The Pharma Innovation Journal 2023; 12(3): 139-151

www.ThePharmaJournal.com

The Pharma Innovation

ISSN (E): 2277-7695
ISSN (P): 2349-8242
NAAS Rating: 5.23
TPI 2023; 12(3): 139-151

www.thepharmajournal.com
Received: 02-12-2022
Accepted: 06-02-2023

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Endophytes: Role and applications in sustainable agriculture

Neerja Rana, Akanksha Rathore, Arti Ghabru and Shivani Chauhan

DOI: https://doi.org/10.22271/tpi.2023.v12.i3b.19528

Abstract
Intensive agriculture which depends on unmanageable processes of agrochemical inputs is environmentally dangerous. The development of these practices to fulfil needs isn't always economically viable. Different practical aspects must be taken into consideration to satisfy the global meals protection undertaking. The plant microbiome has been related to stepped forwards plant productiveness for decades. Rhizospheric bacteria were studied for their capability to promote crop growth and control pathogens. In recent years studies on endophytes have accelerated as a likely alternative to rhizobacteria, for the improvement of Microbial inoculants able to changing some agrochemicals and reducing the environmental impact of agronomic management of crops. This review summarizes the maximum vital characteristics and traits of endophytic microorganism. The presence of rhizomes in soil favours the boom of numerous microbial groups in its rhizosphere. Presently endophytic microorganisms are gaining attention through researchers because of their functionality to synthesizing novel bioactive compounds which might be useful in ailment management of phytopathogens, and some of these compounds are critical in novel drug discovery. For sustainable agriculture, a number of the bacterial and fungal endophytes can be used as plant and soil inoculants to enhance yield and productiveness of plants. Using endophytes as biofertilizers is beneficial and has no unfavorable consequences on the weather, or texture and productiveness of soils, unlike chemical fertilizers. These endophytes may be act as essential biofertilizers, biocontrol agent and help plants to cope up with biotic and abiotic stresses.

Keywords: Endophyte, rhizome, plant growth promoting, biocontrol, biofertilizer, pressure, sustainable agriculture

Introduction

Vegetation is accompanying with numerous groups of microorganisms. Some of the microorganisms that be inherent inside the plant without causing any harm to the host are endophytes. These microbes are inimitable in their diversifications to the precise chemical environment of the host plant (Jasmin *et al*., 2014b; Kumar *et al*., 2016b) [143, 75]. More than 3,00,000 anticipated plant species exist on the earth and every character has been mentioned as host of 1 or more than one endophyte (Theantana *et al*., 2009) [126]. Endophytes are ubiquitous amongst terrestrial flowers, but only 6–7% of the endophyte's existence has been recognized (Zhang *et al*. 2018; Ling *et al*. 2014; Saini *et al*. 2015; Hawksworth 2001) [140, 85, 108, 55].

Therefore, it's very important to explore the potential of micro-organism in sustainable agriculture or as a useful resource for novel bioactive compounds. The diversity and composition of endophytic bacterial communities rely on the supply, age, form of plant, season of sampling and also the surroundings. The variety of bacterial groups inside the endosphere of root is comparatively less than the rhizosphere or bulk soil (Liu *et al*., 2014; Bulgarelli *et al*. 2013) [86, 26]. In plant system, the concentration of endophytic microorganism is greater at the root area than at shoot tissue (Zinniel *et al*. 2002; Theantana *et al*. 2009; Rosenblueth and Martínez-Romero 2006; Degrassi & Carpentieri-Pipolo 2020; Baron & Rigobelo 2022) [142, 126, 106, 28, 18]. Due to its significant effect on various crops, it is considered one of the best agricultural compounds used in the agricultural sector.

Plant Colonization with Endophyte

Endophytic bacteria are commonly present in every plant including seeds, ovules, rhizomes, tubers, roots and stems and leaves (Alibrandi *et al*. 2018; Compant *et al*. 2011; Jasim *et al*. 2014a; Kumar *et al*. 2016a; Gaiero *et al*. 2013; Sturz *et al*. 1997) [4, 34, 63, 74, 47, 123].

Generally, microbes enter into plant tissues via natural opening like stomata, lenticels, wounds, germinating radicles, etc. The entry of endophytes inside the plant tissues is at any point of their life cycle. Most of the reports regarding entry of endophytes inside the host plant are through wounds like broken trichomes, emergence site of root branches, or root hairs.

The importance of lateral root formation for bacterial entry is underlined by the observation that *Bacillus polymyxa* was recovered from inside pine seedlings only after lateral roots had developed (Sturz *et al*. 1999) [122]. Wounds in plant tissues open entry for the endophytic microbes and might be formed by biotic factors like attack of nematodes and insects or abiotic factors like tillage, high temperature fluctuations, grafting, and root pruning (Quadt-Hallmann *et al*. 1997) [102]. The leakage of plant exudates from the wounded tissues allowed favorable conditions for infection and colonization of approaching microbes. However, endophytes can penetrate the plant cells actively as shown in Fig 1. This hypothesis is supported by the presence of cellulytic and pectinolytic enzymes produced by numerous endophytic bacteria like *Azoarcus* sp. (Hurek *et al*. 1994) [59], *Azospirillum irakense* and *Pseudomonas fluorescens* (Benhamou *et al*. 1996; Quadt-Hallmann *et al*. 1997) [21, 102]. Cell membrane degradation by the bacteria secreted enzymes, observed when microbes colonized the roots. This activity can't be seen after colonization of microbes into the intercellular spaces of the foundation cortex. These suggest the induction of cellulase and pectinase enzyme by the endophyte for the penetration into the host plant microbial diversity within the rhizomes of various plant species A rhizome may be a modified subterranean stem diageotropic in nature develop from axillary buds at the lowermost nodes of the erect leafy shoot of the plant (Gizmawy *et al*. 1985) [49].

Endophyte distribution within plants depends on the flexibility to colonize and also the allocation of plant resources. Root endophytes often colonize and penetrate epidermis at sites of lateral root emergence, beneath the basis hair zone, and in root crevices. These colonizers are able to establish populations both intra- and intracellularly (Vurukonda *et al*., 2018; Suarez Moreno *et al*., 2019) [130, 124]. After initial colonization, some endophytes can migrate to other areas of the plant by entering vascular tissues and spreading systemically (Sandhya *et al*., 2017) [109]. Mahlangu *et al*., (2018) [90] reported the bacterial endophytes from surface-sterilized leaves of *Pellaea calomelanos*, a common fern.

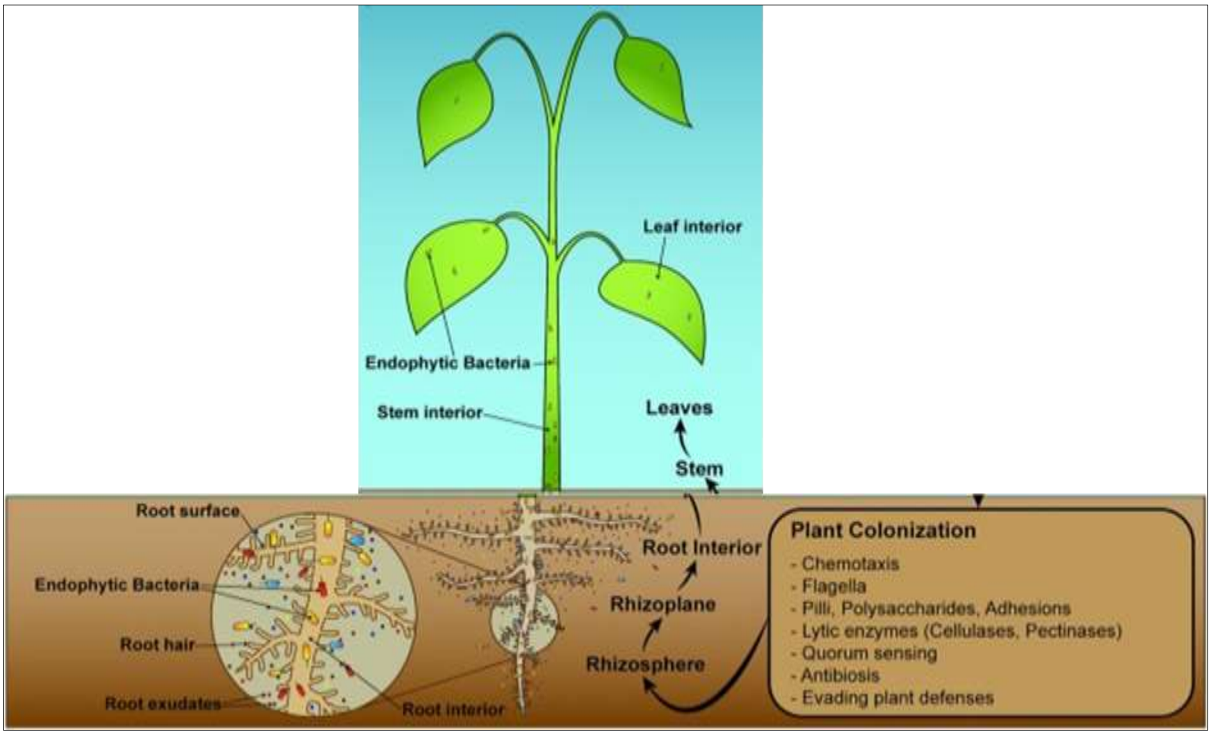

Fig 1: Mode of entry of endophytic bacteria in different parts of plant

Diversity of endophytic rhizomes in the Different Plant Species

The rhizomes of the plant developed from axillary buds, grow horizontally, and retain the power of upward growth of latest shoots (Jang *et al*. 2006) [62]. The rhizome also acts as storehouse of starches, proteins, and other nutrients, these nutrients used during the dormant period of the plants (Jang *et al*. 2006) [62]. Many authors reported the economic and pharmaceutical importance of rhizome or rhizome-derived or stored compounds (Hu *et al*. 2011; Koo *et al*. 2013) [57, 69]. For plant competitiveness and growth, underground stems or rhizomes of plant are of great importance (Hu *et al*. 2011) [57]. Rhizome remains in soil that favors growth of varied microbial communities, i.e., fungi and bacteria in its rhizosphere. Some microbes enter inside the tissues of rhizome and survive as endophyte.

Number of physiological conditions, rhizome tissues is also colonized by diverse microbial communities and impart important role in normal functioning further as maintaining biotic or abiotic stress of the plant (Nongalleima *et al*. 2013; Barik *et al*. 2010; Xu *et al*. 2014) [95, 17, 136]. The variation in microbial communities largely depends upon host plant species, genotypes, plant developmental stages, host tissue types, growth locations, and growth seasons (Theantana *et al*.

2009; Shubin *et al*. 2014: de Almeida Lopes *et al*. 2016; Liu *et al*. 2014) [126, 112, 37, 86]. More than 129 bacterial genera are reported within which, 54 genera have also been found as endophytic bacteria (Seo *et al*. 2010) [110]. *Pseudomonas, Bacillus, Azotobacter, Enterobacter*, etc. are some common bacterial endophytes reported by different authors (Dias *et al*. 2009; Zhao *et al*. 2010; Liu *et al*. 2014; Jasim *et al*. 2014a, b; Kumar *et al*. 2016a, b; Singh *et al*. 2013) [39, 141, 86, 63, 65, 74, 75, 115].

Zingiber officinale (ginger) a common Indian spice and also used as home remedies. The rhizomes of ginger are reported as a potent antimicrobial, antioxidant, and anti-inflammatory and even have cancer-preventive activities because of array of chemical constituents (Aggarwal and Shishodia 2004; Jasim *et al*. 2014a: Anisha *et al*., 2018) [1, 63, 8]. Zhang *et al*. (2018) [140] reported 57 endophytic bacteria from ginger rhizome and classified them into genera *Ochrobactrum, Acinetobacter, Stenotrophomonas, Enterobacter, Serratia, Pseudomonas, Bacillus, Agrobacterium*, and *Tetrathiobacter* which showed rhizome ginger **a** storehouse or host of very diverse community of bacteria. Numerous authors also reported species from *Pseudomonas, Stenotrophomonas, Enterobacter, Serratia, Bacillus*, and *Agrobacterium* as endophytic strains from ginger (Koo *et al*., 2013; Chen *et al*. 2014; Jasim *et al*. 2014b; Anisha *et al*., 2018) [69, 29, 65, 8].

Turmeric (*Curcuma longa* L.) also belonging to the Zingiberaceae family, widely used as a spice and as a remedy extensively applied within traditional folk medicines (Amalraj *et al*. 2017; Kumar *et al*. 2016a, b) [74, 75]. The rhizome of turmeric contains natural phenolic compounds like curcuminoids, sesquiterpenoids, volatile oils and sesquiterpenes are broadly employed in the pharmacology for the treatment of varied human diseases (Ohshiro *et al*. 1990; Rao *et al*. 1995; Srimal 1997; Mukerjee and Vishwanatha 2009; Panahi *et al*. 2014) [96, 104, 120, 93, 99]. The rhizome of the turmeric plant is present within the soil and supports number of microbial communities and interactions. Many authors reported different bacterial and fungal strains as endophytes within the rhizome of turmeric are like *Paenibacillus* sp. that are reported to provide indole-3-acetic acid (Aswathy *et al*. 2013) [13], while *Klebsiella* sp. is documented for plant growth promotion activity (Anisha *et al*. 2013) [9] related to turmeric rhizome. Kumar *et al*. (2016a) [74] reported six endophytic bacterial strains *Bacillus cereus*, *B. thuringiensis*, *Bacillus* sp., *B. pumilus*, *Pseudomonas putida*, and *Clavibacter michiganensis* from the rhizome of turmeric. a number of the fungal endophytes have also been reported from the turmeric plant. Bustanussalam *et al*. (2015) [27] reported 44 fungi, while Jalgaonwala and Mahajan (2014) [61] reported *Eurotium* sp. as fungal endophytes. Krishnapura *et al*. (2016) [71] isolated endophytes from the rhizomes of 5 different medicinal plants that belong to ginger family, and a complete of fifty endophytes (14 bacteria, 22 actinomycetes, and 14 fungi) were isolated from *Curcuma longa*, ginger, *Curcuma amada*, *Hedychium coronarium*, and galangal species. Details about the rhizome-associated endophytes with the various host plants are elucidated in Table 1.

Dutta *et al*., (2016) [41] studied the accumulation of secondary metabolites in response to antioxidant activity of turmeric rhizomes co-inoculated with mycorrhizal fungi & rhizobacteria.

Table 1: Some crop-associated bacterial endophytes and their plant-growth promoting traits

Host plant	Endophyte species	Plant growth- promoting traits	Reference
Potato	*Bacillus* spp.	ACC deaminase activity, phosphate solubilization, siderophore production	Gururani *et al*., 2013 [54]
	Streptomyces spp.	PGP and biological control	Vurukonda *et al*., 2018 [130]
	Pseudomonas putida and *Serratia plymuthica*	Production of the antibiotic 2,4-diacetylphloroglucinol (*Pseudomonas*) and antagonism (Serratia	Berg *et al*., 2005 [22]
	Burkholderia phytofirmans PsJN	ACC deaminase activity and production of indole acetic acid (IAA)	Weilharter *et al*., 2011 [133]
Rice	*Streptomyces* sp. strain A20	Production of three antibiotics: streptothricins D, E and F; production of siderophores and IAA, and P solubilization.	Suarez Moreno *et al*., 2019 [124]
	Bacillus sp.	multiple PGP and antagonistic activity	Etesami & Alikhani 2017 [44]
	Azoarcus sp. BH72	N-fixation	Krause *et al*., 2006 [70]
	Azospirillum sp.	Production of IAA and ACC deaminase	Wisniewski-Dye *et al*., 2011 [134]
	Pseudomonas stutzeri	N-fixation	Yan *et al*., 2008 [138]
	Burkholderia sp.,	Antifungal activity	Kwak MJ *et al*., 2012 [80]
	Kosakonia oryzae	Siderophore production, auxin biosynthesis and N-fixation	Meng *et al*., 2015 [91]
	Herbaspirillum, Pseudomonas, Pantoea, Methylobacterium, Kosakonia, Burkholderia, Rhodococcus, Ralstonia, Brevibacillus, Bacillus	IAA, N-fixing, P solubilization, ACC deaminase, etc.	Chi *et al*., 2005 [31] Bertani *et al*., 2016 [23]
Soybean	*B. subtilis* and *B. thuringiensis*	Production of siderophores, IAA synthesis and ACC-deaminase	Bai *et al*., 2003 [15]
	Pseudomonas, Ralstonia, Enterobacter, Pantoea and *Acinetobacter*	Antifungal activity; phytases; N-fixation; phosphate solubilization	Kuklinsky-Sohral *et al*., 2004 [72]

	Bacillus spp.	Cellulase, pectinase and motility	Hung & Annapurna 2004 [58]
	Agrobacterium, Enterobacter, Kosakonia, Pantoea, Pseudomonas, Ralstonia, Serratia, Rhizobium, Stenotrophomonas, etc.	Production of IAA and exopolysacchardies, P solubilization, etc.	De Almeida *et al.*, 2016; Carpentieri-Pipolo *et al.*, 2019 [58, 28]
	Enterobacter sp., *Bacillus* sp., *Variovorax* sp., *Serratia* sp., *Burkholderia* sp., *Pantoea* sp., *Kosakonia* sp.	Antimicrobial activity	De Almeida *et al.*, 2018 [36]
Wheat	*Bacillus subtilis*	Antifungal activity against Puccinia	Li *et al.*, 2013 [84]
	Bacillus cereus	Biofilm formation, colonization and biocontrol	Xu *et al.*, 2014 [136]
	Bacillus thuringiensis	Biocontrol	
	Azospirillum sp	Phytormone synthesis: IAA, GA, ABA; phosphate solubilization	
	Arthrobacter sp.	Siderophore-production and Zn solubilization	Singh *et al.*, 2018 [114]
	Burkholderia cepacia	Plant growth promotion	Wang *et al.*, 2010 [132]
Sugar Beet	*Bacillus pumilus, Chryseobacterium indologene, Acinetobacter johnsonii*	increased concentration of carbohydrates and growth photosynthetic efficiency	Shi *et al.*, 2010 [111]
Sugar Cane	*Gluconacetobacter diazotrophicus*	N-fixation, plant growth promotion, secretion of organic acids, synthesis of auxin and bacteriocins	Bertalan *et al.*, 2009 [19]
	Azospirillum amazonense, Burkholderia tropica, Herbaspirillum seropedicae, H. rubrisubalbicans, Gluconoacetobacter diazotrophicus	acceleration of budding; increase in biomass; N-fixation; production of siderophores and IAA; phosphate solubilization	Oliveira *et al.*, 2009; de Silva *et al.*, 2012 [97, 113]
Tomato	*Bacillus subtilis*	Control of Alternaria solani and Phytophthora infestans	Chowdappa *et al.*, 2013 [33]
	Burkholderia phytofirmans PsJN	IAA synthesis, ACC deaminase	Weilharter *et al.*, 2011 [133]
	Sphingomonas sp.	Prodution of gibberellins and IAA	Khan *et al.*, 2014 [68]
Common Bean	*Microbacterium testaceum*	Inhibition of bacterial pathogens and quorum sensing	Lopes *et al.*, 2015 [87]
	Rhizobium endophyticum	Solubilization of phytate	Lopes *et al.*, 2010 [88]
Maize	*Bacillus* spp.	Production of lipopeptides active against Fusarium moniliforme	Gond *et al.*, 2015 [52]
	Azospirillum brasilense	Plant growth promotion	Ferreira *et al.*, 2013 [45]
	Enterobacter sp.	Improved photochemical efficiency and flowering anticipation; N-fixation	Naveed *et al.*, 2014 [94]
	Paenibacillus polymyxa	N-fixation and growth promotion	Puri *et al.*, 2016 [101]
	Pseudomonas spp., *Enterobacter asburiae, Sinorhizobium meliloti*	PGP traits and antifungal activity	Sandhya *et al.*, 2017 [109]
Canola	*Bacillus subtilis*	Antibacterial and antifungal activity	Lahlali *et al.*, 2013 [82]
	Burkholderia phytofirmans	ACC deaminase activity and production of IAA	Weilharter *et al.*, 2011 [133]
Coffee	*Escherichia fergusonii, Acinetobacter calcoaceticus, Salmonella enterica, Brevibacillus choshinensis, Pectobacterium carotovorum, Bacillus megaterium, Microbacterium testaceum, Cedecea davisae*	Production of phosphatase and indol acetic acid; control of coffee leaf rust, Hemileia vastatrix	Silva *et al.*, 2012 [113]

Applications of endophytic strains of rhizome

Role of endophytes in plant growth promotion

Endophytic bacteria can affect plant growth between species and strains, so there are usually several ways in which plant growth is promoted by endophytes, not by a single mechanism. Research has been directed regarding the plant growth promoting bacterial endophytes may directly or indirectly affect plant growth (Jasim *et al*., 2013) [64]. Direct stimulation of plant growth occurs when either (i) the bacteria that promote plant growth are able to obtain resources from the environment, including potassium, nitrogen, phosphorous and iron; (ii) modulate plant growth by providing or regulating various plant hormones including cytokinins, auxin or ethylene. Indirect promotion of plant growth by endophytic bacteria through the production of metabolites, HCN and antibiotics against pathogenic bacteria and fungi. PGPR strains ensure nutrient availability, promote plant growth, increase nutrient use efficiency, and reduce biotic and abiotic stresses (Kumar *et al*. 2015a, b, c, 2016a, b) [78, 76, 77, 74, 75]. However, the degree of efficiency of PGPR can vary with crops, cultivars or species, cultural conditions and inoculant strains (Zandi and Basu 2016) [139].

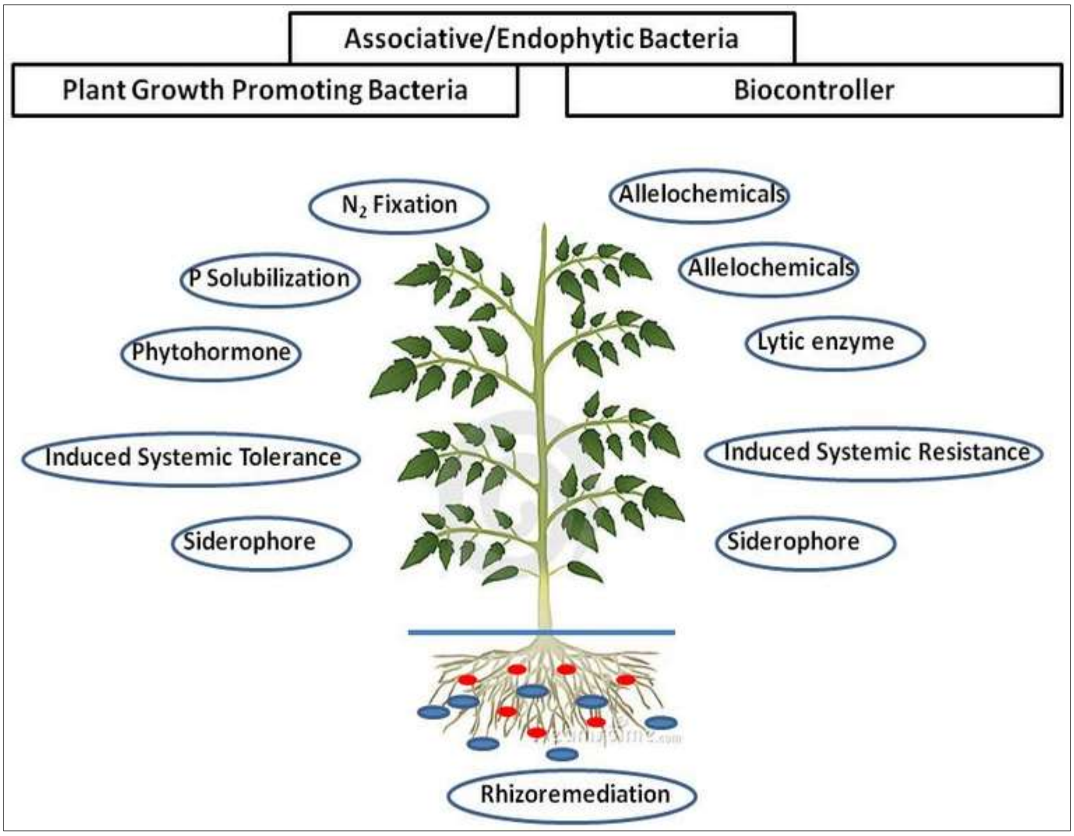

Fig 2: Schematic presentation of role of endophytic bacteria in plant development

Biological nitrogen fixation

Nitrogen (N) is needed by all organisms to synthesize biomolecules such as proteins and nucleic acids. Nitrogen is provided to agricultural land by the use of urea and ammonium nitrate as chemical fertilizers. Microorganisms with biological nitrogen fixation (BNF) capability are responsible for the reduction of N to ammonia (NH) (Glick *et al*. 1999; Glick 2014) [51, 50]. Rhizobium is the best example of nitrogen fixer which fixes nitrogen permanently. These microorganisms were traditionally thought to be responsible for the legume infection process, although rhizobia can also behave as endophytes in nodules and frequent isolation of rhizobial strains from nodules often promotes plant growth. Endophytic rhizobia isolated from nodules after sequencing of various genes were classified into the genera Encifer and Schinella as well as species Rhizobium tropici (Balogh *et al*. 2010; Frampton *et al*. 2012) [16, 46]. Non-availability of good quality seed for low yield and the absence of effective rhizobial inoculation was reported (Jha *et al*., 2011; Gururani *et al*., 2013) [66, 54]. Besides rhizobial endophytes, some promising non-rhizobial endophytic biofertilizers include members of *Azorcus*, *Achromobacter*, *Burkholderia*, *Gluconoacetobacter*, *Herbaspirillum*, *Klebsiella* and *Serratia* (Choudhary *et al*. 2011) [32]. Efficient N supply by endophytic diazotrophic bacteria in sugarcane and cultivar grass suggests a possible pathway for biological nitrogen fixation in plant interior niches. It is clear from reports that the main contributor to endophytic biological nitrogen fixation in sugarcane is *Gluconoacetobacter diazotrophicus* (*Acetobacter diazotrophicus*), and that it has the ability to fix N to approximately 150 kg N ha−1 (García-Fraile *et al*. 2015) [48]. *Azoarcus* is recognized as another potential N2-fixing obligate endophytic diazotroph (Hurek *et al*., 1994) [59]. This cultivar settles in the roots of grasses, and increases grass yield by 20–40 t ha−1 year–1 year–1 in saline sodic, alkaline soils without the addition of any N fertilizer (Vejan *et al*. 2016; Kumar *et al*. 2016a, b) [127, 74, 75]. Rohini *et al*., (2018) [105] studied the remarkable effect of endophytic bacteria as plant growth promotion on ginger rhizome. Carpentteri-Pipolo *et al*., (2019) [28] studied on significant positive effect of endophytic bacteria associated with transgenic and non-transgenic soyabean plant. Kushwaha *et al*., (2020) [79] reported the significant plant growth promoting and antifungal activity of endophytic *Bacillus* strains from pearl millet. The study showed that the endophytic *Bacillus* possess excellent biocontrol and pearl millet growth promotion activities. Rana *et al*., (2021) [103] studied the effect on plant growth promotion of maize (*Zea may* L.) by the endophytic bacteria. These investigations suggest that endophytic diazotrophs have great potential to increase productivity of non-legumes, including important cash crop plants (Singh *et al*. 2017b, c: Zhang *et al*., 2018; Degrassi & Carpentierri 2020; Baron *et al*., 2022) [118, 1117, 140, 38, 18].

a) Phosphorus solution

Phosphorus is an essential macronutrient for plant growth and development involved in important metabolic pathways such as photosynthesis, biological oxidation, nutrient uptake and cell division (Antoun 2012) [10]. Soils around the world are supplemented with inorganic P in the form of chemical fertilizers to support crop production but repeated use of fertilizers results in poor soil quality (Miller *et al*. 2010) [92]. Hence, the current scenario is moving towards more sustainable agriculture. A large amount of phosphorus exists in insoluble forms and is not readily available for plant growth. Organic and inorganic compounds, mainly in the form of insoluble mineral complexes, are the major sources of P available in soil (Wang *et al*. 2007; Oteino *et al*. 2015;

Singh *et al*., 2018) [131, 98, 114]. Phosphate-soluble bacteria soluble inorganic soil phosphates, such as $FePO_4$, $Ca_3(PO_4)_2$ and $AlPO_4$, through the production of siderophores, organic acids and hydroxyl PGPB in agricultural soils (Yadav & Yadav 2017; Vinayarani & Prakash 2018) [137, 128]. Endophytic bacteria have the ability to solubilize phosphate, and it was suggested by the authors that endophytic bacteria from soybean may also participate in phosphate assimilation (Dutta 2014) [41]. Application of phosphate-soluble bacteria increases soil fertility because of their ability to convert insoluble P into soluble P by releasing organic acids, chelation, and ion exchange (Lee *et al*., 2017) [83]. Positive effects of P solubilizers have been reported on food and fodder crops (Rohini *et al*., 2018) [105]. Bader *et al*., (2020) [14] suggested that native trichoderma harzianum strains induce phosphorus solubilization and control wilt disease on tomato (*Solanum lycopersicum* L). Chen *et al*., (2021) [30] reported that multifunctional phosphate solubilizing bacteria significantly increased soil nutrient content and enzyme activity were, such as total N, total P, total K, AP, AK, soil urease, cellulase, sucrase, dehydrogenase, nitrate reductase and acid phosphatase in Chinese fir seedlings. Increased enzyme activity was significantly associated with increased nutrient content.

b) Potassium solubility

Potassium (K) is the third important nutrient required for plant growth and endophytic bacteria are capable of solubilizing the insoluble form of potassium. Potassium soluble microorganisms may provide an alternative technique for making potassium available by plants (Vurukonda *et al*., 2018; Degrassi & Carpentieri-Pipolo 2020) [130, 38]. A wide range of bacteria such as *Pseudomonas, Burkholderia*, *Acidothiobacillus ferrocidans*, *Bacillus mucilaginosus*, *Bacillus edaficus*, *B. circulans* and *Paenibacillus* sp. It has been reported to release potassium in an accessible form from potassium-rich minerals in the soil (Naveed *et al*., 2014) [94]. These potassium soluble bacteria (KSBs) were found to dissolve potassium, silicon and aluminum from insoluble K-bearing minerals such as micas, elite and orthoclase by excreting organic acids, either directly from the rock or chelated silicon ions was dissolved so that K could be brought into solution. (Singh *et al*., 2017). Thus, the application of K-soluble bacteria as a biofertilizer for agricultural improvement can reduce the use of agrochemicals and support environmentally friendly crop production (De Almeida *et al*., 2018) [36].

c) Siderophore production

In plant growth promoting bacteria, the iron in the Fe^{3+}-siderophore complex on the bacterial membrane is reduced to Fe^{2+}, which is further released from the siderophore into the cell via a gating mechanism. Binding of the siderophore to the metal increases the concentration of the soluble metal (Goswami *et al*. 2013) [53]. Bacterial sideophores are released upon elimination of high levels of heavy metal contamination and plants assimilate iron from bacterial siderophores through various mechanisms, for example, release of chelate and iron, direct uptake of the siderophore–Fe complex, or by a ligand exchange. response (Arora *et al*. 2013) [11]. Several studies have been reported of promoting plant growth as compared to siderophore-mediated iron-uptake as a result of siderophore producing rhizobacterial inoculation. Researcher also Evaluated the role of the siderophore-producing *Pseudomonas* strain GRP3 on the Vigna radiata for iron nutrition. After 45 days, plants showed a decline in chlorotic symptoms and increased iron, chlorophyll a and chlorophyll b content in strain GRP3 inoculated plants compared to controls (Kumar *et al*. 2016a, b: Singh *et al*., 2018) [74, 75, 114].

d) Production of indolic compounds

Microbial synthesis of the Phytohormone Auxin has long been well-known (Vinayarani & Prakash 2018) [128]. It is reported that 80% of microbes isolated from the rhizosphere of various crops have the ability to synthesize and release auxins as secondary metabolites. Indole acetic acid (IAA) affects the division, expansion and differentiation of plant cells; stimulates the germination of tubers and seeds; Increases the rate of root and xylem growth; Lateral starts; controls the processes of vegetative growth and adventitious root formation; pigment formation, biosynthesis of various metabolites, mediating reactions to light, gravity and inflorescences; Affects photosynthesis and resistance to stressful situations. IAA possibly produced by plant growth promoting bacteria; Delay the above physiological processes of plants by altering the plant auxin pool. Additionally, the bacterium IAA increases the surface area and length of the root, and thus gives the plant greater access to soil nutrients (Yadav & Yadav 2017: Carpentieri-Pipolo 2019) [137, 28]. Similarly, production of IAA in bacteria relaxes cell walls and enhances the release of exudates and also provides additional nutrients to support the growth of other supporting bacteria of the rhizosphere. Thus, the endophytic bacterium IAA is recognized as an effector molecule in plant–microbe interactions in both pathogenesis and phytostimulation (Boiero *et al*. 2007; Sandhya *et al*., 2017) [24, 109]. Bader *et al*., (2020) Native trichoderma harzianum strains produce indole-3 acetic acid on tomato (*Solanum lycopersicum* L.) and showed significant plant growth.

e) 1-Aminocyclopropane-1-Carboxylate (ACC) Uses

Normally, ethylene is an essential metabolite for the normal growth and development of plants Glick 2014) [50]. This plant growth hormone is produced endogenously by almost all plants and is also produced by various biotic and abiotic processes in the soil and is important in inducing diverse physiological changes in plants. Stress conditions such as waterlogging, drought, salinity, heavy metals and pathogenicity result in an increase in endogenous levels of ethylene which negatively regulates overall plant growth and leads to discoloration and alterations in other cellular processes that contribute to crop growth. Affects performance a lot (Spaepen and Vanderleyden 2011) [119]. At present, bacterial strains exhibiting ACC deaminase activity in a wide range of genera such as *Acinetobacter, Achromobacter, Agrobacterium, Alcaligenes, Azospirillum, Bacillus, Burkholderia, Enterobacter, Pseudomonas, Ralstonia, Serratia* and *Rhizobium* etc. have been identified (Ali *et al*., 2014) [3]. Such bacterial endophytes trap the ethylene precursor ACC and convert it to 2-oxobutanoate and ammonia (Baron & Rigobela 2022) [18]. Puri *et al*., (2016) [101] showed that some forms of stress are rejected by producers of the enzyme ACC deaminase, such as phytopathogenic microorganisms (viruses, bacteria and fungi etc.), and heavy metals, radiation, wounds, insect predation, high salt concentration. Flood resistance to extreme temperatures, high light intensities, and stresses from polyaromatic hydrocarbons.

Pandey and Gupta (2019) [100] reported that *in vivo* study of ACC deaminase producing bacteria promote plant growth both under normal and saline conditions. The production of ACC deaminase and other PGP traits by these isolates project the potential that they could be used as a bio-fertilizer under both normal and saline soils. Dubey *et al*., (2021) [40] studied characterization of bacterial root endophytes for competence and plant growth promotion in soybean **(***Glycine max* (L.) Merr.) under drought stress. Among these three endophytes, AKAD A1-16 performed better than AKAD A1-2 and AKAD A1-1, which was further validated by the ability to produce the enzyme 1-aminocyclopropane-1-carboxylate (ACC) deaminase in the following order: AKAD A1-16 > AKAD A1-2 > AKAD A1-1.

f) Ammonia emissions

Ammonia can be produced by several processes such as nitrite ammonification, degradation and decarboxylation, deamination, urea-mediated hydrolytic degradation of urea, and this ammonia produced by bacteria is taken up by plants as a source of nitrogen for their growth (Chen *et al*., 2014) [29]. Normally, all free-living rhizospheric microbes and some symbiotically associated with the plant fix nitrogen that can be used by the plant for growth, for example, *Gluconacetobacter, Herbaspirillum, Azospirillum, Bacillus, Enterobacter, Klebsiella, Pseudomonas* and *Burkholderia*. These bacteria are appreciated for their importance in agricultural fertility (Awasthy *et al*., 2013; Kumar *et al*., 2018) [13].

g) Production of metabolites

Secondary metabolites are produced either for signalling or defence or in the process of establishing their interaction with the host plant. Microorganisms are used to control various diseases in what is known as a biological and eco-friendly approach (Rohini *et al*., 2018) [105] and these microbes are known as biocontrol agents. The main activities employed by PGPR in biological control and niche exclusion, competition for nutrients, induced systemic resistance and antifungal metabolites (Yadav & Yadav 2017) [137]. Several rhizobacteria have been reported to produce antifungal metabolites such as pyrrolnitrine, phenazine, 2,4-diacetylfluoroglucinol, pileutorin, HCN, viscocinamide and tensin. Some species of bacteria produce and excrete hydrogen cyanide (HCN) which is a potent inhibitor of cytochrome c oxidase and many other metalloenzymes. HCN is a metabolite and has no role in primary metabolism. *Proteobacteria contain* HCN synthase which is a membrane bound flavoenzyme that oxidizes glycine, producing HCN and CO. GacS/GacA (global control) is a two-component system that controls the expression of the HCN gene cascade. This regulation of secondary metabolism expresses itself during the transition from exponential to stationary growth phase (Singh *et al*., 2017c, 2018; Vinayarani & Prakash 2018) [117, 114, 128]. It was found that cyanide produced by the P. fluorescens strain CHA0 is part of the biocontrol ability that suppresses fungal diseases on plant roots. Some bacterial endophytes synthesize antibiotic substances that inhibit the growth of certain plant pathogens. Serratia mercescens and *Bradyrhizobium* sp., both play important roles in plant growth promotion and biocontrol by producing siderophores, IAA, HCN and P solubilization (Singh *et al*., 2017b; Vurukonda *et al*., 2018) [118, 130]. Ahmed *et al*., (2020) reported that endophytic metarhiziumrobertsii promotes maize growth and alters the plant defense gene expression. Previous studies have shown that the synthesis of multiple bioactive secondary metabolites, including alkaloids, sesquiterpenes, polyketones, lactones, organic acids, cyclopeptides, flavonoids, and saponins, with novel applications can be accomplished by endophytes present in host plants (Ek-Ramos *et al*., 2019; Wu *et al*., 2021) [43, 135].

h) Field effectiveness of endophytes

The effect of plant growth promoting rhizobacteria in crop productivity varies due to the unstable environment under greenhouse, field tests and laboratory and it is sometimes difficult to obtain approximate results. Climate heterogeneities also have a great impact on the growth success of plants that promote rhizobacteria, but sometimes unfavorable growth conditions in the region are expected as normal functioning of agriculture is performed.

Do not act independently of each other, but additively IAA, phosphate solubility, N2 fixation, siderophore Biosynthesis, ACC deaminase and antifungal activity, etc. are responsible for promoting plant growth and increasing yield. Both natural agro-ecological locations and controlled soil environments result in significant increases in the yields of various crops. Due to the prevailing worldwide hesitation to encapsulate foods produced by genetically modified plants, PGPR as a bioinoculant may be beneficial for promoting plant growth. Widespread use of PGPR can reduce worldwide dependence on agrochemicals. Likewise, it is a technology that is happily practical for farmers in both developed and developing countries. Some research has shown that endophytes can significantly increase yields in various crops after their inoculation. To reveal the effects of endophytes, various vaccination experiments have been conducted Zhang *et al*. (2018) [140] reported that three out of 14 endophytes improved soybean nodulation and plant weight when combined with *Bradyrhizobium japonicum*. Suryadevara and Ponmurugan (2012) reported the effect of endophytes on soybean plant growth and development, with two isolates having a positive effect on root weight. These isolates increased the total plant biomass by more than 80% compared to the uncultured control. Boominathan and Sivakumaar (2012) [25] reported in their study that endophytic bacterial inoculation had a significant effect on seed germination, root and hypocotyl development of *Solanum nigrum* seedlings; 37 out of 77 different seedlings increase vigor. Of these 37 isolates, 22 improved seed germination by 100% compared to uninfected controls.

Kumar *et al*. (2016b) [75] assessed the effects of non-rhizobial endophytes from surface sterilized root nodules of *Medicago sativa* L. on the growth of alfalfa. Coinfection of all endophytic strains with *Sinorhizobium meliloti* significantly increased the nodule number of alfalfa, but had no significant effect on growth parameters with respect to vaccination with individual *Sinorhizobium meliloti*. Vaccination of *Pseudomonas* sp. in home conditions. PS1 in Greengram greatly increased plant dry weight, leghemoglobin, root N, shoot N, root P, shoot P, nodule number, total chlorophyll content, seed yield and seed protein (Singh *et al*. 2017a, b) [116, 118]. Kumar *et al*. (2014) [73] used Azotobacter chroococcum for inoculation in the rhizome and observed enhancement in leaves number, shoot height, shoot and rhizome biomass as well as curcumin content in turmeric plant. Similarly, Dutta and Neog (2016) [42] described that the nonrhizobial nodule-associated bacterial (NAb) isolate M2N2C and B1N2B (Exigubacterium sp.) showed maximum positive PGP traits. Under home conditions, NAb segregated when combined with the rhizobial strain - S. meliloti, with respect to plant root and shoot length, chlorophyll content, nodulation efficiency and increase in nodule dry weight. Promotes growth. Under field conditions, P. putida strain R-168, P. fluorescens strain R93, P. fluorescens DSM 50090, P. putida DSM291, A. *lipoferum dsm* 1691, a. Brasilens DSM 1690 inoculation in maize crop showed an increase in plant height, seed weight, number of dry weights per ear, leaf area and shoot (Kumar *et al*. 2015c, 2017, 2018) [77]. Similarly, Rohini *et al*. (2018) [77, 105] reported that *Pseudomonas fluorescens* PGPR1, PGPR2, PGPR4 in peanut (*Arachis hypogaea* L.) significantly increased pod yield and nodule dry weight over control under both laboratory and field environment. *Bradyrhizobium* sp. 750, *Pseudomonas* sp., *Lupinus luteus* resulted in both increased biomass, nitrogen content, accumulation of metals (improved phytostabilization capacity) under *Ocrobactrum psittici* inoculation field conditions (Krishnapura *et al*. 2016) [71]. Lee *et al*. (2017) [83] also stated that *Pseudomonas* sp. In wheat field and soybean, increased soil enzyme activities, total productivity and nutrient uptake.

Asghari *et al*., (2020) [12] Induction of systemic resistance to *Agrobacterium tumefaciens* by endophytic bacteria in grapevine The findings revealed the efficacy of the selected endophytic bacteria in triggering grapevine resistance against *A. tumefaciens* and the possible use of these strains as an alternative to chemical control methods in grapevine crown gall disease management. Igiehon *et al*., (2021) [60] studied the **e**ffects of rhizobia and arbuscular mycorrhizal fungi on yield, size distribution of soybean seeds grown under drought stress. The bacteria that were found in the rhizospheric soil were *Verrumicrobia, Proteobacteria, Firmicutes, Bacteroidetes, Planctomycetes* and *Nitospira*. suggesting that the rhizobia and fungi used can also improve soil microbial diversity.

i) Biocontrol Activity

Functional basis of biocontrol activity of diverse endophytic microorganisms has provided deeper insight on interaction between the microbes and plants (Alstrom 2001) [5]. Endophytic strains inhibit the growth or infection of pathogen or proliferation within the host directly via antibiosis, synthesis of cell wall-degrading enzymes, production of antibiotics, and competition indirectly via inducing resistance responses intrinsic to host (Benhamou and Chet 1996; Lahlali and Hijri 2010; Kumar *et al*. 2014, 2015c; Singh *et al*. 2017b) [81, 20, 77, 118]. Endophytic fungi also provide protection from phytopathogens, impart resistance to abiotic stress, and also enhance plant growth (Anisha *et al*. 2018) [8]. They also activate induced systemic resistance (Vu *et al*. 2006) [129] and induce secondary metabolite production in plant, which may convert plant metabolites to antifungal agents. These multi-beneficial impacts of endophytes are very significant as they have commercial potential as agents for successful sustainable agriculture (Kauppinen *et al*. 2016) [67]. Many of the endophytic strains isolated from the rhizome of different plants have also biocontrol potential. Sabu *et al*. (2018) [107] reported endophytic strains of Burkholderia vietnamiensis isolated from *Zingiber officinale* having inhibition potential against Pythium myriotylum *in vitro*. In another study Vinayarani and Prakash (2018) [128] isolated 31 endophytic strains from the rhizome of turmeric and screened their antagonistic activity against *Pythium aphanidermatum* and *Rhizoctonia solani* the causal agent of rhizome rot and leaf blight diseases in turmeric, respectively. Six out of 36 strains showed >70% suppression of test pathogens in antagonistic dual culture assays. The endophyte strain *Trichoderma harzianum* TharDOB-31 showed *in vitro* mycelia growth inhibition against *P. aphanidermatum* (76.0%) and *R. solani* (76.9%) significantly, whereas the antagonistic potential of strains *T. harzianum* TharDOB-31 is followed by *T. asperellum* TaspDOB-19 > 70% against *P. aphanidermatum* and *R. solani*. Anisha *et al*. (2018) [8] reported antagonistic property of processed methanolic extract of *Rhizopycnis vagum* ZM6 and endophytic isolates of ginger against the strains like *Colletotrichum falcatum*, *Fusarium oxysporum*, *Sclerotium rolfsii*, *Phytophthora infestans*, *Corynespora cassiicola*, *Rhizoctonia solani*, and *Pythium myriotylum* by the method of agar well diffusion and observed significant inhibition of all these pathogenic strains. Endophytic microbes have been recently used as a novel source of bioactive compounds (Singh *et al*. 2017a) [116] and being broadly used in the nutraceutical or pharmaceutical industries (Theantana *et al*. 2009) [126].

Maheshwari *et al*., (2019) [89] suggested that the endophytes from *Cicer arietinum and Pisum sativum* possessed plant growth promoting traits, increased the plant growth parameters in pot conditions and explored as bioinoculant in field evaluation. Ambele *et al*., (2020) [7] reported that cocoa seedlings are conducive to endophytic fungal growth either occurring naturally or from artificial inoculation. These findings could possibly lead to an innovative approach to the management of herbivory and subterranean termite pests in cocoa agroforests.

Conclusion

The endophytes have engrossed huge consideration for their ability to promote plant growth through by acting as biocontrol agents. Endophytes must not induce plant disease, should be capable to spread inside plant parts, culturable and must colonize plant parts naturally obligately with species specificness. Though, the rhizospheric environment is somewhat dissimilar from that of internal plant tissues. For example, the variations in abiotic factors such as light emission, soil type, temperature, pH, the availability of oxygen as well as the struggle for nutrients, and the interaction with other organisms in the rhizosphere, can be key factors in the development of different strategies for interaction, lifestyle and survival inside the plant. These endophytic bacteria by various actions make available necessary nutrients which also reduces the application of chemical fertilizers. With a further understanding of the functioning of bacterial endophytes in the future scientists may be able to engineer bacterial endophytes to facilitate their potential to improve plant growth and development. There is a strong need to search for novel entophyte strains with as many desirable characters for enhancing the crop yield. The importance of assessing the ecological and evolutionary relevance of these processes should be stressed. The enhancement of bacterial colonization spurred by specific carbonaceous exudates by plant roots and the capacity of certain bacteria to modulate plant metabolism are key issues for further study, because these could provide insight into possibly mutualistic plant endophyte relationships. Particular endophytes could often have important, if not essential, roles for plant growth and development. Future discovery of pesticides with synergistic effect on endophyte bioinoculant may be able to control the range of pathogens. The development of sprayable endophytes for use along with chemical pesticides will pave the way for commercial pesticide development for effective integrated pest management.

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