

REVIEW

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REVIEW

Harnessing endophytic bacteria as plant growth promoters and biocontrol agents against pests and phytopathogens

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Bacterial endophytes are ubiquitously present and colonize the inner tissues of the plants, and found almost every plant of world. The diversity of endophytic bacteria depends on several factors like nature of the host plant and environment conditions. Some endophytic bacteria have a wide range of host. Plant beneficial endophytic bacteria flourish internal tissues of host plants and have been shown to promote plant growth by assisting plants in developing resistance and absorbing nutrients from the soil as well as to develop strategies for environmental clean-up. They are beneficial to host plants directly by improving nutrient uptake or by producing some phytohormones like Indole acetic acid and indirectly by targeting different pests and pathogens by production of antibiotics and hydrolytic enzymes. Endophytes have “priming” effects when pathogens attack, which makes the plant defend itself more swiftly and successfully. Endophytic bacteria would therefore be effective biological control agents. On the path to creating a biological agent that is commercially viable, there are, however, obstacles to overcome, such as the relatively small number of candidate microorganisms being tested, the selection of microbes based on laboratory test results that do not always replicate in field conditions, the exclusion of microbes that respond to commercial development selection criteria, compatibility with pesticides, quality control, regulations.

Keywords: PGPR, phytohormone, rhizosphere, phytoremediation, inducing plant resistance, biocontrol

INTRODUCTION

Plants can establish partnerships with other components of the ecosystem for the sake of survival in their natural habitat. One of the most significant organisms that associate positively with plants is the microorganism (Santoyo *et al.*, 2016, Adeleke and Babalola, 2020). In nature, microorganisms are ubiquitous and present in nearly all ecosystems. A wide range of microorganisms can be found in plants. The host plant contains these bacteria both inside and outside. A class of bacteria known as “plant beneficial bacteria” offers a variety of advantages to their host plants, including support in enduring biotic and abiotic stresses that impede plant development (Miliute *et al.*, 2015). According to Compant *et al.* (2010), bacteria that are not found in host plants are called epiphytic bacteria, which

are found in the leafy or rhizospheric areas, or in the roots of plants in the soil. Endophytic bacteria are those that survive and grow inside their host plant (Strobel *et al.*, 2004, Hardoim *et al.*, 2008). The term “endophyte” literally means “in the plant,” since endo means “inside” and phyton means “plant.” Various kinds of microorganisms, including bacteria, fungus, and archaea, colonize the inside of plant tissues and undergo all or part of their life cycles without exhibiting any symptoms (Stone *et al.*, 2000).

Plants have the ability to “choose” their microbiome in order to introduce beneficial bacteria to stimulate the growth of host plants (Hardoim *et al.* 2008, Marasco *et al.*, 2012, Rashid *et al.* 2012). Most endophytic microbes originate in the phyllosphere or rhizosphere (Aloo *et al.*, 2019). Some rhizosphere bacteria enter the internal tissue directly from the outer root zone to become endophytes (Nwachukwu *et al.*, 2021).

They employ hydrolytic enzymes (cellulases, pectinases, and proteinases) that break down the host cell wall and enable them to pass through roots in order to aid in their entry into plants through wounds or naturally occurring apertures (Jha, 2023). Chemotactic signals are crucial for colonizing the root surface. The endophytic bacteria then climb and become established in different plant tissues (Sturz and Nowak 2000). All these bacterial groups have a lot in common that encourages plant growth (Compant *et al.*, 2010). They can also help plants thrive in drought-prone areas and limited nutrient-rich soils (Banik *et al.*, 2019, Dubey *et al.* 2021). They have also the ability to choose their microbiomes to stimulate the plant growth. Some of the endophytic bacteria genera such as *Pseudomonas brenneri*, *Ewingella americana*, *Pantoea agglomerans*, *Bacillus cereus*, and *Pseudomonas otitidis* have been reported (Babalola *et al.*, 2021; Dubey *et al.*, 2021; Rana *et al.*, 2021).

DIVERSITY OF ENDOPHYTIC BACTERIA

Endophytic bacteria have been found and reported from a wide range of plant hosts, including agronomic crops, prairie grasslands, wild and perennial plants, as well as plants from severe settings (Afzal *et al.* 2019). There is a significant species richness of plant-associated endophytic bacterial variety, as demonstrated by both culturable and molecular research. Hardoim *et al.* (2015) examined the variety of endophytic bacteria using an assessment of 16s rRNA genes deposited in the International Nucleotide Sequence Database Collaboration (INSDC) repository up until 2014, all endophytic bacteria were classified into 21 taxa. They found that just four bacterial phyla—Proteobacteria (54%), Actinobacteria (20%), Firmicutes (16%), and Bacteroidetes (6%), which together accounted for more than 96% of the total endophytic bacterial population—contributed to the great diversity of endophytic bacteria. The most common genera in the proteobacterial community were *Pseudomonas*, *Enterobacter*, *Pantoea*, *Stenotrophomonas*, *Acinetobacter*, and *Serratia*. Some common endophytic bacterial genera isolated from agronomic plants have been enlisted in Table 1.

A plant's type of endophytic diversity is influenced by a number of factors. A plant's endophytic diversity can be greatly influenced by environmental factors and the host plant in addition to the capacity of bacteria to colonize plants as endophytes. A host plant's endophytic bacterial species might vary depending on its age, genotype, geographic location, and even the tissue under study. Liu *et al.* (2017) assessed the various root endophytic bacterial communities and found that Proteobacteria frequently dominated the plant endorhizosphere (with a relative abundance of 50%), followed by Actinobacteria (10%), Firmicutes (10%), and Bacteroidetes (10%). Furthermore, lesser proportions of bacterial phyla from Verrucomicrobia, Nitrospirae, Armatimonadetes, Chloroflexi, and Cyanobacteria are also frequently recorded. Moreover, a plant's endophytic diversity can be influenced by its host plant growth stages; bacterial variety is higher in plant stages with greater nutrition availability (Shi *et al.*, 2014). Furthermore, climate conditions may affect endophytic invaders of plants (Penuelas *et al.*, 2012). A plant's host species has a significant influence on the composition of its endophytic community (Ding and Melcher, 2016). Endophytic diversity varies significantly among plant species growing in the same soil. As Granér *et al.* (2003) showed for four distinct cultivars of *Brassica napus* with varying endophytic bacterial populations, different cultivars of a plant species grown in the same soil may differ in endophytic diversity. Thus, the kind of endophytic bacteria colonizing a host plant is greatly influenced by the species of the host plant. More intriguingly, a plant's endophytic community may be influenced by the kind of soil it is grown in. Rashid *et al.* (2012) isolated several endophytic bacterial species using one tomato cultivar in fifteen distinct agricultural soils. These findings imply that the diverse character of soil samples and the presence of many endophytes are connected. Diversity of endophytic bacteria isolated from some wild plants have been presented in Table 2.

Rincón and Neelam (2021) examined the endophytic bacterial diversity of common fruits and vegetables and came to the conclusion that the genus *Actinobacteria*, *Arthrobacter*, *Bacillus*,

Table 1: Some common endophytic bacterial genera isolated from agronomic plants

Plant	Endophytic bacterial genera
Wheat (<i>Triticum aestivum</i>)	<i>Bacillus</i> , <i>Burkholderia</i> , <i>Flavobacterium</i> , <i>Klebsiella</i> , <i>Microbispora</i> , <i>Micrococcus</i> , <i>Micromonospora</i> , <i>Mycobacterium</i> , <i>Nacardiodes</i> , <i>Rathayibacter</i> , <i>Streptomyces</i>
Banana (<i>Musa</i> sp)	<i>Azospirillum</i> , <i>Burkholderia</i> , <i>Citrobacter</i> , <i>Herbaspirillum</i> , <i>Klebsiella</i>
Radish (<i>Raphanus sativus</i>)	<i>Proteobacteria</i> , <i>Salmonella</i>
Tomato (<i>Solanum lycopersicum</i>)	<i>Brevibacillus</i> , <i>Escherichia</i> , <i>Pseudomonas</i> , <i>Salmonella</i>
Pineapple (<i>Ananas comosus</i>)	<i>Azospirillum</i> , <i>Burkholderia</i>
Maize (<i>Zea mays</i>)	<i>Achromobacter</i> , <i>Agrobacterium</i> , <i>Arthrobacter</i> , <i>Bacillus</i> , <i>Burkholderia</i> , <i>Corynebacterium</i> , <i>Curtobacterium</i> , <i>Enterobacter</i> , <i>Erwinia</i> , <i>Herbaspirillum</i> , <i>Microbacterium</i> , <i>Micrococcus</i> , <i>Paenibacillus</i> , <i>Phyllobacterium</i> , <i>Pseudomonas</i> , <i>Rhizobium</i> , <i>Serratia</i>
Sugar cane (<i>Saccharum officinarum</i>)	<i>Acetobacter</i> , <i>Gluconacetobacter</i> , <i>Herbaspirillum</i> , <i>Klebsiella</i>
Cotton (<i>Gossypium herbaceum</i>)	<i>Bacillus</i> , <i>Burkholderia</i> , <i>Clavibacter</i> , <i>Erwinia</i> , <i>Phyllobacterium</i> , <i>Pseudomonas</i>
Soybean (<i>Glycine max</i>)	<i>Erwinia</i> , <i>Agrobacterium</i> , <i>Pseudomonas</i> , <i>Klebsiella</i> , <i>Enterobacter</i> , <i>Pantoea</i> , <i>Bacillus</i>
Alfalfa (<i>Medicago sativa</i>)	<i>Bacillus</i> , <i>Erwinia</i> , <i>Microbacterium</i> , <i>Pseudomonas</i> , <i>Salmonella</i>
Clover (<i>Trifolium</i> sp)	<i>Agrobacterium</i> , <i>Bacillus</i> , <i>Methylobacterium</i> , <i>Pseudomonas</i> , <i>Rhizobium</i>
Canola (<i>Brassica napus</i>)	<i>Acidovorax</i> , <i>Agrobacterium</i> , <i>Aureobacterium</i> , <i>Bacillus</i> , <i>Chryseobacterium</i> , <i>Cytophaga</i> , <i>Flavobacterium</i> , <i>Micrococcus</i> , <i>Pseudomonas</i> , <i>Rathayibacter</i> , <i>Acidovorax</i> , <i>Acinetobacter</i> , <i>Actinomyces</i> , <i>Agrobacterium</i> , <i>Alcaligenes</i> , <i>Arthrobacter</i> , <i>Bacillus</i> , <i>Capnocytophaga</i> , <i>Chryseobacterium</i> , <i>Comamonas</i> , <i>Corynebacterium</i> , <i>Curtobacterium</i> , <i>Enterobacter</i> , <i>Erwinia</i> , <i>Klebsiella</i> , <i>Leuconostoc</i> , <i>Methylobacterium</i> , <i>Micrococcus</i> , <i>Paenibacillus</i> , <i>Pantoea</i> , <i>Pseudomonas</i> , <i>Psychrobacter</i> , <i>Serratia</i> , <i>Shewanella</i> , <i>Sphingomonas</i> , <i>Stenotrophomonas</i> , <i>Streptomyces</i> , <i>Vibrio</i> , <i>Xanthomonas</i>
Potato (<i>Solanum tuberosum</i>)	<i>Comamonas</i> , <i>Enterobacter</i> , <i>Klebsiella</i> , <i>Moraxella</i> , <i>Pantoea</i> , <i>Pseudomonas</i> , <i>Rahnella</i> , <i>Rhodococcus</i> , <i>Staphylococcus</i> , <i>Xanthomonas</i>
Grapevine (<i>Vitis vinifera</i>)	<i>Arthrobacter</i> , <i>Bacillus</i> , <i>Curtobacterium</i> , <i>Micrococcus</i> , <i>Pseudomonas</i> , <i>Serratia</i>
Black pepper (<i>Piper nigrum</i>)	
Sugar beet (<i>Beta vulgaris</i>)	<i>Bacillus</i> sp., <i>Erwinia</i> sp., <i>Pseudomonas</i> sp., <i>Corynebacterium</i> sp., <i>Lactobacillus</i> sp., <i>Xanthomonas</i> sp.
Walnut (<i>Juglans regia</i>)	<i>Bacillus subtilis</i> HB1310
Lebanon oak (<i>Quercus libani</i>)	<i>B. firmus</i> , <i>Pseudomonas protegens</i> , <i>Stenotrophomonas maltophilia</i>
Rice (<i>Oryza sativa</i>)	<i>Agrobacterium</i> , <i>Azoarcus</i> , <i>Azorhizobium</i> , <i>Azospirillum</i> , <i>Bacillus</i> , <i>Bradyrhizobium</i> , <i>Burkholderia</i> , <i>Chromobacterium</i> , <i>Enterobacter</i> , <i>Herbaspirillum</i> , <i>Leionella</i> , <i>Klebsiella</i> , <i>Micrococcus</i> , <i>Pantoea</i> , <i>Pseudomonas</i> , <i>Rhizobium</i> , <i>Serratia</i> , <i>Stenotrophomonas</i>
Cucumber (<i>Cucumis sativus</i>)	<i>Agrobacterium</i> , <i>Bacillus</i> , <i>Burkholderia</i> , <i>Chryseobacterium</i> , <i>Clavibacter</i> , <i>Curtobacterium</i> , <i>Enterobacter</i> , <i>Micrococcus</i> , <i>Paenibacillus</i> , <i>Phyllobacterium</i> , <i>Pseudomonas</i> , <i>Serratia</i> , <i>Stenotrophomonas</i>
Red clover (<i>Trifolium pratense</i>)	<i>Acidovorax</i> , <i>Agrobacterium</i> , <i>Arthrobacter</i> , <i>Bacillus</i> , <i>Bordetella</i> , <i>Cellulomonas</i> , <i>Comamonas</i> , <i>Curtobacterium</i> , <i>Escherichia</i> , <i>Klebsiella</i> , <i>Methylobacterium</i> , <i>Micrococcus</i> , <i>Pantoea</i> , <i>Pasteurella</i> , <i>Phyllobacterium</i> , <i>Pseudomonas</i> , <i>Psychrobacter</i> , <i>Rhizobium</i> , <i>Serratia</i> , <i>Sphingomonas</i> , <i>Variovorax</i> , <i>Xanthomonas</i>
Carrot (<i>Daucus carota</i>)	<i>Agrobacterium</i> , <i>Bacillus</i> , <i>Klebsiella</i> , <i>Pseudomonas</i> , <i>Rhizobium</i> , <i>Salmonella</i> , <i>Staphylococcus</i>
Common bean (<i>Phaseolus vulgaris</i>)	<i>Acinetobacter radioresistens</i> , <i>Acinetobacter</i> sp., <i>Agromyces mediolanus</i> , <i>Agromyces</i> sp., <i>B. amyloliquefaciens</i> , <i>B. bataviensis</i> , <i>B. muralis</i> , <i>B. subtilis</i> , <i>B. thuringiensis</i> , <i>B. niacini</i> , <i>Bacillus</i> sp., <i>Brevibacillus agri</i> , <i>Brevundimonas vesicularis</i> , <i>Delftia tsuruhatensis</i> , <i>Dietzia cinnamomea</i> , <i>Enterobacter asburiae</i> , <i>E. hormaechei</i> , <i>Frigoribacterium faeni</i> , <i>Kocuria palustris</i> , <i>Lysinibacillus sphaericus</i> , <i>Microbacterium foliorum</i> , <i>M. phyllosphaerae</i> , <i>M. testaceum</i> , <i>Microbacterium</i> sp., <i>Methylobacterium populi</i> , <i>Micrococcus luteus</i> , <i>Paenibacillus cineris</i> , <i>P. lautus</i> , <i>Paenibacillus</i> sp., <i>Pseudomonas aeruginosa</i> , <i>Rhizobium larrymoorei</i> , <i>Rhodococcus erythropolis</i> , <i>Staphylococcus caprae</i> , <i>S. epidermidis</i> , <i>S. kloosii</i> , <i>S. sanguinis</i> , <i>S. warneri</i> , <i>S. saprophyticus</i> , <i>Staphylococcus</i> sp., <i>Sphingobacterium multivorum</i> , <i>Sphingomonas dokdonensis</i> , <i>Sporosarcina aquimarina</i> , <i>Sporosarcina</i> sp., <i>Stenotrophomonas maltophilia</i> , <i>Stenotrophomonas</i> sp.

(Source: Afzal, et al 2019; Yadav and Yadav, 2019.).

Table 2: Diversity of endophytic bacteria isolated from some wild plants

Plant	Endophytic bacteria	References
<i>Calystegia soldanella</i>	<i>Acinetobacter</i> <i>Arthrobacter</i> <i>Chryseobacterium</i> <i>Curtobacterium</i> <i>Enterobacter</i> <i>Microbacterium</i> <i>Pantoea</i> <i>Pedobacter</i> <i>Pseudomonas</i> <i>Stenotrophomonas</i>	Park <i>et al.</i> , (2005)
<i>Elymus mollis</i>	<i>Acinetobacter</i> <i>Arthrobacter</i> <i>Chryseobacterium</i> <i>Enterobacter</i> <i>Exiguobacterium</i> <i>Flavobacterium</i> <i>Klebsiella</i> <i>Pedobacter</i> <i>Pseudomonas</i> <i>Stenotrophomonas</i>	Park <i>et al.</i> , (2005)
<i>Alyssum bertolonii</i>	<i>Arthrobacter</i> <i>Bacillus</i> <i>Curtobacterium</i> <i>Leifsonia</i> <i>Microbacterium</i> <i>Paenibacillus</i> <i>Pseudomonas</i> <i>Staphylococcus</i>	Barzanti <i>et al.</i> , (2007)
<i>Commelina communis</i>	<i>Arthrobacter</i> <i>Arthrobacter</i> <i>Bacillus</i> <i>Bacillus pumilus</i> <i>Herbaspirillum</i> <i>Microbacterium</i> <i>Sphingomonas</i>	Sun <i>et al.</i> , (2010)
<i>Elsholtzia splendens</i>	<i>Xanthomonas translucens</i> <i>Acinetobacter calcoaceticus</i> <i>Acinetobacter junii</i> <i>Bacillus</i> <i>Bacillus firmus</i> <i>Bacillus megaterium</i> <i>Burkholderia</i> <i>Exiguobacterium aurantiacum</i> <i>Micrococcus luteus</i> <i>Moraxella</i> <i>Paracoccus</i> <i>Serratia marcescens</i>	Sun <i>et al.</i> , (2010)
<i>Pinus contorta</i>	<i>Bacillus</i> <i>Brevibacillus</i> <i>Brevundimonas</i> <i>Cellulomonas</i> <i>Kocuria</i> <i>Paenibacillus</i> <i>Pseudomonas</i>	Bal <i>et al.</i> , (2012)
<i>Alnus firma</i> <i>Thuja plicata</i>	<i>Bacillus</i> sp. <i>Arthrobacter</i> <i>Bacillus</i> <i>Paenibacillus</i>	Shin <i>et al.</i> , (2012) Bal <i>et al.</i> , (2012)

<i>Polygonum pubescens</i>	<i>Pseudomonas</i>	
<i>Pinus sylvestris</i>	<i>Streptovercillium</i>	
<i>Sedum alfredii</i>	<i>Rahnella</i> sp. JN6	He <i>et al.</i> , (2013)
	<i>Bacillus thuringiensis</i>	Babu <i>et al.</i> , (2013)
	<i>Burkholderia</i>	Zhang <i>et al.</i> , (2013)
	<i>Sphingomonas</i>	
	<i>Variovorax</i>	
<i>Noccaea caerulescens</i>	<i>Agreia</i>	Visioli <i>et al.</i> , (2014)
	<i>Arthrobater</i>	
	<i>Bacillus</i>	
	<i>Kocuria</i>	
	<i>Microbacterium</i>	
	<i>Sthenotrophomonas</i>	
	<i>Variovorax</i>	
<i>Cressa cretica</i> ,	<i>Acinetobacter</i>	Arora <i>et al.</i> , (2014)
<i>Salicornia brachiata</i> ,	<i>Arthrobacter</i>	
<i>Suaeda nudiflora</i> ,	<i>Bacillus</i>	
<i>Sphaeranthus indicus</i>	<i>Kocuria</i>	
	<i>Oceanobacillus</i>	
	<i>Paenibacillus</i>	
	<i>Pseudomonas</i>	
	<i>Virgibacillus</i>	
<i>Cannabis sativa</i>	<i>Acinetobacter gyllenbergii</i>	Afzal <i>et al.</i> , (2015)
	<i>Acinetobacter nosocomialis</i>	
	<i>Acinetobacter parvus</i>	
	<i>Acinetobacter pittii</i>	
	<i>Bacillus anthracis</i>	
	<i>Chryseobacterium</i> sp.	
	<i>Enterobacter asburiae</i>	
	<i>Enterococcus casseliflavus</i>	
	<i>Nocardioides albus</i>	
	<i>Nocardioides kongjuensis</i>	
	<i>Pantoea vagans</i>	
	<i>Planomicrobium chinense</i>	
	<i>Pseudomonas taiwanensis</i>	
	<i>Rhizobium radiobacter</i>	
	<i>Streptomyces eurocidicus</i>	
	<i>Xanthomonas gardneri</i>	
<i>Halimione portulacoides</i>	<i>Altererythrobacter</i>	Fidalgo <i>et al.</i> , (2016)
	<i>Hoeflea</i>	
	<i>Labrenzia</i>	
	<i>Marinilactibacillus</i>	
	<i>Microbacterium</i>	
	<i>Salinicola</i>	
	<i>Vibrio</i>	

Bacteroidetes, *Firmicutes*, *Methylobacterium*, *Massilia*, *Proteobacteria*, *Pseudomonas*, *Pantoea* and *Sphingomonas* comprised the most commonly isolated bacterial phyla from fruits and vegetables. Wu *et al.* (2021) discovered a total of eleven orders and eighty-eight genera of endophytic bacteria and highlighted the interactions between bacterial endophytes and medicinal plants from a variety of families. They also found that the orders Bacillales, Enterobacterales, and Pseudomonadales

contained the majority of the encountered bacterial members, accounting for 72.62% of associations. Additionally, making up 58.92% of the entire bacterial community, representatives of the genera *Bacillus*, *Pantoea*, and *Pseudomonas* were the most prevalent. However, a significant number of bacterial endophytes have been identified, evaluated for their capacity to promote plant growth and health, and effectively employed to enhance agronomic features in both conventional and biotic stress scenarios.

FUNCTIONS OF ENDOPHYTIC BACTERIA

Plants can adapt to a variety of biotic (herbivory, pests, and diseases) and abiotic stress factors provided by mutualistic microbes like endophytic bacteria. These benefits include increased resistance or tolerance to drought and water stress, high temperatures and salinities, as well as adaptation under conditions where nutrients are scarce. Soil deficits or nutrient limits can stunt growth and make a plant more vulnerable to a variety of biotic and abiotic challenges. Nitrogen and phosphorus are two examples of essential nutrients that are frequently regarded as the most restrictive requirements for maintaining healthy plant growth and productivity. Phosphorus and nitrogen are frequently found in trace amounts or in non-bioavailable forms. Research has shown that when plants are faced with a lack of nutrients, they attract endophytic bacteria, which helps the plants thrive (Afzal *et al.* 2019). Endophytes benefit plants in two ways: directly (through phytohormone synthesis) and indirectly (by phytoremediation). Nitrogen fixation, modulation of plant hormone levels (auxin, cytokinin, ethylene, and gibberellin), phosphate, iron, and potassium solubilization, synthesis of secondary metabolites, antibiotic activities against various plant pathogens, and enhancing plant responses to abiotic stresses are all ways that endophytic bacteria help plants grow (Rajini *et al.*, 2020). Endophytic bacteria are known to have superior nitrogen-fixing capabilities than their rhizosphere-dwelling counterparts by habitually supplying the fixed nitrogen directly to the host, as demonstrated in sugarcane (Cavalcante *et al.* 2007), rice (Kumar *et al.* 2020), wheat (Afridi *et al.* 2019), and common beans (Lastochkina *et al.* 2021).

Because of their beneficial qualities, phosphate-solubilizing bacteria such *Pseudomonas*, *Burkholderia*, *Paraburkholderia*, *Novosphingobium*, and *Ochrobactrum* have been demonstrated to raise the biomass output of Chinese fir seedlings (Chen *et al.*, 2021). Plant growth promoting endophytic bacteria (PGPEB) involves direct mechanisms such nitrogen fixation and the manufacture of phytohormones like auxin, cytokinin, gibberellin, and abscisic acid (Maheshwari *et al.*, 2019). In addition, they can

increase mineral solubilization (zinc, iron, phosphorus, sulfur, and potassium) and increase survivability under stressful conditions like drought and soil salinity by employing the enzyme 1-aminocyclopropane-1-carboxylate (ACC) deaminase (Dubey *et al.*, 2021). By triggering plant reactions or producing secondary compounds that shield plants against certain phytopathogens, endophytic bacteria might indirectly encourage plant growth (Santoyo *et al.*, 2012). One such indirect technique is called induced systemic resistance (ISR), and it can be carried out by means of specific plant response pathways, including the jasmonic acid (JA) route (Asghari *et al.*, 2020). Endophytic bacteria can trigger defensive reactions in plants by means of various signaling pathways (Montejano-Ramrez *et al.*, 2020). Different factors affecting diversity of endophytic bacteria in host plant, mechanisms of colonization and plant growth promotion have been presented in Fig 1.

MECHANISMS OF PLANT GROWTH PROMOTION

Endophytic bacteria have been shown to directly benefit host plants by assisting them in getting nutrients and enhancing plant growth by controlling hormones associated to growth (Ma *et al.*, 2016). This can help plants grow more effectively in both normal and stressful conditions. Direct and indirect mechanisms used by endophyte to enhance plant growth has been illustrated in Fig.2.

Nutrient acquisition

The macro and micronutrient components required for plant growth are typically insufficiently present in soils. Endophytic bacteria have the ability to help their host plants acquire greater concentrations of nutrients that are limited to plants, such as nitrogen, iron, and phosphorus (Glick, 2012). According to Gupta *et al.* (2013), in nitrogen-limited environments, endophytic bacteria that fix nitrogen can both boost nitrogen fixation and its accumulation in plants.

Nitrogen availability

Endophytic bacteria can boost the availability of nitrogen for their host plants. By exhibiting

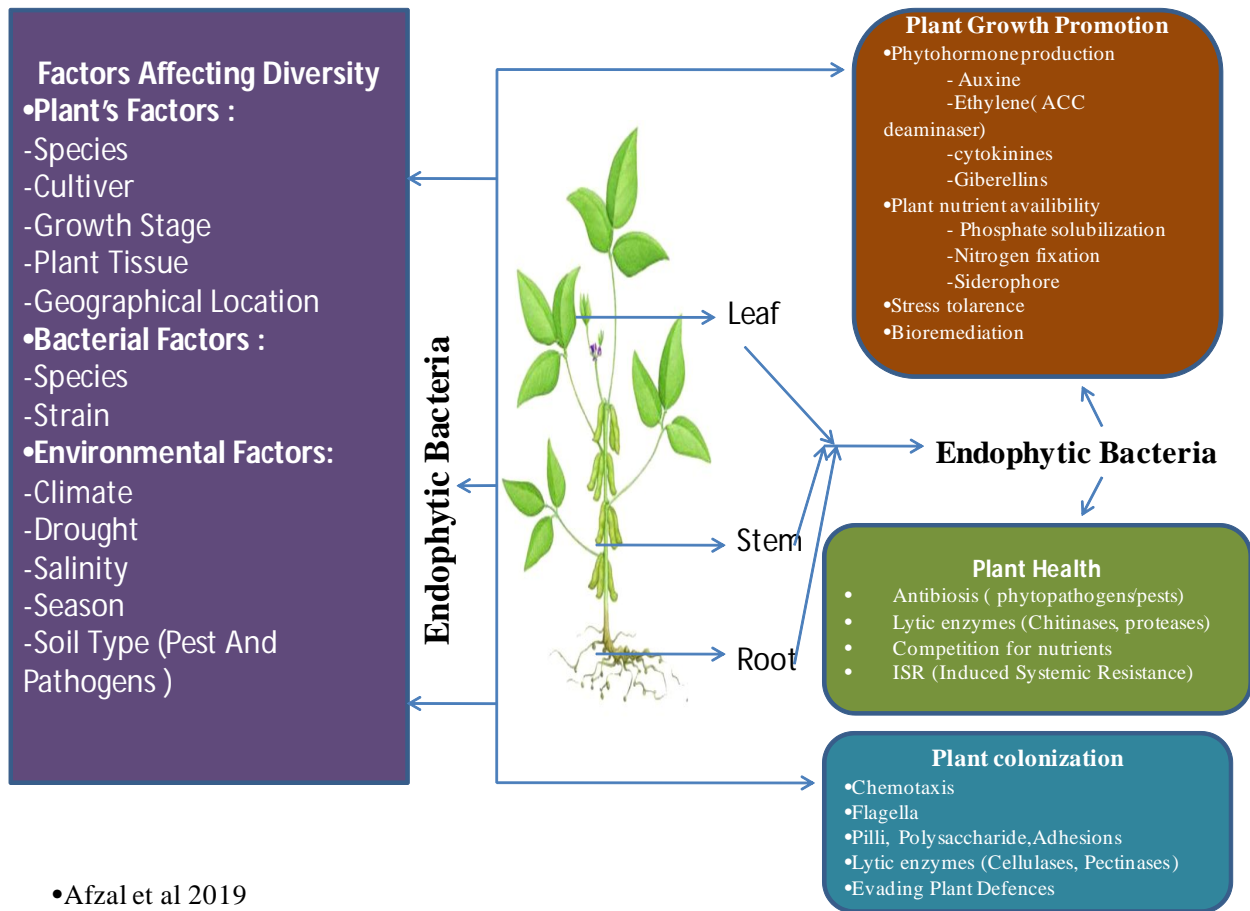


Fig. 1: Different factors affecting diversity of endophytic bacteria in host plant, mechanisms of colonization and plant growth promotion

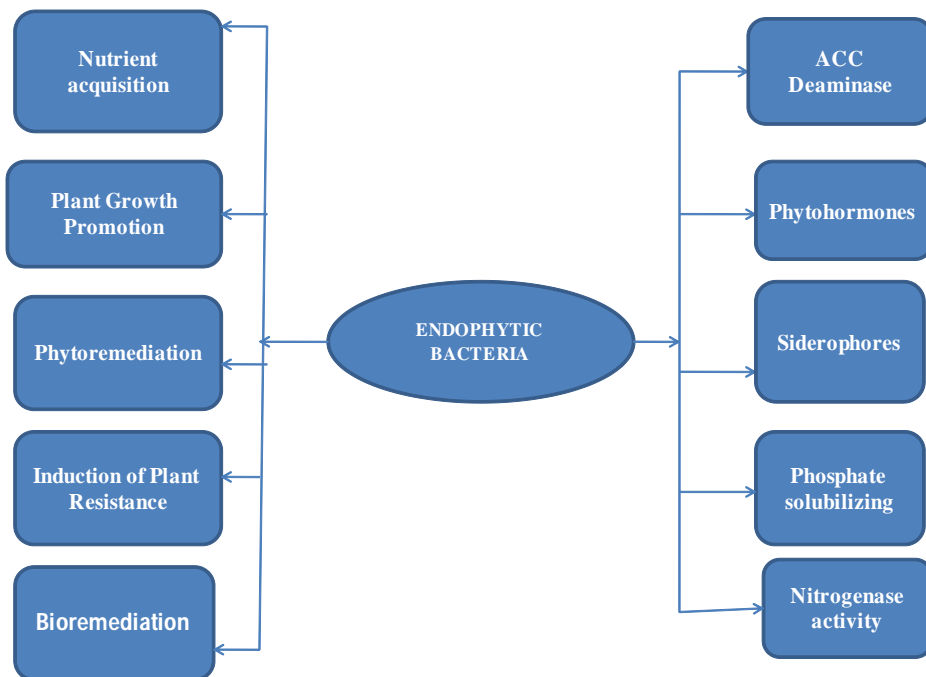


Fig. 2: Direct and indirect mechanisms used by endophyte to enhance plant growth

nitrogenase activity, these bacteria can supply fixed atmospheric nitrogen to their host plants (Montanez *et al.*, 2012). According to Gupta *et al.* (2013), in nitrogen-limited environments, endophytic bacteria that fix nitrogen can both boost nitrogen fixation and its accumulation in plants. *Paenibacillus* strain P22, a nitrogen-fixing endophyte identified in poplar trees, was reported to contribute to the host plant's total nitrogen pool (Scherling *et al.*, 2009). Madhaiyan *et al.* (2013) reported a Nitrogen-fixing endophyte, *Enterobacter* sp. R4-368, that colonised root and stem tissues and enhanced early plant growth and seed productivity in both sterilised and non-sterilised soils.

Phosphate solubilization

Phosphorus solubilization is among endophytic bacteria's most defining traits. By solubilizing precipitated phosphates by processes such as acidification, chelation, ion exchange, and organic acid production, endophytic bacteria can increase the availability of phosphorus for plants (Nautiyal *et al.*, 2000). By secreting acid phosphatase, which can mineralize organic phosphorus, they can also increase the amount of phosphorus available in the soil (Van Der Heijden *et al.*, 2008). One endophytic bacterium from the Enterobacteriaceae family, *Pantoea* sp., for instance, has the ability to solubilize phosphate (Sulbaran *et al.* 2009). Many plants, including canola, have grown more quickly as a result of their capacity to solubilize inorganic phosphate (Rashid *et al.* 2012). Numerous plants, including canola (Rashid *et al.* 2012), tomatoes (Amaresan *et al.* 2012), maize (Pereira and Castro 2014), rice (Walitang *et al.* 2017) and others, have grown more rapidly as a result of their capacity to solubilize inorganic phosphate. In addition to causing changes in the expression of genes linked to gibberellin signaling, endophytes also cause increased expression of genes related to nutrition uptake. Wang *et al.* (2021) observed that the root exudates of endophyte-infected plants showed changed levels of organic acids, amino acids, flavonoids, and phenolic acids.

Siderophores production

Plants can receive iron from bound siderophores by ligand exchange or root-based chelate

breakdown. Endophytic bacteria produce siderophores, which are iron chelating molecules capable of binding insoluble ferric ions (Rajkumar *et al.*, 2009; Ma *et al.*, 2016). Because free iron ions are rare in plant tissues, endophytes that produce siderophores are common (Sessitsch *et al.* 2004). In addition to increasing the bioavailability of metals other than iron, bacterial siderophores hasten plant development (Rajkumar *et al.* 2010).

Phytohormone production

By releasing phytohormones that control growth, endophytic bacteria can assist host plants in acquiring nutrients and metabolic processes. By producing indole acetic acid (Khan *et al.* 2014; Patel and Patel 2014), ethylene (Long *et al.* 2010; Kang *et al.* 2012; Straub *et al.* 2013), gibberellic acid (Khan *et al.* 2014), and auxins (Dutta *et al.* 2014), endophytes boost the yield of legume crops.

IAA production

Indole acetic acid (IAA) was created by endophytic bacteria that were isolated from terrestrial orchids, according to Tsavkelova *et al.* (2007). They found that the culture supernatant of the bacteria significantly increased the length and number of developing roots in kidney beans, boosting root production and suggesting a potential role for bacterial IAA in root growth

Production of cytokinins and gibberellins

Numerous investigations have shown that gibberellins and cytokinins can be produced by a wide variety of plant-beneficial endophytic bacteria. Using the cucumber cotyledon greening bioassay, Bhore *et al.* (2010) detected cytokinin-like substances in the broth extracts of two endophytic bacteria that were isolated from *Gynura procumbens* and identified as *Psuedomonas resinovorans* and *Paenibacillus polymaxa*.

Control of ethylene

By producing aminocyclopropane-1-carboxylic acid (ACC) deaminase, an enzyme that

Table 3: Endophytic bacteria and their plant-growth promoting traits

Endophyte species	Host plant	Plant growth promoting traits	Reference
<i>Azoarcus</i> sp. BH72	Rice	Nitrogen fixation	Krause <i>et al.</i> , (2006)
<i>Klebsiella pneumoniae</i> 342	Maize, Wheat	Nitrogen fixation	Fouts <i>et al.</i> , (2008)
<i>Pseudomonas stutzeri</i> A1501	Rice	Nitrogen fixation	Yan <i>et al.</i> , (2008)
<i>Stenotrophomonas maltophilia</i> R5513	Poplar	IAA synthesis, ACC deaminase	Taghavi <i>et al.</i> , (2009)
<i>Gluconacetobacter diazotrophicus</i> Pa15	Sugarcane, rice, coffee, tea	Nitrogen fixation, auxin synthesis	Bertalan <i>et al.</i> , (2009)
<i>Serratia proteamaculans</i> 568	Soybean	IAA synthesis, ACC deaminase, acetoin and 2,3 butanediol synthesis	Taghavi <i>et al.</i> , (2009)
<i>Enterobacter</i> sp. 638	Poplar	Siderophore, IAA, acetoin and 2,3-butanediol synthesis	Taghavi <i>et al.</i> , (2009)
<i>Pseudomonas putida</i> W619	Poplar	IAA synthesis, ACC deaminase	Taghavi <i>et al.</i> , (2009)
<i>Burkholderia phytofirmans</i> PsJN	Potato, tomato, maize, barley, onion, canola, grapevine	IAA synthesis, ACC deaminase	Weilharter <i>et al.</i> , (2011)
<i>Azospirillum lipoferum</i> 4B	Rice, maize, wheat	Nitrogen fixation, phytohormone secretion	Wisniewski-Dyé <i>et al.</i> , (2011)
<i>Burkholderia</i> spp. KJ006	Rice	ACC deaminase, nif gene cluster, antifungal action (indirect PGP)	Kwak <i>et al.</i> , (2012)

hydrolyzes ACC, a precursor to the plant hormone ethylene, endophytic bacteria can control the amount of ethylene in the host plant. There have been reports of ACC deaminase activity in a variety of plant growth-promoting endophytic bacteria (Zhang *et al.*, 2011; Nikolic *et al.*, 2011; Rashid *et al.*, 2012)

BENEFICIAL ACTIVITIES OF ENDOPHYTIC BACTERIA

Bioremediation

The biological elimination or degradation of pollutants in the environment is known as bioremediation. Plants release a number of toxic metabolites that are not neutralized. Such metabolites need to be bioremediated with “associative bacteria” since they have the potential to impact the ecology of the surrounding area. In several ways, endophytes support plant bioremediation. Plant tissues harbor endophytes that mitigate heavy metal stress (Zhang *et al.*, 2012). and break down toxic substances and their byproducts (Han *et al.* 2011). Endophytes eliminate greenhouse gasses from the atmosphere and stop pests from growing outside of plant tissues (Azevedo *et al.*, 2000; Stpniewska and Kuniar, 2013).

Phytoremediation

Phytoremediation is the process of eliminating pollutants from the environment and soil using

plants. Compared to current engineering solutions, phytoremediation appears to be a less expensive concept in agriculture. The scientific community around the world is paying close attention to this more “green” and practical approach. Endophytes provide plants with the breakdown pathways they need for improved biodegradation and decreased phytotoxicity (Weyens *et al.* 2009). Endophytic bacteria can aid the host plants in phytoremediation by fixing nitrogen, solubilizing minerals, producing phytohormones, generating siderophores, converting nutrients, and ACC (Germaine *et al.*, 2009; Rajkumar *et al.*, 2009; Stpniewska and Kuniar 2013).

In contrast to those that are not symbiotic. By changing how metals are transported and accumulate in plants, endophytic bacteria can lower the toxicity of metals in plants. By boosting biomass and photosynthetic pigment content in *Solanum nigrum* leaves, the endophytic bacterium *Serratia nematodiphila* LRE07 mitigated the effects of Cd (Wan *et al.*, 2012). On sweet sorghum, an endophyte called *Bacillus* sp. SLS18 produced results that were comparable (Luo *et al.*, 2012). Numerous endobacteria are said to aid in the photoextraction of heavy metals (Rajkumar *et al.* 2009). Because genetically modified endophyte strains have so much potential for phytoremediation, their use in

scientific research is growing. For instance, it has been shown that bioengineered *Pseudomonas putida* VM1441 (pNAH7) shields the host plant from the phytotoxic effects of naphthalene (Germaine *et al.* 2009). Another instance genetically modified *Burkholderia cepacia* L.S.2.4 was able to decomposing toluene in plant tissues (Barac *et al.*, 2004).

Biological control and suppression of plant diseases

The endophytic community plays a crucial role in the suppression of disease, because alterations in the endophytic community are linked to disease resistance, (Pavlo *et al.* 2011). The advancement of technology and the ensuing increase in biological knowledge has led to the development of endophytic BCAs as a new tool for managing plant diseases and pests. When contrasting endophytic BCAs with their traditional biocontrol counterparts, there are a few clear benefits. While many phylloplane and rhizosphere microorganisms are susceptible to UV radiation, temperature fluctuations, and moisture variations, endophytes are not. The characteristic that sets an endophytic BCA apart from other BCAs is its interaction with the target pest or pathogen. Before attempting to either feed on the plant or enter and colonize it, the majority of target pests, diseases, and BCA come into contact with the plant in some capacity. But the endophytic BCA has little to no direct contact with the target pest or pathogen.

Endophytic bacteria produce a variety of metabolites that improve host tolerance to various stressors, making them beneficial to plants and able to act as promising biological agents in controlling many plant diseases. Many researchers have reported the biocontrol role of endophytes against various diseases. Main mechanisms by which the endophyte suppresses certain diseases are (a) compete with viruses for a niche and nutrients, (b) production of different lytic enzymes and antimicrobial products (c) to promote system resistance in host plants. Instead of simple structures toxic, plant endophyte metabolites incorporate various bioactive substances that strengthen the host's immunity to pathogens. Therefore using one or

more natural active ingredients as a lead ingredient has a promising mechanism for future green pesticide (Xia *et al.*, 2022). There are, however, a number of obstacles that must be overcome, including the following: (i) many endophytes have never been enlarged and are unknown; (ii) field testing has not always produced consistent results regarding the effects of endophyte biocontrol; (iii) the mechanisms underlying plant-endophyte interactions are not well understood; (iv) there are no databases available for endophyte and its metabolites; and (v) fermentation produces low amounts of metabolites Biocontrol is a natural method of shielding our plants from different phytopathogens (Rybakova *et al.* 2016). Plant viruses are impacted by endophytes either directly or indirectly through changes to the internal ecology (Gao *et al.*, 2010). Similar to rhizosphere bacteria, endophytes lessen phytopathogen resistance through producing antimicrobial compounds and competing with nutrients in the same natural habitat. To reduce phytopathogens in the rhizosphere, certain endophytes transfer antibiotics into the endosphere (Castillo *et al.*, 2003; Franco *et al.*, 2007; Bara *et al.*, 2013). Numerous endophytes produce a range of antibiotics, including coronamycin, ecomycins, kakadumycins, munumbicins, pseudomycins, and xiamycins (Castillo *et al.* 2003; Ezra *et al.*, 2004; Christina *et al.*, 2013). A range of endophytes are resistant to distinct fungal infections. It has been demonstrated that endophytes lessen *Fusarium* wilt in plants, namely in capsicum (Sundaramoorthy *et al.*, 2012), tomato and banana (Chen *et al.*, 2011).

It was discovered that the root endophyte *Pseudomonas fluorescens* PICF7 prevented pathogenic *Verticillium dahlia* from colonizing olive tissues (Prieto *et al.*, 2009). Similar to this, the endophyte *Pseudomonas putida* P9, which was isolated from the potato plant, decreased the disease caused by *Phytophthora infestans* (Andreote *et al.*, 2009). Citrus canker-causing pathogen *Xanthomonas citri* subsp. *citri* (Xcc) has also been demonstrated to be effectively biocontrolled by endophytes (Brunings and Gabriel, 2003). All varieties of commercial oranges are affected by the disease in numerous

Table 4: Endophytic bacteria antagonistic against phytopathogenic fungi

Endophytic bacterial isolates	Host Plant	Pathogenic fungi	References
<i>P. aeruginosa</i> 7 NSK2	Tomato	<i>Botrytis cinerea</i>	Audenaert <i>et al.</i> , (2002)
<i>P. fluorescens</i> EP1	Sugarcane	<i>Colletotrichum falcatum</i>	Senthil <i>et al.</i> , (2003)
<i>Bacillus</i> and <i>Pseudomonas</i>	Wheat	<i>F. graminearum</i>	Nourozian <i>et al.</i> , (2006)
<i>Burkholderia phytofirmans</i> Ps JN	Grapevine	<i>Botrytis cinerea</i>	Compant <i>et al.</i> , (2008)
<i>B. subtilis</i>	Wheat	<i>Gaeamanomyces graminis tritici</i>	Liu <i>et al.</i> , (2009)
<i>B. pumilus</i> SE34	Pea	<i>F. oxysporum</i> f.sp. <i>pisi</i>	Chaudhary <i>et al.</i> , (2009)
<i>Bacillus</i> spp , <i>Pseudomonas</i> spp	Peanut	<i>Sclerotinia sclerotiorum</i> , <i>S. minor</i> , <i>S. rolfsii</i> and <i>Fusarium solani</i>	Tonelli <i>et al.</i> , (2010)
<i>Pseudomonas</i> and <i>Burkholderia</i> <i>P. fluorescens</i> CHA0	Banana	<i>F. oxysporum</i> f.sp. <i>cubense</i>	Fishal <i>et al.</i> , (2010)
<i>Bacillus</i> spp., <i>Pseudomonas</i> spp.	Tomato	<i>Pythium ultimum</i> and <i>F. oxysporum</i> f. sp. <i>pisi</i>	Ardebili <i>et al.</i> , (2011)
	Soybean	<i>R. solani</i> , <i>F. oxysporum</i> . <i>S. rolfsii</i> , <i>C.truncatum</i> , <i>A. alternata</i> , <i>Macrophomina phaseolira</i>	Dalal and Kulkarni (2013)

citrus and tropical citrus regions worldwide (Sharma and Sharma, 2009). Some of the endophytic bacteria having antagonistic activities towards phytopathogenic fungi have been enlisted in Table-4.

The production of diverse antipest proteins, such as lectins for insect control, including recombinant endophytic strains that readily reside within numerous plants, is the most recent technical intervention for managing a variety of plant pests. The endophytic bacteria, which also include *Bacillus subtilis*, which encodes insecticidal lectin, and *Enterobacter* sp. and *Chaetomium globosum* YY-11 gene, which was found from rape plants, produce the *Pinellia ternate* agglutinin (PtA) gene. Using the recombinant endophytic bacterial strain *Enterobacter cloacae*, a bio-insecticide against the white-backed plant hopper *Sogatella furcifera* has been produced (Zhang *et al.* 2011). Copper nanoparticles using the endophyte *Streptomyces capillispiralis* Ca-1, *Culex pipiens* (the mosquito) and *Musca domestica* (the housefly) were inhibited (Hassan *et al.* 2018)

INDUCTION OF RESISTANCE IN PLANT BY ENDOPHYTIC BACTERIA

Endophytic bacteria indirectly promote host plant growth by inhibiting the growth of phytopathogens (Table-5) and pests. Through induced systematic resistance (ISR), endophytic bacteria boost plant tolerance to pathogens (Zamioudis and Pieterse 2012). Endophytic bacteria-induced ISR can protect the host from fungal, bacterial, and viral pathogens (Alvin *et al.*, 2014). Initially, endophytic bacteria interact with their hosts to trigger an immune response, which is similar to the reaction caused by illnesses. Using the endophytic bacterium *Pseudomonas fluorescens* 89B-61, the endophytic organisms then colonize hosts while evading defense responses, as demonstrated in *Bacillus* and *Pseudomonas* (Kloepper and Ryu 2006). This was the first report of ISR induction against cucumber anthracnose in cucumber plants. Salicylic acid (SA), jasmonic acid (JA), and ethylene (ET) mediated pathways, which are usually a network of interconnected signalling pathways are involved in ISR induction, and can

Table 5: Induction of resistance in plants by endophytic bacteria

Endophytic Strain	Host Plant	pathogen	References
<i>Pseudomonas aeruginosa</i> H40, <i>Stenotrophomonas maltophilia</i> H8, <i>Bacillus subtilis</i> H18	<i>Pisum sativum</i> , <i>Brassica oleracea</i> , <i>Capsicum annuum</i>	<i>Rhizoctonia solani</i>	Selim <i>et al.</i> , (2017)
<i>Bacillus</i> sp. 2P2, <i>Klebsiella pneumoniae</i> HR1, <i>Pseudomonas viridiflava</i>	<i>Solanum lycopersicum</i> , <i>Vigna mungo</i> , <i>Brassica napus</i>	<i>Sclerotium rolfsii</i> , <i>Macrophomina phaseolina</i> , <i>Xanthomonas campestris</i> , <i>Sclerotinia sclerotiorum</i> , <i>Leptosphaeria maculans</i>	Sahu <i>et al.</i> , (2019) Dey <i>et al.</i> , (2019) Romero <i>et al.</i> , (2019)
<i>Paecilomyces variotii</i> SJ1, <i>Streptomyces albidoflavus</i> OsiLf-2, <i>Burkholderia gladioli</i> E39CS3	<i>Nicotiana tabacum</i> , <i>Oryza sativa</i> , <i>Crocus sativus</i>	Virus, <i>Magnaporthe oryzae</i> , <i>Fusarium oxysporum</i>	Peng <i>et al.</i> , (2020) Gao <i>et al.</i> , (2020) Ahmad <i>et al.</i> , (2021)

be used by endophytic bacteria to induce ISR (Pieterse *et al.*, 2012). Several investigations have demonstrated that ISR is brought on by chemicals associated to bacteria, including lipopolysaccharides, salicylic acid, siderophores, N-acyl-homoserine lactones, and volatiles like acetoin. They have the ability to create chemicals that antagonize different phytopathogens. Endophytic bacteria can target both bacterial and fungal infections (Lodewyckx *et al.*, 2002). The most typically reported genera for antibacterial activity against phytopathogens are *Actinobacteria*, *Bacillus*, *Enterobacter*, *Paenibacillus*, *Pseudomonas*, and *Serratia* (Aktuganov *et al.*, 2008; Liu *et al.*, 2010). Endophytic bacteria have been demonstrated to efficiently suppress fungal disease in plants such as black pepper, potato, and wheat (Aravind *et al.*, 2009; Coombs *et al.*, 2004; Sessitsch *et al.*, 2004). The antimicrobial activities against fungi are result from the synthesis of different fungal cell-wall targeting enzymes like chitinase, proteases and glucanases (Zarei *et al.*, 2011; Zhang *et al.*, 2012).

CONCLUSION

The capacity of many bacterial endophytes to promote plant development directly or indirectly through biocontrol agents has drawn a lot of interest. Although there may be significant similarities between the processes of plant growth promotion in rhizospheric and endophyte bacteria, the majority of research has focused on rhizosphere bacteria since it is believed that the mechanism is the same in endophytes.

Conversely, the rhizosphere and the interior plant tissues are not the same thing. We still don't fully grasp what changes a rhizospheric bacteria into a plant endophyte. The identification of numerous endophyte genes sheds light on the bacteria's endophytic life. Due to their distinct microenvironment in the endosphere, endophytes have a limited understanding of function currently known. There is little research on endophytes specifically, and little is known about their metabolic processes (Ali *et al.*, 2014). The potential applications of plant-associated beneficial endophytic bacteria as biopesticides and fertilizers is considerable. Even though a large number of these bacteria have been identified and they may infect a variety of animals, in the field they rarely yield reliable findings. Our ignorance of the intricate dynamics governing plant-endophyte interactions is one reason for this. Finally, there is a good probability of finding unique and fascinating bacteria in unidentified wild plants because endophytic diversity has not received enough attention. Due in part to the special endophytes they contain, wild plants are more likely to withstand harsh conditions and overcome biotic and abiotic obstacles. Finding these uncommon and intriguing bacterial endophytes with a wide range of plant-beneficial characteristics is important. Researchers may be able to alter bacterial endophytes to help them fulfill their promise in the future to promote plant growth and development by developing a deeper understanding of the mechanisms behind endophyte function.

On the path to creating a biological agent that is commercially viable, there are, however,

obstacles to overcome, such as the relatively small number of candidate microorganisms being tested, the selection of microbes based on laboratory test results that do not always replicate in field conditions, the exclusion of microbes that respond to commercial development selection criteria, compatibility with pesticides, quality control, regulations, etc. Ecologically significant traits that are required for wild survival during a target functional period have gotten very little, if any, attention. Improved understanding of the process of endophytic bacterial colonization and subsequent interactions with plants is necessary if endophytic bacteria and the microbiome are to be used in practical ways to boost agricultural output. How a plant takes in endophytes and keeps them inside is still a mystery to us. To solve issues, one must understand the relationships between the environment, plants, endophytes, and diseases. Given the current status of agrochemical-induced plant diseases, the use of endophytes to control them will be extremely beneficial to agriculture in the future.

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