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Plant growth promoting endophytic bacteria: Boon to agriculture

Verinder Wahla and Shruti Shukla✉

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Abstract

Endophytic bacteria are group of plant associated bacteria that infects different plant tissues without showing any visual symptoms. This has attracted a great interest of different researchers in the field of agriculture. Endophytes promote plant growth and yield, suppress pathogens, help phosphate solubilization and contribute nitrogen assimilation to plants. Some endophytes are seed borne, but others have mechanisms to colonize the plants. With the intention to provide studies on endophytic bacteria, this review focuses on the role of endophytes with respect to plant growth promotion, phytoremediation, bicontrol and their metabolic potential.

Keywords: plant growth potential, phosphate solubilization, nitrogen assimilation, biocontrol, metabolic potential.

Introduction

There are some bacteria, which live attached to plants and have the ability to promote plant growth. Plants select these bacteria contributing most to their fitness by releasing organic compounds through exudates, creating a very selective environment where diversity is low (Beneduzi *et al.*, 2013). The plant associated bacteria colonize the rhizosphere (rhizobacteria), the phyllosphere (epiphytes) and inside plant tissues (endophytes). The term endophyte (Gr. endon, within; phyton, plant) was first coined by De Bary in 1866 and the presence of endophytes was reported by Vogl in 1898 who revealed a mycelium residing in the grass seed of *Lolium temulentum.* Bacteria living within plant tissues for all or part of their life cycle without causing any visible symptoms of their presence are defined as endophytic bacteria. Bacterial endophytes have been known for more than hundred years. The presence of bacteria resident within healthy plants was first reported in 1926 (Hallman *et al.*, 1997). These can be found at many sites in the plant, such as root, stem, leave, berry, seed, and xylem sap (Mercado-Blanco J. and Bakker Pahm, 2007). A wide variety of endophytic bacteria are found in the roots of many plants, comprising hundreds of species The population density of endophytes is highly variable, depending mainly on the bacterial species and plant genotypes but also on the plant developmental stage, inoculum density, and environmental conditions (Weyens N. *et al.*, 2009 and Hallmann and Berg., 2006). Interest in endophytic bacteria has increased in recent years as they play significant role in plant growth promotion and also prevent pathogenic organisms from colonizing host plant. Extensive colonization of the plant tissue by endophytes creates a "barrier effect", where the local endophytes inhibit pathogenic organisms from taking hold (Berg and Hallmann, 2006), which has subsequently increased the interest of researchers in developing the biofertilizers for enhancing crop productivity (Saini *et al.*, 2015). Endophytes can also be beneficial to their host by producing a range of natural products that could be used in medicine, agriculture and industry (Ruby and Raghunath, 2011). Comprehensive research on the understanding of associative and endophytic ecology will be important determinant to magnify benefits from these bacteria. Considering these points in mind, the present status of these aspects is being reviewed.

Author's Address
Department of Microbiology, Kanya Gurukul Campus, Gurukul Kangri University, Haridwar
E-mail: shruti.shukla34@gmail.com

Distribution And Diversity Of Endophytic Bacteria

Endophytic bacteria can be classified into three main categories based on plant –inhabiting life strategies. Obligate endophytes are which proliferate outside of plants and are transmitted through seed rather than originating from the rhizosphere. Facultative endophytes are free living in soil but will colonize plants when the opportunity arises, through infection (Hardoim et al., 2008). Many endophytes which are responsible for plant growth promotion belong to this group. The passive endophytes belong to the third group, they do not actively colonize the plant, but do so as a result of various open injuries along the root hairs. This passive life strategy is less competitive since the cellular machinery required for plant colonization is lacking (Verma *et al.*, 2004; Rosenblueth and Martínez-Romero, 2006), hence it is consider as less efficient as plant growth promoters. Combination of ability to colonize and also appropriation of plant resources leads to distribution of endophytes. First reliable reports about the isolation of endophytic bacteria from surface sterilized plants (Mundt and Hinkle, 1976) more than 200 bacterial genera from 16 phyla have been reported as endophytes. These include both culturable and unculturable bacteria belonging to *Acidobacteria, Actinobacteria, Aquificae, Bacteroidetes, Cholorobi, Chloroflexi, Cyanobacteria, Deinococcus-Thermus, Firmicutes, Fusobacteria, Gem-matimonadetes, Nitrospira, Planctomycetes, Proteobacteria, Spirochaetes and Verrucomicrobiae* (Mengoni *et al.*, 2009; Manter *et al.*, 2010; Sessitsch *et al.*, 2012). However, the most predominant and studied endophytes belong to three major phyla (*Actinobacteria, Proteobacteria and Firmicutes*) and include members of *Azoarcus* (Krause *et al.*, 2006), *Bacillus* (Deng *et al.*, 2011), *Enterobacter* (Taghavi *et al.*, 2010), *Burkholderia* (Weilharter *et al.*, 2011), *Pseudomonas* (Taghavi *et al.*, 2009), and *Stenotrophomonas* (Ryan *et al.*, 2009).

Endophytic Bacteria As Plant Growth Promoters.

Bacterial endophytes play significant role in plant growth promotion by having beneficial impact on host plant. These bacteria promote plant growth in terms of increased germination rates, biomass, leaf area, chlorophyll content, root and shoot length, nitrogen content, protein content, hydraulic activity, yield and tolerance to abiotic stresses like drought, flood, salinity, etc. These also promote plant growth directly through biological nitrogen fixation, phytohormone production, phosphate solubilization, inhibition of ethylene biosynthesis in response to biotic or abiotic stress or indirectly by inducing resistance to pathogen (Bhattacharya and Jha., 2012). Various beneficial characteristics of different endophytic bacteria reported, are being discussed here.

Nitrogen fixation

Nitrogen is an important limiting factor for plant growth in various environmental conditions, but plant themselves cannot directly reduce atmospheric nitrogen. Application of industrially manufactured nitrogen fertilizer has been one of the most frequently used method to provide nitrogen nutrition to the plants to gain high crop productivity. However, excessive and continuous use of chemically synthesized fertilizer can lead to several adverse consequences.(Bhattacharjee *et al.*, 2008) As a result biological nitrogen fixation is considered to be the most potential way to provide fixed form of nitrogen to the plants. Numerous associative and endophytic bacteria are now known to fix atmospheric nitrogen and supply it to the associated host plants. A variety of nitrogen fixing bacteria like *Arthrobacter, Azoarcus, Azospirillum, Azotobacter, Bacillus, Beijerinckia, Derxia, Enterobacter, Gluconoacetobacter, Herbaspirillum, Klebsiella, Pseudomonas, Serratia* and *Zoogloea* have been isolated from the various plants , which provide fixed nitrogen to the associated plants (Reinhold-Hurek and Hurek, 2011). Effective nitrogen supply by endophytic bacteria in sugarcane and kallar grass have suggested biological nitrogen fixation in interior of plants. Moreover, endophytic bacteria isolated from non-leguminous plants like rice, wheat, maize, sorghum also fix the nitrogen in endophytic manner. It is obvious from the reports that the *Gluconoacetobacter diazotrophicus (Acetobacter diazotrophicus)* has the main contribution in endophytic biological nitrogen fixation in sugarcane, and it has the ability to fix the nitrogen approximately 150 Kg N ha -1 year -1 (Dobereiner *et al* . 1993) . *Azoarcus* is recognized as another potential nitrogen fixing obligate endophyte. It penetrate inside the roots of kallar grass and increased the hay yield upto 20–40 t ha -1 year -1 without inclusion of any nitrogen fertilizer (Hurek and Reinhold-Hurek ., 2003). Growth stimulation of wheat, corn, radish, mustard and certain varieties of rice shoots following seed inoculation with a strain of *Rhizobium leguminosarum* in pot experiment has also been reported (Hoflich *et al* . 1995 and Webster *et al*.,1997).These investigations suggest that endophytic bacteria have a considerable potential to increase the productivity leguminous and non-legumes including important cash crop plants.

Phytohormone production

Phytohormones are chemical messengers that influence plant's capacity to respond to its environment. These are organic compounds that are effective at very low concentration they are mostly synthesized in one part of the plant and are transported to another location. They interact with specific target tissues to cause physiological responses, such as growth or fruit ripening. Each response can be the result of two or more phytohormones acting together. Because phytohormones stimulate or inhibit plant growth, they are also termed as plant growth regulators. There are five major groups of hormones: auxins, gibberellins, ethylene, cytokinins, and abscisic acid. Indole-3-acetic acid (IAA) is a phytohormone commonly produce by endophytic bacteria and is mostly considered the most important native auxin (Ashrafuzzaman *et al*., 2009). It functions as an important signal molecule in the regulation of plant development including organogenesis (root growth), tropic responses, cellular responses such as cell expansion, division, differentiation, and gene regulation (Ryu and Patten, 2008).[31]The production of auxin like compounds increases seed production and germination along with increased shoot growth and tillering (Kevin, 2003).65 bacterial endophytes isolated from stem, root and nodule of two soyabean varieties, *Glycine max* and *Glycine soja* and 56 isolates were capable of producing IAA in different concentrations. Hung and Annapurna (2004).

Phosphate solubilization

Phosphorus (P) is major essential macronutrients for biological growth and development. As nitrogen fixation has significant role in enhancing the soil fertility, similarly phosphate solubilization is too equally important. Phosphorus is mostly applied to soil in the form of phosphate fertilizers. Major portion of soluble inorganic phosphate applied to the soil as chemical fertilizer is immobilized rapidly and becomes unavailable to plants (Goldstein, 1986). Endophytic bacteria offer a biological rescue system capable of solubilizing the insoluble inorganic phosphorus of soil and make it available to the plants. These bacteria have ability to convert insoluble phosphate to an accessible form, like orthophosphate, is an important trait in a plant growth promoting bacteria for increasing plant yields (Rodriguez *et al*., 2006). The use of phosphate solubilizing bacteria as inoculants increases the phosphorus uptake by plants (Chen *et al*., 2006), mechanisms for solubilization from organic bound phosphate involve either enzymes namely C-P lyase, non- specific phosphatases and phytases. Whereas, most of the bacterial genera solubilize phosphate through the production of organic acids such as gluconate, ketogluconate, acetate, lactate, oxalate, tartarate, succinate, citrate and glycolate (Khan *et al*., 2009). The most efficient phosphate solubilizers belong to genera *Bacillus, Rhizobium* and *Pseudomonas* amongst bacteria. A total of 98 non-symbiotic endophytic bacterial strains were isolated from soybean root nodules grown in Heilong Jiang province of China and most of the strains could solubilize mineral phosphate (Li *et al*., 2008). Endophytic bacteria were isolated (e.g. *Bacillus sp., Streptomyces luteogriseus* and *Pseudomonas fluorescens*) from *Carex kobomugi* roots (Matsuoka *et al*., 2013), which exhibited both inorganic phosphate solubilization and siderophore production under Fe or P limiting conditions. Their results suggested that colonization of root tissue by these bacteria contribute to the Fe and P uptakes by C kobomugi by increasing availability in the soil. Further, 136 nodule and 90 root endophytic bacterial isolates were obtained from roots and nodules of legumes and non-legumes. In legume roots, 47.8% and in nodules 56% of bacterial endophytes were solubilizing P (Kumar *et al*., 2013).

Siderophore production

At the time of iron-limiting condition, some microorganisms (also biocontrol agents) produce small molecular weight compound, known as siderophore, which has high iron affinity, they solubilize and competitively acquire ferric ion and provide it to plants and cohabiting microorganism, and thus, deprive pathogen (Compant *et al*., 2005). The bacterium that originally synthesized the siderophores takes up the iron siderophore complex by using a receptor that is specific to the complex and is located in the outer cell membrane. 43 bacterial endophytes isolated and assessed siderophore production. Distinct orange halos were observed with all the 12 *Pseudomonas* isolates with *Flavimonas oryzihabitans* isolates having the largest orange halos. They suggested that *Pseudomonas* isolates could therefore be considered high siderophore producers (Catherine *et al*., 2012).

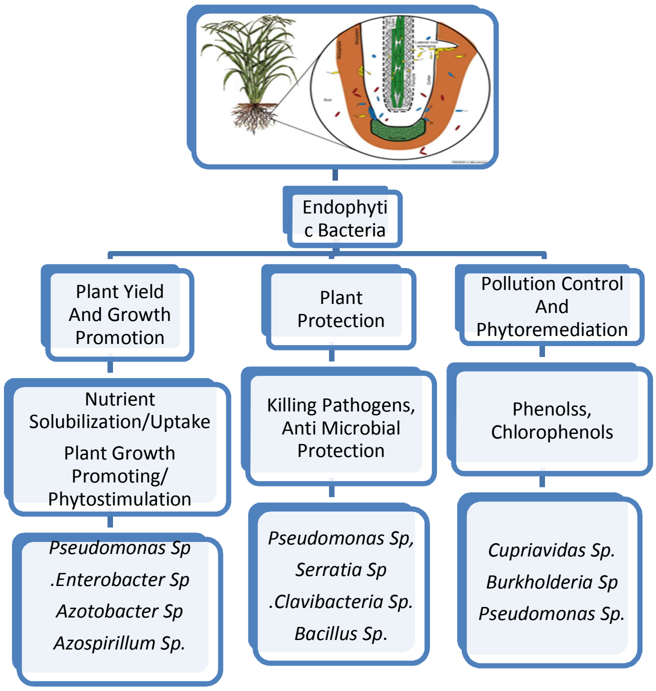

Fig 1. Different functions of endophytic bacteria.

Root Colonization

Plant surface colonization through bacteria is a complicated process that includes relationship between several bacterial traits and genes. There are several steps in colonization process which includes movement of bacteria towards root surface, attachment, distribution along root and growth survival of the bacterial population. In case of endophytic bacteria one additional step is required, that is entry into root and formation of microcolonies inter-or intracellularly (Reinhold-Hurek and Hurek, 2011).Endophytic bacteria mostly arise from the soil, primarily infecting the host plant by colonizing, for example, the cracks formed in lateral root junctions and then rapidly spreading to the intercellular spaces in the root (Chi *et al*., 2005). Whereas other gateways of entering into the plant also exist, for example wounds caused by microbial or nematode phytopathogens, or the stomata found in leaf tissue, root cracks are recognized as the main 'hot spots' for bacterial colonization (McCulley, 2001). Hence, to be ecologically successful, endophytes that infect plants from soil must be competent root colonizers. Apparently, numerous bacterial endophytes are the product of a colonizing process initiated in the root zone (Sturz, et al., 2000), however they may also arise from diverse sources other than the rhizosphere, such as the phyllosphere, the anthosphere, or the spermosphere (Hallman, *et al.*, 1997). *Gluconacetobacter diazotrophicus* and *Herbaspirillum seropedicae* colonize lateral-root junctions in high numbers (James and Olivares 1998). Some rhizospheric bacteria can colonize the internal roots and stems, showing that these bacteria are a source for endophytes (Germaine *et al*., 2004), but also phyllosphere bacteria may be a source of endophytes (Hallmann *et al.*, 1997). It has been proposed that cellulolytic and pectinolytic enzymes produced by endophytes are involved in the infection process (Hallmann *et al.*, 1997). The cellwall–degrading enzymes endogluconase and polygalacturonase seem to be required for the infection of Vitis vinifera by *Burkholderia spp* (Compant *et al.*, 2005).

Endophytic bacteria as biocontrol

The application of microorganism for the control of diseases seems to be one of the most promising ways, as it is eco-friendly and cost-effective. To become an efficient biocontrol agent, micoorganisms should be stable under varying condition of pH, temperature and concentrations of different ions. Nowadays endophytic bacteria are widely used as biocontrol agent as they have capability to prevent plant from adverse effects of pathogenic organisms. To provide benefits to plants, bacterial endophytes follows similar mechanism as described for rhizosphere-associated bacteria (Compant *et al.*, 2005). Endophytic bacteria can exhibit biocontrol activity (antifungal and antibacterial) through production of allelochemicals or antibiotics. Bacteria such as *Pseudomonas* produce 2,4-diacetylphloroglucinol HCN, pyoleutorin, pyrrolnitrin, and phenazines (Lugtenberg and Kamilova, 2009). Bacteria can restrict the growth of pathogens by producing hydrolytic enzymessuch as chitinase, b -1,3-glucanase, protease, laminarinase etc. (Ordentlich *et al* .1988). *Bacillus cepacia* has been reported to destroy *Rhizoctonia solani* , *R. rolfsii* ,and *Pythium ultimum* by producing b -1,3-glucanase (Fridlender et al . 1993). Addition of endophytic bacteria B. cereus 65 directly to soil has been reported to protect cotton seedlings from root rot disease caused by *Rhizoctonia solani* (Pleban *et al* 1997). Secretion of protease and chitinase by endophytic Enterobacter and Pantoea species isolated from cotton were found to protect the plants against fungal pathogen *Fusarium oxysporum f. sp. vasinfectum* (Li *et al* . 2010).

During their interaction with plants, endophytic bacteria results in improving the immune response of plants for future attack by pathogens, a phenomenon called as induced systemic resistance (Van Loon, 2007). In contrast to biocontrol mechanisms, extensive colonization of root system is not required for induced systemic resistance (Lugtenberg and Kamilova, 2009). Induced systemic resistance may induce various genes to immunize the host plant mechanically or metabolically by increasing cell wall strength, alteration of host physiology or metabolic responses, enhanced synthesis of plant defense chemical such as phenolic compounds, pathogenicity related protein, chitinases, peroxidases, phenyl alanine ammonia lyase, phytoalexins, oxidase and or chalcone synthase. These metabolic products shield the host plant from future attacks from pathogens (Compant *et al.*, 2005).

Endophytic microorganisms with the potential to improve phytoremediation

Phytoremediation is a promising, relatively new approach for cleanup of polluted environments. It may be defined as the use of plants to remove, destroy, or sequester hazardous substances from the environment. The technology has so far been used experimentally to remove toxic heavy metals from contaminated soil. One of the major limitations of phytoremediation is that even plants that are tolerant to the presence of these contaminants often remain relatively small, due to the toxicity of the pollutants that they are accumulating or the toxic end products of their degradation. Recently, attention has focused on the role of endophytic bacteria in phytoremediation (reviewed in (Newman, L. A. and Reynolds, C. M. 2005 and Zhuang, X *et al.*, 2007). Plants grown in soil contaminated with xenobiotics naturally recruited endophytes with the necessary contaminant-degrading genes (Siciliano *et al.*, 2001)˙ A phyto-symbiotic strain of *Methylobacterium*, which was isolated from hybrid Poplar was capable of biodegrading numerous nitro-aromatic compounds such as 2,4,6-trinitrotoluene (Van Aken et al. (2004). An application of bacterial endophytes with considerable biotechnological potential was described by (Barac *et al.*, 2004), who showed that engineered *Burkholderia cepacia* G4 could increase plant tolerance to toluene, and decrease the transpiration of toluene to the atmosphere. Because toluene is one of the four components of BTEX contamination, this has the potential to improve phyto-remediation by decreasing toxicity and increasing degradation of the xenobiotic (Barac *et al.*, 2004).

Endophyte and secondary metabolite

Endophyte infection found to alters pattern of gene expression in the host plant. Interaction between endophyte and plant is mainly controlled by the genes of both organism and host plant modulated by the environment. Endophytes from angiosperms as well as gymnosperms have been studied for presence of novel secondary metabolites. Primary metabolites are common in all living cells and are involved in the formation of biomass and generation of energy, in contrary secondary metabolites are produced by one or few species only. These secondary metabolites are low molecular weight compounds, they are not required for growth in pure culture and Are produced as an adaptation for the specific function in nature. Bioprospecting is most frequently used phrase to describe the collection and screening of the biological material for commercial purposes. The importance of natural products in the drug discovery and development has been reported briefly. The natural products produced by endophytes have vast range of bioactivities, representing a vast reservoir offering an enormous potential for exploitation in medicinal and industrial uses (Zhang *et al*., 2006). The natural products produced by endophytes have vast range of bioactivities, representing a vast reservoir offering an enormous potential for exploitation in medicinal, agricultural and industrial uses (Tan and Zou, 2001). Therefore endophytes open up new areas for the biotechnological exploitations.

Conclusion

Endophytic bacteria have ability to accelerate plant growth by different mechanism of action, direct and indirect. The major impact of adoption of such beneficial microorganisms in the field of agriculture is the reduction of use of different agro-chemcials such as pesticides, chemical fertilizers, other artificial chemicals etc. that would make agriculture more productive and sustainable. The challenge and goal is to be able to manage microbial communities to favor plant colonization by beneficial endophytic bacteria. This would be amenable when a better knowledge on endophyte ecology and their molecular interactions is attained. The contributions of this research field may have economic and environmental impacts.

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