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**Review Article** 

# Plant Beneficial Mechanisms and Applications of Endophytic Bacteria

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#### **Abstract**

Endophytic bacteria and fungi reside inside the plant without causing any harmful effects to the host. They have ubiquitous distribution within the plant and can be isolated from different parts by surface sterilization followed by exposing the sterilized parts onto nutrient medium. They have significant impact on physiology and metabolism of the plants. This is due to the evolutionarily adapted multi-potent plant growth promoting and biocontrol mechanisms. Because of their plant beneficial features, they have the promises to develop into microbial inoculants for the field application as biofertilizers, plant strengtheners, phytostimulators or biopesticides. Their exploitation offer promising environment friendly support for emerging organic agricultural applications in worldwide. This review describes the mechanisms of plant beneficial features shown by endophytic bacteria to provide an insight in to their in planta role and applications.

**Key Words:** Endophytic Bacteria; Plant Growth Promoting properties; Biocontrol Agent; Biofertilizers

#### Introduction

Plants are naturally associated with microorganisms in various ways. Bacteria which enter the plant and establish mutualistic association without any harm are known as endophytic bacteria [1, 2, 3]. Here, the host provides unique protective niche for the endophytic organisms, and endophytes in turn synthesise diverse chemical scaffolds [4,5] which mediate increased plant growth, development, nutrient uptake and also protect plant from pathogen. Bacterial endophytes are considered to enter the host from the surrounding soil through wounds in the roots [6] or through root hairs [7] and subsequently it transverse the root cortex and reach various plant organs through vascular system or through the apoplastic routes. The nature and types of endophytes present in the plant is depend on its source, age, tissue type, time of sampling and environment [8,9]. The endophytic bacteria can produce an array of bioactive metabolites and hydrolytic enzymes as adaptive strategy for endophytic association. The endophytes can provide protection to plant from pathogen attack in addition to its plant beneficial properties such as production of indole acetic acid, phosphate solubilization, ammonia production, ACC deaminase activity, nitrogen fixation and siderophore production.

# **History of Endophytes and their Importance**

The term endophyte was first coined by De Bary [10]. Hallmann et al [2] have defined the endophytic bacteria as all the bacteria

that can be detected inside the surface sterilized plant tissues or extracted from inside plants and having no visibly harmful effect on the host plants. Endophytic bacteria have been isolated from diverse range of monocotyledonous and dicotyledonous plants such as oak [11], pear [12], sugar beets and maize [13,14,15,16,17]. The chemicogenomic interaction between plants and endophytes can expect to provide protection to plants from pathogens, insects and grazing animals [4,18].

Endophytic bacteria with plant growth promoting (PGP) and biocontrol properties have applications to enhance crop yield by maintaining ecological balance [19]. The advantage with use of endophyte as a biocontrol agent is their inherent adaptation to live inside the plants with promises to provide reliable disease suppression. They can protect their host from attack by fungi, insect, and mammals by producing secondary metabolites [20]. The endophytic communities mainly include the phyla, *Proteobacteria, Actinobacteria, Planctomycetes, Verrucomicrobia* and *Acidobacteria* [21]. Bacteria of the genera *Pseudomonas, Bacillus, Burkholderia, Stenotrophomonas, Micrococcus, Pantoea* and *Microbacterium* are some of the most commonly identified bacterial endophytes [2,22,23,5,21]. This can be highly complex as there are more than 300000 species of plants are present [24]. Each of these plants can be unique in their endophytic partners.

#### **Endophytic Bacteria**

Based on the types of microorganisms involved, the endophytes can be bacterial, fungal or those of actinomycetes. Bacterial endophytes are well characterized from many plants which include *Azorhizobium caulinodans* from rice [25], *Burkholderia pickettii* from maize [17], *Enterobacter sakazakii* from soybean [26], *Pseudomonas fluorescens*, *Pseudomonas putida* [27] and *Bacillus* spp from citrus plants [28].

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# **Entry of Endophytic Bacteria in Plants**

Endophytic colonization and mobility within host plants are mediated by several factors such as lipopolysaccharides, flagella, pili, and twitching motility [29,30,31]. The endophytic bacteria from the soil get enter into host plant through cracks formed in lateral root junctions followed by quick spread with in the intercellular spaces of the root [32]. Root cracks are recognized as the hot spot for bacterial colonization [33]. Some of the endophytic bacteria can also have the ability to colonize flowers, fruits and seeds but their presence was limited under natural conditions [34].

# **Isolation of Endophytic Bacteria**

There are various methods that have been used for the isolation of endophytic bacteria. Bell et al. [35] have suggested the isolation of endophytic bacteria from grapevine by vaccum or pressure extraction technique. Endophytic bacteria could be easily isolated by the surface sterilization method using 2% sodium hypochlorite followed by wash with sterilized distilled water [36,37]. This simplest procedure of surface sterilization can be followed by exposing the surface sterilized piece of the sample material onto specific media for outgrowth of endophytes [38,39,40]. For the identification of the isolated endophytic bacteria both conventional biochemical tests [41] and rapid method involving 16S rDNA sequence analysis can be used. 16S rDNA based method makes it possible to identify the organism up to genus and possibly to species level by comparing the sequence deposition in available databases [42]. Some of the most common genera of endophytic bacteria characterized from different parts of the plants include Acinetobavter, Acetobacter, Alkaligenes, Arthrobacter, Azospirillum, Azotobacter, Bacillus, Beijerinckia, Burkholderia, Enterobacter, Pseudomonas, Ralstonia and Serratia [43].

#### **Mechanisms of Plant Growth Promotion**

Several studies have been conducted to investigate the mechanisms involved in the plant growth enhancement by endophytic bacteria [44]. These involve direct and indirect mechanisms [45]. The direct mechanisms include (i) those which facilitates the acquisition of nutrients like nitrogen, solubilization of phosphorous and the sequesteration of iron (ii) which modulates plant growth through the production of auxin, cytokinin and ACC deaminase which reduce the level of ethylene. Indirect plant growth support is provided by the production of antibiotics, cell wall degrading enzymes, induced systemic resistance and the production of exopolysaccharides [46,47]. These mechanisms may subject to variation in its expression based on rhizospheric or endophytic life style of organisms.

# **Direct Mechanisms**

**Nitrogen Fixation:** Nitrogen (N) is the most vital nutrient for plant growth and productivity. The atmospheric  $N_2$  is converted into plant-utilizable forms by the process called biological  $N_2$  fixation (BNF). Here nitrogen is converted to ammonia by nitrogen fixing microorganisms with the help of the enzyme system nitrogenase [48]. BNF occurs generally at mild temperature by nitrogen fixing microorganisms, which are widely distributed in nature [49].

Phosphate solubilization: Phosphate solubilization is one of the major mechanisms for plant growth promotion by the plant associated bacteria. Phosphorous is the second most important nutrient required for plants after nitrogen for their growth and development but it exist in soil as mineral salts or incorporated into organic compounds. Plants can only absorb it in two soluble forms, the monobasic (H<sub>2</sub>PO<sub>4</sub>) and the diabasic (HPO<sub>4</sub><sup>2-</sup>) ions. To overcome this P deficiency in soils, phosphatic fertilizers are frequently applied in soils. The challenges like high cost and hazardous effect to the environment demand the need for economically and environment friendly methods for improving crop production even in the low phosphorus soils. In this context, exploring the role of bacteria to release immobilized phosphorous have tremendous applications [50]. They could convert insoluble phosphate compounds such as tri calcium phosphate, dicalcium phosphate, hydroxyapatite, and rock phosphate into available forms for plants via the process of chelation, exchange reaction and by the secretion of organic acids [51,52]. The bacterial genera Azospirillum, Azotobacter, Bacillus, Beijerinckia, Burkholderia, Enterobacter, Erwinia, Flavobacterium, Microbacterium, Pseudomonas, Rhizobium and Serratia have been reported to have tremendous phosphate solubilizing efficiency [53,54].

IAA Production: Indole-3-acetic acid (IAA) is a phytohormone which is known to be involved in root initiation, plant cell division, extension, and differentiation. IAA also affects plant growth and development by stimulating seed and tuber germination, increasing the rate of xylem and root development; controlling processes of vegetative growth, initiating lateral and adventitious root formation, mediating responses to light, gravity and fluorescence, affecting photosynthesis, pigment formation, biosynthesis of various metabolites, and providing resistance to stressful conditions. Production of IAA by endophytic bacteria indicates its role in modulating diverse process in plant physiology. Moreover, IAA producing bacteria promote shoot and root elongation which provide greater access to host plant for nutrient absorption from soil [55].

Microbial production of IAA has been reported to take place by both tryptophan dependent or independent mechanisms. In the presence of tryptophan, microbes release greater quantities of IAA and related compounds [56,57]. Microbial synthesis of IAA occurs through pathways like indole-3-acetonitrile (IAN) pathway, indole-3-acetamide (IAM) pathway, tryptamine pathway, indole-3-acetaldoxime pathway and the indole-3-pyruvate (IPyA) pathway [58,59]. The indole-3-pyruvic acid pathway (IPyA pathway) was found to be the main route for IAA production in the presence of exogenous tryptophan. The first step in this pathway is the conversion of tryptophan into IPyA by an aminotransferase enzyme. Then it undergoes decarboxylation reaction to form indole-3-acetaldehyde (IAAld) by the enzyme indole-3-pyruvate decarboxylase (IPDC) and this IAAld is then oxidized to produce IAA. Biological significance of microbial IAA production has been evidenced by the presence of multiple biosynthetic routes for the same. Even more pathways for the same is also expected due to presence of multiple biosynthetic pathways in some organisms.

Several studies have demonstrated the ability of endophytic fungi

also to synthesise IAA with significant role in the development of plants. The inoculation of IAA producing endophytic *Paecilomyces formosus* on japonica rice has shown to result in increased plant growth with significant differences in plant height and biomass compared with the control [60,61]. The detection and quantification of IAA produced by endophytic bacteria or endophyte fungi has shown to be carried out by using HPLC with same experimental procedure [60,57].

1-Aminocyclopropane-1-Carboxylate (ACC) Deaminase Activity: Ethylene is an important metabolite endogenously produced by all plants for the normal growth and development. Apart from ethylene being a plant growth regulator, it has also been known as a stress hormone because of its role in stress conditions like salinity, drought, water logging, heavy metals and pathogenicity. The biosynthesis of ethylene from methionine takes place in three steps. First, ATP and water binds to methionine which results in the formation of S-adenosyl methionine (SAM) with the release of three phosphates. It is further converted into ACC with the help of an enzyme 1-amino-cyclopropane-1-carboxylic acid synthase (ACC-synthase). Subsequently, ACC is enzymatically converted to ethylene. However presence of increased level of ethylene negatively affects the overall plant growth and development resulting in reduced crop yield [62].

ACC deaminase is a multimeric enzyme with a molecular mass of 35-42kDa [63, 64]. It is a sulfhydryl enzyme that utilizes pyridoxal 5-phosphate as an essential co- factor and several aminoacids such as D- serine and D- cysteine as substrates. It is a sulfhydryl enzyme that utilizes pyridoxal 5-phosphate as an essential co-factor and several amino acids such as D-serine and D-cysteine as substrates. Mechanisms involved in the cleavage of ACC by ACC deaminase includes fragmentation of cyclopropane ring and deamination to form  $\alpha$ -ketobutyrate and ammonia [65].

ACC deaminase produced by endophytic bacteria can have the potential to use ACC from plant root and convert it into α-ketobutyrate and ammonia. The decreased ACC level lowers ethylene production and minimise plant stress. Hence inoculation of plants with ACC deaminase producing bacteria can have the promises to protect plants from stress conditions. Bacterial strains exhibiting ACC deaminase activity have been identified for the genera like *Acinetobacter*, *Achromobacter*, *Agrobacterium*, *Alcaligenes*, *Azospirillum*, *Bacillus*, *Burkholderia*, *Enterobacter*, *Pseudomonas*, *Ralstonia*, *Serratia* and *Rhizobium* [66].

Different types of endophytic bacteria isolated from various parts of the plant have been reported to have diverse mechanisms for plant growth enhancement (Table 1).

#### **Indirect Mechanisms**

Indirect mechanisms generally involve biocontrol properties. Plant growth promoting bacteria (PGPB) can also promote plant growth by protecting the plant from the deleterious pathogens. Mechanisms used by biocontrol organisms to control pathogens have potential applications to reduce the use of chemical pesticides in a cost effective and eco-friendly manner.

#### **Production of Antibiotics and Lytic Enzymes**

Plant growth promoting bacteria produce a wide range of antibiotics and enzymes which protect the plant from phytopathogens. Antibiotics are low-molecular weight, chemically distinct group of organic compounds mostly produced by microorganisms which are deleterious to the growth and metabolic activities of other microorganisms even at very low concentrations [91,92]. There are many reports on the biocontrol properties and applications of *Pseudomonas* spp. due to its abundance in the plant. Recently, more bacterial biocontrol agents other than *Pseudomonas* spp. have also been reported. Antibiotics produced by bacterial biocontrol agents include phenazines (Phz), pyrrolnitrin (PRN) and other lipopeptides [93,94,95,96].

Phenazines: Phenazines are a group of nitrogen containing heterocyclic compounds produced by a variety of bacteria. Both Gram negative and Gram positive species reported to have the ability to synthesise phenazine which include *Nocardia, Sorangium, Brevibacterium, Burkholderia, Erwinia, Pantoea agglomerans, Vibrio* and *Pelagiobacter* [97,98]. Among various bacteria, *Pseudomonads* have been extensively studied for phenazine compounds. In most of the cases, the phenazine production has been identified to be mediated by the core biosynthetic genes which are flanked by one or more genes resulting in the production of additional phenazine derivatives. In our previous study also, endophytic *Pseudomonas aeruginosa* with phenazine-1- carboxylic acid mediated antifungal activity has been reported from ginger rhizome [94].

**Pyrrolnitrin:** Pyrrolnitrin [3-chloro-4-(2-nitro-3- chlorophenyl) pyrrole] is a dichlorinated phenylpyrrole antibiotic. This was primarily used as clinical antifungal agent for the treatment of skin infections caused by the fungus *Trichophyton*. Further, it was used as effective agricultural fungicide [99]. Pyrrolnitrin has previously reported as antifungal basis of *Burkholderia*, *Enterobacter*, *Myxococcus*, *Pseudomonas* as well as by some *Serratia* sp. [100,101,102]. Endophytic *Serratia* sp. G3 from wheat was also reported to have antifungal activity due to the production of pyrrolnitrin, chitinase, and siderophore [103].

**2,4-Diacetylphloroglucinol** (DAPG): 2,4-diacetylphloroglucinol (DAPG) are major group of secondary metabolites which belong to the group of compounds phloroglucinol. These compounds are generally synthesized by species of *Pseudomonads* [104]. Several studies also reported *Serratia* sp. and *Pseudomonas* sp. to have the potential to biosynthesize DAPG and its role in the biocontrol of many phytopathogens [105,106]. DAPG is basically a polyketide which is synthesized by the condensation reaction of acetyl CoA with malonyl CoA. The genes which are included in the biosynthesis are *phlA*, *phlC*, *phlB*, *phlD* and *phlE* [107]. DAPG is reported to have broad range of biological activities including antifungal, anti-helmenthic and herbicidal properties [104].

**Ecomycin:** Ecomycins are novel lipopeptide compounds produced by plant associated fluorescent bacteria called *Pseudomonas viridiflava*. This bacterium is known to exist on or within the tissues of leaves of *Lactuca sativa* and many grass species [108].

**Table.1** Details of selected endophytic bacteria and their plant beneficial features

Endophytic bacteria	Source	Mechanisms of plant growth promotion	References
Paenibacillus sp.	Curcuma longa	Indole-3- acetic acid production	[67, 68]
Klebsiella sp.	Piper nigrum, Curcuma longa	ACC deaminase, phosphate solubilization, siderophore and IAA production.	[69, 70, 71, 72]
Pseudomonas sp.	Zingiber officinale, Elettaria cardamomum	IAA production, ACC deaminase and sidero- phore production, antifungal activity	[73, 74, 75, 76, 77, 78]
Ralstonia sp.	Musa accuminata	Phosphate solubilization, ammonia production, IAA synthesis,	[79, 80]
	cv. Grand Naine	Nitrogen fixation, siderophore production and HCN production	
Bacillus sp.	Capsicum annuum, Eletteria car- damomum, Curcuma longa L	IAA production, ACC	
		deaminase production, phosphate solubilization and siderophore, production, antifungal activity	[75, 81, 82, 83]
Pantoea sp.	Eletteria cardamomum	ACC deaminase production	[75]
Stenotrophomonas sp.	Datura metel	IAA Production, phosphate solubilization	[84]
Agrobacterium sp.	Solanum lycopersicum	IAA production, ACC deaminase, phosphate solubilization, siderophore production	[76]
Rhizobium sp.	Solanum lycopersicum	IAA production, ACC deaminase, phosphate solubilization, siderophore production	[76]
Burkholderia sp.	Vitis vinifera L., Saccharum of-	Phosphate solubilization, IAA production,	[85,86]
Burkholderia australis	ficinarum x spontaneum L.	siderophore production, nitrogen fixation	[55,55]
Novosphingobium sediminicola, Ochrobactrum intermedium, Gluconacetobacter diazotrophicus, Herbaspirillum seropedicae, H. rubrisub albicans and Burkholderia sp.	Saccharum officinarum L.	Nitrogen fixation	[87,88]
Azospirillum			
Amazonense, Rhodopseudomonas palustris, Pantoea ananas, Klebsiella oxytoca, Cytophagales sp., Flavobac- terium gleum	Oryza sativa, Oryza Alta and Oryza. ridleyi	Nitrogen fixation, IAA production	[89]
Sphingomonas paucimobilis, Bacillus megaterium, Pantoea sp., Enterobacter ludwigii	Pennisetum purpureum Schumach	IAA production, ACC deaminase	
		Activity, nitrogen fixation, ammonia	[90]
		production, siderophore production	
		inorganic phosphate solubilization.	

There are mainly three types of ecomycin lipopeptide compounds have been identified and partially purified. These include ecomycin A, B and C. Among them, ecomycin A is structurally similar to the already known antibiotic syringotoxin [109,110]. Ecomycin B and C are novel because of their unique aminoacid composition [108,111,112,113]. This compound was also reported to have broad antifungal properties against human pathogens *Cryptococcus neoformans* and *Candida albicans*.

**Pseudomycin:** The pseudomycins are another group of antifungal peptides identified from plant associated bacterium *Pseudomonas* 

syringae. P. syringae is a member of the Pseudomonadaceae family and belong to the Phylum Proteobacteria. The pseudomycins are lipopeptides which contain non-traditional aminoacids such as L-chlorothreonine, L-hydroxy aspartic acid and diaminobutyric acid and are active against human pathogenic fungi such as Candida albicans and Cryptococcus neoformans as well as phytopathogens including Ceratocystis ulmi and Mycosphaerella fijiensis. The pseudomycins are also being used for the agricultural purpose to manage black sigatoka disease in bananas [4].

Munumbicins and Kakadumycins: Munumbicins and kakadu-

mycins are peptide antibiotics produced by endophytic *Streptomyces* sp. NRRL 30562 and 30566 respectively. These compounds are active against broad range of bacteria such as *Bacillus anthracis*, *Streptococcus pneumoniae*, *Enterococcus faecalis*, *Staphylococcus aureus* and also active against multiple-drug-resistant (MDR) *Mycobacterium tuberculosis*. Munumbicins E-4 and E-5 and kakadumycin A were also found to have activity against *Plasmodium falciparum* and it was found to have more antimalarial activity than the reported chloroquine [114,115].

Other lipopeptides: Lipopeptides are major antimicrobial compounds secreted by Bacillus spp. The antifungal lipopeptides are grouped under iturins and fengycins. Antibiotics that belong to the family iturin are basically cyclic lipopeptides such as iturin A, mycosubtilin, bacillomycin etc. and are one of the most commonly studied compounds produced from Bacillus spp. with promising for their promising antifungal activities [116,117,96]. These are small molecular weight compounds with a mass of 1.1 kDa and consists of a cyclic peptide with 7 amino acid residues and 11-12 carbons atoms at their hydrophobic tail. Due to this structure, the compound exhibits strong amphiphilic nature and thus have high probability to act on target cellular membranes [118]. Biosynthesis of iturins was mostly studied in Bacillus sp. where it consists of an operon with four open reading frames ItuA, ItuB, ItuC, and ItuD [119]. Iturin A specifically shows a strong and broad spectrum antibiotic activity and have the potential to reduce the use of chemical pesticides in agriculture [120]. The fengycin family comprises fengycin A and fengycin B, which differ in a single amino acid in the sixth position (d-alanine and d-valine respectively). Their production was reported from the endophytic bacterium B. amyloliquefaciens ES-2 [121] and B. subtilis B-FS01 [122]. Evaluation of the antifungal activity of the isolated lipopeptides obtained from endophytic Bacillus subtilis showed fengycins to have promising activity [123].

Growth enhancement through the production of cell wall degrading enzymes is another mechanism used by plant growth promoting bacteria to control soil borne pathogens [124]. Certain enzymes produced by the PGPB like  $\beta$ -1, 3-glucanase, chitinase, cellulase, and protease inhibit the growth of fungal pathogens by the degradation of the cell wall. PGPB with one or more of these enzymes have been found to have biocontrol activity against a range of pathogenic fungi including *Botrytis cinerea*, *Sclerotium rolfsii*, *Fusarium oxysporum*, *Phytophthora* spp., *Rhizoctonia solani*, and *Pythium ultimum*. The studies on the biocontrol property of *S. marcescens* B2 against the soilborne pathogens *R. solani* and *F. oxysporum* have been reported as due to the production of the chitinolytic enzyme [125].

**Sequestering of Iron:** Iron (Fe) is the most abundant element on earth which cannot be readily assimilated by either bacteria or plants because of its nature of existence as ferric ion (Fe<sup>+3</sup>). Both microorganisms and plants require a higher level of iron which makes the plant, bacteria and fungi to compete for iron [126]. This limitation has been overcome by some bacteria by synthesizing low-molecular weight compounds (400–1500 Da) called siderophores.

These siderophores binds with ferric ion and make siderophore-ferric ion complex which subsequently binds with membrane receptors at the bacterial cell surface and facilitates the uptake of iron by microorganisms. Plant growth enhancement with the help of bacterial siderophores have been studied extensively and it showed effect of siderophore producing microorganisms on increased iron inside plant tissues leading to improved plant growth. And there are over 500 known types of siderophores with different chemical structures and can be mainly classified into 3 main groups like catecholates (phenolates), hydroxamates and carboxylates.

**Induced Systemic Resistance:** Induced systemic resistance is the physiological state of enhanced defensive capacity elicited by the plant in response to specific environmental stimuli or by the subsequent biotic stresses. Priming of plants with potential organisms can enhance innate defenses against a broad range of plant pathogens. Many bacterial components can affect induced systemic resistance such as lipopolysaccharides (LPS), flagella, siderophores, cyclic lipopeptides, 2, 4-diacetylphloroglucinol, homoserine lactones, and volatiles like, acetoin and 2, 3-butanediol etc.

**Exo polysaccharide Production:** Certain PGPB can have the ability to synthesize exopolysaccharides (EPS). These provide plant growth and development by facilitating the circulation of nutrients and also protecting the plant from pathogen attack. Other functions performed by EPS producing microbes constitute shielding from desiccation, protection against drought, attachment to surfaces, plant invasion defense response in plant-microbe interactions.

In addition to these bacteria, endophytic fungi have also been reported to have several beneficial effects on the plant growth and disease protection which include protection from phytopathogens and enhancement of plant yield through the production of phytohormones like auxins and gibberrillins to increase metabolic activity of the plant [127]. Aureobasidium sp. BSS6 and Preussia sp. BSL10 isolated from Boswellia sacra showed higher potential for indole acetic acid production both by tryptophan-dependent and independent pathways. In vivo evaluation of plant growth enhancement effect of Preussia sp. BSL10 on B. sacra tree showed significant improvement in plant growth parameters and the deposition of photosynthetic pigments [128]. Some endophytic fungi would able to produce different bioactive compounds such as alkaloids, diterpenes, flavonoids, and isoflavonoids to protect plant from biotic and abiotic stresses [129,130]. Plant growthpromoting ability of endophytic fungi isolated from Rosa rugosa, Camellia japonica, Delonix regia, Dianthus caryophyllus and Rosa hybrid collected from Yunnan, Southwest China showed its ability to improve the host plants growth more efficiently [131].

# **Applications of Endophytic Bacteria**

The production of natural products by endophytic bacteria make it an important source in the development of products for various plant diseases. Molecules derived from natural products, particularly those produced by plant and microbes have a great potential for the development of new pharmaceutical

products also. This can be achieved by the discovery of plethora of endophytes (both fungi and bacteria) with broad spectrum activities. So studies on endophytic microorganisms from diverse plants is important. Endophytic microorganisms also have great contribution in production of anti-diabetic [132], anti-cancerous [4], antiviral [133] and even immunosuppressive compounds [134]. Endophytic bacteria include a wide range of antimicrobial producing strains, which make it as a potential source of antimicrobial substances [135]. Endophytic bacteria can also be used for biocontrol purpose because of their well known capability to produce bioactive compounds like surfactin, fengycin, iturin, pyroluetrin etc. [136]. They have the promises for field application as biofertilizers, phytostimulators or as biopescticides. Screening for plant growth promoting and antagonistic properties of bacterial endophytes isolated from potato (Solanum tuberosum L.) have shown their ability to enhance biomass yield of *Phaseolus* vulgaris L and was found to have protective effect against potato pathogens Pectobacterium atrosepticum, Fusarium sambucinum and Clavibacter michiganensis subsp. epedonicus [137]. The endophytic Pseudomonas fluorescens ALEB7B isolated from A. lancea have been reported to have the ability to produce nitrogenous volatiles like formamide and N,N-dimethyl-formamide with significant growth promotion on A. lancea. Moreover, the main bacterial volatile benzaldehyde significantly promoted volatile oil accumulation in A. lancea by activating plant defense responses and thereby enhancing the plant growth and development [138]. Several commercially available microbial products from diverse sources as explained in Table. 2, indicate promises of endophytes also for such applications.

# **Conclusion and Perspectives**

From the emerging understanding on endophytic bacteria, they can consider to have immense promises in the new generation agricultural practices. From the available information on plant beneficial mechanisms of these organisms they can consider to have a heavy deposition of yet to known mechanisms with determining effect for plant growth and development. This also involves mechanisms with promises in their biocontrol application. Hence a detailed insight into plant endophytic interactions can have promising applications.

#### References

- Azevedo JL, Maccheroni W, Pereira JO, Araújo WL (2000) Endophytic microorganisms: a review on insect control and recent advances on tropical plants. Electronic Journal of Biotechnology 3(1): 15-16.
- Hallmann J, Quadt-Hallmann A, Mahaffee WF, Kloepper JW (1997)
   Bacterial endophytes in agricultural crops. Canadian Journal of Microbiology 43(10): 895-914.
- 3. Perotti R (1926) On the limits of biological enquiry in soil science. Proc. Int. Soc.Soil sci 2: 146-161.
- Strobel G, Daisy B (2003) Bioprospecting for Microbial Endophytes and Their Natural Products. 67(4): 491–502. doi: 10.1128/ MMBR.67.4.491.
- Rosenblueth M, Martínez-Romero E (2006) Bacterial endophytes and their interactions with hosts. Molecular plant-microbe interactions 19(8): 827-837.
- Compant S, Clément C, Sessitsch A (2010) Plant growth-promoting bacteria in the rhizo- and endosphere of plants: Their role, colonization, mechanisms involved and prospects for utilization. Soil Biology and Biochemistry 42(5): 669-678. doi:10.1016/j.soilbio.2009.11.024.
- Mercado-Blanco J, Prieto P (2012) Bacterial endophytes and root hairs. Plant Soil 361: 301–306. doi: 10.1007/s11104-012-1212-9.
- Ali S, Charles TC, Glick BR (2012) Delay of flower senescence by bacterial endophytes expressing 1-aminocyclopropane-1-carboxylate deaminase. 1139–1144.

 Table.2 Representatives of microbial inoculants introduced as agricultural products

Organism	Product name	Company	
Pseudomonas	Abtech Pseudo, abtech Pseudochitinase, PSEUDO-GUN, Salavida, Proradix	ABTECH, Maharashtra Bio Fertilizers, India PVT.LTD, Sourcon Padena	
Bacillus spp.	Abtech Bacillus, YiedShield	ABTECH, Bayer Crop Science	
Azospirillum	Abtech Azospirillum, AZOSPIRILLUM, AZOGREEN, Biopromoter	ABTECH, Maharashtra Bio Fertilizers, India PVT.LTD, Omega Ecotech Products India Private Limited, Manidharma Biotech	
Rhizobium	Abtech Rhizobium, RHIZOBIUM	ABTECH, Maharashtra Bio Fertilizers, India PVT.LTD	
Phosphobacteria	Abtech Phosphobacteria	ABTECH	
Azotobacter	AZOTOBACTER	Maharashtra Bio Fertilizers, India PVT.LTD	
Acetobacter	ACETOBACTER	Maharashtra Bio Fertilizers, India PVT.LTD	
Trichoderma viridae	Green Light	Green life Biotech Laboratory	
Serratia plymuthcia HRO-C48	RhizoStar	Prophyta Biologischer Pflanzenschutz	

- Coutinho FH, Meirelles PM, Moreira APB, Paranhos RP, Dutilh BE, et al (2015) Niche distribution and influence of environmental parameters in marine microbial communities: a systematic review. PeerJ 3:e1008. doi: 10.7717/peerj.1008
- De Bary A (1866) Morphologie und Physiologie Pilze, Flechten, und Myxomyceten. Hofmeister's Handbook of Physiological Botany., ed. L. Engelmann. 1866, Germany.
- Brooks DR, Mclennan DA, Carney JP, Dennison MD, Goldman CA (1994) Phylogenetic Systematics: Developing an Hypothesis of Amniote Relationships. Test Stud Lab Teach 390.
- 12. Whitesides SK, Spotts RA (1991) Frequency, distribution, and characteristics of endophytic Pseudomonas syringae in pear trees. Phytopathol 81: 453-457.
- 13. Jacobs MJ, Bugbee WM, Gabrielson DA (1985) Enumeration, location, and characterization of endophytic bacteria within sugar beet roots. Canadian Journal of Botany 63(7): 1262-1265.
- 14. Fisher PJ, Petrini O, Scott HML (1992) The distribution of some fungal and bacterial endophytes in maize (Zea mays L.). New Phytol 122: 299–305. doi: 10.1111/j.1469-8137.1992.tb04234.x
- Gutiérrez-Zamora ML, Martínez-Romero E (2001) Natural endophytic association between Rhizobium etli and maize (Zea mays L.). J Biotechnol 91(2-3): 117–126.
- Lalande R, Bissonnette N, Coutlée D, Antoun H (1989) Identification of rhizobacteria from maize and determination of their plant-growth promoting potential. Plant Soil 115: 7–11. doi: 10.1007/BF02220688
- McInroy JA, Kloepper JW (1995) Survey of indigenous bacterial endophytes from cotton and sweet corn. Plant Soil 173: 337–342. doi: 10.1007/BF00011472.
- 18. Bomke C, Tudzynski B (2009) Diversity , regulation , and evolution of the gibberellin biosynthetic pathway in fungi compared to plants and bacteria. Phytochemistry 70(15-16): 1876–1893. doi: 10.1016/j. phytochem.2009.05.020.
- 19. Trivedi P, Pandey A, Palni L (2012) Bacterial inoculants for field applications under mountain ecosystem: present initiatives and future prospects. In: Maheshwari, D.K. (Ed.), Bacteria in Agrobiology: Plant Probiotics. Springer, Berlin Heidelberg 15–44.
- Wang Y, Zeng Q, Zhang Z, Yan RM, Zhu D (2010) Antagonistic bioactivity of an endophytic bacterium H-6. African Journal of Biotechnology 9: 6140–6145. doi: 10.5897/AJB10.258.
- Shi Y, Yang H, Zhang T, Sun J, Lou K (2014) Illumina-based analysis
  of endophytic bacterial diversity and space-time dynamics in sugar
  beet on the north slope of Tianshan mountain. Applied microbiology and biotechnology 98(14): 6375-6385.
- Marquez-Santacruz HA, Hernandez-Leon R, Orozco-Mosqueda MC, Velazquez-Sepulveda I, Santoyo G (2010) Diversity of bacterial endophytes in roots of Mexican husk tomato plants (Physalis ixocarpa) and their detection in the rhizosphere. Genet Mol Res 9(4): 2372-2380. doi:10.4238/vol9-4gmr921.
- Romero FM, Marina M, Pieckenstain FL (2014) The communities of tomato (Solanum lycopersicum L.) leaf endophytic bacteria, analyzed by 16S-ribosomal RNA gene pyrosequencing. FEMS microbiology letters 351(2): 187-194.
- 24. Smith SA, Tank DC, Boulanger LA, Bascom-Slack CA, Eisenman K, et al. (2008) Bioactive endophytes warrant intensified exploration and conservation. PLoS One 3(8): e3052.

- Engelhard M, Hurek T, Reinhold-Hurek B (2000) Preferential occurrence of diazotrophic endophytes, *Azoarcus spp.*, in wild rice species and land races of *Oryza sativa* in comparison with modern races. Environ Microbiol 2(2): 131-141.
- Kuklinsky-Sobral J, Araújo WL, Mendes R, Geraldi IO, Pizzirani-Kleiner AA, et al. (2004) Isolation and characterization of soybean-associated bacteria and their potential for plant growth promotion. Environ Microbiol 6(12): 1244-1251. doi:10.1111/j.1462-2920.2004.00658.x
- 27. Surette MA, Sturz AV, Lada RR, Nowak J (2003) Bacterial endophytes in processing carrots (Daucus carota L. var. sativus): their localization, population density, biodiversity and their effects on plant growth. Plant Soil 253(2): 381–390. doi: 10.1023/A:1024835208421.
- 28. Araujo WL, Maccheroni W Jr, Aguilar-Vildoso CI, Barroso PA, Saridakis HO, et al. (2001) Variability and interactions between endophytic bacteria and fungi isolated from leaf tissues of citrus rootstocks. Canadian Journal of Microbiology. 47(3): 229-236.
- Duijff BJ, Gianinazzi-Pearson V, Lemanceau P (1997) Involvement of the outer membrane lipopolysaccharides in the endophytic colonization of tomato roots by biocontrol Pseudomonas fluorescens strain WCS417r. New Phytologist 135(2): 325-334. doi:10.1046/ j.1469-8137.1997.00646.x.
- 30. Dorr J, Hurek T, Reinhold-Hurek B (1998) Type IV pili are involved in plant-microbe and fungus-microbe interactions. Mol Microbiol 30(1): 7-17.
- 31. Bohm M, Hurek T, Reinhold-Hurek B (2007) Twitching motility is essential for endophytic rice colonization by the N2-fixing endophyte Azoarcus sp. strain BH72. Mol Plant Microbe Interact 20(5): 526-533. doi:10.1094/MPMI-20-5-0526.
- 32. Chi F, Shen S, Cheng H, Jing Y, Yanni YG, et al. (2005) Ascending Migration of Endophytic Rhizobia , from Roots to Leaves, inside Rice Plants and Assessment of Benefits to Rice Growth Physiology. Appl Environ. Microbiol 71(11): 7271–7278.
- 33. Sorensen J, Sessitsch A (2006) Plant-associated bacteria lifestyle and molecular interactions. In: Van Elsas J.D., Jansson J.D., Trevors J.T., editors. 2nd. CRC Press 211–236.
- 34. Hallmann J (2001) Plant interactions with endophytic bacteria. In: Jeger, M.J., Spence, N.J. (Eds.), Biotic Interactions in Plante Pathogen Associations. CABI Publishing, Wallingford, United Kingdom.
- 35. Bell C, Dickie GA, Harvey WLG, Chan JWYF (1995) Endophytic bacteria in grapevine. Canadian journal of Microbiology 41(1): 46-53.
- 36. Stoltzfus JR, So R, Malarvithi PP, Ladha JK, de Bruijn FJ (1997) Isolation of endophytic bacteria from rice and assessment of their potential for supplying rice with biologically fixed nitrogen. Plant Soil 194(1): 25–36. doi: 10.1023/A:1004298921641.
- Gyaneshwar P, James EK, Mathan N, Reddy PM, Reinhold-Hurek B, et al (2001) Endophytic Colonization of Rice by a Diazotrophic Strain of Serratia marcescens. J Bacteriol 183: 2634–2645. doi: 10.1128/ JB.183.8.2634.
- 38. Berg G, Hallmann J (2006) Microbial Root Endophytes. In: Schulz BJE, Boyle CJC, Sieber TN (eds). Springer Berlin Heidelberg, Berlin, Heidelberg 53–69.
- Hallmann J, Berg G (2006) Spectrum and Population Dynamics of Bacterial Root Endophytes, in Microbial Root Endophytes, B.J.E. Schulz, C.J.C. Boyle, and T.N. Sieber, Editors. Springer Berlin Heidelberg: Berlin, Heidelberg 15-31

- Xia Y, DeBolt S, Dreyer J, Scott D, Williams MA (2015) Characterization of culturable bacterial endophytes and their capacity to promote plant growth from plants grown using organic or conventional practices. Front Plant Sci 6: 490. doi: 10.3389/fpls.2015.00490
- 41. Zvyagintsev DG (1991) Methods for Soil Microbiology and Biochemistry. Moscow: Moscow State University [in Russian].
- 42. Vandamme P, Pot B, Gillis M, de Vos P, Kersters K, et al (1996) Polyphasic taxonomy, a consensus approach to bacterial systematics. Microbiol Rev 60: 407–438.
- Sharma SK, Johri BN, Ramesh A, Joshi OP, Sai Prasad SV (2011) Selection of plant growth-promoting *Pseudomonas spp.* that enhanced productivity of soybean-wheat cropping system in Central India. J Microbiol Biotechnol 21(11): 1127-1142.
- 44. Ahemad M, Kibret M (2014) Mechanisms and applications of plant growth promoting rhizobacteria: Current perspective. J King Saud Univ Sci 26(1): 1–20. doi: 10.1016/j.jksus.2013.05.001
- 45. Castro RO, Cantero EV, Bucio JL (2008) Plant growth promotion by Bacillus megaterium involves cytokinin signaling. Plant Signal Behav 3(4): 263–265. doi: 10.1094/MPMI-20-2-0207.
- 46. Yaish MW, Antony I, Glick BR (2015) Isolation and characterization of endophytic plant growth- promoting bacteria from date palm tree ( Phoenix dactylifera L .) and their potential role in salinity tolerance. Antonie Van Leeuwenhoek 107(6): 1519-1532. doi: 10.1007/ s10482-015-0445-z
- van Loon LC (2007) Plant responses to plant growth-promoting rhizobacteria. Eur J Plant Pathol 119(3): 243–254. doi: 10.1007/ s10658-007-9165-1
- 48. Kim J, Rees DC (1994) Nitrogenase and biological nitrogen fixation. Biochemistry 33(2): 389-397.
- 49. Raymond J, Siefert JL, Staples CR, Blankenship RE (2004) The Natural History of Nitrogen Fixation. Molecular Biology and Evolution 21(3): 541-554.
- Richardson AE, Hadobas PA, Hayes JE, O'Hara CP, Simpson RJ (2001)
   Utilization of phosphorus by pasture plants supplied with myoinositol hexaphosphate is enhanced by the presence of soil microorganisms. Plant Soil 229(1): 47–56. doi: 10.1023/A:1004871704173
- 51. Chung H, Park M, Madhaiyan M, Madhaiyana M, Seshadri S, et al (2005) Isolation and characterization of phosphate solubilizing bacteria from the rhizosphere of crop plants of Korea. Soil Biol Biochem 37(10): 1970–1974. doi: 10.1016/j.soilbio.2005.02.025
- 52. Gulati A, Sharma N, Vyas P, Sood S, Rahi P, et al. (2010) Organic acid production and plant growth promotion as a function of phosphate solubilization by Acinetobacter rhizosphaerae strain BIHB 723 isolated from the cold deserts of the trans-Himalayas. Arch Microbiol 192(11): 975-983. doi:10.1007/s00203-010-0615-3
- 53. Sturz A, Nowak J (2000) Endophytic communities of rhizobacteria and the strategies required to create yield enhancing associations with crops. Appl Soil Ecol 15(2): 183–190. doi: 10.1016/S0929-1393(00)00094-9

- 54. Pérez-Montaño F, Alías-Villegas C, Bellogín RA, del Cerro P, Espuny MR, et al (2014) Plant growth promotion in cereal and leguminous agricultural important plants: from microorganism capacities to crop production. Microbiol Res 169(5-6): 325–336. doi: 10.1016/j. micres.2013.09.011
- Boiero L, Perrig D, Masciarelli O, Penna C, Cassán F, et al (2007) Phytohormone production by three strains of Bradyrhizobium japonicum and possible physiological and technological implications. Appl Microbiol Biotechnol 74(4): 874–880. doi: 10.1007/s00253-006-0731-9
- Lee S, Flores-Encarnación M, Contreras-Zentella M, Garcia-Flores L, Escamilla JE, et al (2004) Indole-3-acetic acid biosynthesis is deficient in Gluconacetobacter diazotrophicus strains with mutations in cytochrome c biogenesis genes. J Bacteriol 186: 5384–5391. doi: 10.1128/JB.186.16.5384-5391.2004
- 57. Jasim B, Jimtha John C, Shimil V, Jyothis M, Radhakrishnan EK (2014) Studies on the factors modulating indole-3-acetic acid production in endophytic bacterial isolates from Piper nigrum and molecular analysis of ipdc gene. J Appl Microbiol 117(3): 786–799. doi: 10.1111/ jam.12569
- Prinsen E, Costacurta a, Michiels K, Van Onckelen H, Vanderleyden J (1993) Azospirillum brasilense Indole-3-Acetic Acid Biosynthesis: Evidence for a Non-Tryptophan Dependent Pathway. Mol Plant-Microbe Interact 6: 609–615.
- 59. Mano Y, Nemoto K (2012) The pathway of auxin biosynthesis in plants. Journal of Experimental Botany 63(8): 2853-2872. doi:10.1093/jxb/ers091
- 60. Fouda AH, Hassan SE, Eid AM, Ewais EE (2015) Biotechnological applications of fungal endophytes associated with medicinal plant Asclepias sinaica (Bioss.). Annals of Agricultural Sciences 60(1): 95–104. doi: 10.1016/j.aoas.2015.04.001
- 61. Waqas M, Khan AL, Shahzad R, Ullah I, Khan AR, et al. (2015) Mutualistic fungal endophytes produce phytohormones and organic acids that promote japonica rice plant growth under prolonged heat stress. J Zhejiang Univ Sci B 16(12): 1011–1018. doi: 10.1631/jzus. B1500081
- Saleem M, Arshad M, Hussain S, Bhatti AS (2007) Perspective of plant growth promoting rhizobacteria (PGPR) containing ACC deaminase in stress agriculture. Journal of Industrial Microbiology & Biotechnology 34(10): 635-648.
- 63. Onofre-Lemus J, Hernández-Lucas I, Girard L, Caballero-Mellado J (2009) ACC (1-aminocyclopropane-1-carboxylate) deaminase activity, a widespread trait in Burkholderia species, and its growth-promoting effect on tomato plants. Appl Environ Microbiol 75(20): 6581–6590. doi: 10.1128/AEM.01240-09
- 64. Zhang Yf, He LY, Che ZJ, Wang QY, Qian M, et al. (2011) Characterization of ACC deaminase-producing endophytic bacteria isolated from copper-tolerant plants and their potential in promoting the growth and copper accumulation of Brassica napus. Chemosphere 83(1): 57-62.

- 65. Glick BR (2005) Modulation of plant ethylene levels by the bacterial enzyme ACC deaminase. FEMS Microbiol Lett 251(1): 1–7. doi: 10.1016/j.femsle.2005.07.030
- Zahir ZA, Munir A, Asghar HN, Shaharoona B, ArshadM (2008) Effectiveness of rhizobacteria containing ACC deaminase for growth promotion of peas (Pisum sativum) under drought conditions. J Microbiol Biotechnol 18(50: 958-963.
- 67. Aswathy AJ, Jasim B, Jyothis M, Radhakrishnan EK (2013) Identification of two strains of Paenibacillus sp. as indole 3 acetic acid-producing rhizome-associated endophytic bacteria from Curcuma longa. 3 Biotech 3(3): 219–224. doi: 10.1007/s13205-012-0086-0
- Phi QT, Park YM, Seul KJ, Ryu CM, Park SH, et al. (2010) Assessment of root-associated paenibacillus polymyxa groups on growth promotion and induced systemic resistance in pepper. J Microbiol Biotechnol 20(12): 1605-1613.
- 69. Jasim B, John Jimtha C, Jyothis M, Radhakrishnan EK (2013) Plant growth promoting potential of endophytic bacteria isolated from Piper nigrum. Plant Growth Regul 71(1): 1–11. doi: 10.1007/s10725-013-9802-y
- Gundogan N, Yakar Ua (2007) Siderophore Production, Serum Resistance, Hemolytic Activity And Extended-Spectrum B-Lactamase-Producing Klebsiella Species Isolated From Milk And Milk Products.
   J Food Saf 27(3): 251–264. Doi: 10.1111/J.1745-4565.2007.00077.X
- Sachdev DP, Chaudhari HG, Kasture VM, Dhavale DD, Chopade BA (2009) Isolation and characterization of indole acetic acid (IAA) producing Klebsiella pneumoniae strains from rhizosphere of wheat (Triticum aestivum) and their effect on plant growth. Indian J Exp Biol 47(12): 993–1000.
- Jha PN, Kumar A (2007) Endophytic colonization of Typha australis by a plant growth-promoting bacterium Klebsiella oxytoca strain GR-3. J Appl Microbiol 103(4): 1311–1320. doi: 10.1111/j.1365-2672.2007.03383.x
- Jasim B, Rohini S, Anisha C, Radhakrishnan EK (2013) Antifungal and plant growth promoting properties of endophytic Pseudomonas aeruginosa from Zingiber officinale. J Pure Appl Microbiol 7(2): 1003–1009.
- Long HH, Schmidt DD, Baldwin IT (2008) Native bacterial endophytes promote host growth in a species-specific manner; phytohormone manipulations do not result in common growth responses. PLoS One 3(7): e2702.
- Jasim B, Anish MC, Shimil V, Jyothis M, Radhakrishnan EK (2015) Studies on Plant Growth Promoting Properties of Fruit-Associated Bacteria from Elettaria cardamomum and Molecular Analysis of ACC Deaminase Gene. Appl Biochem Biotechnol 177(1): 175–189. doi: 10.1007/s12010-015-1736-6
- Abbamondi GR, Tommonaro G, Weyens N, Thijs S, Sillen W, et al (2016) Plant growth-promoting effects of rhizospheric and endophytic bacteria associated with different tomato cultivars and new tomato hybrids. Chem Biol Technol Agric 3:1. doi: 10.1186/s40538-015-0051-3
- Ma Y, Prasad MN, Rajkumar M, Freitas H (2011) Plant growth promoting rhizobacteria and endophytes accelerate phytoremediation of metalliferous soils. Biotechnol Adv 29(2): 248-258. doi:10.1016/j. biotechadv.2010.12.001

- Shaharoona B, Arshad M, Zahir ZA (2006) Effect of plant growth promoting rhizobacteria containing ACC-deaminase on maize (Zea mays L.) growth under axenic conditions and on nodulation in mung bean (Vigna radiata L.). Lett Appl Microbiol 42(2): 155-159. doi:10.1111/j.1472-765X.2005.01827.x
- Sarr PS, Yamakawa T, Asatsuma S, Sakai M (2010) Investigation of endophytic and symbiotic features of Ralstonia sp TSC1 isolated from cowpea nodules. African J Microbiol Res 4(19): 1959–1963.
- Jimtha JC, Smitha P V, Anisha C, Deepthi T, Meekha G, et al (2014) Isolation of endophytic bacteria from embryogenic suspension culture of banana and assessment of their plant growth promoting properties. Plant Cell Tissue Organ Cult 118(1): 57–66. doi: 10.1007/ s11240-014-0461-0
- Jasim B, Geethu PR, Mathew J, Radhakrishnan EK (2015) Effect of endophytic Bacillus sp. from selected medicinal plants on growth promotion and diosgenin production in Trigonella foenum-graecum. Plant Cell, Tissue Organ Cult 122(3): 565–572. doi: 10.1007/s11240-015-0788-1
- 82. Wani PA, Khan MS (2010) Bacillus species enhance growth parameters of chickpea (*Cicer arietinum L.*) in chromium stressed soils. Food Chem Toxicol 48(11): 3262-3267. doi:10.1016/j.fct.2010.08.035
- 83. Kumar A, Singh R, Yadav A, Giri DD, Singh PK, et al. (2016) Isolation and characterization of bacterial endophytes of Curcuma longa L. 3 Biotech 6(1): 1–8. doi: 10.1007/s13205-016-0393-y
- 84. Ben A, Rania A, Jabnoun-khiareddine H, Nefzi A, Mokni-Tlili S, et al (2016) Endophytic bacteria from Datura metel for plant growth promotion and bioprotection against Fusarium wilt in tomato promotion and bioprotection against Fusarium wilt in tomato. Biocontrol Science and Technology 26(8): 1139-1165. doi: 10.1080/09583157.2016.1188264
- Rachel M, Lins R, Fontes JM, Marques N, Mamede D, et al (2014) Plant growth promoting potential of endophytic bacteria isolated from cashew leaves. African J Biotechnol 13(33): 3360–3365. doi: 10.5897/AJB2014.13835
- 86. Paungfoo-Lonhienne C, Lonhienne TGA, Yeoh YK, Webb RI, Lakshmanan P, et al. (2014) A new species ofBurkholderiaisolated from sugarcane roots promotes plant growth. Microbial Biotechnology 7(2): 142-154. doi:10.1111/1751-7915.12105
- 87. Muangthong A, Youpensuk S, Rerkasem B (2015) Isolation and Characterisation of Endophytic Nitrogen Fixing Bacteria in Sugarcane. Trop Life Sci Res 26(1): 41-51.
- 88. Boddey RM, Urquiaga S, Alves BJR, Reis V (2003) Endophytic nitrogen fixation in sugarcane: present knowledge and future applications. Plant and Soil 252(1): 139-149. doi:10.1023/a:1024152126541
- Elbeltagy A, Nishioka K, Suzuki H, Sato T, Sato Y, et al. (2000) Isolation and characterization of endophytic bacteria from wild and traditionally cultivated rice varieties. Soil Science and Plant Nutrition 46(3): 617-629. doi:10.1080/00380768.2000.10409127
- Li X, Geng X, Xie R, Fu L1, Jiang J, et al. (2016) The endophytic bacteria isolated from elephant grass (Pennisetum purpureum Schumach) promote plant growth and enhance salt tolerance of Hybrid Pennisetum. Biotechnology for Biofuels 9(1): 190. doi:10.1186/s13068-016-0592-0

- 91. Fravel DR (1988) Role of Antibiosis in the Biocontrol of Plant Diseases\*. Annu Rev Phytopathol 26: 75–91. doi: 10.1146/annurev. py.26.090188.000451
- 92. Thomashow LS, Weller DM (1996) Current concepts in the use of introduced bacteria for biological disease control: mechanisms and antifungal metabolites. In: Stacey G, Keen NT (eds) Plant microbe interactions. Chapman & Hall, New York, NY 187–235
- Kwak YS, Weller DM (2013) Take-all of Wheat and Natural Disease Suppression: A Review. plant Pathol J 29(2): 125–135. doi: 10.5423/ PPJ.SI.07.2012.0112
- Jasim B, Anisha C, Rohini S, Kurian JM, Jyothis M, et al (2014) Phenazine carboxylic acid production and rhizome protective effect of endophytic Pseudomonas aeruginosa isolated from Zingiber officinale. World J Microbiol Biotechnol 30(5): 1649–1654. doi: 10.1007/s11274-013-1582-z
- 95. Jasim B, Mathew J, Radhakrishnan EK (2016) Identification of a novel endophytic Bacillus sp. from Capsicum annuum with highly efficient and broad spectrum plant probiotic effect. J Appl Microbiol 124(4): 1079–1094. doi: 10.1111/jam.13214
- Jasim B, Sreelakshmi KS, Mathew J, Radhakrishnan EK (2016) Surfactin, Iturin, and Fengycin Biosynthesis by Endophytic Bacillus sp. from Bacopa monnieri. Microb Ecol 72(1): 106–119. doi: 10.1007/s00248-016-0753-5.
- Mavrodi DV, Bonsall RF, Delaney SM, Soule MJ, Phillips G, et al. (2001) Functional analysis of genes for biosynthesis of pyocyanin and phenazine-1-carboxamide from Pseudomonas aeruginosa PAO1. J Bacteriol 183(21): 6454-6465. doi:10.1128/JB.183.21.6454-6465.2001
- 98. Mentel M, Ahuja EG, Mavrodi DV, Breinbauer R, Thomashow LS, et al. (2009) Of two make one: the biosynthesis of phenazines. Chembiochem 10(14): 2295-2304. doi:10.1002/cbic.200900323
- Burkhead KD, Schisler DA, Slininger PJ (1994) Pyrrolnitrin Production by Biological Control Agent Pseudomonas cepacia B37w in Culture and in Colonized Wounds of Potatoes. Appl Environ Microbiol 60(6): 2031-2039.
- 100. Arima K, Imanaka H, Kousaka M, Fukuda A, Tamura G (1964) Pyrrolnitrin, a new antibiotic substance, produced by *Pseudomonas*. Agric. Biol. Chem 28(8): 575–576.
- 101. Haas, Dieter, Defago G (2005) Biological Control of Soil-Borne Pathogens by Fluorescent Pseudomonads. Nat Rev Micro 3(4): 307–319.
- 102. Hammer PE, Hill DS, Lam ST, Van Pee KH, Ligon JM (1997) Four genes from *Pseudomonas fluorescens* that encode the biosynthesis of pyrrolnitrin. Appl Environ Microbiol 63(6): 2147–2154.
- 103. Liu X, Jia J, Atkinson S, Cámara M, Gao K, et al. (2010) Biocontrol Potential of an Endophytic Serratia Sp. G3 and Its Mode of Action. World Journal of Microbiology and Biotechnology 26(8): 1465–1471. doi:10.1007/s11274-010-0321-y.
- 104. Yang F, Cao Y (2012) Biosynthesis of phloroglucinol compounds in microorganisms review. 93(2): 487–495. doi: 10.1007/s00253-011-3712-6
- 105. Mercado-Blanco J, Bakker PA (2007) Interactions between plants and beneficial *Pseudomonas spp.*: exploiting bacterial traits for crop protection. Antonie van Leeuwenhoek 92(4): 367-389. doi:10.1007/ s10482-007-9167-1

- 106. Raaijmakers JM, Vlami M, de Souza JT (2002) Antibiotic production by bacterial biocontrol agents. Antonie van Leeuwenhoek 81(1/4): 537-547. doi:10.1023/a:102050142083
- 107. Delany I, Sheehan MM, Fenton A, Bardin S, Aarons S, et al (2000) Regulation of production of the antifungal metabolite 2,4-diacetylphloroglucinol in *Pseudomonas fluorescens* F113: genetic analysis of phIF as a transcriptional repressor. Microbiology 146 ( Pt 2): 537–543. doi: 10.1099/00221287-146-2-537
- 108. Miller, Miller, Garton K, Redgrave B, Sears J, et al. (1998) Ecomycins, unique antimycotics from Pseudomonas viridiflava. Journal of Applied Microbiology 84(6): 937-944. doi:10.1046/j.1365-2672.1998.00415.x
- 109. Ballio A, Bossa F, Collina A, Gallo M, Iacobellis NS, et al. (1990) Structure of syringotoxin, a bioactive metabolite of *Pseudomonas syringae pv. syringae*. FEBS Lett 269(2): 377-380.
- 110. Christina A, Christapher V, Bhore SJ (2013) Endophytic bacteria as a source of novel antibiotics: An overview. Pharmacogn Rev 7: 11–16. doi: 10.4103/0973-7847.112833
- 111. Harrison L, Teplow DB, Rinaldi M, Strobel G (1991) Pseudomycins, a family of novel peptides from Pseudomonas syringae possessing broad-spectrum antifungal activity. J Gen Microbiol 137(12): 2857-2865. doi:10.1099/00221287-137-12-2857.
- 112. Isogai A, Fukuchi N, Yamashita S, Suyamab K, Suzuki A (1990) Structures of syringostatins A and B, novel phytotoxins produced by pseudomonas syringae pv. syringae isolated from lilac blights. Tetrahedron Letters 31(5): 695-698.
- 113. Segre A, Bachmann RC, Ballio A, Bossa F, Grgurina I, et al. (1989) The structure of syringomycins A1, E and G. FEBS Lett 255(1): 27-31.
- 114. Castillo U, Harper JK, Strobel GA, Sears J, Alesi K, et al. (2003) Kakadumycins, novel antibiotics from Streptomyces sp NRRL 30566, an endophyte of Grevillea pteridifolia. FEMS Microbiol Lett 224(2): 183-190.
- 115. Castillo UF, Strobel GA, Mullenberg K, Condron MM, Teplow DB, et al. (2006) Munumbicins E-4 and E-5: novel broad-spectrum antibiotics from Streptomyces NRRL 3052. FEMS Microbiol Lett 255(2): 296-300. doi:10.1111/j.1574-6968.2005.00080.x
- 116. Moyne A-L, Cleveland TE, Tuzun S (2004) Molecular characterization and analysis of the operon encoding the antifungal lipopeptide bacillomycin D. {FEMS} Microbiol Lett 234(1): 43–49.
- 117. Gond SK, Bergen MS, Torres MS, White JF Jr (2015) Endophytic Bacillus spp. produce antifungal lipopeptides and induce host defence gene expression in maize. Microbiological Research 172: 79-87. doi:10.1016/j.micres.2014.11.004
- 118. Aranda FJ, Teruel JA, Ortiz A (2005) Further aspects on the hemolytic activity of the antibiotic lipopeptide iturin A. Biochim Biophys Acta 1713(1): 51–56. doi: 10.1016/j.bbamem.2005.05.003
- 119. Tsuge K, Inoue S, Ano T, Itaya M, Shoda M (2005) Horizontal Transfer of Iturin A Operon , itu , to *Bacillus subtilis* 168 and Conversion into an Iturin A Producer. Antimicrob Agents Chemother 49(11): 4641–4648. doi: 10.1128/ AAC.49.11.4641
- 120. Hsieh FC, Lin TC, Meng M, Kao SS (2008) Comparing methods for identifying Bacillus strains capable of producing the antifungal lipopeptide iturin A. Current microbiology 56(1): 1-5.

- 121. Sun L, Lu Z, Bie X, Lu F, Yang S (2006) Isolation and characterization of a co-producer of fengycins and surfactins, endophytic *Bacillus amyloliquefaciens* ES-2, from Scutellaria baicalensis Georgi. World Journal of Microbiology and Biotechnology 22(12): 1259-1266. doi:10.1007/s11274-006-9170-0
- 122. Hu LB, Shi ZQ, Zhang T, Yang ZM (2007) Fengycin antibiotics isolated from B-FS01 culture inhibit the growth of Fusarium moniliformeSheldon ATCC 38932. FEMS Microbiology Letters 272(1): 91-98. doi:10.1111/j.1574-6968.2007.00743.x
- 123. Malfanova N, Franzil L, Lugtenberg B, Chebotar V, Ongena M (2012) Cyclic lipopeptide profile of the plant-beneficial endophytic bacterium Bacillus subtilis HC8. Archives of Microbiology 194(11): 893-899. doi:10.1007/s00203-012-0823-0
- 124. Neeraja C, Anil K, Purushotham P, Suma K, Sarma P, et al (2010) Biotechnological approaches to develop bacterial chitinases as a bioshield against fungal diseases of plants. Crit Rev Biotechnol 30(3): 231–241. doi: 10.3109/07388551.2010.487258
- 125. Wang K, Yan PS, Cao LX, Ding QL, Shao C, et al (2013) Potential of chitinolytic Serratia marcescens strain JPP1 for biological control of Aspergillus parasiticus and aflatoxin. Biomed Res Int 2013: 397142. doi: 10.1155/2013/397142
- 126. Robin A, Mougel C, Siblot S, Vansuyt G, Mazurier S, et al (2006) Effect of ferritin overexpression in tobacco on the structure of bacterial and pseudomonad communities associated with the roots. FEMS Microbiol Ecol 58(3): 492–502. doi: 10.1111/j.1574-6941.2006.00174.x
- 127. Waqas M, Khan AL, Kamran M, Hamayun M, Kang SM, et al (2012) Endophytic Fungi Produce Gibberellins and Indoleacetic Acid and Promotes Host-Plant Growth during Stress. Molecules 17(9): 10754–10773. doi: 10.3390/molecules170910754
- 128. Khan AL, Al-Harrasi A, Al-Rawahi A, et al. (2016) Endophytic Fungi from Frankincense Tree Improves Host Growth and Produces Extracellular Enzymes and Indole Acetic Acid. PLOS ONE 11(6): e0158207. doi:10.1371/journal.pone.0158207
- 129. Firakova S, Sturdíkova M, Muckova M (2007) Bioactive secondary metabolites produced by microorganisms associated with plants. Biologia 62(3): 251–257. doi:10.2478/s11756-007-0044-1
- 130. Rodriguez RJ, White Jr JF, Arnold AE, Redman RS (2009) Fungal endophytes: diversity and functional roles. New Phytologist 182(2): 314-330. doi:10.1111/j.1469-8137.2009.02773.x
- 131. Zhou Z, Zhang C, Zhou W, Li W, Chu L, et al. (2014) Diversity and plant growth-promoting ability of endophytic fungi from the five flower plantspecies collected from Yunnan, Southwest China. Journal of Plant Interactions 9(1): 585-591. doi:10.1080/17429145.2013.873959
- 132. Yu H, Zhang L, Li L, Zheng C, Guo L, et al (2010) Recent developments and future prospects of antimicrobial metabolites produced by endophytes. Microbiol Res 165(6): 437–449. doi: 10.1016/j.micres.2009.11.009
- 133. Guo B, Wang Y, Sun X, Tang K (2008) Bioactive natural products from endophytes: A review. Appl Biochem Microbiol 44(2): 136–142. doi: 10.1007/s10438-008-2002-2
- 134. Lee SA, Hong SS, Han XH, Hwang JS, Oh GJ, et al (2005) Piperine from the Fruits of *Piper longum* with Inhibitory Effect on Monoamine Oxidase and Antidepressant-Like Activity. Chem Pharm Bull 53(7): 832–835. doi: 10.1248/cpb.53.832

- 135. Ryan RP, Germaine K, Franks A, Ryan DJ, Dowling DN (2008) Bacterial endophytes: recent developments and applications. 278(1): 1–9. doi: 10.1111/j.1574-6968.2007.00918.x
- 136. Arrebola E, Jacobs R, Korsten L (2010) Iturin A is the principal inhibitor in the biocontrol activity of Bacillus amyloliquefaciens PPCB004 against postharvest fungal pathogens. J Appl Microbiol 108(2): 386–395. doi: 10.1111/j.1365-2672.2009.04438.x
- 137. Pageni BB, Lupwayi NZ, Akter Z, Larney FJ, Kawchuk LM, et al. (2014) Plant growth-promoting and phytopathogen-antagonistic properties of bacterial endophytes from potato (*Solanum tuberosum L.*) cropping systems. Canadian Journal of Plant Science 94(5): 835-844. doi:10.4141/cjps2013-356
- 138. Zhou JY, Li X, Zheng JY, Dai CC (2016) Volatiles released by endophytic Pseudomonas fluorescens promoting the growth and volatile oil accumulation in Atractylodes lancea. Plant Physiology and Biochemistry 101: 132-140. doi:10.1016/j.plaphy.2016.01.026