



Endophytic bacteria and their potential application in agriculture: A review

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ABSTRACT

Evolution and biodiversity of plants may depend on their mutual relationship with soil microbes. Endophytes are such microbes that grow within the plants and can be isolated from leaves, stem, roots, seeds, fruits and flowers. This review gives information on the importance of endophytic bacteria and their role in agriculture by giving some of the products which is more beneficial in improving the agriculture and a detailed knowledge about the potential biotechnological applications of endophytic bacteria in agriculture.

Key words: Auxin production, Endophytes, Induced resistance, Nitrogen fixation, Siderophore.

Microorganisms such as fungi and bacteria associate with host plant tissues without causing any adverse effects and promote plant growth by secreting various bioactive substances are called endophytes (Strobel *et al.*, 2004). As reported by Kusari *et al.* (2012), the term endophyte (endo-inside, phyte-plant) was introduced by De Bary in 1866 and the first endophyte was isolated from *Lolium temulentum* by Freeman in 1904. Endophytes are involved in the synthesis of siderophores, in the production of plant hormones, in nitrogen fixation, solubilization of immobilized phosphorus, in nutrient cycling, production of volatile organic compounds, pathogenic resistance and stress tolerance. Normally plant roots help the plant tissues to grow by absorbing the water and nutrients and in addition a rich source of organic acids, amino acids and sugars are released into the soil which makes the soil to colonize with microorganisms around the surface of plant roots. In addition, any seeds during germination also release low molecular weight organic compounds into the surroundings thereby attracting the microbes in the rhizosphere and rhizoplane (Thrall *et al.*, 2007). Many endophytes were reported to be found in rhizosphere (Rosenblueth and Martinez-Romero, 2004). Some selected microorganisms occupy the internal root tissues and reaches the xylem. At this stage the microorganism gets differentiated into pathogenic, associative, symbiotic, or neutralistic adaptation within the plant, and plant beneficial microorganism become endophytic (Hayat *et al.*, 2010). Moreover, endophytes can enter plants through lenticles, wounds (which occurs at emerging site of lateral root and root tips), through vascular system or xylem vessels or germinating radicles, secondary roots, stomata or through foliar damage and also through seeds and leaves (Mano and Morisaki, 2008). Inside seeds, they found to be present in the embryonic stage through the

endospore. Later, when the seeds germinate, the endophytes are released into the external environment and invade into the internal tissues of the growing plants (Johnston-Monje and Raizada, 2011). By this mode, endophytes are transferred from generation to generation. The endophytes entering the plants through various routes can be localized at a single point or may spread to the whole plant (Strobel *et al.*, 2004). The organic compounds of plants act as chemoattractants and facilitate the movement of bacteria by flagellum-mediated chemotaxis (Buschart *et al.*, 2012). Plant secondary metabolites like flavanoids are chemoattractants for colonization of bacteria (Santi *et al.*, 2013; Bhattacharyya and Jha, 2012; Chamam *et al.*, 2013). Plants growing in low phosphate environment release organic acids like malic acid to attract the microbes (Pineros *et al.*, 2002). Similarly, the products of microbes produced during their metabolism influences the plant colonization (Surette *et al.*, 2003). It was reported that endophyte has lipopolysaccharides on their surface and plant derived isoflavanoids recognize these lipopolysaccharide (Chang *et al.*, 2009). Endophytes such as *Azospirillum brasilense* move towards the extract of seeds like cereals with strong adhesion due to its protein called Major Outer Membrane Protein (MOMPS) present in their glycosylated flagellum (Lugtenberg and Kamilova, 2009) whereas *Pseudomonas* species involves the use of type IV pili in colonizing the plants (Reinhold-Hurek *et al.*, 2006). Besides, *Pseudomonas fluorescens* uses secretion system such as SSIII for their entry into plant roots (Preston, 2007) and *Azoarcus* endophyte uses type IV pili and twitching motility for their colonization (Dulla *et al.*, 2012).

Isolation of endophytes: The bacterial endophytes are isolated from all types of plants such as from wild to agricultural crops (Bacon and White, 2000; Arnold, 2007). From a single plant, different species of bacterial endophytes

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are also identified and reported (Gaiero *et al.*, 2013). Endophytic bacteria can be isolated from all the plant organs such as leaf, root, stem and fruits.

Endophytic bacteria and pathogenic bacteria: The beneficial microbes and pathogen invading the plants are differentiated by the plants' defence mechanism. Increase in an intracellular calcium ion by a plant cell can activate such a defence gene mechanism during pathogenic entry and establish the beneficial interaction for endophytes through a casual balance (Vadassery and Oelmüller, 2009). In addition, plants can sense the entry of pathogen by cellwall integrity (Hematy *et al.*, 2009). Further, pathogen-associated (or microbe-associated) molecular patterns (PAMPs/MAMPs) is the another defence response of the plants that recognizes the pathogens (Martínez-Viveros *et al.*, 2010) which act as a true filter in selecting the beneficial microbes (Hardoim *et al.*, 2008). Quorum sensing is the technique that differentiates endophytic bacteria from pathogen where communication process is made by pathogenic bacteria by producing signal molecules called auto inducers to track the density of population.

Plant growth promoting endophytes: "True endophyte" is the term given to endophytes which can able to reinfect the nonhost plants (Rosenblueth and Martínez-Romero, 2006). The clover nodulating bacteria *Leguminosarum trifolii* was isolated from rice roots when it was grown on rotation with clover (Yanni *et al.*, 1997). Specific endophytic bacteria are used in agriculture, medicine, pharmaceuticals and also in pollution control (Taechowisan *et al.*, 2005). In agriculture, through mutual relationship with plants, endophytic bacteria involves in their host plant growth promotion (Beattie, 2006). They are used in agricultural applications as biofertilizer and biocontrol agents (Botta *et al.*, 2013). Phytohormones are essential for growth and development of plants. Plants can adapt to environmental stress by altering their phytohormone levels (Bhattacharyya and Jha, 2012). Even endophytic bacteria that produce phytohormones can regulate the endogenous plant hormone levels and eventually have an influence on plant growth and development (Vanstraelen and Benkova, 2012). In the study reported by Kannan *et al.* (2018), endophytic bacteria from mango roots produces auxin and siderophore.

Phytohormone producing endophytic bacteria: Auxin is the most common phytohormone secreted by endophytic bacteria within the plant to stimulate root growth that results in the formation of lateral, adventitious roots and root hairs thereby increasing the root surface area (Hilbert *et al.*, 2012). For an efficient plant growth promotion, there should be an optimal level of total phytohormone produced by the plant and endophytes (Sgroy *et al.*, 2009). Increase in auxin level stimulates ethylene synthesis in high concentration and vice-versa. Further, cytokinin stimulated apical dominance of roots is counteracting by auxins (Woodward and Bartel,

2005). Indeed, endophytes improve the plant to absorb more nutrients and help to form nodulation in legumes by the production of auxin. Maximum secretion of auxin occurs in logarithmic to stationary phase of endophytes. In addition, auxin can protect the plant by increasing the resistance against external stress (Bianco and Defez, 2009). It was found that during stress condition plants synthesized auxin get depleted and endophytic bacteria helps the plant to cope up with stress by supplying auxin (Spaepen *et al.*, 2007).

Cytokinins produced by microorganisms are correlated with increased plant growth (Arkhipova *et al.*, 2005; Garcia de Salamone *et al.*, 2001). Cytokinin helps in controlling and retarding senescence. Cytokinin-like compound producing endophytes could be used to increase the shelf-life of cut-flowers, leafy vegetables and fruits (Bhore *et al.*, 2010). *Azotobacter chroococcum* was the most important producer of cytokinin when compare to other endophytes like *Azotobacter beijerinckii*, *Pseudomonas fluorescens* and *Pseudomonas putida*. Endophytes isolated from tropical legume crops were found to secrete cytokinin (Dudeja *et al.*, 2012).

Gibberellins are diterpenes involved in seed germination, growth of stem, root, leaf, flower and also fruit (Lange *et al.*, 2005). *Azotobacter* insynthesizing GA-like substances was reported by (Azcón and Barea, 1975) and other diazotrophic endophyte producing GA-like substance were observed in leguminous plants like *Lupinus luteus*, *Phaseolus vulgaris* and *Pisum sativum*. These endophytes increase the GA level in plants by hydrolyzing the inactive form into active GA (Bottini *et al.*, 2004).

Ethylene acts as a signaling molecule between plants and bacteria for plant development, sex determination and fruit ripening which is secreted by plants in response to stress and when secretes in higher amount, can reduce plant performance (Saleem *et al.*, 2007). Endophytes indirectly regulate ethylene level by synthesizing 1-amino cyclopropane-1-carboxylate (ACC) deaminase which hydrolyses ACC into nitrogen and carbon source thereby inhibit the production of ethylene and protect plants against stress (Glick *et al.*, 2007; Blaha *et al.*, 2006; Strader *et al.*, 2010). When endophytes activate induced systemic resistance (ISR), these ethylene act as a signaling molecule in protecting the plants against pathogen (Weingart *et al.*, 2001).

Nitrogen fixation: About 80% of nitrogen in atmosphere is in the form of dinitrogen gas and cannot be taken up by the plants because plants absorb nitrogen only in the form of ammonium and nitrate (Steenhoudt and Vanderleyden, 2000). N-based fertilizers are used to compensate the lacking of such nitrogen bioavailability. Only a lower amount is used by the plants and the remaining part accumulates in soil resulting in nitrate contamination (Santi *et al.*, 2013). Diazotrophic bacteria are able to fix atmospheric nitrogen by forming root nodules in the legume plants with the help

of nitrogenase enzyme (Dobbelaere and Okon, 2007). Most likely, endophytic bacteria like *Azospirillum spp.*, *Azoarcus spp.* and *Herbaspirillum* are involved in biological nitrogen fixation even in non-legume plants (Desbrosses and Stougaard, 2011; Doty *et al.*, 2009). Nitrogen fixing bacterium, *Gluconacetobacter diazotrophicus* was reported for colonization of crops like maize, rice, wheat and other major non-legume crops, such as oilseed rape and tomato (Cocking *et al.*, 2005).

Phosphate solubilization: The phosphorus present as inorganic phosphate remains unavailable for the plants. Endophytes play a central role in getting these phosphorus to the plants by converting them into a soluble form of phosphate with secretion of organic acid or by mineralizing the organic phosphorus and produces different phosphatases thereby solubilizing the phosphorus (Ramachandran *et al.*, 2007). Among other endophytes *Bacillus*, *Pseudomonas*, *Erwinia*, *Agrobacterium* and *Flavobacterium spp.*, are involved in solubilizing the inorganic phosphate compounds by phosphatases (Rodríguez and Fraga, 1999). *Enterobacter*, *Micrococcus*, *Azotobacter*, *Bradyrhizobium*, *Salmonella*, *Alcaligenes*, *Chromobacterium*, *Arthrobacter*, *Streptomyces*, *Thiobacillus*, *Serratia* and *Escherichia spp.*, are some endophytic bacteria that secrete organic acid to solubilize the insoluble phosphorus (Zhu *et al.*, 2011). Endophytic fungal strain of *Aspergillus* isolated from the leaf of *Schima wallichii* was found to possess good phosphate solubilizing and IAA producing ability (Sarbadhikary *et al.*, 2018).

Siderophore production: Siderophores are the low molecular weight iron binding molecules secreted by endophytes for binding of iron present in the soil. With siderophores, endophytes can bind iron and make it available for plant growth. Hydroxamate-type and catecholate-type are the two types of siderophores produced by endophytes (Sharma and Johri, 2003). Moreover, siderophores of bacteria has higher affinity for iron than the pathogenic siderophores of fungus and scavenge the iron present in the soil and prevent pathogen from taking the iron thereby protect the plants from fungal pathogen. *Pseudomonas spp.*, and *Bacillus spp.*, are known endophytes that involve in siderophore production (Pedraza *et al.*, 2007).

Induced systemic resistance: Chemical pesticides when used may lead to pathogenic resistance and sometimes the pesticide against the pathogenic attack is ineffective (Compant *et al.*, 2005). Biocontrol agents make an alternative to such a problem and studies on endophytic bacteria as a control agent shows their ability to prevent the entry of pathogen (Haas and Defago, 2005). In general, plants protect themselves against microbial pathogens by induced resistance. Systemic Acquired Resistance (SAR) is a pathogen induced mechanism and the plant shows hypersensitive reaction in non-infected parts to increase the

resistance for pathogens (Heil and Bostock, 2002). Similar to SAR, endophytic bacteria can stimulate Induced Systemic Resistance (ISR) to protect the plants against the pathogens without showing any hypersensitive reaction (Kang *et al.*, 2007). It helps in the synthesis of ethylene/jasmonic acid pathway other than salicylic acid pathway (Carvalhais *et al.*, 2013). Salicylic acid is said to be induced by SAR (Van Wees *et al.*, 2008).

Bioremediation: Plants can degrade the xenobiotic pollutants only to a lesser extent and results in phytotoxicity (Barac *et al.*, 2004; Weyens *et al.*, 2009). Endophytes associated with plants are involved in degrading the toxins and named as bioremediators (Newman and Reynolds, 2005). Engineered endophytes carrying new metabolic properties proved to be a successful strategy in phytoremediation (Mastretta *et al.*, 2009). During Trichloroethylene (TCE) degradation, vinyl chloride and cis-dichloroethylene are produced which may be toxic when remain in the environment for a long time. Using microbes like dehalococoides group can metabolize TCE to ethylene thereby contributing more to the overall bioremediation costs. Bioremediation is useful for various pollutants like xenobiotics, petroleum, BTEX (benzene, toluene, ethyl benzene, xylene) and even heavy metals (Khan and Doty, 2011). Inoculating the plants with *Pseudomonas putida* protects the plant from the phytotoxic effects of naphthalene (Germaine *et al.*, 2009).

Endophytes in plants stress tolerance: The term 'induced systemic tolerance' (IST) was given for PGPB induced tolerance in plants that brings improved physical and chemical changes in plants (Yang *et al.*, 2009). Endophyte-mediated plants can alter its mechanism by causing reductions in root diameter and root production close to soil surface but increases the root hair length. This alteration may cause increased plant water absorption and decrease susceptibility to drought stress (Thrall *et al.*, 2007). Other tolerance mechanisms such as changes in osmotic levels (the accumulation of solutes to retain cell turgor under water stress), changes in secondary metabolites by stomatal closure has been reported in endophyte-infected plants than endophyte-free plants (Malinowski *et al.*, 2005). Osmotic adjustment in endophytic related plants occur through improved accumulation of solutes (Theocharis *et al.*, 2012). Further, endophytes can promote plant water efficiency even in terms of lesser water availability and promotes soil moisture conservation (Morse *et al.*, 2002). They influence the hormonal status of the plants like ethylene and abscisic acid in response to stress and jasmonic acid known to occur during saline stress is mediated by endophytes (Khan *et al.*, 2011).

When plants exposed to stress, their common adaptation mechanism involves changes in root morphology where phytohormone plays an important role (Wittenmayer

and Merbach, 2005). Such modification in root growth can be influenced by endophytes (Luo *et al.*, 2009). Regulating ACC by ACC deaminase is another characteristic feature of endophytes in exerting beneficial effects on abiotically stressed plants. ACC deaminase causes the hydrolysis of ACC that leads to a decrease in plant ethylene level and increased root growth (Saleem *et al.*, 2007). Nitric oxide production by endophytes also causes changes in root morphology. Endophytes involves in increasing the ethylene levels when the plant is exposed to different levels of stress, as ethylene plays a key role in stress-related signal transduction pathways. Apart from ACC deaminase activity, elevated phosphorous and potassium uptake of plants by endophytes might play a role in salt tolerance (Mayak *et al.*, 2004).

In the study conducted by Mayak *et al.* (2004), the salinity in tomato plants was alleviated by inoculating them with *Achromobacter piechaudii*. *A. piechaudii* eliminates ethylene level in tomato plants by its ACC deaminase production and thereby controls salinity. *Bacillus subtilis* produced volatile organic compounds shown to induce IST in response to saline stress (Ryu *et al.*, 2004). When salt stressed maize was inoculated with *Azospirillum*, the selectivity of sodium, potassium and calcium was altered thereby high K⁺/Na⁺ ratios were noticed by Hamdia *et al.* (2004) in combination with high relative water, chlorophyll and low proline contents. *Azospirillum* mitigating salt stress has been observed in barley seedlings (Zawoznik *et al.*, 2011). By inoculation with genetically modified *A. lipoferum* the damaging effects of salt in wheat seedlings were reduced (Bacilio *et al.*, 2004) and similar positive results were noted

when inoculating chick pea with *Azospirillum* (Siddiqui, 2006). Inoculation of pepper with *Bacillus spp.*, results in relief from osmotic stress (Jung *et al.*, 2003). Endophyte *Piriformospora indica* elevated the ascorbic acid level in barley exposed to salinity (Baltruschat *et al.*, 2008). Several PGPBs, including *Pseudomonas fluorescens*, *Pseudomonas putida*, *Bacillus pumilus*, *Serratia marcescens*, *Paenibacillus alvei*, *Acinetobacter lwoffii*, *Chryseobacterium balustinum*, and *Azospirillum brasilense* colonize roots and protect on a large variety of plant species, including vegetables, crops, and even trees (Loon, 2007).

CONCLUSION

To improve stress tolerance of cultivated plants and to alleviate the deleterious effects of salinity on plant growth, the action of endophytes has emerged as a new field of interest. Many reports have assessed the endophytic effects on grain yield of annual crops with less use of agrochemicals. The inoculants can be formulation containing one or more species prepared with economic carrier material. Mixed inoculants can interact synergistically. Recent studies have shown that the beneficial effects of individual endophyte on plants can be enhanced by co-inoculation with other microorganisms which increased growth and yield providing the plants with more balanced nutrition, and improved absorption of nitrogen, phosphorus and mineral nutrients. The practice of inoculating the plants with microorganisms started in early 20th century where the product with *Rhizobium* sp. was used as formulation (Bashan, 1998). Proper formulation involves the techniques such as inoculum preparations, the selection of an adequate carrier, and the design of correct delivery methods.

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