Endophytic Microbiome and Plant Growth

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Endophytic bacteria are plant-associated bacteria that live in the internal tissues of the plant without harming the host plant.

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1. Introduction

The plant root is the primary site of interaction between plants and associated microorganisms and constitutes the main components of plant microbiomes that impact crop production. The endophytic bacteria in the root zone have an important role in plant growth promotion. Diverse microbial communities inhabit plant root tissues, and they directly or indirectly promote plant growth by inhibiting the growth of plant pathogens, producing various secondary metabolites. Mechanisms of plant growth promotion and response of root endophytic microorganisms for their survival and colonization in the host plants are the result of complex plant-microbe interactions. Endophytic microorganisms also assist the host to sustain different biotic and abiotic stresses. Better insights are emerging for the endophyte, such as host plant interactions due to advancements in ‘omic’ technologies, which facilitate the exploration of genes that are responsible for plant tissue colonization. Consequently, this is informative to envisage putative functions and metabolic processes crucial for endophytic adaptations. Detection of cell signaling molecules between host plants and identification of compounds synthesized by root endophytes are effective means for their utilization in the agriculture sector as biofertilizers. In addition, it is interesting that the endophytic microorganism colonization impacts the relative abundance of indigenous microbial communities and suppresses the deleterious microorganisms in plant tissues. Natural products released by endophytes act as biocontrol agents and inhibit pathogen growth. The symbiosis of endophytic bacteria and arbuscular mycorrhizal fungi (AMF) affects plant symbiotic signaling pathways and root colonization patterns and phytohormone synthesis. In this review, the potential of the root endophytic community, colonization, and role in the improvement of plant growth has been explained in the light of intricate plant-microbe interactions.

2. Role of Microbial Signals Modulate PGPR Functions

2.1. Regulation of Quorum Sensing by Plant-Associated Bacteria

A population density-based phenomenon known as quorum sensing (QS) makes bacteria able to communicate by synthesizing small signaling molecules. Most widely studied are acyl-homoserine lactone (AHL) molecules produced by Proteobacteria, which move in and out of the cell either passively or actively. Signaling compounds involved in the QS process are called autoinducers [1]. In this process, Gram −ve bacteria use acyl-homoserine lactone (AHL), and Gram +ve bacteria use auto-inducing peptide (AIP) molecule as signaling molecules. The QS Process depends upon the cell density of bacteria. Plant growth and development are also improved by QS. PGPR colonization in the rhizosphere of the plant root exudates is also mentored by Quorum sensing [2]. In the colonization and biofilm formation process on the root surface, plant-associated bacteria used AHL biosensors to produce the AHL substances [3]. QS regulates the process of antibiosis, biofilm formation, exopolysaccharide production, virulence factors secretion, bioluminescence, sporulation, and competence process, in addition to the expression of many PGP attributes. PGPR may influence the cell-to-cell communications among itself and other bacteria and fungi, inhabiting and sharing the microenvironment of roots. This is facilitated through changes in the bacterial density by synchronizing gene expression [4], while some of the bacterial signals are not related to cell density, they may still use chemical signals such as AHL for this purpose. AHL production is commonly found in endophytic *Pseudomonas* spp. than soil-borne *Pseudomonas* spp. and such strains are more available in plant tissues than in the rhizosphere [5]. It has been reported that signaling compounds secreted by one species could induce density-dependent responses in other species [6]. In *S. plymuthica*, an endophyte of rice plants, QS was observed to regulate the antifungal activities by affecting the exoenzymes release, though it was unfavorable towards the production of IAA [7]. *Azospirillum lipoferum* B518, an endophyte of rice plants was able to release AHL signals [8] and

thus terminate the pectinase activity, in addition to enhanced synthesis of siderophore and reduction in the production of IAA. However, it has no impact on cellulase activity [9]. Crosstalk among species having a similar AHL signal or framework has been noticed within the root-associated bacteria of wheat and tomato [10]. AHL-mimics impede bacterial QS and regulate the assertion of plant-beneficial activities [11].

2.2. Role of Quorum Sensing in Plant Defense and Biocontrol

Cellular signal molecules play a key role in regulating plant immune responses and reduce infection by retarding the pathogen proliferation. Bacterial cyclopeptide (CDP), N-acyl-L-homoserine-lactone, AHL produced by QS helps the plant to induce its defense responses. In the case of the ISR of plants, the QS response of bacteria is thought to be of great importance. Endophytic bacteria have been reported to initiate ISR mediating different pathways salicylic acid (SA), Jasmonic acid (JA), and ethylene (ET), which are the signaling pathways involved in ISR induction [12] (Figure 1). Different members of the root endophyte, for example, *Pseudomonas, Serratia, Burkholderia* [13][14][15] have been found effective in inducing plant defense with QS response. The role of QS in ISR elicited by *Serratia marcescens* strain 90–166 in two tobacco plants harboring genes for either AHL degradation (AiiA) or AHL production (AHL) was examined. Root treated with *S. marcescens* strain 90–166 showed increased ISR to the bacterial pathogens (*Pectobacterium carotovorum* subsp. *carotovorum,* and *Pseudomonas syringae* pv. *tabaci*) in AHL plants and ISR was found to be reduced in AiiA plants. On the other hand, bacterial treatment in AHL plants decreased ISR in the *Cucumber mosaic virus*, however; it was improved in AiiA plants [16].

The first line of evidence on defense response in plants induced by AHL was demonstrated with AHL producing isolate—*Serratia liquefaciens* MG1, which could suppress the pathogenicity of *Alternaria alternate*, the tomato fungal leaf pathogen, more effectively, than compared to the AHL negative mutant [17]. Endophytic *Serratia* sp. G3 was reported to confer biocontrol activities through AHL-mediated QS molecules. It was found to produce 10 AHLs signal molecules of which the most abundant AHLs detected were 3-oxo-C6-HSL (N-hexonoyl-homoserine lactone), C4-HSL (N-butanoyl-homoserine lactone), C6-HSL (N-hexanoyl-homoserine lactone), 3-OH-C6-HSL (N-3-hydroxy-hexanoyl-homoserine lactone), and 3-oxo-C7-HSL (N-3-oxo-heptanoyl-homoserine lactone) [18]. This led to a new phenomenon of AHL-induced resistance. Another remarkable finding showed the rhizobacteria *Bacillus pumilus* SE3 could cause changes in root cell walls of the plants challenged with *Fusarium oxysporum*, due to increased callose deposition and phenolic compounds, thereby creating hindrance in fungal infection [19]. A similar study was conducted on *Arabidopsis thaliana*. The plant treated with exogenous AHL molecules generated a priming response by enhanced deposition of callose, lignin, and phenolic materials upon bacterial infection [20].

3. Root Colonization and Rhizosphere Competence

Endophytic colonization involves complex communication between the microbe and the host plant, and usually, it starts by colonizing roots where endophytic microbes require recognition of specific compounds released by the roots [21]. Endophytic bacteria are specialized bacteria that can invade plant roots, and inside the roots they infect adjacent plant tissues [22]. Rhizosphere colonization by PGPR improves plant growth by colonizing the root system and suppresses deleterious rhizosphere microorganisms [23]. PGPR improves the anatomy and plant tissue function present within a particular length from the settled site similar to a shoot; firstly, there is PGPR, which intensifies the intake of nutrients uptake considering the roots of the plant. Alternatively, endophytic plant growth-promoting bacteria trigger plant defense response pathways regulating endophytic colonization. Endophytic colonization by *Klebsiella pneumoniae* 342 activated the ethylene signaling pathway in *Medicago truncatula*. An ethylene insensitive mutant of *Medicago truncatula* was observed to be hypercolonized by Kp342, however, colonization was further found to be reduced with the addition of 1-methylcyclopropene, which is an ethylene function inhibitor. Colonization of *Salmonella enterica* serovar *typhimurium* strain 14,028 (that does not harm plant) was observed to be affected by both salicylic acid (SA)-dependent and independent responses. Mutants lacking extracellular components such as flagella or type III secretion system encoded by *Salmonella* pathogenicity island 1 (TTSS-SPI1) also influenced the endophytic colonization in *Medicago* spp. in either SA-dependent or SA independent responses [24]. Diazotrophic endophytes *Gluconacetobacter diazotrophicus* PAL5 and *Herbaspirillum rubrisulbalbicans* HCC103 inoculation in sugarcane exhibited modulation in the expression pattern of a putative ethylene receptor (SCER1) and two putative ERF transcription factors (SCERF1 and SCERF2). The gene expression profile of these factors could establish efficient or inefficient associations with the diazotrophic endophytes, which shoqed a high or low rate of nitrogen fixation, respectively. This revealed SCER1, SCERF1, and SCERF2 contribution in ethylene signaling cascade(s) that could identify endophytic association [25].

Endophytic bacterial colonization in the rhizosphere and their entrance into the endorhiza could progress with the secretion of cell wall degrading enzymes. An endophytic bacterium *B. phytofirmans* strain PsJN, earlier known as *Pseudomonas* sp. [26], was later classified as *B. phytofirmans* PsJN^T [27]. The *B. phytofirmans* strain PsJN was observed to enter into the endorhiza by secreting endoglucanase and endopolygalacturonase, endo-β-D-cellobiosidase, and exo-β-1,4-glucanase. Colonization of peripheral cylinders, mainly xylem vessels and endodermis barrier by the endophytic bacteria, allowed it to spread inside plants [28]. Root endophytes were described to colonize and penetrate the epidermis below the root hair zone and in root cracks [29]. The transport of endophytes from seeds into plant tissues and roots had been demonstrated by endophytes labeled with a green fluorescent protein and their movement was observed to continue throughout the root [30]. The *B. phytofirmans* strain PsJN migrated from endorhiza to inflorescence organs of grapevine, which would use non-functional vessels, and the strain was detected in the lumen of xylem vessels, which allowed for bacterial progression within plants [28]. Previously it had been assumed that pathogens move through the xylem vessel and endophytes colonized non-functional vessels or transport through the apoplast to reach the aerial parts of the plant [31].

Diazotrophic endophytic bacteria colonize and modify the environment of the host plant through nitrogen fixation. Transcriptomic analysis has indicated the upregulation of *nif* genes that are involved in nitrogen fixation when bacteria attach to the root surface [32]. Bacteria moving from plant rhizosphere to the endosphere should overcome plant defense responses most importantly through the production of reactive oxygen species (ROS) and reactive nitrogen species (RNS). Endophytic bacteria require detoxification of ROS and RNS to adapt to the environment. The importance of ROS detoxification was observed in *Gluconacetobacter diazotrophicus* PAL5 during root colonization by superoxide dismutase and glutathione reductase [33].

4. Endophytic Arbascular Mycorhiza (AMF)

Arbuscular mycorrhizal fungi and root endophytic fungi are the root symbionts that positively affect plant growth and nutrition [34]. The role of AMF in high phosphorus uptake through activating a specific group of phosphate transporters in plants is well documented [34]. The symbiosis between nitrogen-fixing bacteria (rhizobia and actinorhizas), AMF, and plants affects several functional elements, which includes plant symbiotic signaling pathways, root colonization strategies, the formation of the host-microbe interface, and phytohormone release for root development [35]. Co-inoculation of AMF, *Cochliobolus sativus*, *Diaporthe* sp., and *Phoma exigua* var. *exigua* exhibited a beneficial effect on biomass yield in *Verbascum lychnitis*. AMF was found to increase the rate of photosynthesis and abundance of photosystem II core protein (PsbC) revealed an upregulation in plants when the plants were colonized by *Epichloe typhina,* showing an increase when the negative effect of fungal endophyte was attenuated by AMF [36]. Synergistic interaction of endophytic *B. subtilis* and AMF showed a significant increase in shoot and root dry weight, nodulation, nutrient acquisition and alleviate the adverse effect of saline stress in *Acacia gerrardii* [37]. Bacterial diversity and its effect on mycorrhizal symbiosis has been investigated by Deveau et al. [38]. They suggested that bacterial communities in the bulk soil, sporocarps and ectomycorrhizal (EM) root tips of *Tuber melanosporum* exhibited significant changes in sporocarp formation, while little variation was observed in EMs. AMF represent an important niche for interaction with bacteria because the fungi have a large surface area that allows access to photosynthetically derived carbon to the colonizing endophytic bacteria, as observed in *Pinus sylvestris* [39] and *P. muricata* [40]. High throughput sequencing elucidated the impact of AMF inoculation on indigenous root microbial communities, which showed inoculation modified the abundance of indigenous AMF and other members of fungi and showed enrichment in several bacterial communities with the introduction of new bacterial species. Members of *Microbacterium*, *Cellulomonas*, *Burkholderia*, *Streptomyces,* and *Sphingomonas* were observed to have closely interacted with the introduced AMF while members of *Acetobacteraceae*, *Alicyclobacillaceae, Armatimonadaceae*, and *Methylobacteriaceae* were observed to be reduced with the inoculation [41]. An association of endobacterium *Candidatus* Glomeribacter gigasporarum with AMF *Gigaspora margarita* showed a significant increase in fungal primary metabolism and respiration by 50% [42]. Therefore, the interaction between AMF, endophyte and host plant require attention for its holistic role in the alleviation of stress and plant growth.

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