Abstract

An eco-friendly organic agricultural system is a significant prospect for sustainable agriculture. Application of microbes associated with plants for escalating crop yield and overcoming the drawbacks of the existing conventional methods using agrochemicals is gaining impetus globally. The plant rhizosphere with its incredibly rich microbial diversity exhibits a harmonious interaction between plant and microbes. Such interactions facilitate microbial colonization in the root tissues. These root-colonizing active microbes, categorized as endophytes, are beneficial showing positive relationships with plants. They directly or indirectly benefit plants by promoting growth through the various phytohormones, secondary compounds or signal molecules secreted or modulated by them. The symbiotic interaction between the root-colonizing endophytic microbes enables establishment of association with the crop plants overcoming nutrient deficiencies and environmental stresses. Integration of beneficial endophytes in agricultural practices as biofertilizers could efficiently neutralize the effect of agrochemicals, thereby reducing their harmful environmental impact. Endophytic microbial biofertilizers could also become an economical and sustainable approach to acquire higher crop yields. Understanding the significance of endophytes in agriculture ensures various possibilities for formulating novel endophytic bioproducts such as potent bioinoculants for

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their prospective application in larger agricultural fields. This comprehensive review is a compilation of research on the functional role of root-colonizing endophytic microbes and highlights the mechanism of colonization of the endophytic rhizomicrobiome. The review also discusses the operational details of plant growth promoting endophytic microbes and their significant use in agrobiotechnology for crop improvement programs to ensure future food security.

Keywords: Rhizosphere, endophytes, plant growth promoter, biofertilizer, sustainable agriculture.

I. INTRODUCTION

The rhizosphere- the most versatile and highly intricate soil entity surrounding the root zone- attracts distinctive microbial community with its rich rhizodeposition (Manoharan *et al*., 2017; Gouda *et al*., 2018). These root exudates are sources of microbial energy capable of initiating a strong plant root-microbial interaction (Philippot *et al*., 2013; Bai *et al*., 2015; Cole *et al*., 2017; Bhupendra *et al*., 2019). These interactions often promote a gamut of useful plant-microbe associations which effectively encourage microbial colonization within root tissues. Such root-colonizing active microbes are categorized as rhizospheric endophytes (Lacava *et al*., 2022). The strong root tissue-endophyte interactions equip the rhizospheric endophytes to initiate a steady relationship with the plant host compared to the free-living rhizo-microbes. These mutualistic trophobiotic associations with the host plants confer rhizospheric endophytes the competence to subsequently improve plant growth and health (Ryan *et al*., 2008; Santoyo *et al*., 2016; Afzal *et al*., 2019).

Rhizospheric endophytes comprises of a distinct soil microorganism group involved in plant growth promotion. These plant growth-promoting endophytes (PGPE) are associated with the internal root tissues of every plant species and exhibit an alternate diphasic life cycle between root tissues and soil (Ryan *et al*., 2008; Ma *et al*., 2011; Sessitsch *et al*., 2012). With easier access to nutrients, PGPE proliferates in the root apoplast region with less competition and stays protected from environmental stress (Senthilkumar *et al*., 2011). The diverse group of rhizospheric PGPE are highly beneficial to plants and provide numerous agriculturally promising traits. They are gaining attention for their environmentally benign approach to sustainable agriculture.

The root colonizing PGPE modulates plant growth via direct mechanisms and accelerates plant nutrient absorption and distribution, secretion of phytohormones and plant growth-promoting enzymes. Indirectly they facilitate plant disease resistance, enable allelopathic responses, and mediate host stress tolerance thereby maintaining overall plant health (Mei and Flinn, 2010; Chukwuneme *et al*., 2020; Adeleke and Babalola*,* 2020). These qualities of the PGPE could be utilized to formulate potential bioinoculants to efficiently substitute synthetic plant growth regulators and agrochemicals for enhancing the productivity of crops and practising safe agriculture.

Endophytes associated with crop roots are being taken into consideration worldwide in view of their active role in bio-fertilization and bio-controlling of various plant diseases. Developing the rhizosphere endophytic community as a potential means to practice sustainable agriculture and improving prospective agri management aptitude, depends on comprehensive scientific research on PGPE-mediated plant growth stimulation. Such indepth research provides better perception relating to the microbe-plant root interactions and colonization mechanisms leading to enhanced plant growth. This would expedite formulations appropriate for isolating and developing potent microbial strains that can endure varied agronomic environments.

II. COLONIZATION AND INTERACTION OF PLANT-ASSOCIATED RHIZOSPHERIC ENDOPHYTES

Endophytes are ranked as a subcategory of the rhizospheric microbial system, that invades and inhabits host plant tissues internally (Hallmann and Berg, 2007; Marquez-Santacruz *et al*., 2010). The colonization of endophytes depends on the varietal difference of plants, their developmental phase, the environmental condition, microbial species, and the abundance of the microbial community (Tan *et al*., 2003). The other attributes which influence endophytic colonization includes the biological, chemical, and physical environment of the rhizosphere.

Endo-rhizosphere colonization is highly affected by physical factors like temperature, water availability (including precipitation) and soil (type, texture, pH, and topography). Chemical characteristics like the presence of mineral elements, inorganic and organic substances, exudates, and other metabolites also significantly contribute towards endophytic colonization. Biological factors greatly determine the abundance, colonization and diversity of rhizoendophytes. The distribution of other competitive and inhibitory microorganisms like bacteria, fungi, viruses, nematodes, and other plant-beneficial growth promoters (Ojuederie *et al*., 2019) can regulate the colonization and persistance of rhizospheric microbes either negatively or positively.

Endophytic microbes adopt various survival strategies for colonizing their host based on which they are catogorized distinctly into three types- obligate, facultative, and passive endophytes (Hardoim *et al*., 2008). Endophytes which thrive only within the plant tissues and get disseminated through seeds are the Obligate types. Facultative endophytes are free-living soil microbes. Signalling molecules mediate their entry into the host tissues. Both these cendophyte categories sport a prominent part in plant growth regulation. The third type of endophytes enter the host tissues via minute wounds on the root hairs without any signalling cues and have little impact on growth modulation in plants (Verma *et al*., 2004; Swarnalakshmi *et al*., 2019).

Each plant microbiome is a hub of diverse microbial communities. Endophytic microbial establishment within the plants follows a series of events akin to rhizomicrobial colonization. This is influenced by an array of microbial traits and intricate plant-microbial communication (Afzal *et al*., 2019). The endophytic microorganisms commonly establish their entry through the root zone (Zinniel *et al*., 2002). Following the penetration, the microbes colonize adjacent root tissues (Afzal *et al*., 2019). Progression of colonization is initiated by the plant roots by secreting endophyte-specific root exudates that signal the root colonizing endophytes (Rosenblueth and Martinez-Romero, 2006). These signalling molecules accelerate the formation of a strong bond between the endophytic microbes and the plant host. This lays the foundation for the plant-endophyte interactions which are beneficial to growth promotion and disease management in plants (Compant *et al*., 2005) along side various other functionalities.

1. Rhizosphere Colonization of Endophytic Microbes

The rhizo-microbial diversity is distinct from the ordinary soil microbial community. Plant root metabolic exudates like amino acids, sugars, alkaloids, and phenolic compounds attract microorganisms including endophytes towards the rhizosphere making it the most viable region surrounding the plant root (Vandana *et al*., 2021). These organic nutrients and plant transudes act as signals that drive microbial growth and development. Compared to normal soil, they support 10 to 50 fold bacterial growth and 5 to 10 fold fungal growth (Ortiz-Castro *et al*., 2009). These root exudates enrich the rhizome-microbiome by serving as a rich carbon source within the rhizosphere, helping to sustain wide range of microbial population associated with roots.

Microbial communities of root microbiome interact and compete for their nutrients (Pervaiza, 2020). The competitive rhizospheric microbe interactions are crucial for efficacious root colonization. Endophytic microbes strive fiercely to occupy the rhizosphere for procuring nutrients (Azevedo, 1998, Oliveira *et al*., 2003). Only those endophytes successfully colonizing the rhizospheres flourish in this space and contribute towards growth and development of plants. Such endophytes may subsequently colonize the entire rhizoplane and certain extracellular cells, resulting in the development of rhizodermal microbial colonies (Benizri *et al*., 2001).

Successful colonization of rhizospheric endophytes is dependent on microbial traits like signal recognition, attachment, motility, nutrient utilization, growth rate, antagonistic substance and enzyme secretion, besides polysaccharide synthesis (Compant *et al*., 2010; Santoyo *et al*., 2016; Santos *et al*., 2018). At a later stage, rhizospheric colonizers secrete metabolites that alter the cell wall of roots, conceivably enabling endophytic growth initiation within the root cortex. These structural alterations in root cell walls are induced by the rhizospheric microbe-mediated change in plant gene expression. The metabolic regulations also associated with altered plant gene expression following rhizosphere colonization by endophytes pave the way to their entry into the root tissues.

2. Root Colonization of the Endophytic Microbes

Rhizospheric endophytes enter the internal root tissues after colonizing the rhizoplane and establish within the intracellular region as an endophytic sub-population (Hallmann, 2001). Chemo-attraction mediated by exudates from root often stimulates plant-specific endophyte colonization (Berg *et al*., 2005; Hardoim *et al*., 2008). The extent of rootmicrobial interaction often determines the specificity of the rhizosphere microbes. For example, rhizobial colonization in Fabaceae is initiated via root tips which leads to nodule formation in roots (Desbrosses and Stougaard, 2011). Furthermore, initial infection of host plant by rhizospheric endophytes happens following the colonization at lateral root emerging break points. Later they invade the root cortex and exhibit plant-beneficial properties (Chi *et al*., 2005; Pothier *et al*., 2007; Combes-Meynet *et al*., 2011).

Plant-microbial interaction is initiated through the adhesion of the microbes with the extracellular region of the root tissues. Specific receptors and signalling molecules modulate this, thereby providing a tissue-specific colonization strategy which is unique for each endophyte (Zachow *et al*., 2010). Following their establishment in the extracellular region, rhizospheric endophytes use specialized approaches for invading the internal root tissues.

Rhizospheric endophyte colonization within the root tissues would be either active or passive. Active colonization gets modulated via systematic events like signal recognition, attachment, and colonization while, passive colonization of rhizospheric endophytes happens along the root tips or the wounds formed at the root arising region, or through the injuries produced by the pathogenic microbes (Hardoim *et al*., 2008).

Bacterial colonization and movement within the internal root tissues are mediated through receptor-ligand signalling, chemotaxis, quorum sensing, twitching motility, lipopolysaccharides, flagella, and pili (Böhm *et al*., 2007, Suárez-Moreno *et al*., 2010). Bioactive secondary metabolites like alkaloids, phenolics, and enzymes help the endophytic fungal strains to recognize the host tissue. Fungi secrete specific enzymes like cellulases and pectinases to degrade the root cell wall for colonization. Similarly, secretion of cell-divider debasing compounds (CWDEs) is seen within the cortical cells colonized by microbes (Lodewyckx *et al*., 2002).

III. PGPE MEDIATED GROWTH PROMOTION MECHANISM IN PLANTS

Rhizospheric endophytes are a distinct microbial subpopulation colonizing the root tissues internally. They adopt various plant growth promotion strategies. In nature, the interaction between the host plant and rhizosphere colonizing microbes is established by the colonization potential inherited within the plant and the microbe. However, microbial growth may be hampered by variations in soil conditions like pH, availability of water, and temperature. Additionally, rhizospheric bacteria also compete with the endophytes and strive for colonizing plant roots (Santoyo *et al*., 2016). Once established, PGPEs coexist within the plant tissues, supporting the overall physiological and biochemical functioning of their host plant.

Plant-beneficial rhizospheric endophytes could be bacteria or fungi in association with a wide array of crops. Tables 1 and 2 summarises details of some rhizosperic microbes showcasing efficacy to promote plant growth. Some of the the common endorizhal endophytes blong to bacterial genera like *Arthrobacter*, *Actinobacteria*, *Azospirillum, Azotobacter, Escherichia coli, Bacillus, Enterobacter, Pantoea, Paenibacillus, Pseudomonas, Rhizobium and Serratia* (Hungria *et al*., 2013, Patel and Archana, 2017; Issa *et al*., 2018; Ali *et al*., 2019; Dubey *et al.,* 2021; Cun *et al.,* 2022). Fungal endophytes, which include *Aspergillus, Paecilomyces, Penicillium, Trichoderma,* mycorrhizal fungi, and the non-pathogenic strains of *Alternaria, Fusarium, Verticillium* actively colonize the root tissue and expedite plant growth promotion and trigger the host plant defense system (Doni *et al*., 2014, Lone *et al*., 2015; Ikram *et al*., 2018; Ali *et al*., 2019).

Root-colonizing PGPEs exist in every agronomic ecosystem. They regulate both rootendophyte association and microbial interactions between the rhizomicrobes. They hold metabolically active traits that promote directly or indirectly growth and development in plants (Fig.1). The rhizospheric PGPEs directly facilitate nutrient acquisition, phytohormone production, and enzyme synthesis which are essential for plant growth under both normal and stressed environments (Wakelin *et al*., 2004; Bhardwaj *et al*., 2014). PGPEs mediate nutrient acquisition through biological nitrogen fixation and solubilization of minerals like phosphorus, potassium, iron, zinc, and other micronutrients which are vital for plant growth promotion.

PGPEs synthesize lytic enzymes, and antimicrobial compounds efficiecnt to suppress phytopathogen growth. This improves plant defense mechanisms to protect the host from further pathogen attack, thus indirectly enhancing plant growth (Miliute *et al*., 2015). The strategies exhibited by the rhizospheric endophytes coincide, depending on their nature and provenance. All these features act concurrently for plant growth enhancement and disease resistance, and ensure higher crop productivity for achieving agricultural sustainability (Omomowo and Babalola, 2019).

Table 1: Effective plant growth-promoting strains of rhizospheric bacterial endophytes and their host crops

Table 2: Rhizospheric Endophytic Fungi Showing Effiecient Plant Growth Promotion in Crop Plants

Figure 1: PGPE mediated growth promotion mechanism in plants

1. Plant growth promotion by PGPE: Direct Mechanism

PGPE promotes growth directly by a number of mechanisms beneficial to plants. These can be categorized as (1) biofertilization- plant growth improvement by enabling the bioavailability of plant nutrients and (2) phytostimulation- the production of plant growth regulators like phytohormones, and enzymes (Beneduzi *et al*., 2012). PGPE is an alternative to maximize nutrient acquisition and can be efficiently exploited as an easily accessible microbial source for enhancing agriculture production. Nitrogen fixation, solubilization of insoluble phosphates, sulfur oxidation, and iron chelation are the major pathways through which PGPEs maximize nutrient acquisition (Wakelin *et al*., 2004; Krause *et al*., 2006; Long *et al*., 2008; Yadav and Yadav, 2019). They also mediate the synthesis of vitamins that are vital for plant growth (Pirttila *et al*., 2004). Additionally, rhizospheric endophytes regulate plant growth by facilitating osmotic adjustment, regulating stomatal opening and closure, modifying root morphology, improving photosynthetic efficiency, and enhancing mineral metabolism (Compant *et al*., 2005, Polesi, 2011).

- **A. Biofertilization- Nutrient Acquisition by PGPE:** Soil is the most essential medium that supplies nutrients for growth and development in plants. Often there might be deficiency of one or the other nutrient components required for plant growth. PGPE is well known for enhancing nutrient availability for plant growth stimulation. Endophytes colonizing the root zone facilitate the absorption of limiting plant nutrients, like nitrogen, phosphorus, and iron (Balachandar *et al*., 2006; Glick, 2012).
	- **Nitrogen Bioavailability:** Nitrogen is an indispensable element for plant growth and development. Molecular nitrogen is converted to ammonia by the fundamental process of nitrogen fixation. Rhizospheric PGPE has a vital part in enhancing the bioavailable nitrogen to their host plant. This is achieved through biological nitrogen fixation by nitrogenase enzyme activity. Root-associated endophytes execute efficient

nitrogen fixation enabling better utilization of nitrogen in nitrogen-deficient environments. This PGPE includes species of the Rhizobiaceae family which colonize leguminous plant roots and independent endophytes including *Frankia* and cyanobacterial genera like *Azotobacter, Azocarus, Azospirillum*, and *Gluconacetobacter* that establish colonization of non-leguminous plant roots (Ahemad and Khan, 2012; Bhattacharyya and Jha, 2012)*.* A number of nitrogenfixing endophytes including *Rhizobium* sp., *Bacillus* sp., *Pseudomonas* sp., *Azosporillim* sp., *Enterobacter* sp., *Alcaligene* sp., *Herbaspirillum* sp., *Klebsiella* sp., were identified from rice and maize root (Triplett, 1996; James *et al*., 2000). Inoculating the crops with PGPE like *Burkholderia* sp., *Azospirillum amazonense, Gluconacetobacter diazotrophicus, Herbaspirillum seropedicae,* and *H. rubrisubalbicans* is effective in enhancing nitrogen content (Oliveira *et al.,* 2002).

 Phosphate Solubilization: Phosphorus is another indispensable and limiting macronutrient following nitrogen. It is a significant nutrient involved in enzyme activation involved in major physiological processes governing plant growth and development (Gyaneshwar *et al*., 2002, Ahemad, 2015). It is typically found as mineral salt in the soil and is sporadically soluble in nature. Thus, the majority of phosphorous in soil is still not available to plants (Miller *et al*., 2010). Rhizospheric endophytes can act as the potential source of phosphorus for their host plant as and when needed. Phosphate solubilization is a key feature of endophytic genera including *Erwinia, Bacillus, Azotobacter, Enterobacter, Burkholderia, Microbacterium, Flavobacterium, Pseudomonas, Serratia, Rhizobium*, etc. (Bhattacharyya and Jha, 2012). Around half the population of rhizospheric endophytes colonizing strawberries, sunflower, legumes and soybean are efficient phosphate solubilizers (Forchetti *et al*., 2007; Dias *et al*., 2009; Palaniappan *et al*., 2010).

Phosphate mobilization by PGPE is achieved through precipitating the available phosphate by synthesizing organic acids. Processes like chelation and ion exchange are also modes through which phosphate solubilization is achieved by the PGPEs (Nautiyal *et al*., 2000). They produce organic phosphate digesting enzymes like acid phosphatase thereby enhancing the availability of phosphorus (Van Der Heijden *et al*., 2008).

 Potassium Solubilization: Potassium is yet another essential macronutrient other than nitrogen and phosphorus. Potassium deficiency leads to abnormal development in plants causing improper root development, low viability of seeds, reduced growth, and decreased yield (Kumar and Dubey, 2012). In its original state Potassium is insoluble as it exists as a silicate mineral. The insoluble nature of potassium makes it less available to plants. Plants absorb only the dissolved form of potassium from soil (Parmar and Sindhu, 2013). PGPE like *Pseudomonas* sp., *Bacillus edaphicus, B. mucilaginosus*, *Ewingella* sp., *Pantoea* sp., *Ferrooxidans* sp., *Paenibacillus* sp., and *Acidithiobacillus* sp., are reliable potassium solubilizers (Liu *et al*., 2012; Cun *et al.,* 2022; Watts *et al.*, 2023). These bacteria efficiently solubilize minerals of potassium into plant-accessible form by secreting organic acid (Liu *et al*., 2012).

Zinc Solubilization: Zinc (Zn) - a vital micronutrient playing a prominent part in plant growth and development, regulates different biochemical and physiological processes. It is required for enzyme activation, redox reactions and metabolic process regulations. Zn is crucial for nitrogen assimilation, protein synthesis, carbohydrate metabolism, auxin biosynthesis, regulation of chlorophyll and other plant pigments, and modulation of cytochrome (Hafeez *et al*., 2013; Surabhi *et al*., 2022).

Reduced Zn availability in the soil owing to its low solubility leads to persisting Zn deficiency in plants (Singh *et al.,* 2005; Iqbal *et al*., 2010). Several factors like the presence of bicarbonate ions, excess organic matter content, increased magnesium-calcium ratio, persistent phosphate and iron content, and pH of the soil highly influence Zn availability. An increase in soil pH decreases the Zn solubility (Ahemad, 2011; Prasad *et al*., 2019). To mitigate the Zn deficiency inorganic fertilizers containing Zn serve the plants. However, a major percentage of Zn gets readily transformed into its insoluble state within a few days of application. Mere application of Zn fertilizers to the fields may not alleviate Zn deficiencies in crop plants as it gets rapidly transformed to its insoluble form (Saravanan *et al*., 2004). Zinc-solubilizing microbes serve the plants by ensuring the bioavailability of Zn in the soil. PGPE actively solubilizes the insoluble form and facilitates enhanced Zn absorption by plants, subsequently promoting plant development and productivity (Prasad *et al*., 2019).

 Iron Availability: Iron is the most essential micronutrient for every life form. Enzymes and proteins with iron as a core element play a key role in the regulation of important physiological activities including respiration, transpiration and photosynthesis (Ma *et al.*, 2016). Iron in its natural form - Fe^{3+} (ferric), retained as insoluble hydroxides or oxyhydroxides, is unavailable to both microbes and plants. Microbial siderophores are the major supplier of iron for plants. Siderophores are iron-chelating low molecular weight molecules capable of binding with insoluble ferric ions (Rajkumar *et al*., 2009). Their high binding affinity for complexing iron makes this possible (Ma *et al*., 2016). Microbial siderophores are the key compounds that solubilize iron from different mineral sources under an iron deficit environment. They convert the insoluble form of iron into an easily accessible source of iron. Rhizobacteria bear an iron-siderophore complex on the cell membrane that releases Fe²⁺ into the cell by the reduction of Fe³⁺ in the Fe³⁺-Siderophore complex. Degradation or recycling of these siderophore molecules are also effected (Rajkumar *et al*., 2010; Priyanka, 2018).

PGPE shows a strong affinity for iron complexes by secreting iron-chelating siderophores. Major siderophores produced by PGPEs include rhizobactin, enterobactin, and ferrioxamine. *Strenotrophomonas maltophilia* genome sequence revealed the ability to produce enterobactin, a catechol-type siderophore (Ryan *et al*., 2009). Endophytes that produce siderophores were identified in the root tissues of major crops (Loaces *et al*. 2011). Siderophores produced by PGPE are assimilated by plants via various methods, such as ligand-signalling reactions, chelating and degrading siderophore in order to absorb the iron component, or through direct absorption of the iron-siderophore complex. Therefore, bio-inoculation of siderophore-producing PGPE can facilitate iron absorption and mediate plant growth.

PGPEs vary in their ability to metabolize siderophores. While some are competent in siderophore utilization, others are poor in cross-linking siderophores. The second category consumes the iron-rich molecules released by other rhizomicrobes (Khan *et al*., 2009). Rhizomicrobial strains that can efficiently invade the root tissues were recognized as efficient siderophore producers. Plant growth promoting endophytic siderophores have much important rhizospheric significance. Siderophore-producing endophytic bacteria limit the bioavailability of iron in the plant tissues and in the surrounding soil, thereby restraining the growth of phytopathogens including pathogenic moulds (Calvente *et al*., 2001; Ahmad *et al*., 2008). *Bacillus subtilis* (Patil *et al*., 2014) *and Pseudomonas putida* (Kloepper *et al*., 1980) efficiently inhibit the growth of wilt and dry root rot-causing fungi - *Fusarium oxysporium*.

Soil fungi like *Penicillium chrysogenum* and *P. aeruginosa* are actively involved in siderophore production. They effectively control phytopathogens and aid nodule formation for nitrogen fixation which stimulates plant growth. They also secrete organic acids and are useful for direct abiotic stress management (Mahmod and Allah, 2001). In addition, endophytic actinomycetes are efficiently involved in the biocontrol of the phytopathogen *Pythium* in crops like cucumber and wheat (Franco, 2006; El-Tarabily, 2009). *Trichoderma* is known to release bio-chelators that suppress the growth of fungal pathogens.

Siderophores comes under the most heterogeneous categories of microbial biomolecules. They execute a variety of tasks including plant growth promotion either directly or indirectly and assist in plant health management. They promote heavy metal stress tolerance by forming complexes with the metal ions in the soil (Rajkumar *et al*., 2010). Heavy metal-resistant rhizobacterial endophytic strains like *Pseudomonas fluorescens* G10 and *Microbacterium sp*. G16 exhibits plant growth promotion and lead accumulation in *Brassica napus* (Sheng *et al*., 2008). PGPE like *Methylobacterium mesophilicum* and *Sphimgomonas sp*. were identified to be tolerant to heavy metals like nickel. Their endophytic habit enables them to survive under lower iron concentrations in the plant tissues (Idris *et al*., 2004). Consequently, microbial siderophore assimilation offers additional benefits to plants by inhibiting the growth of phytopathogens by limiting their nutrient and mineral availability in the soil, thereby conferring stress tolerance (biotic and abiotic) in addition to plant growth promotion.

B. Phytostimulation: Phytostimulation is the synthesis of growth-regulating compounds by plants owing to microbial activities (Kumari *et al*., 2021). Phytostimulation primes the secretion of phytohormones and other regulatory molecules associated with plant growth promotion (Santos *et al*., 2018). Endophytic colonization is crucial for the secretion of phytohormones (Gravel *et al*., 2007; Shi *et al*., 2014). PGPE mediates direct plant growth promotion by synthesizing phytohormones like auxin, cytokinin, gibberellin (GA), and abscisic acid (Maheshwari *et al*., 2019). Indole-3-acetic acid (IAA) and ethylene biosynthesis are influenced by plant-microbial interaction (Afzal *et al.,* 2019). Auxin, cytokinins, and GA enhance root morphogenesis and improve uptake of water and nutrients (Santos *et al*., 2018).

 Regulation of IAA (Indole-3-Acetic Acid) Level in Plants: IAA is a naturally occurring auxin. Every aspect of plant growth and development is influenced by IAA signalling. It induces plant cell division, differentiation, and cell elongation. IAA enhances seed and tuber germination. Besides increasing xylem development, IAA significantly stimulates the formation of pigments and initiates the lateral and adventitious root growth. Regulation of photosynthesis, triggering the stimulimediated response, activation of defense mechanism in plants and modulation of secondary metabolite synthesis also comes under the purview of IAA. In addition, IAA controls cell communication (Spaepen *et al*., 2007) and stress response in plants (Navarro *et al*., 2006; Glick, 2012).

PGPE of various plants actively synthesize and secrete IAA as a secondary compound that enhances plant growth (Patten and Glick, 1996; Gravel *et al*., 2007). In plants, IAA synthesized by root endophytes induce root formation laterally and increased root biomass (Tsavkelova *et al*., 2007, Dias *et al*., 2009). Rhizobacterial strains like *Agrobacterium, Rhizobium, Xanthomonas, Pseudomonas* (Gravel *et al*., 2007)*, Bacillus, Azotobacter, Arthrobacter, Acinetobacter,* and *Burkholderia*, colonize the root tissues and prompt IAA production (Tsakelova *et al*., 2006; Mitter *et al*., 2021). Endophytic species of *Pseudomonas* enhance the host IAA level and are efficient plant growth promoters (Kang *et al*., 2014). Cellular accumulation of IAA varies according to endophytic activation, which sequentially influences many of the plant's metabolic processes. IAA mediates root nodule formation. Genetically modified *Rhizobium leguminosarum* bv. viciae with enhanced IAA biosynthetic pathway showed increased nitrogen fixation and nodule formation than the wild variety (Camerini *et al*., 2008).

PGPE not only mediates IAA synthesis, but also take part in IAA degeneration, correspondingly enhancing plant growth and development. *Pseudomonas putida* Strain 1290 inhibited the effect of exogenous IAA that induced root elongation in radish by degrading the derived IAA and helped to stabilize the IAA concentration benefiting their host plant (Leveau and Lindow, 2005).

2. Plant Growth Promotion by PGPE: Indirect Mechanism

An environment-friendly approach to plant disease management employed using antagonistic microorganisms is one of the indirect mechanisms of plant growth promotion and is a form of biological control for phytopathogens (Lugtenberg and Kamilova, 2009). PGPE are potential biocontrol agents that mediate indirect plant growth promotion without inducing any environmental toxicity in contrast to synthetic pesticides (MacGregor, 2006; Mishra *et al*., 2015). Endophytes survive in the protective microenvironment of the host, ensuring safer survival benefits and many additional advantages above rhizosphere microorganisms. The occurrence of a suppressive rhizomicrobiome by the plant rootendophyte interaction sustains plant growth and maintains health even during phytopathogen infection. Rhizospheric endophytes inhibit the incursion of phytopathogens through different mechanisms like competitive exclusion of the phytopathogen by efficiently utilizing the microbial niche and the essential nutrients, the secretion of antimicrobial compounds and initiating Induced Systemic Resistance- ISR (Compant *et al*., 2005; Beneduzi *et al*., 2012; Teixeira *et al*., 2019).

For eradicating plant pathogens, the most sort after microbial defense mechanisms include production of various antimicrobial compounds. Antibiotics, volatile organic compounds, antifungal toxins, hydrolytic enzymes and siderophores fall in this category (Sheoran *et al*., 2015). Plant-beneficial root endophytes also facilitate ISR to protect plants by suppressing pathogens. ISR-mediated responses protect plants from bacterial, fungal, and viral diseases (Alvin *et al*., 2014). ISR is the principal plant defense mechanism that guides the host plants by stimulating resistance against the pest and pathogens, even in the uninfected plant parts and ensures future protection from further pathogenic infections (Afzal *et al*., 2019). These mechanisms are beneficial against phytopathogens as they can reduce or prevent the proliferation of these pathogens through antagonistic interactions.

A. Antibiosis: Endophytes regulate the internal environment of the plants. They suppress pathogen growth and maintain overall plant health. Endophytes effectively reduce the intensity of virulence by vying for nutrients in the same ecological niche as that of plant pathogens and secrete chemicals toxic to them. Root endophytes secrete antibiotics onto the endosphere, inhibiting the rhizosphere-invading phytopathogens (Gao *et al*., 2010; Bara *et al*., 2013).

Rhizospheric endophytes produce a variety of antimicrobial compounds during the stationary phase where the cells are liable to produce secondary metabolites uninvolved in the active microbial growth. Major ones being antibiotics like coronamycin, ecomycins, kakadumycins, munumbicins, pseudomycins and xiamycins (Castillo *et al*., 2003; Ezra *et al*., 2004; Christina *et al*., 2013) and antifungal toxins like hydrogen cyanide, 2,4-diacetylphloroglucinol, tensin, phenazines, pyrrolnitrin, pyoluteorin, and viscosinamide (Bhattacharyya and Jha, 2012). These antimicrobial substances act antagonistically towards pathogens.

With their vast array of antimicrobials, endophytic bacterial communities suppress the different phytopathogens. They effectively target nematodes, viruses, bacteria, and fungal pathogens (Raza *et al.,* 2016). The bacterial endophytic population is more prominent in the root than in the aerial portions. Root colonizing endophytic bacteria from the genera *Arthrobacter*, *Actinobacteria*, *Bacillus, Enterobacter, Pantoea, Paenibacillus, Pseudomonas, Rhizobium*, and *Serratia* are known for their antimicrobial activity (Lodewyckx *et al*., 2002; Liu *et al*., 2010). *Bacillus subtilis* antimicrobials are antagonists for phytopathogen *Erwinia carotovora* (Deng *et al*., 2011). Rhizospheric endophytic bacterial strains *Bacillus megaterium* BP17 and *Curtobacterium luteum* TC10 show nematicidal activity (Aravind *et al*., 2009).

Host-specific endophytes are more efficient biocontrol agents due to their favourable microenvironment. Rhizospheric endophytic genera including *Bradyrhizobium, Enterobacter, and Pseudomonas* were isolated from rice (*Oryza sativa*). Root colonizing PGPEs proficiently eliminate diseases in plants like maize, soybean, sorghum, millets, cowpea, sugarcane, cotton, wheat, rice, black pepper, and potatoes (Zarei *et al*., 2011; Adeleke and Babalola*,* 2020). Species of *Bacillus* are efficient endophytic biocontrol agents and reported to suppress pathogens in millets (*Pennisetum glaucum*), and *Citrus* varieties. *Enterobacter, Pantoea*, and *Pseudomonas* promote the biocontrol of pathogens in Sugarcane (*Saccharum officinarum*) (Shen *et al*., 2019; Adeleke and Babalola*,* 2020). Additionally, PGPE that

are effective against plant pests has been genetically engineered by developing *Pseudomonas fluorescens* that express Cry toxin of *Bacillus thuringiensis* and chitinase activity of *Serratia marcescens* that successfully target larvae of Sugarcane Borer worm (*Eldana saccharina*) (Downing *et al*., 2000).

Endorhizal microbes act antagonistically towards phytopathogenic fungi. *Fusarium* root wilt of *Musa sp., Lycopersicon esculentum*, and *Capsicum* has been efficiently controlled by rhizospheric endophytes (Benhamou *et al*., 1998; Chen *et al*., 2011; Sundaramoorthy *et al*., 2012). Pseudobactin, a siderophore metabolized by pseudomonads, is effective in suppressing potato soft-rot-causing pathogenic fungi *Erwinia cartovora* (Kloepper *et al*., 1980). Similarly, pyroverdine is a class of pseudomonas-based siderophore with potential biocontrol properties. Endorhizhal strain *Pseudomonas fluorescens* PICF7 actively curtailed the fungal growth in olive (Prieto *et al*., 2009). Infection and proliferation of *Phytophthora infestans* late blight disease-causing pathogen, is inhibited by the antimicrobials of *Pseudomonas putida* P9 (Andreote *et al*., 2009).

Similar to the rhizospheric bacterial endophytes, fungal endophytes also maintain mutualistic relations with the host plant and negative associations with plant pathogens. Mycorrhiza-forming fungi colonize the root internal tissues and sustain strong interactions that in turn protect the plants from disease-causing agents (Verzeaux *et al*., 2017). Endophytic fungi secrete a variety of antimicrobial substances that control pest and pathogen invasion (Segaran and Sathiavelu, 2019). Entomopathogenic fungi efficiently control plant pests (Jaber and Ownley, 2018). These entomopathogenic fungi are promising biocontrol agents which could be processed into commercial products. The species of *Trichoderma* exert antimicrobial activities against many bacterial and fungal pathogens (Vizcaino *et al*., 2005). Root endophytic fungi suppress the growth of nematodes like *Meloidogyne incognita* by secreting antimicrobial compounds. *Verticillium chlamydosporium* synthesizes phomalactone, which slows down the mobility of the nematodes immediately after application (Khambay *et al*., 2000).

Plants release low molecular weight secondary metabolites known as phytoalexins to attract endorhizal microbes. PGPE in turn produces certain plant-signalling polyphenolic metabolites like flavonoids with enhanced antimicrobial properties. The antimicrobial effect of endophytic *Trichoderma* sp. of *Vinca* plant is attributed to the myriad of secondary metabolites like, polyketides, gliotoxin, gliotoxin, pyrones, terpenes and peptaibols produced by them (Vinale *et al*., 2008). Thus, the plant-endophyte interaction mediated through secondary metabolite secretion determines the rhizospheric microbial diversity. Consequently, endorhizal microbial metabolites are promising resources that can be efficiently exploited as a substitute for agrochemicals.

B. Induced Systemic Resistance (ISR): Root colonizing PGPE efficiently inhibits the proliferation of phytopathogens causing plant diseases and helps prevent yield loss. The application of endorhizal microflora in agriculture considerably protects plants against phytopathogens. Induced Systemic Resistance (ISR) is triggered as a defence response to pathogen infection or endophytes. This in turn leads to plant-inherent resistance against pathogens. ISR facilitates plant disease resistance via multiple mechanisms. ISR stimulation alters the structural stability of the cell wall in plants by changing the composition and increasing the wall density, which inhibits pathogen invasion into the cortical tissues (Benhamou *et al*., 1996). In plants, ISR accelerates the expression of plant defensive compounds such as hydrogen peroxide, antioxidant enzymes like peroxidase, polyphenol oxidase, glutathione peroxidase, glutathione reductase, superoxide dismutase, etc. Pathogenesis-related proteins like phytoalexins, chitinase, and phenylalanine ammonia-lyase are also elevated by ISR (Harish *et al*. 2009; Gamalero and Glick, 2011).

PGPE elicits phytohormone biosynthesis as a result of ISR. ISR activates signalling pathways which are usually linked together. Ethylene biosynthetic pathway, jasmonic acid (JA) pathway and salicylic acid (SA) pathyway get modulated according to ISR responses (Pieterse *et al*., 2012). For colonizing the plant host, endophytes has to bypass the ISR-mediated plant defense mechanism (Ma *et al*., 2016). Root colonizing PGPE are greater contestants that induce ISR and are found to impart broad spectrum resistance against phytopathogens.

Endophytic strains like *Bacillus, Pseudomonas*, and *Serratia* trigger plant defence by ISR and induce protection against different pathogens (Kloepper and Ryu, 2006; Pieterse *et al*., 2012). In *Arabidopsis thaliana,* endo bacterial strains of *Bacillus* mediate ISR by activating pathways of SA and JA-ethylene against plant pathogens and inducing resistance (Niu *et al*., 2011). Endophyte inoculation in *A. thaliana* enhance ISR reactions conferring resistance against *P. syringae*varieties (Kavino *et al*., 2007; Kumar *et al*., 2007; Harish *et al*., 2009). Actinomycete inhabitants of *A. thaliana* also modulate ISR-mediated defense pathway. This provides plant protection from the soilborne pathogens *Erwinia carotovora* and *Fusarium oxysporum*. Nevertheless, the defense pathways differed for both pathogens. *E. carotovora* pathogen resistance was activated through the JA- ethylene pathway and SA mediated pathway provided resistance against *F. oxysporum* (Conn *et al*., 2008)*.* PGPE also stimulates ISR response against viral pathogens. Endophytic strains of *Bacillus subtilis*, *B. amyloliquefaciens* and *B. pumilus* facilitated ISR response against the Cucumber Mosaic Virus (CMV) (Zehnder *et al*., 2000). In bananas, endophytes evoked ISR towards Banana Bunchy Top Virus (BBTV) (Kavino *et al*., 2007; Harish *et al*., 2008).

By secreting compounds like chitinase, cellulase, lipopolysaccharides, siderophores, 2,4-diacetyl phloroglucinol, homoserine lactones, volatiles compounds like, monoterpene β-ocimene, limonene, linalool, myrcene, nonanal acetoin, 2,3-butanediol and other metabolites like indole and methyl salicylate, PGPE successfully induces ISR (Lugtenberg and Kamilova, 2009; Russo *et al*., 2012; Rybakova *et al*., 2015). Root colonizing mycorrhizal fungi of higher plants accumulate lignin in the cell wall of host root tissues which act as a structural barrier against pathogens and elicit ISR (Dehne and Schoenbeck, 1979). Endorhizal *Trichoderma sp.* induces chitinase and cellulase secretion when it comes in contact with the pathogen (Russo *et al*., 2012).

IV. APPLICATION OF ENDOPHYTIC MICROBES IN AGRICULTURE

Endophytes originate from the microbial population associated with plants in the rhizosphere, the region of soil surrounding the roots (Hardoim *et al*., 2008). Endophytic microorganisms are highly potent tools capable of improving plant growth, reducing susceptibility to plant pathogens and pests, and enhancing tolerance to plant stress postendophytic inoculation (Watts *et al.*, 2023). Endophyte-associated plants increased fresh and dry weight twofold by improved nutrient uptake during zinc and iron-deficient conditions. The presence of endophytes also increases IAA and phytosiderophore synthesis thereby improving the availability of soil nutrients (Singh *et al*., 2018). Biofortification of crops for essential micronutrients by endophyte application is one of the practical approaches towards high-quality crop production. The most effective strategy for the application of endophytes in crop production is still being studied. The most reliable approach is to use them as soil inoculum or by seed priming (Cocq *et al*., 2017).

Owing to the complex relationship between the existing soil microorganisms and plants, recruiting plant growth-promoting rhizospheric endophytes into field crops is more challenging (Khaksar *et al*., 2016). Priming of seeds or seedlings with PGPE is an intricate process. It is highly competitive with subsequent colonizing microorganisms and is often affected by the biochemical inhibitors of the seeds **(**Gaiero *et al*., 2013**).** Introducing crop-specific plant growth-promoting rhizospheric endophytes can be a potent solution for the specific concern. On the whole, PGPE application within the initial hours of planting is more likely to establish long-term colonization and sustained presence in matured plants (Watts *et al*., 2023). Intensive research for exploiting the crop-specific rhizospheric endophytes would lead to the discovery of potential compatible sources of PGPE.

Rhizospheric endophytes perform a key function in biological nitrogen fixation, solubilization of elements like phosphate, potassium, zinc etc., phytohormone synthesis, plant stress tolerance and disease resistance. These beneficial microbial endophytes could be exploited to improvise soil health to enhance plant growth and productivity.

V. CONCLUSION AND FUTURE PERSPECTIVES

Root endophytes could influence plant growth and development significantly. Knowledge relating to the rhizosphere-plant-microbial interactions can be exploited to improvise productivity of crop plants and maintain ecosystem sustainability. Rhizospheric microbes exhibit competitive, mutualistic as well and neutral relationships with the plants. Mutualistic plant-microbe communications is important since it form endophytic relationships with plants. Plant-rhizospheric endophyte relationships are influenced by the quality of plant-microbe interactions which substantially increase plant growth. The agroecosystem can be improved by employing microbial bio inoculums or engineered bioformulations or their metabolites to increase agricultural productivity. This can be executed by elucidating the mechanism underlying rhizospheric endophyte-mediated plant growth promotion that favours an eco-friendly mode of plant cultivation.

Recent advancements in agrobiotechnology and agromicrobiolgy have made it possible to modify PGPE in an efficient way that could be beneficial for agriculture. Nextgeneration sequencing techniques have transfigured the analysis of endophytic communities (Adeleke *et al.,* 2021). In addition, elucidation of the relative diversity of the microbiota, genomic and proteomic techniques including metagenomics and metaproteomics, have thrown light towards the taxonomic and functional profiling of microbial endophyte communities (Adeleke and Babalola, 2022). Enevthough, identification of many efficient PGPEs were made so far, appropriate techniques to enhance the plant growth-promoting potential through genetic engineering remains a challenge. Moreover, the efficacy of genetically engineered PGPE may be subjected to few challenges but can exhibit vibrant agricultural significance as PGPE has the potential to revolutionize agriculture by making crops more productive and resilient.

To exploit the biological, ecological and functional approaches of endophytic rhizomicrobiome, a concerted effort with a multidisciplinary approach integrating the different advanced areas of research like agro microbiology, agrobiotechnology, nanotechnology, chemical engineering, and material science would be required. This would offer novel microbial formulations which could be employed as potential biofertilizers and biocontrol inoculants at a large scale. These emerging techniques can also be employed to develop potential microbial consortia that would find prospective application in larger agricultural fields. Sustainable agriculture towards eco-friendly and safer food production will be a fruition in the immediate future.

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