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Antagonistic Compounds Producing Plant Growth Promoting Rhizobacteria: A Tool for Management of Plant Disease

Himanshu Singh[1], Vishakha Jaiswal[2], Siddhi Singh[2], S. P. Tiwari[1], Bharti Singh[3] and Deepmala Katiyar[4*]

[1]Department of Microbiology, Veer Bahadur Singh Purvanchal University, Jaunpur, India.
[2]Department of Biochemistry, Veer Bahadur Singh Purvanchal University, Jaunpur, India.
[3] Vitae Gen Biotech-Educational and Research Institute, Varanasi, India.
[4]Department of Plant Physiology, Institute of Agricultural Sciences, Banaras Hindu University, Varanasi, India.

Authors' contributions

This work was carried out in collaboration between all authors. Authors HS, VJ and SS wrote the first draft of the manuscript. Authors SPT and BS managed the literature searches. Author DK had proposed the topic for review and revised the manuscript. All authors read and approved the final manuscript.

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ABSTRACT

Agriculture is facing struggle to meet the various confront of reducing plant diseases for an increasing world population food security. Great quantities of synthetic fertilizers and pesticides are required for high productivity which can damage ecosystem structures and functions, including the soil microbial community which plays an important role in agriculture sustainability. Soil is an excellent niche of growth of much plant growth promoting rhizobacteria. PGPR are naturally occurring soil bacteria that aggressively colonize in plant roots and play a vital role in crop

**Corresponding author: E-mail: deepmala.katiyar@gmail.com;*

protection, growth promotion and in the improvement of soil health. Scientific researchers involve multidisciplinary approaches to understand adaptation of PGPR, effects on plant physiology and growth induced systemic resistance, biocontrol of plant pathogens and biofertilization. The primary mechanism of biocontrol by PGPR involves the production of antibiotics such as carboxylic acid, 2,4-diacetyl phloroglucinoloomycin,pyoluteorin,pyrrolnitrin,kanosamine,zwittemycin-A and pantocin. A cascade of endogenous signals such as sensor kinases, N-acyl homoserine lactones and sigma factors regulates the synthesis of antibiotics. Some of these antibiotics have broad spectrum against many plant pathogens like fungi, viruses and bacteria, affecting crop plants. These antibiotics also serve as determinants in triggering induced systemic resistance (ISR) in the plant system.

Keywords: Antibiotic; plant growth promoting rhizobacteria; indirect plant growth promotion; rhizosphere.

1. INTRODUCTION

Plant growth promoting rhizobacteria (PGPR) are naturally occurring heterogenous group of soil bacteria that are found in rhizosphere, and actively colonized in plant root and increase plant growth directly and indirectly [1]. The term PGPRs was coined by Joe Kloepper in late 1970 and was defined by Kloepper and Schroth [2]. PGPRs are known to influence plant growth by various mechanisms (Fig. 1).

PGPR is being used as biofertilizer and bioenhancer for different crop plant as an alternative source of chemical fertilizer. In present scenario, 72 bacterial isolates have been reported as efficient PGPR which belong to *Azotobacter, Pseudomonas, Mesorhizobium*, *Bacillus* and *Serratia* [3,4,5]. After various studies, it was found that *P. fluorescens*, annual plant, co-inoculate with more than one biological control agent. Biocontrol is the phenomenon in which organisms (or their metabolites) are used as a natural fighter or inhibitor of a pest or Phytopathogen [6] to reduce or remove its bad effect on the plant physiology or its product. PGPR have been reported to be present in high populations in the rhizosphere and as endophytes of many crops. They include species of *Enterobacter, Bacillus, Klebsiella, Herbaspirillum, Burkholderia, Azospirillum,* and *Gluconacetobacter* [7,8]. The presence of biocontrol activity of organism or agents in the environment is the important reason behind that many agricultural products are not completely destroyed by pathogens and diseases because those organisms have ability to antagonizing with pathogen by the reduction of its unnecessary or harmful effects [9]. According to various studies, it was shown that antibiotic production elucidates mechanism of action on antagonistic microorganism [10].

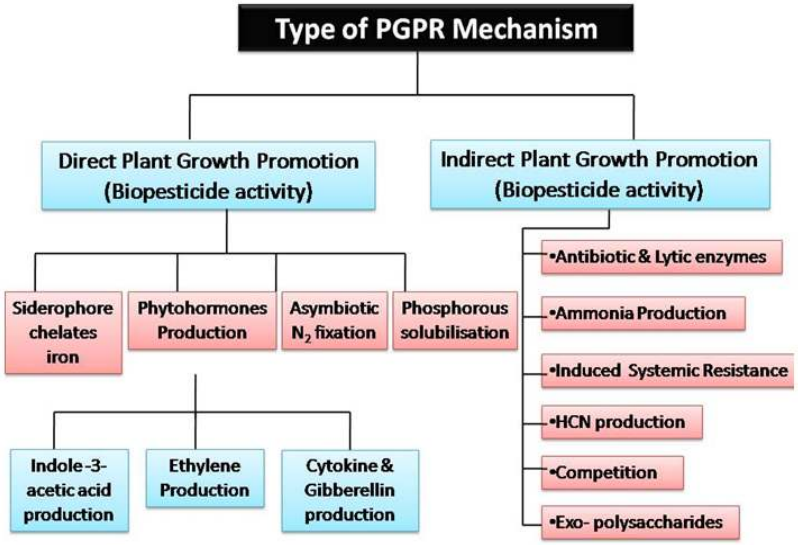

Fig. 1. Type of plant growth promoting rhizobacteria mechanism

2. MECHANISM OF ACTION OF PGPR (DIRECT AND INDIRECT)

The mechanism by which PGPR promote plant growth are not fully understood [I] The ability to produce or change the concentration of plant growth regulators like indole-acetic acid, gibberellic acid, cytokinins and lowering plant level [11,5] [II] Asymbiotic N_2 fixation [12]. [III] Antagonism against phytopathogenic Microorganism by production of antibiotics [13] and cyanide [14]. [IV] Solubilization of mineral phosphate (biological phosphate mineralization) and other nutrient that release complexing or mineral dissolving compound e.g. organic acid anions, protons, hydroxyl ion and carbon di hydroxides [15,16]. [V] *Azospirillum, Pseudomonas* and *Azotobacter* strains could affect seed germination and seedling growth. In natural ecosystem, beneficial plant associated bacteria play an important role in supporting and increasing plant health and growth [17]. Some soil borne microorganisms can enter roots and stabilized subpopulation ranging from 10^5 to 10^7 CFU g^{-1} FW. The good result obtained *in vitro* cannot always be dependably reproduced under field conditions [18,19,20].

3. ANTAGONISTIC COMPOUNDS, MODE OF ACTION AND PPGR TARGETS

Antibiotics are heterogeneous group and are low molecular weight of organic compound that are harmful to the growth and metabolic activity of microorganisms [21]. Most of the antibiotics are peptides in nature and effective or active against fungal growth like as cyanide lipopeptide, phosphoro-oligopeptide and phosphoro-dipeptide [22]. Antagonistics produced by bacteria include volatile compounds (hydrogen cyanide, aldehydes, alcohols, ketones, and sulfides) and nonvolatile antibiotics: polyketides (diacetylphloroglucinol; DAPG and mupirocin), heterocyclic nitrogenous compounds (phenazine derivatives: pyocyanin, phenazine-1-carboxylic acid; phenazine-1- carboxylate (PCA), and phenazine-1-carboxamide (PCN) and hydroxyphenazines) [23] and phenylpyrrole antibiotic (pyrrolnitrin) [24] (Fig. 2). The most widely studied group of rhizospheric bacteria described as being implicated in biocontrol was phenazine fluorescent *Pseudomonads* [25]. Numerous types of antibiotics have been isolated from fungal and bacterial strains and this diversity includes mechanisms of action that inhibit synthesis of pathogen cell walls, influence membrane structures of cells and inhibit the formation of initiation complexes on the small subunit of the ribosome [26]. Pyrrolnitrin, the antibiotic produced by the *P. fluorescens*BL915 strain, is able to prevent the damage of *Rhizoctonia solani* during damping-off of cotton plants. In soils, antibiotic 2, 4 diacetylphloroglucinol (2, 4- DAPG) producing *Pseudomonas* sp. was reported for biocontrol of disease in wheat caused by the fungus *Gaeumanomyces graminis* var. *Tritici* Bacterization of wheat seeds with *P. fluorescens* strains producing the antibiotic phenazine-1-carboxylic acid (PCA) resulted in significant suppression of take-all in about 60% of field trials [27].

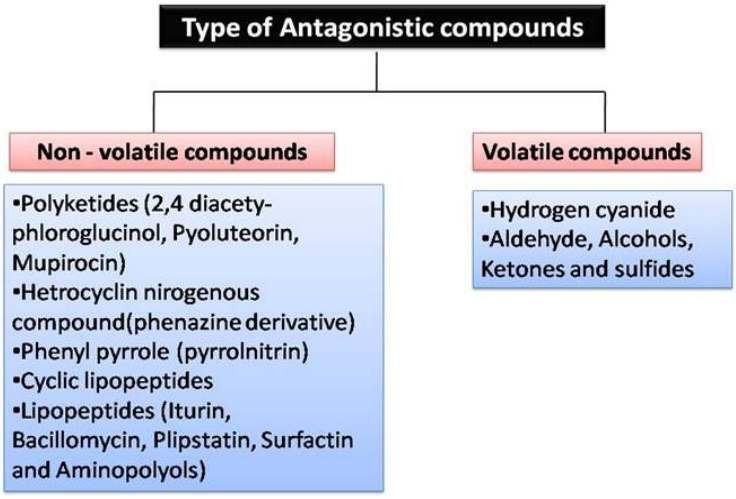

Fig. 2. Major two group of antagonistic compounds for the suppression of plant pathogens

4. TYPE OF ANTAGONISTIC COMPOUNDS

Synthesis of natural antibiotics by plant growth promoting rhizobacteria (PGPR) include 2,4 diacetalphloroglucinol, phenzine-1-carboxylic acid, phenazine-1-carboxamide, pyoluteorin, pyrolnitrin, oomycin, antitumor antibiotics FR901463, butyrolactones, kanosamin, zwittermycin A, aerogine, rhamnolipids, cepacimide A, pseudomonic acid, azomycin A, cepafungins and antiviral antibiotics karalicin. All these antibiotics have antiviral, antimicrobial, antihelminthic, phytotoxic, antioxidant and cytotoxic effect and they are also helpful in plant growth [28]. Each of the antibiotics have different way of work based on different action some of which attack the cellular membrane and some other have inhibitory effect on ribosome and other cellular organism [28] that's why some of them are susceptible to some antibiotics but not other depending on the specific form of cellular organelles. Six classes of antagonistic compounds such as phenazines and phloroglucinol, pyoluteorin, pyrrolnitrin, cyclic lipopeptide (all of which are diffusible in nature) and HCN are much more related to the biocontrol of root disease [29]. Recently discovered lipopeptide, biosurfactants produced by *Pseudomonas* and *Bacillus* species have been apply in bio control because of their potential positive effect of competitive interaction with organism which include bacteria, fungi, oomycetes, protozoa, nematodes, and plants [30,31].

Zwittermycin, Kanosamine are Novel class of antibiotics produce by *B. cereus* UV85. In antibiotics synthesis, *B. cereus* modifies the ionic composition of medium in which it grows and raises the pH, sequesters Ca^{++}, and excretes ammonia. This combination is highly toxic to zoospores of oomycete pathogens, causing rapid swelling of the expulsion vacuole, followed by zoospore lysis [32].

Sigma factor are important for regulation of antibiotic production in *florescence Pseudomonad;* housekeeping factor sigma [70] and the stress-related sigmas have important role in production of antibiotic metabolites in disease suppression [29].

Table 1 lists the heterogeneous group of organic compound that prevent the development of pathogens and its metabolic activity and very helpful in plant growth and development.

5. POSSIBLE MECHANISMS THAT INCREASE RESISTANCE

5.1 Antibiotic

Natural Antibiotic synthesizer must contain some antibiotic resistance mechanism to stop them committing suicide through formation of their own toxins. Environment of soil is very important for research into the mechanism of antibiotic resistance, including possible mechanism which is not yet seen in clinical microbiology [54].On a given population when antibiotics are a constant pressure then antibiotic resistance occur; those organisms with natural resistance can survive easily and also reproduce easily whereas those organisms which do not have resistance factor are die [55]. Once a resistance factor has developed, it can be rapidly spread within a population where DNA is transfer from one bacterium to another bacterium [56]. Transfer of DNA containing antibiotic genes can do by three processes (1) Transformation (2) Transfection (3) Conjugation.

Production of natural antibiotic by bacteria mainly *Pseudomonads*, seems to be closely regulated by two- component system involving an environmental sensor (a membrane protein) and cytoplasmic response factor [57]. In biocontrol bacteria, most known cases involve the AHL (N-acetyl homoserine lactone) control of phenazines antibiotics synthesized by rhizospheric *Pseudomonads*. Recent findings demonstrate that phenazines are not only group of biocontrol related antibiotics, but its synthesis or production is regulated through QS System (Quorum Sensing System). *Bacillus polymyxa* strain Pw-2R and *Pseudomonas fluorescence* strain Sw5-RN a spontaneous antibiotic-resistant derivatives of the naturally occurring parental strains *B. polymyxa* Pw-2 and *P. fluorescence* Sw5 respectively [58]. Expression of several phenotypic characteristics in bacteria e.g. bioluminescence, biofilm formation, motility, production of virulence factors, exoenzymes and antibiotics is often a cell-density-dependent phenomenon mediated by cell-to-cell communication in a process known as quorum sensing (QS). The main QS system, known as Lux IR, operates to control the response, mainly via production of N-acylated homoserine lactone (AHL) signaling [59]. Various PGPR, which are able to protect plant from fungal and bacterial disease, have been found to produce AHL and other QS signals [60]. Antibiotics are major determinants of antagonism against fungi by

various PGPR, among the fluorocent *Pseudomonads*, many strains produce one or more potent metabolites with antifungal activity, the best-characterized are simple compounds such as phenazines, 2-4 diacetylphloroglucinol, 3-chloro-4- (20 - nitrochlorophenyl) pyrrole (pyrrolnitrin) and pyoluteorin [61]. However, only a few examples of the role of QS system in the regulation of these secondary metabolites production have been described. Most known cases involve the AHL control of phenazines antibiotics [60,39]. Four different LuxRI/AHL QS systems have been described in *Serratia* [61, 62]. These systems control population surface migration, biofilm development and production of the bio-surfactant serrawettin, the antibiotics carbapenem and prodiogosin, chitinases, proteases and other exoenzymes [63,64,65, 66,67]. These lipopeptides displayed dose-dependent antifungal activity against a broad spectrum of phytopathogens and were weakly antagonistic to *Staphylococcus aureus*. Lipopeptides produced by this strain were isolated, purified by HPLC system, elucidated by NMR spectroscopy and MS spectrometry techniques, and the antimicrobial activities were evaluated with paper disc–agar diffusion assay. The cytotoxic activities were based on 3-(4,5 dimethylthiazol-2-yl)-2,5-diphenyltetrazolium bromide assay. On the other hand, bacteria can produce a wide variety of compounds with antimicrobial activity used as defense systems. These include broad-spectrum antibiotics, lactic acid produced by lactobacilli, lytic agents such as lysozymes, numerous types of exotoxins and bacteriocins, which also have a bactericidal mode of action [68]. Siderophores, bacteriocins and antibiotics are three of the most effective and well known mechanisms that an antagonist can employ to minimize or prevent phytopathogenic proliferation.

5.2 Bacteriocin as another Defense Molecule

Bacteriocins are bacterially product synthesized peptides (protein) that are either may be bacteriostatic or may be bacteriocidal against strains related to the synthesizer strain [69]. Various types of bacteriocinsare identified (Table 2). Although determining the sequence of amino acid of bacteriocins can often be difficult, due to presence of modified amino acid. In microbial defense system other defense molecule are used as bacteriocins. Researcher reported that the nature of bacteriocins differ from traditional antibiotics in one critical manner [68]. They commonly have a relatively narrow killing spectrum and are only harmful or toxic for closely related to the bacteriocins producing strain. Near about all the bacterium may make at least one bacteriocin and many types of bacteriocins isolated from Gram- negative bacteria appear to have been created by recombination between existing bacteriocins [70]. The colicin proteins are very representative bacteriocin produced by some strain of *E. coli* that are lethal for related strain *E. coli* is a Gram negative bacterium and the colicin's name derived from *E. coli;* therefore, other bacteriocins have been thusdefined. Interestingly bacteriocins from *Bacillus* spp. are increasingly becoming much more important because of their sometimes broader spectra of inhibition (As compared with most lactic bacterial bacteriocins).

5.3 Bacteriocin Classes

Several classes of bacteriocins have been described based on their size, post-translational modification, production and heat liability [71,72] as follows:

Class I- Includes the lantibiotics, bacteriocins that possess the characteristic lanthionine moiety and are after produced by lactic acid bacteria [73].

Class II- Exclude the lantibiotics and contain heat stable bacteriocins. This class is also subdivided into section a, b and c members.

ClassII a- Is conserved sequence homology of at least YGNGVXC.

ClassII b- Bacteriocins need two bacteriocins for antibiotics activity.

ClassII c- Comprises all other class II bacteriocins [71].

Class III– Contain larger (730 KDa) heat labile bacteriocins

Class IV– Contain bacteriocins that are modified with either Lipid or Carbohydrate components [72].

The recently discovered PGPR is *Bacillus thuringiensis* NEB17 that help to enhance the growth of soybean [74]. This strain also synthesizes a bacteriocin, thuricin 17, which is a low molecular weight peptide (3162 KDa). It presents an inhibitory or a harmful effect against *Bacillus* strains [75]. Thuricin 17 is stable across a pH range of 1.0 to 9.25, highly heat resistant and is inactivated by treatment with proteolytic enzymes [75].

Table 1. Plant growth promoting rhizobacteria and their mode of action

S. N.	Antibiotics	Source	Target organism	Mode of action	Reference
1	Bacillomycin	*Bacillus*	*Aspergillus flavus*	-	[33]
2	Kanosamine (Aminoglycoside)	*Bacillus cereus*	*Phytophthora medicaginis*	Contribute to biocontrol of alfalfa dumping off	[34,35]
3	Zwittermicin A	*B. cereus UW85 strain*	*Phytophthora*	Suppresses Oomycete pathogens	[34,38]
4	Pyrrolnitrine (From this fungicide fluidioxonil can be derived)	*Pseudomonas fluoroscens BL915 strain* *Pseudomonas* sp.	*R. solani*	Able to prevent the damage of *R. solani* during dumping of cotton plant and this fungicide is used for seed treatment and foliar spray or soil drench	[36,37]
5	2,4 diacetylfluoroglucinol (DAPG)	*Pseudomonads*	*Phythium* species and particularly zoospores of oomycete	Membrane damage to phythium species and is particularly inhibitory to zoospore of oomycete	[37,13]
6	Phenazine	*Pseudomonads*	*F. oxysporum* and *Gaeumahnomyces graminis*	Posses redox activity and can suppress pathogen of plant	[39]
7	Phenazine- 1-carboxamide	*P. chlororaphis PCL 1391 strain*	-	Which is able to release soluble iron from insoluble ferric oxide at neutral pH, raising the possibility that phenazenes might contribute to iron mobilization in soil	[40,41]
8	Polymyxin,Circulin and Calistin	*Bacillus sp*.	Gram positive Gram negative bacteria and as well as many pathogenic Fungi	-	[26]
9	Streptomycin and Oxytetracyclin	*Pseudomonas sp.*	*Erwinia amylovora*	Control of fire blight (some pathogenic strain resistant to the antibiotic appears in several growing region) by Streptomycin And a disease of pear apple coused by *E. amylovora* (oxytetracyclin is less effective than Streptomycin for suppression on antibiotic sensitive population *of E. amylovora*)	[42]
10	Iturin	*B. subtilis*	*Phythiumultimum, R. soloni, F. oxysporum, S. sclerotiorum* and *M. phaseolin*	-	[43]

S. N.	Antibiotics	Source	Target organism	Mode of action	Reference
11	Iturin A and Surfactin	*Bacillus* sp.	*R. soloni*	-	[44]
12	Phenazin-1-carboxylic acid	*Pseudomonas* sp.	Antifungal	-	[45]
15	Pyrrolnitrin	*Pseudomonas* sp.	Antifungal	-	[37]
14	Pyuteorin	*Pseudomonas* sp.	Antifungal	-	[46]
15	Oomycin	*Pseudomonas* sp.	Antifungal	-	[47]
16	Copaciamide A	*Pseudomonas* sp.	Antifungal	-	[48]
17	Ecomycins	*Pseudomonas* sp.	Antifungal	-	[49]
18	DDR	*Pseudomonas* sp.	Antifungal	-	[50]
19	Viscosinamide	*Pseudomonas* sp.	Antifungal	-	[51]
20	Butyrolactones	*Pseudomonas* sp.	Antifungal	-	[52]
21	Sulphonamide	*Pseudomonas* sp.	Antifungal	-	[47]
22	Pyocyanin	*Pseudomonas* sp.	Antifungal	-	[52,53]

Table 2. Bacteriocins of plant growth promoting rhizobacteria and their source

Sl. No.	Bacteriocins	Source	References
1	Thuricin 439A and Thuricin 439B (share the partial N-terminal sequence WVAXVGAXGTAALASGGVV)	*Bacillus thuringiensis* 439	[76]
2	Cerein7(N-terminal sequence-GWGDVL)	*Bacillus cereus* Bc7	[77]
3	Bacthuricin F4 (N-terminal sequence- DWTXWSXL)	*B. thuringiensis* spp. Kurstaki strain BUPM	[78]
4	Pyocins	*P. pyogenes strain*	[79]
5	Cloacins	*Enterobacter cloacae*	[79]
6	Marcescins	*Serratia marcescens*	[79]
7	Megacins	*B. megaterium*	[79]
8	Thuricin17	*B. thuringiensis NEB17*	[75]

6. CONCLUSION

Plant pathologists are facing major challenges for the management of soil-borne plant pathogens. Excessive use of pesticides against plant pathogens has resulted in environmental pollution and resistance among pathogens. Subsequently, identification of suppressive soils to various soil borne plant pathogens such as *Gaeumanomyces graminis*, Var. tritici. [80]. This present review revealed that environment is confer with an intensify biodiversity of PGPR. The prevailing bacterial microfloras in the PGPR community include *Pseudomonas* spp., *Enterobacter* spp. and *Bacillus* spp. Among the wide genetic biodiversity of prokaryotes, plant growth promoting rhizobacteria (PGPR) play a vital role in the management of plant diseases to increase crop productivity via various mechanisms [2]. Considerable progress has been made over the past two decades to elucidate the mechanisms by which fluorescent *Pseudomonads* suppress diseases. The primary mechanism of biocontrol by fluorescence *Pseudomonads* involves production of antibiotics such as 2, 4-diacetylphloroglucinol, pyoluteorin, pyrrolnitrin, phenazine-1-carboxyclic acid, 2- hydroxyphenazines and phenazine-1-carboxamide. In addition to direct antipathogenic action, antibiotics also serve as determinants in triggering induced systemic resistance (ISR) in the plant system and contribute to disease suppression by conferring a competitive advantage to biocontrol agents. Synergism between antibiotics and ISR may further increase host resistance to plant pathogens. Though several modes of action are responsible for the suppression of plant pathogens, this review focused on new insights in biocontrol of plant pathogens by PGPR through antibiotics.

COMPETING INTERESTS

Authors have declared that no competing interests exist.

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