



## OPEN ACCESS

## EDITED BY

Mamoona Rauf,  
Abdul Wali Khan University Mardan,  
Pakistan

## REVIEWED BY

Julio Alves Cardoso Filho,  
Federal University of Alagoas, Brazil

## \*CORRESPONDENCE

Muhammad Adnan Shahid  
✉ mshahid@ufl.edu  
Muhammad Shafiq  
✉ shafiq.iags@pu.edu.pk

## SPECIALTY SECTION

This article was submitted to  
Plant Symbiotic Interactions,  
a section of the journal  
Frontiers in Plant Science

RECEIVED 07 November 2022

ACCEPTED 22 December 2022

PUBLISHED 18 January 2023

## CITATION

Mushtaq S, Shafiq M, Tariq MR, Sami A,  
Nawaz-ul-Rehman MS, Bhatti MHT,  
Haider MS, Sadiq S, Abbas MT,  
Hussain M and Shahid MA (2023)  
Interaction between bacterial  
endophytes and host plants.  
*Front. Plant Sci.* 13:1092105.  
doi: 10.3389/fpls.2022.1092105

## COPYRIGHT

© 2023 Mushtaq, Shafiq, Tariq, Sami,  
Nawaz-ul-Rehman, Bhatti, Haider,  
Sadiq, Abbas, Hussain and Shahid. This is  
an open-access article distributed under  
the terms of the [Creative Commons  
Attribution License \(CC BY\)](https://creativecommons.org/licenses/by/4.0/). The use,  
distribution or reproduction in other  
forums is permitted, provided the  
original author(s) and the copyright  
owner(s) are credited and that the  
original publication in this journal is  
cited, in accordance with accepted  
academic practice. No use,  
distribution or reproduction is  
permitted which does not comply with  
these terms.

# Interaction between bacterial endophytes and host plants

Sehrish Mushtaq<sup>1</sup>, Muhammad Shafiq<sup>2\*</sup>,  
Muhammad Rizwan Tariq<sup>3</sup>, Adnan Sami<sup>4</sup>,  
Muhammad Shah Nawaz-ul-Rehman<sup>5</sup>,  
Muhammad Hamza Tariq Bhatti<sup>1</sup>, Muhammad Saleem Haider<sup>1</sup>,  
Saleha Sadiq<sup>6</sup>, Muhammad Taqqi Abbas<sup>7</sup>, Mujahid Hussain<sup>8</sup>  
and Muhammad Adnan Shahid<sup>8\*</sup>

<sup>1</sup>Faculty of Agricultural Sciences, University of the Punjab, Lahore, Pakistan, <sup>2</sup>Department of Horticulture, Faculty of Agricultural Sciences, University of the Punjab, Lahore, Pakistan,

<sup>3</sup>Department of Food Science, Faculty of Agricultural Sciences, University of the Punjab, Lahore, Pakistan, <sup>4</sup>Department of Plant Breeding and Genetics, Faculty of Agricultural Sciences, University of the Punjab, Lahore, Pakistan, <sup>5</sup>Virology Lab, Centre of Agricultural Biochemistry and Biotechnology (CABB), University of Agriculture Faisalabad Pakistan, Faisalabad, Pakistan, <sup>6</sup>Institute of Biochemistry, Biotechnology, and Bioinformatics (IBBB), The Islamia University of Bahawalpur, Bahawalpur, Pakistan, <sup>7</sup>Department of Plant Pathology, Faculty of Agricultural Sciences, University of the Punjab, Lahore, Pakistan, <sup>8</sup>Horticultural Science Department, North Florida Research and Education Center, University of Florida/IFAS, Quincy, FL, United States

Endophytic bacteria are mainly present in the plant's root systems. Endophytic bacteria improve plant health and are sometimes necessary to fight against adverse conditions. There is an increasing trend for the use of bacterial endophytes as bio-fertilizers. However, new challenges are also arising regarding the management of these newly discovered bacterial endophytes. Plant growth-promoting bacterial endophytes exist in a wide host range as part of their microbiome, and are proven to exhibit positive effects on plant growth. Endophytic bacterial communities within plant hosts are dynamic and affected by abiotic/biotic factors such as soil conditions, geographical distribution, climate, plant species, and plant-microbe interaction at a large scale. Therefore, there is a need to evaluate the mechanism of bacterial endophytes' interaction with plants under field conditions before their application. Bacterial endophytes have both beneficial and harmful impacts on plants but the exact mechanism of interaction is poorly understood. A basic approach to exploit the potential genetic elements involved in an endophytic lifestyle is to compare the genomes of rhizospheric plant growth-promoting bacteria with endophytic bacteria. In this mini-review, we will be focused to characterize the genetic diversity and dynamics of endophyte interaction in different host plants.

Endophytic bacteria are mainly present in the plant's root systems. Endophytic bacteria improve plant health and are sometimes necessary to fight against adverse conditions. There is an increasing trend for the use of bacterial endophytes as bio-fertilizers. However, new challenges are also arising regarding the management of these newly discovered bacterial endophytes. Plant growth-promoting bacterial endophytes exist in a wide host range as part of their microbiome, and are proven to exhibit positive effects on plant growth. Endophytic bacterial communities within plant hosts are dynamic and affected by abiotic/biotic factors such as soil conditions, geographical distribution, climate, plant species, and plant-microbe interaction at a large scale. Therefore, there is a need to evaluate the mechanism of bacterial endophytes' interaction with plants under field conditions before their application. Bacterial endophytes have both beneficial and harmful impacts on plants but the exact mechanism of interaction is poorly understood. A basic approach to exploit the potential genetic elements involved in an endophytic lifestyle is to compare the genomes of rhizospheric plant growth-promoting bacteria with endophytic bacteria. In this mini-review, we will be focused to characterize the genetic diversity and dynamics of endophyte interaction in different host plants.

## KEYWORDS

host endosymbiont interactions, mechanism of interaction, bacterial endophytes, plants, endophytic

## 1 Introduction

Plants interact with diverse microbial populations in the ecosystem (Delaux et al., 2015). Microorganisms can colonize on plants' surfaces or internal parts depending on the host genotype and the molecular signals released by plant roots. Microorganisms can colonize on plants' surfaces or internal parts depending on the host genotype and the molecular signals released by plant roots. Endophytes are prokaryotic bacteria found within the healthy host tissue (Brader et al., 2014). Bacterial endophytes can benefit the host in several ways, such as biotic and abiotic stress resistance, increased availability of nutrients, degradation of toxic molecules, and production of phytohormones (Kandel et al., 2015).

Plant population dynamics have soil microbial intermediation. The plant has a microbial population in the phyllosphere, endophytes, or rhizospheric microbes. The ecology and phenotype of the plants can be affected by the influence of symbiotic microbes on the atmosphere and competition for soil resources.

The plant genotype affects the microbial make-up of the phyllosphere, rhizosphere, and endophytic microorganisms (Lynch et al., 2001). Although the precise method involves the plant-associated microorganisms and ecosystem function, the other specific mechanism is still unknown. Because they are co-evolved with bacteria, plants are immobile and need to control the results of their intricate interactions (Schnitzer and Klironomos, 2011). Different sorts of chemicals are continuously produced by plant roots, gathered, and secreted into the soil (Wood et al., 2012) known as the root exudates which contain enzymes, water, mucilage, H<sup>+</sup> ions, and primary, secondary compounds made up of carbon (Singh, 2015). Every plant species' rhizosphere is known to have a microorganism population that is 100 times higher than soil and is mostly controlled by compounds generated by roots (Jonkers et al., 2003; Bever, 2003). The favorable plant-soil microbial response enhances the microbial populations' spatial spread (Schimel et al., 2007), while negative reaction results in plant replacement, which demands recolonization of locally specific roots (Bever et al., 2010; Pedrotti et al., 2013).

It has been proposed that endophytic bacteria vary from rhizobacteria in their genetic architecture, which may account for their capacity to colonise plant tissues internally. However, no specific gene or gene family has been found to explain the endophytic regime. In a 2014 study, the whole genomes of nine Proteobacteria were compared to identify a list of genes that may play a role in the endophytic activity. So yet, only a few of those genes have undergone experimental testing to determine whether they are involved in endophytic colonisation (Shen et al., 2013; Ouyabe et al., 2019). In this study, we have documented some mechanisms involved in plant endophyte interaction at the molecular level.

## 2 Plant growth promotion by endophytes

PGPEs enhance plant development through three interconnected mechanisms: phytostimulation, biofertilization, and biocontrol. Phytostimulation is the production of phytohormones for direct plant development (Vishwakarma et al., 2021). The amount of the plant hormone ethylene frequently declines as a result of the enzyme 1-aminocyclopropane-1-carboxylate (ACC) deaminase (Cruz Barrera et al., 2020). According to numerous studies, the pea plant and the pepper plant (*Pseudomonas putida* and *Piper nigrum*, respectively) both have bacterial endophytes that release ACC deaminase to aid plant growth (Ruduś et al., 2013). By controlling ethylene levels in plants, ACC deaminase production may minimize abiotic stress because an increase in ethylene can obstruct DNA synthesis, root and shoot growth, and cell division. However, the specific method for enhanced plant development is still unknown (González Candia, 2021). Bacterial strains also produced other hormones which include abscisic acid, indole-3-acetic acid, and jasmonic acid, to stimulate plant growth (Forchetti et al., 2007). The endophytes can enhance plant growth by increasing the availability of important nutrients known as bio-fertilization.

Nitrogen fixation is the most studied phenomenon of bio-fertilization which is the conversion of atmospheric nitrogen into ammonia (Mishra and Arora, 2016). Bacterial species like *Azospirillum* spp., *Pantoea agglomerans*, and *Azoarcus* spp. all are known to be involved in a substantial amount of nitrogen fixation in plant roots (Indragandhi et al., 2008). Nonetheless, only 21 PGPEs can increase plant phosphorus availability by solubilizing phosphate. The metal cation linked to phosphorous is chelated as a result of the release of low molecular weight acids, making it more available to plants. The researchers have isolated, identified, and assessed the ability of *Achromobacter xiloxidans* and *Bacillus pumilus* to solubilize phosphate in sunflowers (Barrera et al., 2020). PGPEs were utilized to treat corn, lowering the quantity of artificial phosphorus fertilizer required while increasing yields by up to 50% (Cruz Barrera et al., 2019).

The protection of plants from phytopathogens and their growth promotion is known as biological control. Antibiotic and siderophores production are involved in biological control mechanisms. Siderophores like pyochelin and alicyclic acid and chelate iron are not directly involved in disease control due to their competition with pathogens for trace metals (Leopold, 1964). The disease can be suppressed in plants by antimicrobial metabolites secreted by bacterial endophytes such as 2,4-diacetylphloroglucinol (DAPG). Seed treatment of eggplant (*Solanum melongena*) with DAPG-producing bacterial endophytes reduced 70% of eggplant wilt caused by *Ralstonia solanacearum* (Rana et al., 2020a).

*Burkholderia*, *Bacillus*, *Pseudomonas*, *Enterobacter*, and *Serratia* are just a few of the bacterial endophyte strains that are successful at preventing the growth of pathogenic germs in

both *in vitro* and *in vivo* settings (Khan and Doty, 2009). Aside from that, bacteria from the genera *Bacillus*, *Enterobacter*, *Arthrobacter*, *Azotobacter*, *Isolpitericola*, *Streptomyces*, and *Pseudomonas* improved the crop's stress resistance from heat, drought, and salt (Rana et al., 2020b; Khalil et al., 2021). The most important interaction between these endophytes and symbiotic plants allowed the plants to significantly increase their biomass and height while lowering stress. Although, it is not yet clear how bacterial endophytes lessen abiotic stress (Liu et al., 2014).

## 2.1 Rhizobium and process of nodule formation

Rhizobium is a member of the family *Rhizobiaceae* and the class *Alphaproteobacteria*. Rhizobium, was the name given to this genus for the first time by Frank in 1889. There are 11 non-rhizobial species and 49 rhizobial species in the family *Rhizobiaceae* at the moment (Ledermann et al., 2021). The

rhizobial species induce the nodules on the roots of plants (*Fabaceae* family) and are linked to symbiotic nitrogen-fixing bacteria. The nodule's nitrogen fixation activity is extremely oxygen sensitive. The host plant receives continual supplies of reduced nitrogen from the bacterial enzyme system in this symbiotic connection, and the bacteria in exchange receive nutrients and energy from the plant (Van Rhijn and Vanderleyden, 1995). Nodules can occur in about 10% of legumes. The majority of the rhizobacteria in soil are oxygen sensitive and feed on the decomposing remains of other organisms.

In roots, nitrogen-fixing bacteria occur as irregular cells known as bacteroids, which are frequently Y, club-shaped and appear as straight rods with a regular structure (Figure 1). Bacteroids encode genes that determine the rhizobium's host specificity (Lodwig and Poole, 2003). Rhizobia that generate nodules but are unable to fix nitrogen are sometimes referred to as ineffective strains, whereas effective strains cause nitrogen fixation in nodules. Nodule development is controlled by certain genes known as nod genes i.e. nodF, nodE, nodL, nodP, nodQ,

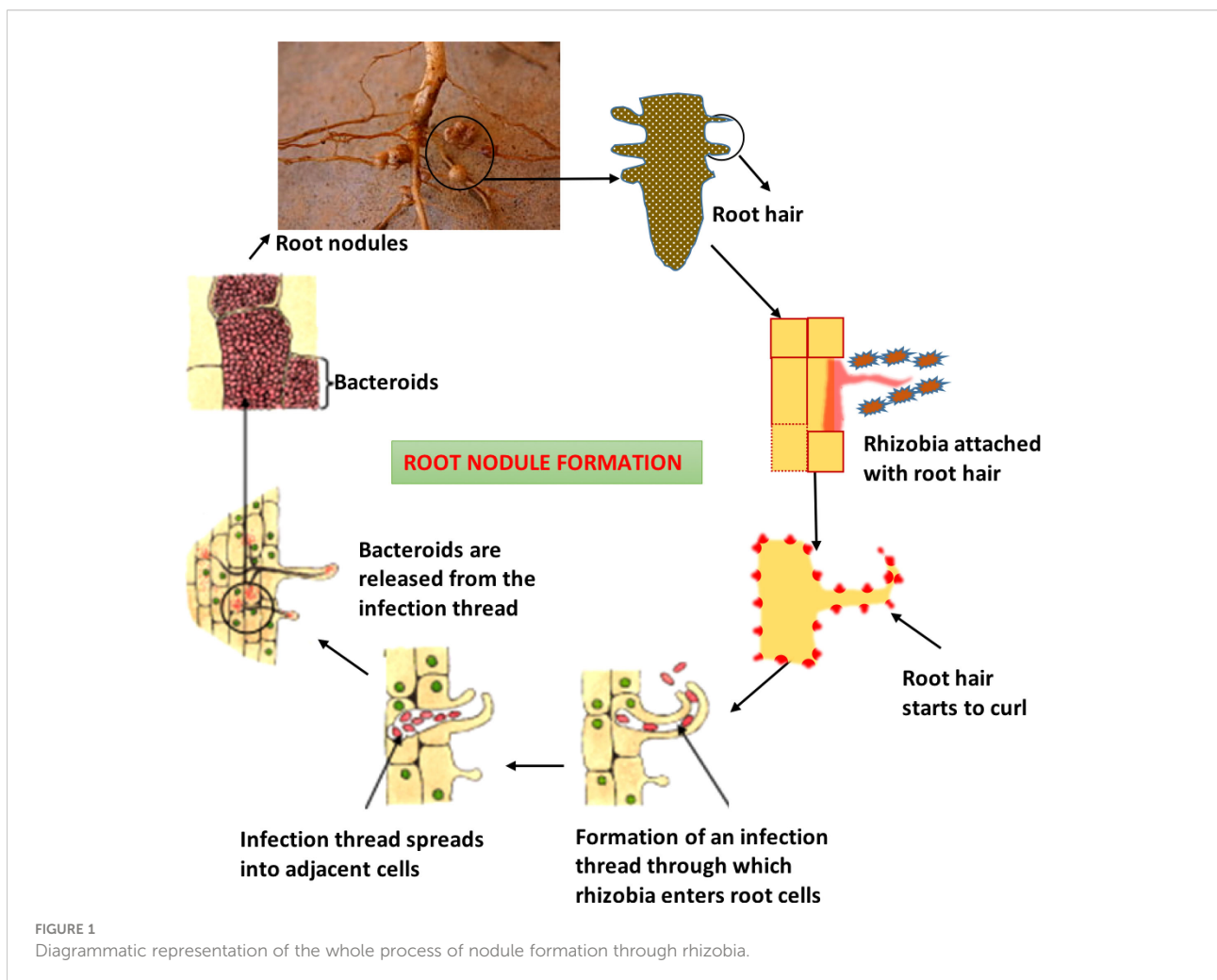


FIGURE 1  
Diagrammatic representation of the whole process of nodule formation through rhizobia.

and nodH (Basile and Lepek, 2021). Some substances, such as flavonoids, are released by the root cells and trigger the production of nodules in bacteria by activating the nod gene. In essence, these chemicals are in charge of identifying the proper host and attaching to the root hairs.

The nod factors, which are secreted by bacteria, cause the root hairs to curl (Moran, 1997). The root hair tip is damaged by rhizobia, which also causes the infection thread to arise. The thread then extends to neighboring cells by thread branching, and the bacteria continue to grow within the growing network of tubes, continuing to create nod factors that encourage the growth of the root cells and ultimately result in the formation of root nodules (Oldroyd et al., 2011). Following a week of infection, nodules are visible with the unaided eye and each nodule contains thousands of living rhizobium bacteria, the majority of which are malformed and are referred to as bacteroids. Small sections of the plant cell membranes called symbiosomes, which may or may not include multiple bacteroids, are located next to bacteroids and are active sites for nitrogen fixation (Ratu et al., 2021). Through the *Nitrogenase enzyme*, also known as Nitrogenase catalysis, nitrogen gas from the atmosphere is converted inside legume nodules into ammonia, which is then assimilated into amino acids, DNA, and RNA as well as significant energy molecules like ATP or other chemicals like vitamins, flavones, and hormones (Bergersen, 1961). The Nitrogenase complex is protected by a variety of mechanisms used by aerobic free-living bacteria, including physical barriers and fast metabolic rates. Azotobacter, for instance, circumvents this issue by maintaining the lowest oxygen concentration in its cells and the greatest rate of respiration of any organism. In the instance of Rhizobium, the nodule's red iron-containing protein, similar to hemoglobin in function to bond with oxygen, maintains control over the oxygen level (Lindström and Mousavi, 2020). However, this avoids the accumulation of free oxygen to prevent the loss of Nitrogenase activity while still providing enough oxygen for the metabolic functioning of bacteroids. Rhizobia and plants work together to make leghemoglobin, something neither of them could ever do on their own. Even in poor soil with few nutrients and insufficient nitrogen to support the growth of other plants, these nodules increase crop output (Lodwig and Poole, 2003).

## 2.2 Spread and variation of microbes from seed to plants

Plants and their microbial diversity vary throughout their life span of plants. These factors, prompt the structure and variety of the microbial community (Honma and Shimomura, 1978). Seed-born microbes gain entry into the germinating plant and take advantage of other colonizing microbes as well as opportunistic pathogens from the surrounding soil (Glick et al., 1999; Oteino et al., 2015). Hence the overall microbial biota and population changed dramatically throughout the life cycle of plants. The important ways of entry

into host plants are through root hair cells, root cracks, and wounds whereas other sources include stomata particularly of young stems and leaves; lenticels, and germinating radicles (Figure 2). Vertical seed transmission is another possible way to receive endophytic bacteria through plant host generations (Bergersen, 1961).

## 2.3 Presence of plant microbes in different parts of plants

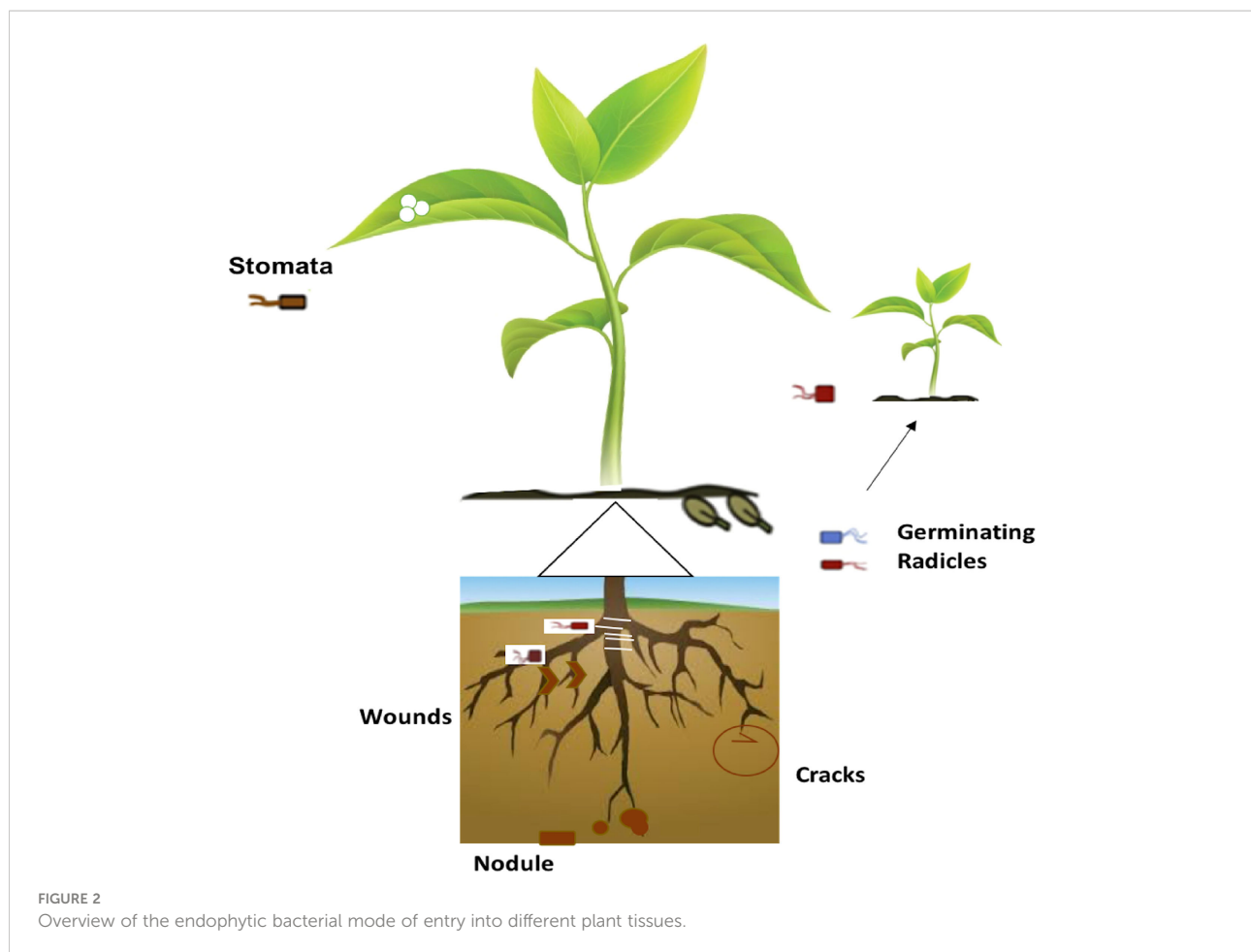
Microorganisms associated with plants formed a complex network. Different studies suggested that plant-associated microbes live inside plant tissues or on the surface of plant parts such as leaves, stems, fruit, and roots (Clarholm, 1985). The microbiome studies of *A. thaliana* leaves showed that plant genotype, surrounding plants, and abiotic features affected the microbial population structure (Teixeira et al., 2013). These interactions are responsible for expediting the defense signals between plants and the efficacy of natural biological control agents (Morgan et al., 2005). Microbial populations might indirectly affect the other taxa of microbes by altering the host growth response or metabolites without direct interaction with microbes.

## 3 Beneficial effects of microbes on plant growth and development

Plants usually take nutrients from the soil which constitutes a pool for microscopic life forms including bacteria, fungi, actinomycetes, algae, and protozoa. So, among them, the bacteria are the most common ones and have the maximum proportion in soil. The maximum number of bacteria present in the rhizosphere near the roots of plants is different from bulk soil (Luu et al., 2020). As these bacteria are present in more concentration in the soil so the bacteria may affect a plant through three different pathways (Edwards and Harding, 2004). PGPEs can promote plant growth directly by expediting the procurement of compounds or modifying levels of plant hormones and reducing the inhibitory effect of plant growth and pathogenicity by acting as biocontrol agents (Yan et al., 2019). The benefits provided by the endophytes to the host plants and their mechanisms are described in (Table 1).

## 4 Role of PGPEs against biotic stress

Throughout their lives, plants are exposed to harmful abiotic and biotic stresses. The damage that bacteria, fungi, viruses, nematodes, viroids, and insects do to plants is referred to as "biotic stress." Rhizobacteria that promote plant growth by generating phytohormones or facilitating the uptake of particular nutrients might affect plant growth through biotic stress (Tiwari et al., 2020). However, PGPR reduces or even



eliminate the negative impacts of plant pathogens. For example, *Pseudomonas fluorescens* produces 2,4-Diacetyl Phloroglucinol, which inhibits the development of pathogenic fungi in plants (Suslow and Schroth, 1982). Chitinase and laminarinase, two extracellular enzymes generated by *P. stutzeri*, caused the lysis of *Fusarium solani* mycelia and root rot (Cano-Salazar et al., 2011). During a seven-month field trial, the endophytic *B. cenocepacia* reduced the prevalence of fusarium wilt disease in banana plants by 3.4%, compared to 24.5% in untreated infected plants (Sapak et al., 2008). The antibiotic Pyrrolnitrin, which helps to reduce cotton damping off losses brought on by *Rhizoctonia solani*, was developed by several endophytic *Pseudomonas fluorescens* strains (Timper et al., 2009). *Fusarium oxysporum*, which was used as a bio-agent to create resistance in tomato plants, was successfully protected against *P. fluorescens* in flowering plants (Dudai, 2011). A bacteria that inhabit plant roots called *Bacillus amyloliquefaciens* has the power to control plant diseases and promote plant growth (Vardi et al., 2021).

In a study, it was discovered that bacterial endophytes shield cucumber plants from the cucumber anthracnose produced by *Pseudomonas fluorescens* (Akköprü et al., 2021). It was once believed that *Achromobacter* sp., *Streptomyces* sp., and *Bacillus*

*licheniformis* were responsible for the foliar disease known as downy mildew. The downy mildew disease infestation level was lowered by *Pseudoperonospora cubensis* (Basu et al., 2022), which ultimately resulted in an increased yield.

The management of pests, which has become a challenge for most crops since pests have evolved a tolerance to pesticides, is another use for these endophytic bacteria (Deng et al., 2014). Entomopathogenic bacteria have been used to combat pests that are immune to insecticides (Figure 3). A few fungi from the genera *Podonectria*, *Verticillium*, *Hirsutella*, *Sphaerostilbe*, *Agerata*, *Metarhizium* *Aschersonia*, and *Myriangium* are used for the biological management of pests. *Brevibacillus laterosporus* is effective against nematodes, Lepidoptera, Coleoptera, and toxic fungi in plants in addition to insects (Skinner et al., 2014).

## 5 Identification of endophytic bacteria interaction with Host

In recent years, next-generation sequencing (NGS) techniques have been utilized to study the whole population of

TABLE 1 Examples of plant growth-promoting rhizobacteria tested for various crop types.

PGPR	Plant	Benefits to plant growth	References
<i>Pseudomonas</i> sp.	Green gram	Increased plant dry weight, number of nodules, total chlorophyll content, root/shoot N, P seed protein, and yield.	(Del Carmen Orozco-Mosqueda et al, 2020)
	Soybean Wheat	Increased soil enzyme activity, nutrient absorption, and yield	(Kalyani et al., 2008)
	Chickpea	An enhanced fresh and dry weight of plants	(Berendsen et al., 2012)
	Rice	More ability to control fungal and bacterial pathogens	(Bulgarelli et al., 2012)
	Canola	Encouraged growth and cadmium accumulation in plants	(Aglar et al., 2016)
	Mustard	Improved growth and reduced Cr contents among plants	(Foster, 1988)
	Soybean, mung bean, wheat	Promotes growth of plants	(Bertin et al., 2003)
<i>Pseudomonas putida</i>	Mung bean	The ethylene production repressed in treated plant Increase the growth and decreases Pb and Cd uptake	(Glick, 2012) (Ahemad and Khan, 2012)
	Lectuca	Enhancement of shoot/root length attained through concentrated inoculants	(Sharma et al., 2011)
	Artichoke	PSB along with N fixers increase in shoot length/weight, germination percentage seedling vigor, and reduction in germination time	(Tank and Saraf, 2010)
<i>Pseudomonas aeruginosa</i>	Maize	Endorsed plant growth and helped soil metal utilization, increase Pb and Cr uptake	(Lawongsa et al., 2008)
	Black gram	Reduced Cd deposition in tissues, widespread rooting, and increased plant growth	(Wu et al., 2015)
	Indian mustard and pumpkin	Increased in plant growth, decrease in Cd uptake	(Rajkumar et al., 2006)
	Tomato, Okra, African spinach	Increase in Dry weight of tomato, okra, and spinach	(Gupta et al., 2002)
<i>Pseudomonas fluorescens</i>	Alfalfa	Enhanced Fe and Cu movement from root/shoot	(Mayak et al., 1999)
	Peanut	Increase in pod yield and nodule dry weight	(Lobo et al., 2019)
	Soybean	Increased plant growth	(Rekha et al., 2007)
	Canola	Protect plants against the inhibitory effects of Cd	(Jahanian et al., 2012)
	Maize	Increase of plant growth, height, seed weight, no. of seed/ear, leaf area, shoot dry weight	(Curá et al., 2017)
<i>Azospirillum amazonense</i>	Rice	Grain dry matter deposition, panicle count, and nitrogen buildup at the grain maturity stage all increase	(Sant'anna et al., 2011)
<i>Azospirillum brasilense</i>	Common bean	Increase of Root growth in plants	(Adesemoye et al, 2008)
<i>Azospirillum lipoferum</i>	Cotton	An increase in soil microorganisms, plant height, and seed production was observed, but no changes in boll weight or staple length.	(Fayez and Daw, 1987)
<i>Azotobacter chroococcum</i>	Chinese mustard	Increased plant development and metal toxicity protection for the plant	(Jha, 2017)
<i>Azospirillum brasilense</i>	Rice	Increased grain yield	(Gupta et al., 2005)
<i>Kluyvera ascorbate</i>	Mustard, Tomato Canola,	Heavy metals reduce plant growth but do not boost metal uptake.	(Safronova et al., 2006)
<i>Bradyrhizobium</i>	Green gram	The development traits at all of the studied pesticide dosages (quizalafop-p-ethyl and clodinafop)	(Wani et al., 2007)
	Soybean and yellow Lupin	Increased biomass, nitrogen content, deposition of metals	(Dell'amico et al, 2008)

(Continued)

TABLE 1 Continued

PGPR	Plant	Benefits to plant growth	References
	Green gram	Increase of nodule number, seed yield, grain protein, root/shoot N at 290 mg Ni/kg soil	(Burd et al., 2000)
<i>Brevundimonas</i>	Canola	Isolated cadmium directly from the solution	(Gholami et al., 2009)
<i>Enterobacter cloacae</i>	Canola	Significant increases in root and shoot length were observed.	(Bashan and González, 1999)
<i>Klebsiella oxytoca</i>	Maize	Increase of plant growth parameters	(Remans et al., 2008)
<i>Enterobacter sakazakii</i>			
<i>Brevibacillus</i>	White clover	Increased plant growth and nutrition and decreased zinc conc.	Anjum et al., 2007)
<i>Methylobacterium oryzae</i> , <i>Berkholderia</i> sp.	Tomato	Significant increase in shoot/root length attained through bacterial cells inoculation	(Wu et al., 2006)
<i>Sinorhizobium</i> sp.	Brown mustard	Increased the efficacy of Pb	(Thakuria et al., 2004)
<i>Bacillus</i> spp	Barley	Increased root/shoot weight	(Dary et al., 2010)
<i>Rhizobium</i> sp.	Pea	Increase of the dry matter, nodule numbers, root/shoot nitrogen	(Lugtenberg and Kamilova, 2009)
<i>Mycobacterium</i> sp.	Canola	Prevent plant against the inhibitory effects of cadmium	(Wani et al., 2008)
<i>Bacillus</i> sp. <i>Paenibacillus</i> sp.	Rice	Considerably encouraged the root/shoot growth.	(Robinson et al., 2001)

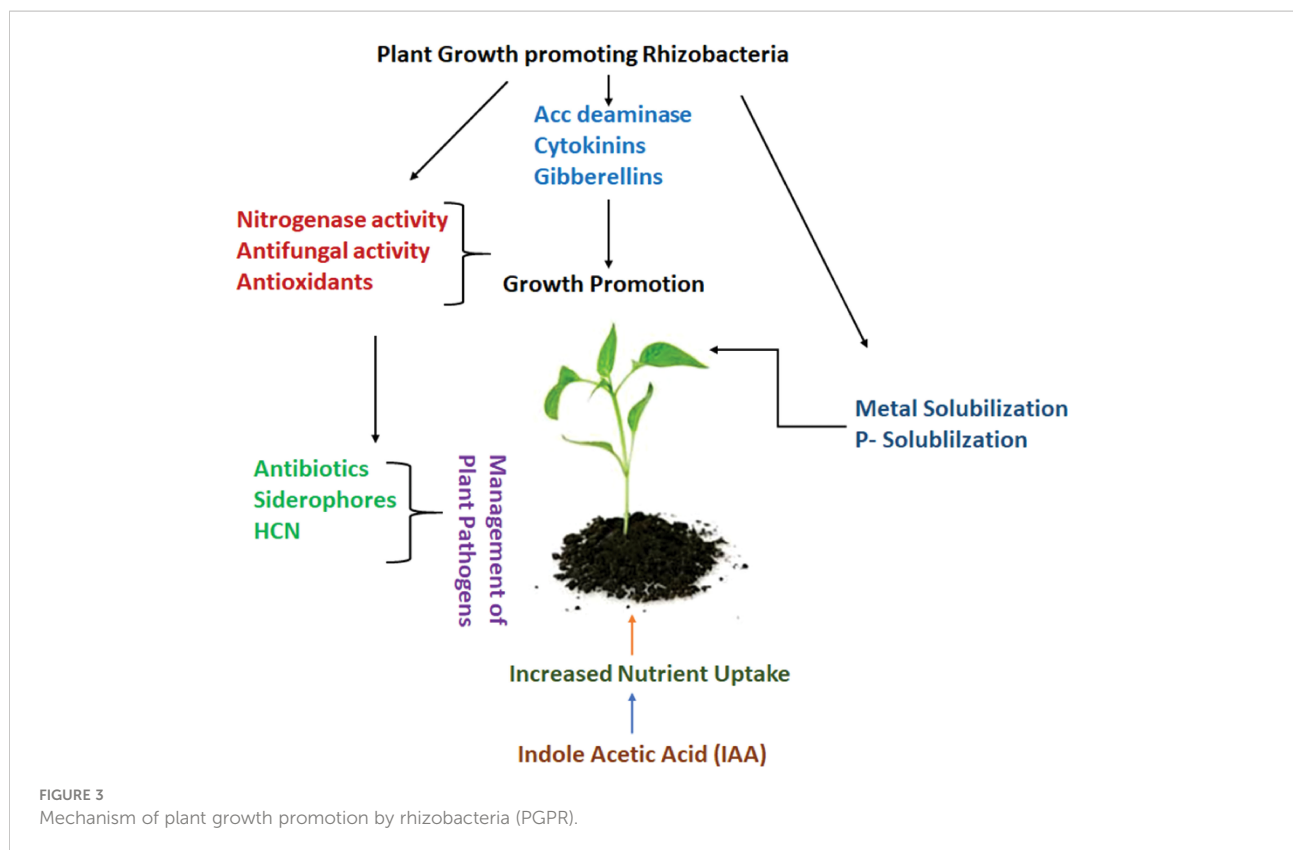
cultivable or non-cultivable bacteria inside plants, as well as their genomes. The interaction of host and bacterial endophytes has insightful concerns for the biological functioning of plants. As a result of interactions, rapid changes in host phenotype occurs also it is assumed as a driving force for the speciation and co-evolution of both the genetic system of host and bacteria (Fawcett, 1944). Though old genetic techniques to study plant-microbe interaction are less efficient, time-consuming, costly, and labor-intensive required a wide range of experiments and are usually limited to certain known genes (De Oliveira et al., 2004) in comparison to investigating the host-microbe interactions in molecular levels, it is needed to understand the phenotypic phenomena and genomics in depth. So the development of NGS technologies or metagenomic studies has provided the best way to understand the host-pathogen system. Through this technology, we can construct genome models of different organisms, which includes strains, their natural populations over time and their evolutionary histories (Navas et al., 2017; Sharma et al., 2021).

These complicated interactions can be analyzed and integrated by viewing plant microbiomes as a system. To better understand endophytism, contemporary genomic investigations incorporating metaomics and comparative studies can be quite beneficial (Dubey et al., 2020). A better understanding of endophyte interactions could be used to improve agricultural management by increasing plant development, biocontrol, and bioremediation (Alaimo et al., 2018). Some of the tools being utilized or that could be used to understand the link between plants and endophytes

include genome sequencing, comparative genomics, microarray, next-generation sequencing, metagenomics, and metatranscriptomics (Dixit et al., 2022). To study endophytes and their apparent function in host plant ecology, contemporary methods and approaches need to be investigated (Gaiero et al., 2013).

Another way to identify the endophytic bacteria interact with the plant is to isolate the endophytic bacteria culture and then classify based on its phenotypic traits, and a few isolates from each category are identified further through partial sequencing of the 16S rRNA gene (Khare et al., 2018). The results of partial sequencing show that the isolates belonged to the genera *Pseudomonas*, *Stenotrophomonas*, *Bacillus*, *Pantoea*, and *Serratia* of bacteria (Liu et al., 2017>2552). These isolates are tested for their ability to produce siderophores, phosphate solubilization, atmospheric nitrogen fixation, protease, and hydrogen cyanide, as well as phytohormones like auxin and gibberellin (Eid et al., 2019). Auxin and gibberellin, two plant growth hormones, can be produced by all strains, though to varying degrees. Almost all strains could solubilize phosphate (Lata et al., 2019). The outcomes of protease, siderophore, and atmospheric nitrogen-fixing ability vary between strains. These findings provide information on the relationship between endophytic bacteria and their host plant (Vandana et al., 2021).

Furthermost genomic methods require recognition of variations among sequences within species or populations, like point mutations, Addition/deletions, and structural variations in structures (Bulgarelli et al., 2013).



## 5.1 Evolution of new pathogenic strains of microbes

One of the great evolutionary changes in life is the development of advantageous symbioses between eukaryotic (plants) and prokaryotic creatures (Chebotar et al., 2015). According to certain theories, the relationship between endophytic bacteria and plants frequently depends on two fundamental elements: currency and a system for exchanging currency. The currency could be, for instance, a root exudate that bacteria can take up in the context of interactions between plants and endophytic bacteria (Mercado-Blanco and JJ Lugtenberg, 2014). Similarly, bacteria may release hormones that encourage plant growth, such as auxin and gibberellins, which may be favorable for plant growth (Maksimov et al., 2018). It is anticipated that selection will favor the evolution of mutualism when the exchange of currencies between the two parties is balanced. Therefore, it is hypothesized that increased mutualistic dependency develops through reciprocal co-evolution or adaptation by one of the partners through the selection of features directly related to the mutualistic interaction (Chen et al., 2021).

Competition for scarce shared resources like iron may also lead to asymmetrical currency exchange, which could help to explain why some plant-microbe interactions are hostile (Hong and Park, 2016). Furthermore, because the rhizosphere is open,

the free diffusion of resources derived from plants may promote higher levels of cheating in which mutant bacterial genotypes take benefit of “public goods” without producing substances that aid plant growth (Pandey et al., 2017). Because of this, mutualistic plant-microbe interactions may need additional enforcement from the plant, such as penalizing dishonest bacterial genotypes or positively identifying genotypes that promote plant growth (Ryan et al., 2008). Intriguing research would also be done to see whether endophytic bacteria and plants may coevolve from first neutral interaction and whether plants can coevolve in response to rhizosphere bacteria (Santos et al., 2018). In conclusion, by showing that plant-associated bacteria can quickly evolve along the symbiotic connection within a few growth cycles, our results urge eco-evolutionary management of endophytic bacteria and plants interactions in agriculture (Aswani et al., 2020).

## 5.2 Endophytic bacteria in disease management

Crop productivity is impacted by a number of common plant diseases that are present worldwide. Some of the serious ones are wilt disease, root rot, powdery mildew, leaf spot, leaf curl, and blight. To counter these phytopathogens, endophytic bacteria are crucial (Latha et al., 2019).



By producing proteins associated with pathogenesis (PRPs) and defense enzymes that stop the growth of phytopathogens that cause disease, endophytic bacteria can produce siderophores, antimicrobial compounds, and systemic resistance (Pandey et al., 2019). Bacterial endophytes are also potentially useful biocontrol agents. Plant diseases degrade plant performance and crop quality, which reduces crop output (Muthukumar et al., 2017). It has been shown that the nitrogen-fixing bacteria *Azotobacter chroococcum*, the phosphate-solubilizing bacteria PSB (*Pseudomonas cepacia*), the endophytic bacterial strains *Lysinibacillus* sp. and *Bacillus subtilis*, and their combination as bio-fertilizers can reduce the incidence of bacterial wilt disease in chili plants by up to 80% (Tewari et al., 2019).

The endophytic bacterial strain *B. subtilis* showed the strongest (80%) illness suppression (Jacob et al., 2020). This endophyte could also considerably aid the growth of the chili. Chemical pesticides are typically used to manage such phytopathogens, but this tactic has raised concerns about environmental contamination and contributed to the emergence of resistance to specific chemicals over time (Prasad et al., 2020). New insecticides must always be developed to address this. Chemical pesticides are thought to be ineffective when compared to endophytic bacteria acting as biocontrol agents or bioinsecticides. A broad array of mechanisms, including direct antagonism via the generation of antibiotics, siderophores, hydrogen cyanide, hydrolytic enzymes (chitinases, proteases, and lipases), etc., are involved in the biocontrol of plant diseases (Puri et al., 2017).

## 6 Conclusion

Some of the bacterial endophytes or PGPR are commonly used to control different diseases and as biological control agents so nowadays most of the focus is the understanding of complex interactions and their mechanisms and outcome either beneficial or harmful. It is hard to find the exact mechanism of interaction among complex microbial populations residing in the soil and environment near to host. So that proper characterization and management strategies can be devised according to the current need of time. In recent time peoples are preferring organic food and disliked the use of fertilizers and chemicals in agriculture. As the world population is increasing and food shortage issues are

raised, in the current situation food security is an important topic for debate. Hence bacterial endophytes can be used as an alternative to chemical fertilizers, nutrient sources, and biological control agents for various plant pathogens. Scientists are focusing on the use of these endophytes in the form of biopesticides, and biofertilizers with different trade names for the control of different diseases and sustainable agricultural systems. Although the application of these endophytes in combination may lead to the development of optimum PGPEs inoculants that robust, and slight variation of environmental factors will not affect the plant growth promotion.

## Author contributions

SM, MN, MH, MS, and MA conceived and conceptualized the study. MAS, AS, MB provided materials and technical assistance. SM, MS wrote original draft. SS, MSH, MS and MT technically reviewed and finalized the draft. All authors contributed to the article and approved the submitted version.

## Acknowledgments

The authors are thankful to the University of the Punjab Lahore, Pakistan for providing the facilities for study.

## Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

## Publisher's note

All claims expressed in this article are solely those of the authors and do not necessarily represent those of their affiliated organizations, or those of the publisher, the editors and the reviewers. Any product that may be evaluated in this article, or claim that may be made by its manufacturer, is not guaranteed or endorsed by the publisher.

## References

- Adesemoye, A., Obini, M., and Ugoji, E. (2008). Comparison of plant growth-promotion with *pseudomonas aeruginosa* and *bacillus subtilis* in three vegetables. *Braz. J. Microbiol.* 39, 423–426. doi: 10.1590/S1517-83822008000300003
- Agler, M. T., Ruhe, J., Kroll, S., Morhenn, C., Kim, S.-T., Weigel, D., et al. (2016). Microbial hub taxa link host and abiotic factors to plant microbiome variation. *PLoS Biol.* 14, e1002352. doi: 10.1371/journal.pbio.1002352

- Ahemad, M., and Khan, M. S. (2012). Effect of fungicides on plant growth promoting activities of phosphate solubilizing pseudomonas putida isolated from mustard (*Brassica campestris*) rhizosphere. *Chemosphere* 86, 945–950. doi: 10.1016/j.chemosphere.2011.11.013
- Akköprü, A., Akat, Ş., Özkatan, H., Gül, A., and Akbaba, M. (2021). The long-term colonization dynamics of endophytic bacteria in cucumber plants, and their effects on yield, fruit quality and angular leaf spot disease. *Scientia Hort.* 282, 110005. doi: 10.1016/j.scienta.2021.110005
- Alaimo, S., Marceca, G. P., Giugno, R., Ferro, A., and Pulvirenti, A. (2018). Current knowledge and computational techniques for grapevine meta-omics analysis. *Front. Plant Sci.* 8, 2241. doi: 10.3389/fpls.2017.02241
- Anjum, M., Sajjad, M., Akhtar, N., Qureshi, M., Iqbal, A., and Rehman, A. (2007). Response of cotton to plant growth promoting rhizobacteria (PGPR) inoculation under different levels of nitrogen. *J. Agric. Res. (Pakistan)*.
- Aswani, R., Jishma, P., and Radhakrishnan, E. (2020). “Endophytic bacteria from the medicinal plants and their potential applications,” in *Microbial endophytes* (Elsevier). Available at: <https://www.sciencedirect.com/science/article/pii/B9780128187340000024>.
- Barrera, M. C., Jakobs-Schoenwandt, D., Gómez, M. I., Serrato, J., Ruppel, S., and Patel, A. V. (2020). Formulating bacterial endophyte: Pre-conditioning of cells and the encapsulation in amidated pectin beads. *Biotechnol. Rep.* 26, e00463. doi: 10.1016/j.btre.2020.e00463
- Bashan, Y., and González, L. E. (1999). Long-term survival of the plant-growth-promoting bacteria azospirillum brasilense and pseudomonas fluorescens in dry alginate inoculant. *Appl. Microbiol. Biotechnol.* 51, 262–266. doi: 10.1007/s002530051391
- Basile, L. A., and Lepek, V. C. (2021). Legume–rhizobium dance: an agricultural tool that could be improved? *Microbial Biotechnol.* 14, 1897–1917.
- Basu, S., Sarkar, S., Prasad, R., and Kumar, G. (2022). Current approaches for alleviating abiotic stress tolerance in crops: Role of beneficial microorganisms. *Beneficial Microorganisms Agric.*, 231–248. doi: 10.1007/978-981-19-0733-3\_9
- Berendsen, R. L., Pieterse, C. M., and Bakker, P. A. (2012). The rhizosphere microbiome and plant health. *Trends Plant Sci.* 17, 478–486. doi: 10.1016/j.tplants.2012.04.001
- Bergersen, F. (1961). The growth of rhizobium in synthetic media. *Aust. J. Biol. Sci.* 14, 349–360. doi: 10.1071/BI9610349
- Bertin, C., Yang, X., and Weston, L. A. (2003). The role of root exudates and allelochemicals in the rhizosphere. *Plant Soil* 256, 67–83. doi: 10.1023/A:1026290508166
- Bever, J. D. (2003). Soil community feedback and the coexistence of competitors: conceptual frameworks and empirical tests. *New Phytol.* 157, 465–473. doi: 10.1046/j.1469-8137.2003.00714.x
- Bever, J. D., Dickie, I. A., Facelli, E., Facelli, J. M., Klironomos, J., Moora, M., et al. (2010). Rooting theories of plant community ecology in microbial interactions. *Trends Ecol. Evol.* 25, 468–478. doi: 10.1016/j.tree.2010.05.004
- Brader, G., Compant, S., Mitter, B., Trognitz, F., and Sessitsch, A. (2014). Metabolic potential of endophytic bacteria. *Curr. Opin. Biotechnol.* 27, 30–37. doi: 10.1016/j.copbio.2013.09.012
- Bulgarelli, D., Rott, M., Schlaeppli, K., Ver Loren Van Themaat, E., Ahmadinejad, N., Assenza, F., et al. (2012). Revealing structure and assembly cues for arabidopsis root-inhabiting bacterial microbiota. *Nature* 488, 91–95. doi: 10.1038/nature11336
- Bulgarelli, D., Schlaeppli, K., Spaepen, S., Van Themaat, E. V. L., and Schulze-Lefert, P. (2013). Structure and functions of the bacterial microbiota of plants. *Annu. Rev. Plant Biol.* 64, 807–838. doi: 10.1146/annurev-arplant-050312-120106
- Burd, G. I., Dixon, D. G., and Glick, B. R. (2000). Plant growth-promoting bacteria that decrease heavy metal toxicity in plants. *Can. J. Microbiol.* 46, 237–245. doi: 10.1139/w99-143
- Cano-Salazar, L., Gregorio-Jáuregui, K. M., Juárez-Ordaz, A. J., Leon-Joubanc, E., Perez-Molina, A., Martínez-Hernández, J. L., et al. (2011). Thermodynamics of partitioning of chitinase and laminarinase in a soya lecithin liposome system and their antifungal effect against fusarium oxysporum. *Biocatalysis Biotransformation* 29, 60–70. doi: 10.3109/10242422.2011.563445
- Chebotar, V., Malfanova, N., Shcherbakov, A., Ahtemova, G., Borisov, A. Y., Lugtenberg, B., et al. (2015). Endophytic bacteria in microbial preparations that improve plant development. *Appl. Biochem. Microbiol.* 51, 271–277. doi: 10.1134/S0003683815030059
- Chen, W., Wang, E., Ji, Z., and Zhang, J. (2021). Recent development and new insight of diversification and symbiosis specificity of legume rhizobia: mechanism and application. *J. Appl. Microbiol.* 131, 553–563. doi: 10.1111/jam.14960
- Clarholm, M. (1985). Interactions of bacteria, protozoa and plants leading to mineralization of soil nitrogen. *Soil Biol. Biochem.* 17, 181–187. doi: 10.1016/0038-0717(85)90113-0
- Cruz Barrera, F. M. (2019). Development of an integrated fermentation and formulation approach for the endophytic bacterium *Kosakonia radicincitans* DSM16656T as a novel plant biostimulant.
- Cruz Barrera, M., Jakobs-Schoenwandt, D., Persicke, M., Gómez, M. I., Ruppel, S., and Patel, A. V. (2020). Anhydrobiotic engineering for the endophyte bacterium *Kosakonia radicincitans* by osmoadaptation and providing exogenously hydroxyectoine. *World J. Microbiol. Biotechnol.* 36, 1–16.
- Curá, J. A., Franz, D. R., Filosofía, J. E., Balestrasse, K. B., and Burgueño, L. E. (2017). Inoculation with azospirillum sp. and herbaspirillum sp. bacteria increases the tolerance of maize to drought stress. *Microorganisms* 5, 41.
- Dary, M., Chamber-Pérez, M., Palomares, A., and Pajuelo, E. (2010). “In situ” phytostabilisation of heavy metal polluted soils using lupinus luteus inoculated with metal resistant plant-growth promoting rhizobacteria. *J. Hazardous Materials* 177, 323–330. doi: 10.1016/j.jhazmat.2009.12.035
- Delaux, P.-M., Radhakrishnan, G. V., Jayaraman, D., Cheema, J., Malbreil, M., Volkening, J. D., et al. (2015). Algal ancestor of land plants was preadapted for symbiosis. *Proc. Natl. Acad. Sci.* 112, 13390–13395. doi: 10.1073/pnas.1515426112
- Del Carmen Orozco-Mosqueda, M., Glick, B. R., and Santoyo, G. (2020). ACC deaminase in plant growth-promoting bacteria (PGPB): an efficient mechanism to counter salt stress in crops. *Microbiological Res.* 235, 126439. doi: 10.1016/j.micres.2020.126439
- Dell’amico, E., Cavalca, L., and Andreoni, V. (2008). Improvement of brassica napus growth under cadmium stress by cadmium-resistant rhizobacteria. *Soil Biol. Biochem.* 40, 74–84. doi: 10.1016/j.soilbio.2007.06.024
- Deng, M.-C., Li, J., Liang, F.-R., Yi, M., Xu, X.-M., Yuan, J.-P., et al. (2014). Isolation and characterization of a novel hydrocarbon-degrading bacterium achromobacter sp. HZ01 from the crude oil-contaminated seawater at the daya bay, southern China. *Mar. Pollut. Bull.* 83, 79–86. doi: 10.1016/j.marpolbul.2014.04.018
- De Oliveira, E. J., Rabinovitch, L., Monnerat, R. G., Passos, L. K. J., and Zahner, V. (2004). Molecular characterization of *Brevibacillus laterosporus* and its potential use in biological control. *Appl. Environ. Microbiol.* 70, 6657–6664. doi: 10.1128/AEM.70.11.6657-6664.2004
- Dixit, R., Kamat, S., Srivastava, A., and Kumari, M. (2022). “Molecular basis of plant-PGP interactions during amelioration of biotic stress,” in *Microbial biocontrol: Food security and post harvest management* (Springer). Available at: [https://link.springer.com/chapter/10.1007/978-3-030-87289-2\\_5](https://link.springer.com/chapter/10.1007/978-3-030-87289-2_5).
- Dubey, A., Malla, M. A., Kumar, A., Dayanandan, S., and Khan, M. L. (2020). Plants endophytes: unveiling hidden agenda for bioprospecting toward sustainable agriculture. *Crit. Rev. Biotechnol.* 40, 1210–1231. doi: 10.1080/07388551.2020.1808584
- Dudai, N. (2011). “Domestication and breeding of wild medicinal and aromatic plants—thirty years of experience in Israel,” in *1 International symposium on medicinal, aromatic and nutraceutical plants from mountainous areas (MAP-mountain 2011)*, vol. 955, 175–183. Available at: [https://www.actahort.org/books/955/955\\_25.htm](https://www.actahort.org/books/955/955_25.htm).
- Edwards, R., and Harding, K. G. (2004). Bacteria and wound healing. *Curr. Opin. Infect. Dis.* 17, 91–96. doi: 10.1097/00001432-200404000-00004
- Eid, A. M., Salim, S. S., Hassan, S. E.-D., Ismail, M. A., and Fouda, A. (2019). “Role of endophytes in plant health and abiotic stress management,” in *Microbiome in plant health and disease* (Springer). Available at: [https://link.springer.com/chapter/10.1007/978-981-13-8495-0\\_6](https://link.springer.com/chapter/10.1007/978-981-13-8495-0_6).
- Fawcett, H. (1944). Fungus and bacterial diseases of insects as factors in biological control. *Botanical Rev.* 10, 327–348. doi: 10.1007/BF02861103
- Fayez, M., and Daw, Z. (1987). Effect of inoculation with different strains of azospirillum brasilense on cotton (*Gossypium barbadense*). *Biol. fertility soils* 4, 91–95. doi: 10.1007/BF00280357
- Forchetti, G., Masciarelli, O., Alemanno, S., Alvarez, D., and Abdala, G. (2007). Endophytic bacteria in sunflower (*Helianthus annuus* L.): isolation, characterization, and production of jasmonates and abscisic acid in culture medium. *Appl. Microbiol. Biotechnol.* 76, 1145–1152. doi: 10.1007/s00253-007-1077-7
- Foster, R. (1988). Microenvironments of soil microorganisms. *Biol. fertility soils* 6, 189–203. doi: 10.1007/BF00260816
- Gaiero, J. R., Mccall, C. A., Thompson, K. A., Day, N. J., Best, A. S., and Dunfield, K. E. (2013). Inside the root microbiome: bacterial root endophytes and plant growth promotion. *Am. J. Bot.* 100, 1738–1750. doi: 10.3732/ajb.1200572
- Gholami, A., Shahsavani, S., and Nezarat, S. (2009). The effect of plant growth promoting rhizobacteria (PGPR) on germination, seedling growth and yield of maize. *Int. J. Agric. Biosyst. Eng.* 3, 9–14.
- Glick, B. R. (2012). Plant growth-promoting bacteria: mechanisms and applications. *Scientifica* 2012. doi: 10.6064/2012/963401

- Glick, B. R., Holguin, G., Patten, C., and Penrose, D. M. (1999). *Biochemical and genetic mechanisms used by plant growth promoting bacteria* (World Scientific). Available at: [https://books.google.com.pk/books?hl=en&lr=&id=vPq3CgAAQBAJ&oi=fnd&pg=PP9&dq=Glick,+B.+R.,+Holguin,+G.,+Patten,+C.+%26+Penrose,+D.+M.+1999.+Biochemical+and+genetic+mechanisms+used+by+plant+growth+promoting+bacteria,+World+Scientific.&ots=7T3cBYAz5r&sig=5R7x1cvIBN5AVox2Xx\\_847srclY&redir\\_esc=y#v=onepage&q=Glick%2C%20B.%20R.%2C%20Holguin%2C%20G.%2C%20Patten%2C%20C.%20%26%20Penrose%2C%20D.%20M.%201999.%20Biochemical%20and%20genetic%20mechanisms%20used%20by%20plant%20growth%20promoting%20bacteria%2C%20World%20Scientific.&f=false](https://books.google.com.pk/books?hl=en&lr=&id=vPq3CgAAQBAJ&oi=fnd&pg=PP9&dq=Glick,+B.+R.,+Holguin,+G.,+Patten,+C.+%26+Penrose,+D.+M.+1999.+Biochemical+and+genetic+mechanisms+used+by+plant+growth+promoting+bacteria,+World+Scientific.&ots=7T3cBYAz5r&sig=5R7x1cvIBN5AVox2Xx_847srclY&redir_esc=y#v=onepage&q=Glick%2C%20B.%20R.%2C%20Holguin%2C%20G.%2C%20Patten%2C%20C.%20%26%20Penrose%2C%20D.%20M.%201999.%20Biochemical%20and%20genetic%20mechanisms%20used%20by%20plant%20growth%20promoting%20bacteria%2C%20World%20Scientific.&f=false).
- González Candia, P. (2021). *Rizobacterias que promueven el enraizamiento de miniestacas de híbridos de eucalyptus SP. y sus posibles mecanismos de acción*. Available at: <http://repositorio.udec.cl/handle/11594/9362>.
- Gupta, A., Meyer, J. M., and Goel, R. (2002). Development of heavy metal-resistant mutants of phosphate solubilizing pseudomonas sp. NBRI 4014 and their characterization. *Curr. Microbiol.* 45, 323–327. doi: 10.1007/s00284-002-3762-1
- Gupta, A., Rai, V., Bagdwal, N., and Goel, R. (2005). *In situ* characterization of mercury-resistant growth-promoting fluorescent pseudomonads. *Microbiological Res.* 160, 385–388. doi: 10.1016/j.micres.2005.03.002
- Hong, C. E., and Park, J. M. (2016). Endophytic bacteria as biocontrol agents against plant pathogens: current state-of-the-art. *Plant Biotechnol. Rep.* 10, 353–357. doi: 10.1007/s11816-016-0423-6
- Honma, M., and Shimomura, T. (1978). Metabolism of 1-aminocyclopropane-1-carboxylic acid. *Agric. Biol. Chem.* 42, 1825–1831.
- Indiragandhi, P., Anandham, R., Kim, K., Yim, W., Madhaiyan, M., and Sa, T. (2008). Induction of defense responses in tomato against pseudomonas syringae pv. tomato by regulating the stress ethylene level with methylbacterium oryzae CBMB20 containing 1-aminocyclopropane-1-carboxylate deaminase. *World J. Microbiol. Biotechnol.* 24, 1037–1045. doi: 10.1007/s11274-007-9572-7
- Jacob, J., Krishnan, G. V., Thankappan, D., and Amma, D. K. B. N. S. (2020). “Endophytic bacterial strains induced systemic resistance in agriculturally important crop plants,” in *Microbial endophytes* (Elsevier). Available at: <https://www.sciencedirect.com/science/article/pii/B9780128196540000041>.
- Jahanian, A., Chaichi, M., Rezaei, K., Rezayazdi, K., and Khavazi, K. (2012). The effect of plant growth promoting rhizobacteria (PGPR) on germination and primary growth of artichoke (*Cynara scolymus*). *Int. J. Agric. Crop Sci. (IJACS)* 4, 923–929.
- Jha, A. K. (2017). Effect of lime, compost and microbial inoculants on micronutrient removal by mustard and maize in trace metal contaminated soil of Jharkhand. *Curr. Agric. Res. J.* 5, 196. doi: 10.12944/CARJ.5.2.07
- Jonkers, H. M., Ludwig, R., De Wit, R., Pringault, O., Muijzer, G., Niemann, H., et al. (2003). Structural and functional analysis of a microbial mat ecosystem from a unique permanent hypersaline inland lake: ‘La salada de Chiprana’ (NE Spain). *FEMS Microbiol. Ecol.* 44, 175–189. doi: 10.1016/S0168-6496(02)00464-6
- Kalyani, D. C., Patil, P. S., Jadhav, J. P., and Govindwar, S. P. (2008). Biodegradation of reactive textile dye red BLI by an isolated bacterium pseudomonas sp. SUK1. *Bioresource Technol.* 99, 4635–4641. doi: 10.1016/j.biortech.2007.06.058
- Kandel, S., Herschberger, N., Kim, S., and Doty, S. (2015). Diazotrophic endophytes of poplar and willow for growth promotion of rice plants in nitrogen-limited conditions. *Crop Sci.* 55, 1765–1772. doi: 10.2135/cropsci2014.08.0570
- Khalil, A. M. A., Hassan, S. E.-D., Alsharif, S. M., Eid, A. M., Eweis, E. E.-D., Azab, E., et al. (2021). Isolation and characterization of fungal endophytes isolated from medicinal plant *ephedra pachyclada* as plant growth-promoting. *Biomolecules* 11, 140. doi: 10.3390/biom11020140
- Khan, Z., and Doty, S. L. (2009). Characterization of bacterial endophytes of sweet potato plants. *Plant Soil* 322, 197–207. doi: 10.1007/s11104-009-9908-1
- Khare, E., Mishra, J., and Arora, N. K. (2018). Multifaceted interactions between endophytes and plant: developments and prospects. *Front. Microbiol.* 9, 2732. doi: 10.3389/fmicb.2018.02732
- Lata, R. K., Divjot, K., and Nath, Y. A. (2019). Endophytic microbiomes: biodiversity, ecological significance and biotechnological applications. *Res. J. Biotechnol.* 14, 10.
- Latha, P., Karthikeyan, M., and Rajeswari, E. (2019). *Plant Health under biotic Stress*.
- Lawongsa, P., Boonkerd, N., Wongkaew, S., O’gara, F., and Teaumroong, N. (2008). Molecular and phenotypic characterization of potential plant growth-promoting pseudomonas from rice and maize rhizospheres. *World J. Microbiol. Biotechnol.* 24, 1877–1884. doi: 10.1007/s11274-008-9685-7
- Ledermann, R., Schulte, C. C., and Poole, P. S. (2021). How rhizobia adapt to the nodule environment. *J. bacteriology* 203, e00539–e00520. doi: 10.1128/JB.00539-20
- Leopold, A. C. (1964). “Plant growth and development,” in *Plant growth and development*. Available at: <https://www.cabdirect.org/cabdirect/abstract/19670701019?freeview=true>.
- Lindström, K., and Mousavi, S. A. (2020). Effectiveness of nitrogen fixation in rhizobia. *Microbial Biotechnol.* 13, 1314–1335. doi: 10.1111/1751-7915.13517
- Liu, H., Carvalhais, L. C., Crawford, M., Singh, E., Dennis, P. G., Pieterse, C. M., et al. (2017>2552). Inner plant values: diversity, colonization and benefits from endophytic bacteria. *Front. Microbiol.* 8. doi: 10.3389/fmicb.2017.02552
- Liu, W., Hou, J., Wang, Q., Ding, L., and Luo, Y. (2014). Isolation and characterization of plant growth-promoting rhizobacteria and their effects on phytoremediation of petroleum-contaminated saline-alkali soil. *Chemosphere* 117, 303–308. doi: 10.1016/j.chemosphere.2014.07.026
- Lobo, C. B., Tomás, M. S. J., Viruel, E., Ferrero, M. A., and Lucca, M. E. (2019). Development of low-cost formulations of plant growth-promoting bacteria to be used as inoculants in beneficial agricultural technologies. *Microbiological Res.* 219, 12–25. doi: 10.1016/j.micres.2018.10.012
- Lodwig, E., and Poole, P. (2003). Metabolism of rhizobium bacteroids. *Crit. Rev. Plant Sci.* 22, 37–78. doi: 10.1080/713610850
- Lugtenberg, B., and Kamilova, F. (2009). Plant-growth-promoting rhizobacteria. *Annu. Rev. Microbiol.* 63, 541–556. doi: 10.1146/annurev.micro.62.081307.162918
- Luu, M., Monning, H., and Visekruna, A. (2020). Exploring the molecular mechanisms underlying the protective effects of microbial SCFAs on intestinal tolerance and food allergy. *Front. Immunol.* 11. doi: 10.3389/fimmu.2020.01225
- Lynch, J. M., Brimecombe, M. J., and De Leij, F. A. (2001). Rhizosphere. *e LS.* doi: 10.1038/npg.els.0000403
- Maksimov, I., Maksimova, T., Sarvarova, E., Blagova, D., and Popov, V. (2018). Endophytic bacteria as effective agents of new-generation biopesticides. *Appl. Biochem. Microbiol.* 54, 128–140. doi: 10.1134/S0003683818020072
- Mayak, S., Tirosh, T., and Glick, B. (1999). Effect of wild-type and mutant plant growth-promoting rhizobacteria on the rooting of mung bean cuttings. *J. Plant Growth Regul.* 18, 49–53. doi: 10.1007/PL00007047
- Mercado-Blanco, J., and Jj Lugtenberg, B. (2014). Biotechnological applications of bacterial endophytes. *Curr. Biotechnol.* 3, 60–75. doi: 10.2174/22115501113026660038
- Mishra, J., and Arora, N. K. (2016). *Bioformulations: For Sustain. Agric.*
- Moran, R. (1997). The little nitrogen factories. *Biol. Sci. Rev.* 10, 2–6.
- Morgan, J., Bending, G., and White, P. (2005). Biological costs and benefits to plant-microbe interactions in the rhizosphere. *J. Exp. Bot.* 56, 1729–1739. doi: 10.1093/jxb/eri205
- Muthukumar, A., Udhayakumar, R., and Naveenkumar, R. (2017). “Role of bacterial endophytes in plant disease control,” in *Endophytes: crop productivity and protection* (Springer). Available at: [https://link.springer.com/chapter/10.1007/978-3-319-66544-3\\_7](https://link.springer.com/chapter/10.1007/978-3-319-66544-3_7).
- Navas, L. E., Amadio, A. F., Ortiz, E. M., Sauka, D. H., Benintende, G. B., Berretta, M. F., et al. (2017). Complete sequence and organization of pFR260, the bacillus thuringiensis INTA Fr-7-4 plasmid harboring insecticidal genes. *Microbial Physiol.* 27, 43–54. doi: 10.1159/000451056
- Oldroyd, G. E., Murray, J. D., Poole, P. S., and Downie, J. A. (2011). The rules of engagement in the legume-rhizobial symbiosis. *Annu. Rev. Genet.* 45, 119–144. doi: 10.1146/annurev-genet-110410-132549
- Oteino, N., Lally, R. D., Kiwanuka, S., Lloyd, A., Ryan, D., Germaine, K. J., et al. (2015). Plant growth promotion induced by phosphate solubilizing endophytic pseudomonas isolates. *Front. Microbiol.* 6, 745. doi: 10.3389/fmicb.2015.00745
- Ouyabe, M., Kikuno, H., Tanaka, N., Babil, P., and Shiwachi, H. (2019). Endophytic nitrogen-fixing bacteria of water yam (*Dioscorea alata* L.) in relation with fertilization practices. *Trop. Agric. Dev.* 63, 122–130.
- Pandey, P. K., Samanta, R., and Yadav, R. N. S. (2019). Inside the plant: addressing bacterial endophytes in biotic stress alleviation. *Arch. Microbiol.* 201, 415–429. doi: 10.1007/s00203-019-01642-y
- Pandey, P. K., Singh, M. C., Singh, S., Kumar, A., Pathak, M., Shakywar, R., et al. (2017). Inside the plants: endophytic bacteria and their functional attributes for plant growth promotion. *Int. J. Curr. Microbiol. Appl. Sci.* 6, 11–21. doi: 10.20546/ijemas.2017.602.002
- Pedrotti, L., Mueller, M. J., and Waller, F. (2013). Piriformospora indica root colonization triggers local and systemic root responses and inhibits secondary root colonization of distal roots. *PLoS One* 8, e69352. doi: 10.1371/journal.pone.0069352
- Prasad, M., Srinivasan, R., Chaudhary, M., Mahawer, S. K., and Jat, L. K. (2020). “Endophytic bacteria: Role in sustainable agriculture,” in *Microbial endophytes* (Elsevier). Available at: <https://www.sciencedirect.com/science/article/pii/B9780128187340000036>.
- Puri, A., Padda, K. P., and Chanway, C. P. (2017). “Plant growth promotion by endophytic bacteria in nonnative crop hosts,” in *Endophytes: crop productivity and*

protection (Springer). Available at: [https://link.springer.com/chapter/10.1007/978-3-319-66544-3\\_2](https://link.springer.com/chapter/10.1007/978-3-319-66544-3_2).

- Rajkumar, M., Nagendran, R., Lee, K. J., Lee, W. H., and Kim, S. Z. (2006). Influence of plant growth promoting bacteria and Cr6+ on the growth of Indian mustard. *Chemosphere* 62, 741–748. doi: 10.1016/j.chemosphere.2005.04.117
- Rana, K. L., Kour, D., Kaur, T., Devi, R., Yadav, A. N., Yadav, N., et al. (2020a). Endophytic microbes: biodiversity, plant growth-promoting mechanisms and potential applications for agricultural sustainability. *Antonie Van Leeuwenhoek* 113, 1075–1107. doi: 10.1007/s10482-020-01429-y
- Rana, K. L., Kour, D., Kaur, T., Sheikh, I., Yadav, A. N., Kumar, V., et al. (2020b). Endophytic microbes from diverse wheat genotypes and their potential biotechnological applications in plant growth promotion and nutrient uptake. *Proc. Natl. Acad. Sciences India Section B: Biol. Sci.* 90, 969–979. doi: 10.1007/s40011-020-01168-0
- Ratu, S. T. N., Teulet, A., Miwa, H., Masuda, S., Nguyen, H. P., Yasuda, M., et al. (2021). Rhizobia use a pathogenic-like effector to hijack leguminous nodulation signalling. *Sci. Rep.* 11, 1–15. doi: 10.1038/s41598-021-81598-6
- Rekha, P., Lai, W.-A., Arun, A., and Young, C.-C. (2007). Effect of free and encapsulated pseudomonas putida CC-FR2-4 and bacillus subtilis CC-pg104 on plant growth under gnotobiotic conditions. *Bioresource Technol.* 98, 447–451. doi: 10.1016/j.biortech.2006.01.009
- Remans, R., Beebe, S., Blair, M., Manrique, G., Tovar, E., Rao, I., et al. (2008). Physiological and genetic analysis of root responsiveness to auxin-producing plant growth-promoting bacteria in common bean (*Phaseolus vulgaris* L.). *Plant Soil* 302, 149–161. doi: 10.1007/s11104-007-9462-7
- Robinson, B., Russell, C., Hedley, M., and Clothier, B. (2001). Cadmium adsorption by rhizobacteria: implications for new Zealand pastureland. *Agriculture Ecosyst. Environ.* 87, 315–321. doi: 10.1016/S0167-8809(01)00146-3
- Rudúš, I., Sasiak, M., and Kępczyński, J. (2013). Regulation of ethylene biosynthesis at the level of 1-aminocyclopropane-1-carboxylate oxidase (ACO) gene. *Acta Physiologiae Plantarum* 35, 295–307. doi: 10.1007/s11738-012-1096-6
- Ryan, R. P., Germaine, K., Franks, A., Ryan, D. J., and Dowling, D. N. (2008). Bacterial endophytes: recent developments and applications. *FEMS Microbiol. Lett.* 278, 1–9. doi: 10.1111/j.1574-6968.2007.00918.x
- Safronova, V. I., Stepanok, V. V., Engqvist, G. L., Alekseyev, Y. V., and Belimov, A. A. (2006). Root-associated bacteria containing 1-aminocyclopropane-1-carboxylate deaminase improve growth and nutrient uptake by pea genotypes cultivated in cadmium supplemented soil. *Biol. Fertility Soils* 42, 267–272. doi: 10.1007/s00374-005-0024-y
- Sant'anna, F. H., Almeida, L. G., Cecagno, R., Reolon, L. A., Siqueira, F. M., Machado, M. R., et al. (2011). Genomic insights into the versatility of the plant growth-promoting bacterium azospirillum amazonense. *BMC Genomics* 12, 1–14. doi: 10.1186/1471-2164-12-409
- Santos, M. L. D., Berlitz, D. L., Wiest, S. L. F., Schünemann, R., Knaak, N., and Fiuzza, L. M. (2018). Benefits associated with the interaction of endophytic bacteria and plants. *Braz. Arch. Biol. Technol.* 61. doi: 10.1590/1678-4324-2018160431
- Sapak, Z., Meon, S., and Ahmad, Z. A. M. (2008). Effect of endophytic bacteria on growth and suppression of ganoderma infection in oil palm. *Int. J. Agric. Biol.* 10, 127–132.
- Schimel, J., Balsler, T. C., and Wallenstein, M. (2007). Microbial stress-response physiology and its implications for ecosystem function. *Ecology* 88, 1386–1394. doi: 10.1890/06-0219
- Schnitzer, S. A., and Klironomos, J. (2011). Soil microbes regulate ecosystem productivity and maintain species diversity. *Plant Signaling Behav.* 6, 1240–1243. doi: 10.4161/psb.6.8.16455
- Sharma, S., Chandra, D., and Sharma, A. K. (2021). “Rhizosphere plant–microbe interactions under abiotic stress,” in *Rhizosphere biology: Interactions between microbes and plants* (Springer). Available at: [https://link.springer.com/chapter/10.1007/978-981-15-6125-2\\_10](https://link.springer.com/chapter/10.1007/978-981-15-6125-2_10).
- Sharma, S. K., Johri, B. N., Ramesh, A., Joshi, O. P., and Sai Prasad, S. (2011). Selection of plant growth-promoting pseudomonas spp. that enhanced productivity of soybean-wheat cropping system in central India. *J. Microbiol. Biotechnol.* 21, 1127–1142. doi: 10.4014/jmb.1012.12018
- Shen, W., Cevallos-Cevallos, J. M., Nunes Da Rocha, U., Arevalo, H. A., Stansly, P. A., Roberts, P. D., et al. (2013). Relation between plant nutrition, hormones, insecticide applications, bacterial endophytes, and candidatus liberibacter ct values in citrus trees infected with huanglongbing. *Eur. J. Plant Pathol.* 137, 727–742. doi: 10.1007/s10658-013-0283-7
- Singh, J. S. (2015). Microbes play major roles in the ecosystem services. *Climate Change Environ. Sustainability* 3, 163–167.
- Skinner, M., Parker, B. L., and Kim, J. S. (2014). Role of entomopathogenic fungi in integrated pest management. *Integrated Pest Manage.*, 169–191. doi: 10.1016/B978-0-12-398529-3.00011-7
- Suslow, T., and Schroth, M. (1982). Role of deleterious rhizobacteria as minor pathogens in reducing crop growth. *Phytopathology* 72, 111–115. doi: 10.1094/Phyto-72-111
- Tank, N., and Saraf, M. (2010). Salinity-resistant plant growth promoting rhizobacteria ameliorates sodium chloride stress on tomato plants. *J. Plant Interact.* 5, 51–58. doi: 10.1080/17429140903125848
- Teixeira, L. C., Yergeau, E., Balieiro, F. C., Piccolo, M. C., Peixoto, R. S., Greer, C. W., et al. (2013). Plant and bird presence strongly influences the microbial communities in soils of admiralty bay, maritime Antarctica. *PLoS One* 8, e66109. doi: 10.1371/journal.pone.0066109
- Tewari, S., Shrivastava, V. L., Hariprasad, P., and Sharma, S. (2019). “Harnessing endophytes as biocontrol agents,” in *Plant health under biotic stress* (Springer). Available at: [https://link.springer.com/chapter/10.1007/978-981-13-6040-4\\_10](https://link.springer.com/chapter/10.1007/978-981-13-6040-4_10).
- Thakuria, D., Talukdar, N., Goswami, C., Hazarika, S., Boro, R., and Khan, M. (2004). Characterization and screening of bacteria from rhizosphere of rice grown in acidic soils of Assam. *Curr. Sci.*, 978–985.
- Timper, P., Kone, D., Yin, J., Ji, P., and Gardener, B. B. M. (2009). Evaluation of an antibiotic-producing strain of pseudomonas fluorescens for suppression of plant-parasitic nematodes. *J. Nematol.* 41, 234.
- Tiwari, R. K., Lal, M. K., Naga, K. C., Kumar, R., Chourasia, K. N., Subhash, S., et al. (2020). Emerging roles of melatonin in mitigating abiotic and biotic stresses of horticultural crops. *Scientia Hort.* 272, 109592. doi: 10.1016/j.scienta.2020.109592
- Vandana, U. K., Rajkumari, J., Singha, L. P., Satish, L., Alavilli, H., Sudheer, P. D., et al. (2021). The endophytic microbiome as a hotspot of synergistic interactions, with prospects of plant growth promotion. *Biology* 10, 101. doi: 10.3390/biology10020101
- Van Rhijn, P., and Vanderleyden, J. (1995). The rhizobium-plant symbiosis. *Microbiological Rev.* 59, 124–142. doi: 10.1128/mr.59.1.124-142.1995
- Vardi, R., Mittermeier, J. C., and Roll, U. (2021). Combining culturomic sources to uncover trends in popularity and seasonal interest in plants. *Conserv. Biol.* 35, 460–471. doi: 10.1111/cobi.13705
- Vishwakarma, K., Kumar, N., Shandilya, C., and Varma, A. (2021). “Unravelling the role of endophytes in micronutrient uptake and enhanced crop productivity,” in *Symbiotic soil microorganisms* (Springer). Available at: [https://link.springer.com/chapter/10.1007/978-981-13-6040-4\\_10](https://link.springer.com/chapter/10.1007/978-981-13-6040-4_10).
- Wani, P. A., Khan, M. S., and Zaidi, A. (2007). Effect of metal tolerant plant growth promoting bradyrhizobium sp.(vigna) on growth, symbiosis, seed yield and metal uptake by greengram plants. *Chemosphere* 70, 36–45. doi: 10.1016/j.chemosphere.2007.07.028
- Wani, P. A., Khan, M., and Zaidi, A. (2008). Effect of metal-tolerant plant growth-promoting rhizobium on the performance of pea grown in metal-amended soil. *Arch. Environ. Contamination Toxicol.* 55, 33–42. doi: 10.1007/s00244-007-9097-y
- Wood, T. E., Cavaleri, M. A., and Reed, S. C. (2012). Tropical forest carbon balance in a warmer world: A critical review spanning microbial-to ecosystem-scale processes. *Biol. Rev.* 87, 912–927. doi: 10.1111/j.1469-185X.2012.00232.x
- Wu, W., Jin, Y., Bai, F., and Jin, S. (2015). “Pseudomonas aeruginosa,” in *Molecular medical microbiology* (Elsevier). Available at: <https://www.sciencedirect.com/science/article/pii/B978012397169200041X>.
- Wu, C. H., Wood, T. K., Mulchandani, A., and Chen, W. (2006). Engineering plant-microbe symbiosis for rhizoremediation of heavy metals. *Appl. Environ. Microbiol.* 72, 1129–1134. doi: 10.1128/AEM.72.2.1129-1134.2006
- Yan, L., Zhu, J., Zhao, X., Shi, J., Jiang, C., and Shao, D. (2019). Beneficial effects of endophytic fungi colonization on plants. *Appl. Microbiol. Biotechnol.* 103, 3327–3340. doi: 10.1007/s00253-019-09713-2