microbial	Insecticidal			
Rhodopseudomonas palustris	12814					○							[58]
Streptomyces asoensis Streptomyces cacaoi	NA								○				[59]
Streptomyces carpinensis	NA							○					[60]
Streptomyces fradiae (*Streptomyces roseoflavus*)	NA							○					[61]
Streptomyces griseochromogenes	NA								○				[62]
Streptomyces griseus	NA							○					[63]
Streptomyces halstedii	NA							○					[64]
Streptomyces niger	NA												NA
Streptomyces violaceusniger	NA							○					[65]
Tetrathiobacter kashmirensis (*Advenella kashmirensis*)	NA												NA

[a] The () signifies name from the previous taxonomy

[b] The ○ sign denotes species exhibiting PGP activities in the respective activity while species inside the parenthesis. Unknown PGP activities were left blank

Table 2 Regulated bacterial species in South Korea and their KACC strains without reference for PGP qualities

Species	KACC strain	PGPR function
Paenibacillus amylolyticus	11263	Unknown
Paenibacillus chibensis	11242	Unknown
Paenibacillus chibensis	11526	Unknown
Brevibacterium flavum (*Corynebacterium glutamicum*)[a]	20786	Unknown
Frateuria aurantia	11384	Unknown
Lactobacillus bulgaricus	12420	Unknown
Lysinibacillus boronitolerans	15323	Unknown
Pediococcus halophilus Tetragenococcus halophilus	12355	Unknown
Pseudomonas nitroreducens	15288	Unknown
Rhodobacter azotoformans	14390	Unknown
Streptococcus cremoris (*Lactococcus lactis cremoris*) (*Streptococcus lactis*)	13438	Unknown
Streptococcus thermophilus (*Streptococcus salivarius subsp. thermophiles*)	11857	Unknown

[a] Species inside the parenthesis () signifies name from the previous taxonomy

plants from pathogens. While the fundamentals of how PGPR promote growth are well known, there is still much more to learn about the mechanisms underlying plant–microbe interactions for commercial production for the microbes as an alternative to chemical fertilizers.

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