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Chapter 1: Entry, colonization and distribution of endophytic microorganisms in plants

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ABSTRACT

Inside plants, microbial communities live as endophytes without causing any disease symptoms or adverse impacts to the host plant. These microbial communities may comprise bacteria, fungi, archaea. In the last few decades endophytic microbes have been broadly used in sustainable agriculture as biofertilizers, biocontrols, or inducers of abiotic stress tolerance. Successful colonization by endophytes in the host plant is a key factor for beneficial plant microbe interaction that results in various plant growth promoting mechanisms. Colonization includes a series of phenomenon such as attachment, entry, motility, transmission, and multiplication of endophytic populations within the host plant. In this chapter we will discuss the mechanisms of colonization, the rhizophagy cycle, and genomic insights of endophytic behaviour and functions that will aid in the advancement and application of endophytes in various aspects of sustainable agriculture.

Keywords: Colonization, Diversity, Endophyte, Rhizophagy cycle, Transmission

1. Introduction

Plants interact with large numbers of microbial communities, in which some of them enter and reside in the plant tissue without causing any disease or otherwise negative impact. These intimately associated microbes are called as endophytes. The word “endophyte” is derived from two Greek words "endon" means within, and "phyton" means plant (Chanway, 1996). The term “endophyte” was first introduced by De Bary (1866) for the microorganisms growing inside plant tissues. Later on, definition and types of endophytes were modified as per researcher observations. Hallmann et al. (1997) have defined endophyte as the microbes that can be isolated from the surface-disinfected tissues of plants, and those microbes that could survive inside their host system without causing any disease. Some researchers have also categorized endophytes on the basis of their types i.e. bacteria or fungi, and their relationship with the plants such as facultative or obligate (Rosenblueth and Martínez-Romero, 2006). However, Haridom et al. (2015) have characterized endophytes on the basis of colonization niche instead of their function. Initially the term “endophyte” was used for the fungi that were documented from the internal cells/tissues of host plants but later on the concept had been changed and the bacterial communities also considered as endophytes (Chanway, 1996; Haridom et al., 2015). Currently, it has been considered that endophytes are present in all plant species (Strobel and Daisy, 2003; Huang et al., 2007), and have been demonstrated to share a complex relationship with their host plants.

2. The rhizosphere and its role in endophytic associations

The entry or colonization of endophytic bacteria into the host plant is a complex phenomenon and involves a series of events. The process of colonization usually starts from the communication between the specific components of the root exudates and the associated microbial communities (de Weert et al., 2002; Rosenblueth and Martínez-Romero, 2006). The rhizosphere can be described as the region of soil adhered to the root and is directly influenced by plants and their associated microbiota, species, growth stages, and the physiology of the host plant. The roots of plants release significant amounts of exudates that influence diverse microbial communities in the rhizosphere (Singh et al., 2017;2018). Root exudates are rich in organic substrates such as carbohydrates, lipids, phenolics, amino acids, phytosiderophores, and flavonoids, these serve as chemoattractants and facilitate the communication between roots and microbes that ultimately help in recruiting bacterial

endophytes from the rhizosphere and start colonization of host plant tissue (Badri and Vivanco, 2009).

There are various reports available showing the evidence of direct involvement of root exudates in initializing the host tissue colonization by microbial entities. Oku et al. (2102) reported the role of amino acids present in root exudates of tomato plants and noticed their role as chemo attractants in the colonization of *Pseudomonas fluorescens* Pf0-1. The evidence in support was gathered from genomic studies pertaining to three genes namely *ctaA*, *ctaB*, and *ctaC* coding for sensory proteins Pfl01_4431, Pfl01_0124, and Pfl01_0354, respectively. These genes are homologous to *Pseudomonas aeruginosa* PAO1 *pctA* gene, exhibiting positive response towards 20, L-amino acids during initial root colonization in tomato (Oku et al., 2012).

In another study Kost et al. (2014) reported the role of oxalate in root colonization by a strain of *Burkholderia*. The plant growth promoting strains were reported to utilize oxalate as a carbon source but pathogenic strains such as *B. glumae*, and *B. plantarii* did not degrade the oxalate. Interestingly, the mutant strain *Burkholderia phytofirmans* PsJN lacked the ability to metabolize oxalate could not colonize lupin and maize, indicating oxalotrophy as a prerequisite for colonization by this endophytic species. In similar ways metabolites like malate and benzoates also act as chemoattractants and provide help in effective colonization of the plant (Lopez-de-Victoria and Lovell, 1993). Flavonoids have also been recognized as one of the important components of root exudates secreted by several plant species and could play effective role in endophytic colonization within the root hairs (Khare et al., 2018). The specificity and effectiveness is considerably determined by the chemical structure of flavonoids as reported by Scervino et al. (2006). There are various reports available confirming the participation of flavonoids as chemotaxis agents during host tissue colonization by endophytic strains of *Rhizobium* (Dharmatilake and Bauer, 1992; Khandual, 2007; Faure et al., 2009). Furthermore, some of the authors have also illustrated the role of flavonoids in effective colonization of host tissue by the endophytic strain *Serratia* sp. EDA2 and *Azorhizobium caulinodans* ORS571 (Webster et al., 1998; Balachandar et al., 2006). In this connection, Steinkellner et al. (2007) also studied the various functional aspects of flavonoids including hyphal growth differentiation and root colonization and concluded the role of flavonoids as effective signalling molecule in the various plant species and their active participation in plant–microbe interaction. In case of legume–rhizobium endophytic

association, flavonoids facilitates chemotactic response and start signalling through nod factors, culminating into symbiotic association (Garg and Geetanjali, 2007).

Strigolactone (SL), the phytohormones secreted by plant roots has also been demonstrated to act as signalling molecules. In a study, López-Ráez et al. (2017) have discussed the role of SL hormone and concluded that treatment was able to activate the release of oligomers acting as signalling molecules and provided help in tissue colonization. Further, Rozpádek et al. (2018) also reported the role of strigolactone as a signalling molecule during the initial colonization of host tissue by endophytic strain of *Mucor* sp.

3. Endophytes and host plant surfaces

The entry or host tissue colonization by microbes is a complex phenomenon and is controlled by signalling molecules, proteins, and/or the secretory products of the plants as well as microbes. Generally, adhesion of a particular microbial strain to the host surface is considered as the first step of colonization. Subsequently, the microbes migrate towards the host surface in response to root exudates via chemotactic movement that precedes attachment (Begonia and Kremer, 1994) (**Fig.1.**).

The attachment of bacterial cells to the plant surface is one of the most crucial step during endophyte colonization; in this process various structural components such as flagella, fimbriae, pili and the secretory products like EPS (exopolysaccharides), LPS (lipopolysaccharide) or cell surface polysaccharides may directly involve in the attachment (Sauer and Camper, 2001). There are various reports available that confirm the role of microbial appendages in surface attachment. Croes et al. (1993) have reported the role of flagella in the primary attachment of *Azospirillum brasilense* with the root surface of wheat. However, flagella-deficient mutants did not show attachment with the wheat roots. Dörr et al. (1998) have reported the association of type IV pili in the attachment of endophytic strain *Azoarcus* sp. BH72, with the root surface of rice. These small appendages flagella and pili have also been described to act as propellers leading to movement of microbes towards the plant surface via chemotactic response and developed a weak attractive force to withstand any repulsive barriers that might originate due to electrostatic charges present on the cell envelope (Berne et al., 2015; Zheng et al., 2015).

The bacterially synthesized product exopolysaccharides (EPS) could also facilitate bacterial attachment to the host plant surface during early stages of colonization as mentioned by Janczarek et al. (2015) for *Rhizobium leguminosarum*. Similarly, Meneses et al. (2011) have

mentioned the role of EPS secreted by endophyte *Gluconacetobacter diazotrophicus* in the attachment and colonization of rice root endosphere. However, besides attachment EPS have also been reported to offer other advantages including protection of bacterial cell and host plant from oxidative damage and elevated level of free radicals. Similarly, Marczak et al. (2017) reported the role of exopolysaccharides secreted by *Rhizobium* in symbiosis and colonization with the legume plants. Balsanelli et al. (2010) have described the role of lipopolysaccharide (LPS) secreted by endophytic bacterial strain *Herbaspirillum seropedicae* in attachment and colonization of maize root. In addition, reports are also available in literature emphasizing the role of lipopolysaccharides N-acetyl glucosamine in binding with lectins present in maize root, and concluded their involvement as an essential in bacterial attachment and subsequent colonization in the host roots (Balsanelli et al., 2013).

Plants respond differentially after attachment of microbial strain with the host surface that leads to significant variation in the pattern of gene expression as reported by Sauer and Camper (2001) in case of *Pseudomonas putidia*. Further, in depth study was conducted by De Mot and Vanderleyden (1991) pertaining the proteomics of outer membrane porin F (OprF) proteins and their role in attachment and host tissue colonization by *Pseudomonas fluorescens*. OprF is a multifunctional outer membrane proteins commonly present on the outer surface of *Pseudomonas* and helps in the attachment with various surfaces and molecules (Bodilis and Barray, 2006). The function of OprF proteins as adhesive had also been observed in various plant species such as barley, sunflower, maize (De Mot and Vanderleyden, 1991) cucumber, and tomato roots (Crespo and Valverde, 2009). Similarly, arabinogalactan proteins (AGPs), a glycoprotein present on the plant's cell wall has also been documented to help in initial colonization of microbes at the different growth stages of the plants (Nguema-Ona et al., 2013). In a similar fashion, the important contribution of flagellin, a globular proteins of flagella during the attachment with host surface as reported in case of *Azospirillum brasilense* strain (Rodríguez Navarro et al., 2007) is also evidenced. The responsible genes for the glycosylation of flagellin and lipopolysaccharides are the same, and it had been seen that mutation in these genes results in impairment of the attachment of *Azospirillum brasilense* (Rossi et al., 2016).

4. Entry and colonization of plants by bacterial endophytes

After establishing in the rhizosphere and rhizoplane, bacterial endophytes are known to make their way inside the plant root, with sub-populations ranging from 10^5 - 10^7 cfu/g fresh weight

(Hallmann, 2001). During colonization, pattern and sites are specific for each of the endophytic strain (Zachow et al., 2010). After attachment to the host surface, endophytes start penetrating in order to enter to the host tissue. Endophytic bacteria, however, may prefer various sites to enter the plant tissue; the most preferred entrance path is via root zone, aerial parts of the plants, including stems, leaves, flowers and cotyledons (Zinniel et al., 2002). The process of penetration into the host can be mediated by passive or active process. The passive penetration occurs at the site of cracks present in the areas of root emergence, root tips that are created by deleterious organisms (Hardoim et al., 2008), whereas active penetration is achieved through attachment and proliferation of EPS, LPS, structural components, quorum sensing, providing considerable help in the movement and multiplication of endophytes inside the plant tissues (Böhm et al., 2007; Dörr et al., 1998; Duijff et al., 1997; Suárez-Moreno et al., 2010).

There are numerous reports present that have shown different entry modes and colonization patterns of endophytic strains. Apart from this, specialized and frequently studied interaction between nodulating bacteria and legumes is less well understood. Although not experimentally proven, it has been proposed that endophytic bacteria produce low levels of cell-wall degrading enzymes as compared to phytopathogens that could produce deleteriously high levels of these enzymes and thus endophytes may avoid triggering plant defence systems (Elbeltagy et al., 2000). Furthermore, another way by which endophytic bacteria escape their detection as a pathogen by host tissue is maintenance of low cell densities (2-6 log cfu/gfw) as compared to pathogenic bacteria

During entry or colonization, microbial strains prefer the site having thin surfaces such as root hairs, or the elongation zone of the apical root meristem serving as one of the preferred site of rhizoplane. At favourable sites, endophytic microbial strain secretes some lytic enzymes such as lysozymes, cell wall degrading enzymes, cellulases, facilitating the entry of bacterial strain through hydrolysing external covering or plant cells (Compant et al., 2005; Reinhold-Hurek et al., 2006; Naveed et al., 2014). Reinhold-Hurek et al. (2006) have reported *Azoarcus* sp. BH72 species at the entry site having endoglucanase, a kind of cellulase and further confirmed the role of endoglucanase in endophyte colonization by mutant analysis of *eglA* gene. The mutant endophyte lacking *eglA* genes was unable to colonize plant tissues, whereas wild type strain invaded and colonized the host surface. Suzuki et al. (2005) have reported a non-specific wax-degrading enzyme helping in colonization of *Streptomyces galbus* on the *Rhododendron*. Taking together, all these

previous investigations have shown the ability of bacteria to utilize certain plant metabolites as an essential mechanism for successful establishment as endophyte.

Successful colonization of endophyte involves compatible plant-microbe interactions. As the endophyte invades the host surface, it is recognized by the plant and cross-talk of signalling molecules is initiated (Rosenblueth and Martínez-Romero, 2006; Compant et al., 2010; Brader et al., 2014). The colonization of endophytic microbes depends upon various factors including microbial strains, host genotype, biotic and abiotic factors, nutrients limitation, UV light etc. and most importantly, the strains better adapted to these factors are comparatively more efficient in getting entry into the plant tissues via various routes like natural opening such as hydathodes, stomata etc. followed by colonization of host tissue (Hallmann, 2001; Hardoim et al., 2015). To date, numerous reports have presented the details regarding the colonization routes of endophytic microbial strains. In a study, Alvarez et al. (2010) reported the colonization pattern of *Ralstonia solanacearum* strain and concluded that strains firstly attached to surface followed by invasion of the extension of roots such as root hairs, root tips, lateral roots; however, they may also prefer to enter through mechanical binding during initial colonization. After entering the host tissues, strain may spread themselves upwardly in the plants via xylem vessels. In another study, Compant and his co-workers (2005; 2008) studied the colonization route of strain *Paraburkholderia phytofirmans* PsJN and reported that endophytic strain entered through the exodermis layer of roots following cortical cells and crossed the barrier of endodermal layer leading to its access to the central zone. From this zone, the endophyte spread towards the upper part of plants through xylem vessels. At the site of xylem colonization, very few bacterial strains are able to cross the endodermal layer. Generally, the endophytic strains prefer unsubsided endodermal cells of the apical root zone to get entry inside host tissues (James et al., 2002; Roncato-Maccari et al., 2003; Compant et al., 2005; Gasser et al., 2011). Studies have demonstrated low concentrations of nutrients in the xylem tissues or plant sap that could be sufficient for the growth of endophytic bacteria (Madore and Webb, 1981; Sattelmacher, 2001; Bacon and Hinton, 2006). At the site of cortex colonization, once the bacterial strains have crossed the exodermal barrier, they may remain localized at the site of entry (Timmusk et al., 2005) or move deeper into the host system such as cortex of the plant (Roncato-Maccari et al., 2003; Compant et al., 2005; Gasser et al., 2011).

In phyllosphere colonization, bacterial strains are firstly attached to the surface of leaf and randomly distributed throughout. Some of them may enter into the leaf tissue via natural

openings such as stomata, hydathodes and influence their local environment. At this site, bacterial strains multiply and form a thin layer of biofilm, however, some of them may enter into the leaf tissue and start surviving as endophytes (Yaron and Römmling, 2014). In a study James et al. (2001) have reported stomata as an entry site during colonization of *Gluconobacter diazotrophicus* strain in the sugarcane.

Currently, various reports have confirmed the utilization of plant nutrient as source of energy by the endophytic microbes (Rasche et al., (2009) and carbon has been reported as the most preferred source for growth and survival of endophytes (Krause et al., 2011; Malfanova et al., 2013). However, Iwai et al. (2003) have reported endophytic *pseudomonads* isolated from cucumber plants with the ability to utilize L-arabinose as one of the most abundant sugars available in the xylem fluid utilized by endophyte as nutrient source. In another study, Krause et al. (2011) reported alcohol dehydrogenases as an essential component in the colonization of *Azoarcus* sp. BH72 in waterlogged rice. They also concluded from their study that, in waterlogged rice, alcohol was present abundantly and may be utilized as carbon source by the colonizing bacterial strain *Azoarcus* sp. BH72.

Some reports have described the local colonization of endophytic strains and further there was no transmission to other parts of the host after successful colonization as documented in the case *Pseudomonas fluorescens* strain invading olive plants (Prieto et al., 2011). Similar studies by Moulin et al. (2015) have also reported the colonization of *Rhizobium* strain only in the symbiotic zone of root nodule of legume. After colonization or entry of endophytic strains into the plant tissue, they may colonize locally or spread systemically (Afzal et al., 2019) to the upper parts of the host tissues. It has been mentioned that 10^3 - 10^4 cfu/gfw population density is established in the ground tissue of root and stem (Compant et al., 2010). The above ground migration of endophytes depends upon their functional and physiological requirements and the strain could move upwardly as above ground tissues are well adapted for the particular environment and endophytic niche (Hallmann, 2001). The movement of the endophytic strain within the host tissue is however, largely executed by lateral appendages such as flagella, pilli, or the transpiration stream of the plants similar to transport of plant nutrients (Compant et al., 2005; James et al., 2002).

5. Plant internalization and extraction of nutrients from microbes in the rhizophagy cycle:

Recent studies have shown that plants internalize soil microbes (bacteria and fungi) into plant roots and oxidatively extract nutrients from them in a process that has been termed 'rhizophagy' (Paungfoo-Lonhienne et al., 2010, 2013) or 'rhizophagy cycle' (White et al., 2018). In the rhizophagy cycle, plants attract soil microbes to the root tip meristem with root exudates, and then internalize microbes into root meristem cells, which have soft cell walls. The precise mechanism by which microbes are internalized into root meristem cells remains unknown but may involve previously discussed processes. After internalization microbes become situated in the periplasmic space (between cell wall and plasma membrane) of root cells. The root cell plasma membrane secretes superoxide (produced on membrane bound NADPH oxidases) onto microbes and this strips the cell walls from microbes, resulting in formation of microbe protoplasts (White et al., 2018). Superoxide causes microbe protoplasts to become porous and leak nutrients that are absorbed by root cells. Through the action of cyclosis (cytoplasm rotation or streaming) in root cells, microbe protoplasts are circulated around the periphery of root cells and broken into many smaller protoplasts, rapidly replicating the intracellular microbes. Intracellular microbes in root cells accumulate in the tips of root hairs and trigger root hair elongation by an as yet unknown mechanism; without microbes root hair elongation does not occur (Verma et al., 2017). Microbe protoplasts are ejected into the soil through pores that form in the elastic wall at tips of elongating root hairs after a wave of vacuolar expansion propagates from the base of the root hair to the tip. It is unknown what triggers the periodic ejection of microbes from root hairs. Once ejected from root hairs, microbes reform cell walls and move out into the rhizosphere soil to acquire additional nutrients. The rhizophagy cycle appears to occur in all plants that form root hairs, and may be an important mechanism for acquisition of nitrogen and soil micronutrients like iron, zinc and magnesium (White et al., 2015; 2018). It seems evident that the rhizophagy cycle is a mechanism whereby plants employ soil microbes as carriers of difficult to acquire nutrients (**Fig. 2**). Work is still being done to evaluate details of the rhizophagy cycle mechanism and determine its importance to plant growth (Domka, Rozpadek and Turnau, 2019).

6. Genomic insights into host and endophyte interaction:

Comparative genomics studies of close mutualistic or pathogenic endophytic strains have shown very similar genetic contents (López-Fernández et al., 2015; Sheibani-Tezerji et al., 2015) and this similarity may be used in differentiating strains as a pathogen or beneficial microbe for the host on the basis of genetic analyses. López-Fernández et al. (2015) when

comparing the virulence genes in endophytes and other symbiotic bacteria lead to the conclusion that there are only minor differences between endophytes and pathogens and that the similarities between these two groups are set above the species level.

In plant microbe interactions secretion of protein is a determinant factor and is required for beneficial interaction. The transport of specific proteins for particular functions such as biocontrol is of considerable importance as the immunity of host plant is enhanced multiple orders after transport of effector proteins from microbes to the host, and thus helping in marking a particular microbe as a endophyte or parasite (Jones and Dangl, 2006). These effector proteins are recognized by the plant immune system and are demonstrated to participate in activation of effector-triggered immune responses particularly T3SSs and T6SSs genes in the plant (Jones and Dangl, 2006). Interestingly, in the case of mutualistic endophytes, genes for T3SSs are missing (Hardoim et al., 2015; Mitter et al., 2017, Reinhold-Hurek and Hurek, 2011). Reinhold-Hurek and Hurek (2011) have proposed the view that missing T3SSs showed characteristics of an endophytic life style. Iniguez et al. (2005) have also reported a similar observation; mutants of T3SSs of *Typhimurium* showed increased endophytic colonization in *Medicago truncatula*. However, some reports are also available that have shown endophytic establishment of *Pseudomonas* strain in the root even in the presence of T3SS gene (Preston et al., 2001). Endophytic microbes generally contain genes for T6SSs, conferring them with the potential for plant–microbe interaction (Mitter et al., 2013, Reinhold-Hurek and Hurek, 2011). There are various reports in the literature showing the contribution of T6SSs genes in the control of phytopathogens and disease management (Mattinen et al., 2008; Schell et al., 2007). In addition, Nod genes are also responsible factors for nodulation and symbiotic association between host and bacterial strain. Various authors have reported nod genes in the genome sequence of nodule-forming bacteria such as *Burkholderia phymatum* strain STM815A (Amadou et al., 2008.), *Bradyrhizobium japonicum* USDA110 (Kaneko et al., 2002), and *Frankia* spp. strain CcI3 (Normand et al., 2007).

7. Transmission of endophytes:

Plant associated microbes interact with plants through various ways, and during colonization they may vector horizontally (plant or soil to plant), vertically (parent plant to seed) or in a mixed way (Bright and Bulgheresi, 2010). The transmission mode may also depend upon the ecological and evolutionary relationship between host and microbe. Microbes displaying symbiotic relationship with the host plant generally follow vertical transmission (Moran,

2006) and during transmission, parents (seeds, and pollens) fulfil nutrient requirements. In many vertically transmitted symbioses, the symbiont is obligate and spends its entire life inside the host plant (Bright and Bulgheresi, 2010; Herre et al., 1999). Some of the fungal species are known to prefer vertical mode of transmission via the seeds and is well documented by various authors (Schardl, 2001; Wilkinson and Sherratt, 2001; Foster and Wenseleers, 2006). Generally bacterial endophytes employ a horizontal route of transmission and it has been also seen that bacterial count in the soil or in other environment is higher than the seed or the seed grown under artificial conditions (Hardoim et al., 2012). Some of the naturally existing bacteria, after entry to the host tissue, may act as endophytes and thus may be transmitted to the next generation in a similar way as pathogens. Many of the bacterial species are known to infect different plant species through the similar horizontal mode (Ma et al., 2011; Compant et al., 2005; Khan et al., 2012). The horizontal transmission mode of beneficial bacteria appears optimal for the host system, because endophytic strains provide resistance against various biotic and abiotic stresses that may directly influence the plants (Carroll, 1988; Schlaeppi and Bulgarelli, 2015; Bulgarelli et al., 2012; Lundberg et al., 2012; Peiffer et al., 2013; Schlaeppi et al., 2014; Edwards et al., 2015; Verma et al., 2017). Some of the endophytic bacterial strains, however, may employ a mixed mode of transmission and this may depend upon the surrounding environmental conditions. There are various reports available that have confirmed the existence of bacterial inhabitants as endophyte inside the seed or the vertical mode of transmission. In the last few decades, the microbiome of seeds is gaining high importance and attracting researchers to explore their hidden potentials (Verma and White, 2019). The endophytic microbial isolates from different plant seeds have been reported by various authors from hosts such as alfalfa (Charkowski et al., 2001), rice (Hardoim et al., 2012; Cottyn et al., 2001; Bacilio-Jiménez et al., 2001; Kaga et al., 2009; Okunishi et al., 2005; Verma et al., 2017), maize (Liu et al., 2013; Johnston-Monje and Raizada, 2011), tobacco (Mastretta et al., 2009), coffee (Vega et al., 2005), quinoa (Pitzschke, 2016), common bean (López-López et al., 2010), grapevine (Pitzschke, 2016), barley (S Zawoznik et al., 2014), and pumpkin (Fürnkranz et al., 2012). Different parts of seeds such as seed coat, endosperm, and embryonic tissue have been reported to be occupied by various types of bacterial communities (Mitter et al., 2017; Compant et al., 2011; Glassner et al., 2018). Rhizomes of plants may also act as seed and harbour various groups of bacteria as endophyte (Kumar et al., 2016). There are numerous bacterial genera such as *Bacillus*, *Pseudomonas*, *Klebsiella*, *Burkholderia*, *Paenibacillus*, *Staphylococcus*, *Pantoea*, *Acinetobacter* that have been the most commonly reported seed endophytes. Inside seeds,

these endophytic bacterial strains mediate various beneficial interactions such as nutrient acquisition, synthesis of growth regulators, along with biotic and abiotic stress management. However, it is not necessary that all the inhabiting seed bacteria colonize the seedlings or are transferred from parent to offspring plants.

The best evidence in support of vertical transfer of endophytes via seed comes from the studies demonstrating overlap in endophyte taxa between seed and seedling (Ferreira et al., 2008; Gagne-Bourgue et al., 2013; Ringelberg et al., 2012; Verma and White, 2019). Other studies have also reported the continued transfer of particular endophytic strains across generations in rice and maize (Mukhopadhyay et al., 1996; Liu et al., 2012), thus supporting vertical transfer. And at least in maize, there is some evidence of long-term conservation in the seed endophytic community; noteworthy, seeds of some genetically related maize hybrids have been found to host similar bacterial taxa (Liu et al., 2012). In an experimental investigation based on terminal restriction fragment length polymorphism (RFLP) of 16S rDNA, the presence of the same genera across several genotypes of maize, including its ancestor teosinte was documented (Johnston-Monje and Raizada, 2011). Further, different bacterial species can colonize the seeds horizontally from the external environment via flowers, fruits and during seed dispersal.

8. Endophytic diversity

In the last few years, exploration and isolation of endophytic microbes have been carried out using new technologies and “omics”. Every plant species, which is growing in the natural environment has endophytic microbial communities, and it is a peculiar exception if any plant does not have an endophytic community of microbes (Partida-Martinez and Heil, 2011; Afzal et al., 2019). Currently more than 16 phyla or 200 genera of bacteria have been reported as endophytes in various plant species. These bacterial genera include both cultivable and uncultivable strains (Malfanova et al., 2013); Proteobacteria followed by Actinobacteria, Firmicutes, and Bacteroidetes (Edwards et al., 2015) are the most dominant phyla, and contain numerous groups of bacteria such as *Pseudomonas* (Kumar et al., 2016), *Bacillus* (Deng et al., 2011) *Burkholderia* (Weilharter et al., 2011), *Enterobacter* (Taghavi et al., 2010), *Serratia* (Taghavi et al., 2009).

There are various reports that show similar types of observations inside roots. Marques et al. (2015) reported Gamma-Proteobacteria (including *Enterobacter*, *Pseudomonas* and *Stenotrophomonas* genera) was the dominant group in the endosphere of sweet potato. Sun et al. (2008) studied endophytic bacterial diversity of rice roots and revealed Beta-Proteobacteria (27.08% of the total clones) was the most dominant phylum among bacteria communities, whereas *Stenotrophomonas* was the dominant genus among all the endophytes. Similar observations in rice were reported by Ferrando and Scavino (2015) and Ren et al. (2015a). Mendes et al. (2007) studied the endosphere of sugarcane, and found *Burkholderia*, *Pantoea*, *Pseudomonas*, and *Microbacterium* were the common genera whereas *Burkholderia* genus was the most dominant in the endosphere. Similarly Han et al. (2009) studied the interior root tissues of moso bamboo, and reported, 22 bacterial genera in which majority of root endophytic bacteria belong to phyla of Proteobacteria (67.5%). *Burkholderia* was the most common genus inside the roots, comprising 35.0% of the total isolates from root domain. However, in the leaf microbiome the endophytic bacterial genera were also dominated by *Proteobacteria*, *Actinobacteria* and *Firmicutes* as reported by Costa et al. (2012) in the common bean plants. The overlapping of endophytic bacterial communities in the root and leaf confirm upward movement of bacterial group with the translocation through xylem. It is likely that the concentration of available nutrients in xylem is decreasing along the plant axis. This can explain the facts that the diversity and population density of endophytic bacteria decreases with the distance from the root and that only a small number of bacteria reaches the upper parts of shoots, the leaf apoplast and reproductive organs such as flowers, fruits and seeds (Compant et al., 2010; Frnkranz et al. 2011).

Endophytic bacteria are generally present in plant parts, including roots, stems, leaves, seeds, fruits, tubers and ovules (Benhizia et al., 2004; Hallmann et al., 1997) (Table 1). Since 1940, there have been numerous reports of indigenous endophytic bacteria in various plant tissues including seeds and ovules (Mundt and Hinkle, 1976), tubers (Trevet, 1948), roots (Philipson and Blair, 1957), stems and leaves (Henning and Villforth, 1940), and fruits (Samish et al., 1961; Sharrock et al., 1991). The microbiomes of the root endosphere is significantly less diverse than the rhizosphere and bulk soil (Liu et al., 2017) and it has been estimated, inside the root microbial population varies in between 10^4 – 10^6 per gram of root tissues which is very much less than the bulk or rhizospheric soil (10^6 – 10^9) bacterial cells (Bulgarelli et al., 2013). The diversity of endophytic microbes varies with their height, altitude, and organs.

The diversity of endophytic communities varies with the differences in host plant species, genotype, location growth stages of the host plant, and the local environmental (Hallmann and Berg, 2006; Shi et al., 2014 Ding and Melcher, 2016). Besides these factors, the omics approaches used to enumerate endophytic populations are also a major limiting factors. During isolation of endophyte strains surface sterilization of the host tissues is the first or important phenomenon that influences the diversity and composition of endophytic communities, which in nature, concentration and treatment time of the sterilizing agent also influences the diversity and population of endophytic microbial communities (Hallmann and Berg, 2006, Hallmann et al., 1997). It has been found that different plant species growing in the same soil have different patterns of microbial communities. Graner et al. (2003) reported diversity in the endophytic bacterial communities in different cultivars of *Brassica napus*, which were growing in the same type of soil. In another study, Rashid et al. (2012) observed different endophytic bacterial communities in the same tomato species which were growing in different types of soil; similar observations were reported in the in roots of canola plants grown at three different places (Germida et al., 1998). The surrounding of the host plant, including biotic and abiotic stress factors, also govern the diversity of endophytic microbial communities. In a study Siciliano et al. (2001) reported that plants growing in a petroleum contaminated site had endophytic bacterial strains that contained genes for degrading the contaminants.

9. Conclusion or future prospective

Endophytic microbes are fascinating life forms surviving in a range of host plants. Their entry inside the intricate system of diverse plants holds a promising research area in the field of microbiology and agricultural sciences. Involvement of different plant as well as microbe-derived molecules has been proposed to play an important role in development of symbiotic relationship with different plants. Their entry inside the plants has been documented to offer different advantages to host systems including tolerance to numerous biotic and abiotic stresses and enhancement in crop nutrients and productivity. In spite of well-developed plant immune system, endophytes have evolved the strategy for entry into the host system. It has also been proposed that plants have evolved to internalize microbes for purposes of acquiring nutrients and defence. So far limited numbers of genes have been identified and proposed to contribute in the invasion of hosts in order to enter tissues of the host plant. Many endophytes employ natural openings for entering into the host system and their survival and transfer to other parts of the host system is considerably determined by the nutrient materials available

in the xylem sap. In the rhizophagy cycle microbial endophytes are internalized into root cells prior to hardening of the plant root cell walls in the root tip meristem; and they are ejected back into the soil from tips of root hairs through pores that form in the wall of the expanding root hair tip. Identifying the genes facilitating the entry of endophytes inside the host tissue could be utilized to inoculate desirable microbial endophytes into plants.. For instance, the identification of genes favouring the colonization of nitrogen fixing microorganism and exploring the existing biochemical mechanisms to overcome the plant immune response could be a viable option to enhance the agricultural productivity without, or minimizing, the application of fertilizers. Further, detailed investigations of a huge diversity of endophytic microorganisms could help in identifying unexplored genes having possible application as drugs or medicines. The integrated involvement of scientists from different disciplines, including microbiology, agriculture, biochemistry, genetics and molecular biology, could be helpful in developing a better understanding of how plant endophytes function, and in identifying applications..

References:

- Afzal, I., Shinwari, Z.K., Sikandar, S. and Shahzad, S., 2019. Plant beneficial endophytic bacteria: Mechanisms, diversity, host range and genetic determinants. *Microbiol. Res.* 221, p. 36-49
- Álvarez, B., Biosca, E.G., López, M.M., 2010. On the life of *Ralstonia solanacearum*, a destructive bacterial plant pathogen. *Current research, technology and education topics in applied microbiology and microbial biotechnology.* 1, 267-279.
- Amadou, C., Pascal, G., Mangenot, S., Glew, M., Bontemps, C., Capela, D., Carrère, S., Cruveiller, S., Dossat, C., Lajus, A., Marchetti, M., 2008. Genome sequence of the β -

rhizobium *Cupriavidus taiwanensis* and comparative genomics of rhizobia. *Genome Res.* 18(9), 1472-1483.

- Amaresan, N., Jayakumar, V., Kumar, K. and Thajuddin, N., 2012. Isolation and characterization of plant growth promoting endophytic bacteria and their effect on tomato (*Lycopersicon esculentum*) and chilli (*Capsicum annuum*) seedling growth. *Annals of microbiology*, 62(2), pp.805-810.
- Araújo, W.L., Maccheroni, W. and Azevedo, J.L., 2009. Characterization of an endophytic bacterial community associated with *Eucalyptus* spp. *Genetics and Molecular Research*, 8(4), pp.1408-1422.
- Aung, T.N., Nourmohammadi, S., Sunitha, E.M. and Myint, M., 2011. Isolation of endophytic bacteria from green gram and study on their plant growth promoting activities. *Intl J Appl Biol Pharmacol Tech*, 2, pp.525-536.
- Babu, A.G., Kim, J.D. and Oh, B.T., 2013. Enhancement of heavy metal phytoremediation by *Alnus firma* with endophytic *Bacillus thuringiensis* GDB-1. *Journal of hazardous materials*, 250, pp.477-483.
- Bacilio-Jiménez, M., Aguilar-Flores, S., del Valle, M.V., Pérez, A., Zepeda, A., Zenteno, E., 2001. Endophytic bacteria in rice seeds inhibit early colonization of roots by *Azospirillum brasilense*. *Soil Biol Biochem.* 33(2), 167-172.
- Bacon, C.W., Hinton, D.M., 2007. Bacterial endophytes: the endophytic niche, its occupants, and its utility. In *Plant-associated bacteria* (pp. 155-194). Springer, Dordrecht.
- Badri, D.V., Vivanco, J.M., 2009. Regulation and function of root exudates. *Plant Cell Environ.* 32(6), 666-681.
- Bai, Y., D'Aoust, F., Smith, D.L. and Driscoll, B.T., 2002. Isolation of plant-growth-promoting *Bacillus* strains from soybean root nodules. *Canadian Journal of Microbiology*, 48(3), pp.230-238.
- Balachandar, D., Sandhiya, G.S., Sugitha, T.C.K., Kumar, K., 2006. Flavonoids and growth hormones influence endophytic colonization and in planta nitrogen fixation by a diazotrophic *Serratia* sp. in rice. *World J Microbiol Biotechnol.* 22(7), 707-712.

- Balsanelli, E., Serrato, R.V., De Baura, V.A., Sasaki, G., Yates, M.G., Rigo, L.U., Pedrosa, F.O., De Souza, E.M., Monteiro, R.A., 2010. *Herbaspirillum seropedicae* rfbB and rfbC genes are required for maize colonization. *Environ Microbiol.* 12(8), 2233-2244.
- Balsanelli, E., Tuleski, T.R., de Baura, V.A., Yates, M.G., Chubatsu, L.S., de Oliveira Pedrosa, F., de Souza, E.M., Monteiro, R.A., 2013. Maize root lectins mediate the interaction with *Herbaspirillum seropedicae* via N-acetyl glucosamine residues of lipopolysaccharides. *PLoS One.* 8(10), p.e77001.
- Begonia, M.F.T., Kremer, R.J., 1994. Chemotaxis of deleterious rhizobacteria to velvetleaf (*Abutilon theophrasti* Medik.) seeds and seedlings. *FEMS Microbiol Ecol.* 15(3-4), 227-235.
- Benhizia, Y., Benhizia, H., Benguedouar, A., Muresu, R., Giacomini, A., Squartini, A., 2004. Gamma proteobacteria can nodulate legumes of the genus *Hedysarum*. *Syst Appl Microbiol.* 27(4), 462-468.
- Berne, C., Ducret, A., Hardy, G.G., Brun, Y.V., 2015. Adhesins involved in attachment to abiotic surfaces by Gram-negative bacteria. *Microbiol Spectr.* 3(4).
- Bhore, S.J., Ravichantar, N. and Loh, C.Y., 2010. Screening of endophytic bacteria isolated from leaves of Sambung Nyawa [*Gynura procumbens* (Lour.) Merr.] for cytokinin-like compounds. *Bioinformation*, 5(5), p.191.
- Bodilis, J., Barray, S., 2006. Molecular evolution of the major outer-membrane protein gene (*oprF*) of *Pseudomonas*. *Microbiol.* 152(4), 1075-1088.
- Böhm, M., Hurek, T., Reinhold-Hurek, B., 2007. Twitching motility is essential for endophytic rice colonization by the N₂-fixing endophyte *Azoarcus* sp. strain BH72. *Mol Plant Microbe Interact.* 20(5), 526-533.
- Brader, G., Compant, S., Mitter, B., Trognitz, F., Sessitsch, A., 2014. Metabolic potential of endophytic bacteria. *Current Opin Biotechnol.* 27, 30-37.
- Bright, M., Bulgheresi, S., 2010. A complex journey: transmission of microbial symbionts. *Nat Rev Microbiol.* 8(3), p.218.
- Brimecombe, M.J., De Leij, F.A.A.M., Lynch, J.M., 2007. Rhizodeposition and microbial populations. The rhizosphere biochemistry and organic substances at the soil-plant interface. CRC Press, Boca Raton, Florida. 73-109.

- Bulgarelli, D., Rott, M., Schlaeppi, K., van Themaat, E.V.L., Ahmadinejad, N., Assenza, F., Rauf, P., Huettel, B., Reinhardt, R., Schmelzer, E., Peplies, J., 2012. Revealing structure and assembly cues for *Arabidopsis* root-inhabiting bacterial microbiota. *Nat.* 488(7409), 91.
- Bulgarelli, D., Schlaeppi, K., Spaepen, S., van Themaat, E.V.L. and Schulze-Lefert, P., 2013. Structure and functions of the bacterial microbiota of plants. *Annual review of plant biology*, 64, pp.807-838.
- Cankar, K., Kraigher, H., Ravnikar, M. and Rupnik, M., 2005. Bacterial endophytes from seeds of Norway spruce (*Picea abies* L. Karst). *FEMS microbiology letters*, 244(2), pp.341-345.
- Carroll, G., 1988. Fungal endophytes in stems and leaves: From latent pathogen to mutualistic symbiont. *Ecol.* 69, 2–9.
- Chanway, C.P., 1996. I Endophytes: they're not just fungi! *CP Chanway. Can J Bot.* 74, 321-322.
- Charkowski, A.O., Sarreal, C.Z., Mandrell, R.E., 2001. Wrinkled alfalfa seeds harbor more aerobic bacteria and are more difficult to sanitize than smooth seeds. *J Food Prot.* 64(9), 1292-1298.
- Chen, L., Luo, S., Xiao, X., Guo, H., Chen, J., Wan, Y., Li, B., Xu, T., Xi, Q., Rao, C. and Liu, C., 2010. Application of plant growth-promoting endophytes (PGPE) isolated from *Solanum nigrum* L. for phytoextraction of Cd-polluted soils. *Applied soil ecology*, 46(3), pp.383-389.
- Chung, E.J., Park, J.H., Park, T.S., Ahn, J.W. and Chung, Y.R., 2010. Production of a phytotoxic compound, 3-phenylpropionic acid by a bacterial endophyte, *Arthrobacter humicola* YC6002 isolated from the root of *Zoysia japonica*. *The Plant Pathology Journal*, 26(3), pp.245-252.
- Compant, S., Clément, C., Sessitsch, A., 2010. Plant growth-promoting bacteria in the rhizo- and endosphere of plants: their role, colonization, mechanisms involved and prospects for utilization. *Soil Biol Biochem.* 42(5), 669-678.

- Compant, S., Kaplan, H., Sessitsch, A., Nowak, J., Ait Barka, E., Clément, C., 2008. Endophytic colonization of *Vitis vinifera* L. by *Burkholderia phytofirmans* strain PsJN: from the rhizosphere to inflorescence tissues. *FEMS Microbiol Ecol.* 63(1), 84-93.
- Compant, S., Mitter, B., Colli-Mull, J.G., Gangl, H., Sessitsch, A., 2011. Endophytes of grapevine flowers, berries, and seeds: identification of cultivable bacteria, comparison with other plant parts, and visualization of niches of colonization. *Microb Ecol.* 62(1), 188-197.
- Compant, S., Reiter, B., Nowak, J., Sessitsch, A., Clément, C., Barka, E.A., 2005. Endophytic Colonization of *Vitis vinifera* L. by Plant Growth- Promoting Bacterium *Burkholderia* sp. Strain PsJN. *Appl Environ Microbiol.* 71, 1685–1693.
- Costa, L.E.D.O., Queiroz, M.V.D., Borges, A.C., Moraes, C.A.D. and Araújo, E.F.D., 2012. Isolation and characterization of endophytic bacteria isolated from the leaves of the common bean (*Phaseolus vulgaris*). *Brazilian Journal of Microbiology*, 43(4), pp.1562-1575.
- Cottyn, B., Regalado, E., Lanoot, B., De Cleene, M., Mew, T.W., Swings, J., 2001. Bacterial populations associated with rice seed in the tropical environment. *Phytopathol.* 91(3), 282-292.
- Crespo, M.C.A., Valverde, C., 2009. A single mutation in the oprF mRNA leader confers strict translational control by the Gac/Rsm system in *Pseudomonas fluorescens* CHA0. *Curr Microbiol.* 58(2), 182-188.
- Croes, C.L., Moens, S., van Bastelaere, E., Vanderleyden, J., Michiels, K.W., 1993. The polar flagellum mediates *Azospirillum brasilense* adsorption to wheat roots. *Microbiol.* 139(9), 2261-2269.
- De Bary, A., 1866. *Morphologie und Physiologie der Pilze, Flechten, und Myxomyceten.* Hofmeister's handbook of physiological Botany. W.Engelmann, Leipzig.
- De Mot, R., Vanderleyden, J., 1991. Purification of a root-adhesive outer membrane protein of root-colonizing *Pseudomonas fluorescens*. *FEMS Microbiol Lett.* 81(3), 323-327.

- de Weert, S., Vermeiren, H., Mulders, I.H., Kuiper, I., Hendrickx, N., Bloemberg, G.V., Vanderleyden, J., De Mot, R., Lugtenberg, B.J., 2002. Flagella-driven chemotaxis towards exudate components is an important trait for tomato root colonization by *Pseudomonas fluorescens*. *Mol Plant Microbe Interact.* 15(11), 1173-1180.
- Deng, Z.S., Zhao, L.F., Kong, Z.Y., Yang, W.Q., Lindström, K., Wang, E.T. and Wei, G.H., 2011. Diversity of endophytic bacteria within nodules of the *Sphaerophysa salsula* in different regions of Loess Plateau in China. *FEMS microbiology ecology*, 76(3), pp.463-475.
- Dharmatilake, A.J., Bauer, W.D., 1992. Chemotaxis of *Rhizobium meliloti* towards nodulation gene-inducing compounds from alfalfa roots. *Appl Environ Microbiol.* 58(4), 1153-1158.
- Dias, A.C., Costa, F.E., Andreote, F.D., Lacava, P.T., Teixeira, M.A., Assumpção, L.C., Araújo, W.L., Azevedo, J.L. and Melo, I.S., 2009. Isolation of micropropagated strawberry endophytic bacteria and assessment of their potential for plant growth promotion. *World Journal of Microbiology and Biotechnology*, 25(2), pp.189-195.
- Ding, T., Melcher, U., 2016. Influences of plant species, season and location on leaf endophytic bacterial communities of non-cultivated plants. *PloS one* 11, e0150895
- Domka, A.M., Rozpadek, P., Turnau, K. 2019. Are endophytes merely mycorrhizal copycats? The role of fungal endophytes in the adaptation of plants to metal toxicity. *Frontiers Microbiol* DOI: 10.3389/fmicb.2019.00371.
- Dörr, J., Hurek, T., Reinhold-Hurek, B., 1998. Type IV pili are involved in plant–microbe and fungus–microbe interactions. *Mol Microbiol.* 30(1), 7-17.
- Duijff, B.J., Gianinazzi-Pearson, V., Lemanceau, P., 1997. Involvement of the outer membrane lipopolysaccharides in the endophytic colonization of tomato roots by biocontrol *Pseudomonas fluorescens* strain WCS417r. *New Phytol.* 135(2), 325-334.
- Edwards, J., Johnson, C., Santos-Medellín, C., Lurie, E., Podishetty, N.K., Bhatnagar, S., Eisen, J.A., Sundaresan, V., 2015. Structure, variation, and assembly of the root-associated microbiomes of rice. *Proc Natl Acad Sci.* 112(8), E911-E920.

- Edwards, R.A., McNair, K., Faust, K., Raes, J. and Dutilh, B.E., 2015. Computational approaches to predict bacteriophage–host relationships. *FEMS microbiology reviews*, 40(2), pp.258-272.
- Elbeltagy, A., Nishioka, K., Suzuki, H., Sato, T., Sato, Y.I., Morisaki, H., Mitsui, H., Minamisawa, K., 2000. Isolation and characterization of endophytic bacteria from wild and traditionally cultivated rice varieties. *Soil Sci Plant Nutr.* 46(3), 617-629.
- El-Deeb, B., Fayez, K. and Gherbawy, Y., 2013. Isolation and characterization of endophytic bacteria from *Plectranthus tenuiflorus* medicinal plant in Saudi Arabia desert and their antimicrobial activities. *Journal of plant interactions*, 8(1), pp.56-64.
- Faria, D.C., Dias, A.C.F., Melo, I.S. and de Carvalho Costa, F.E., 2013. Endophytic bacteria isolated from orchid and their potential to promote plant growth. *World Journal of Microbiology and Biotechnology*, 29(2), pp.217-221.
- Faure, D., Vereecke, D., Leveau, J.H., 2009. Molecular communication in the rhizosphere. *Plant and soil.* 321(1-2), 279-303.
- Ferrando, L. and Fernández Scavino, A., 2015. Strong shift in the diazotrophic endophytic bacterial community inhabiting rice (*Oryza sativa*) plants after flooding. *FEMS microbiology ecology*, 91(9).
- Ferreira, A., Quecine, M.C., Lacava, P.T., Oda, S., Azevedo, J.L., Araújo, W.L., 2008. Diversity of endophytic bacteria from *Eucalyptus* species seeds and colonization of seedlings by *Pantoea agglomerans*. *FEMS Microbiol Lett.* 287(1), 8-14.
- Forchetti, G., Masciarelli, O., Alemano, S., Alvarez, D. and Abdala, G., 2007. Endophytic bacteria in sunflower (*Helianthus annuus* L.): isolation, characterization, and production of jasmonates and abscisic acid in culture medium. *Applied microbiology and biotechnology*, 76(5), pp.1145-1152.
- Foster, K.R., Wenseleers, T., 2006. A general model for the evolution of mutualisms. *J Evol Biol.* 19(4), 1283-1293.
- Fürnkranz, A., Köster, I., Chun, K.J., Metzner, A., Mathew, S., Konstantinidou, M., Ouyang, F., Kuck, K.H., 2011. Cryoballoon temperature predicts acute pulmonary vein isolation. *Heart Rhythm.* 8(6), 821-825.

- Fürnkranz, M., Lukesch, B., Müller, H., Huss, H., Grube, M., Berg, G., 2012. Microbial diversity inside pumpkins: microhabitat-specific communities display a high antagonistic potential against phytopathogens. *Microb Ecol.* 63(2), 418-428.
- Gagne-Bourgue, F., Aliferis, K.A., Seguin, P., Rani, M., Samson, R., Jabaji, S., 2013. Isolation and characterization of indigenous endophytic bacteria associated with leaves of switchgrass (*Panicum virgatum* L.) cultivars. *J Appl Microbiol.* 114(3), 836-853.
- Gagne-Bourgue, F., Aliferis, K.A., Seguin, P., Rani, M., Samson, R. and Jabaji, S., 2013. Isolation and characterization of indigenous endophytic bacteria associated with leaves of switchgrass (*Panicum virgatum* L.) cultivars. *Journal of applied microbiology*, 114(3), pp.836-853.
- Garg, N., Geetanjali., 2007. Symbiotic nitrogen fixation in legume nodules: process and signaling. A review. *Agron Sustain Dev.* 27, 59-68.
- Gasser, I., Cardinale, M., Müller, H., Heller, S., Eberl, L., Lindenkamp, N., Kaddor, C., Steinbüchel, A., Berg, G., 2011. Analysis of the endophytic lifestyle and plant growth promotion of *Burkholderia terricola* ZR2-12. *Plant and soil.* 347(1-2), 125.
- Germida, J.J., Siciliano, S.D., Renato de Freitas, J., Seib, A.M., 1998. Diversity of root associated bacteria associated with field-grown canola (*Brassica napus* L.) and wheat (*Triticum aestivum* L.). *FEMS Microbiol. Ecol.* 26, 43-50.
- Glassner, H., Zchori-Fein, E., Yaron, S., Sessitsch, A., Sauer, U., Compant, S., 2018. Bacterial niches inside seeds of *Cucumis melo* L. *Plant and soil.* 422(1-2), 101-113.
- Govarathanan, M., Mythili, R., Selvankumar, T., Kamala-Kannan, S., Rajasekar, A. and Chang, Y.C., 2016. Bioremediation of heavy metals using an endophytic bacterium *Paenibacillus* sp. RM isolated from the roots of *Tridax procumbens*. *3 Biotech*, 6(2), p.242.
- Granér, G., Persson, P., Meijer, J. and Alström, S., 2003. A study on microbial diversity in different cultivars of *Brassica napus* in relation to its wilt pathogen, *Verticillium longisporum*. *FEMS microbiology letters*, 224(2), pp.269-276.

- Hallmann, J., 2001. Plant interactions with endophytic bacteria. In *Biotic Interactions in Plant-Pathogen Associations*, ed. MJ Jeger, NJ Spence, pp. 87–120. Wallingford, UK: CABI Publ.
- Hallmann, J., Berg, G., 2006. Spectrum and population dynamics of bacterial root endophytes. In *Microbial root endophytes*: Springer, pp. 15-31.
- Hallmann, J., Quadt-Hallmann, A., Mahaffee, W., Kloepper, J., 1997. Bacterial endophytes in agricultural crops. *Can. J. Microbiol.* 43, 895-914.
- Hallmann, J., Quadt-Hallmann, A., Mahaffee, W.F., Kloepper, J.W., 1997. Bacterial endophytes in agricultural crops. *Can J Microbiol.* 43(10), 895-914.
- Han, J., Xia, D., Li, L., Sun, L., Yang, K. and Zhang, L., 2009. Diversity of culturable bacteria isolated from root domains of moso bamboo (*Phyllostachys edulis*). *Microbial ecology*, 58(2), pp.363-373.
- Hardoim, P.R., Hardoim, C.C., Van Overbeek, L.S., Van Elsas, J.D., 2012. Dynamics of seed-borne rice endophytes on early plant growth stages. *PLoS One.* 7(2), p.e30438.
- Hardoim, P.R., Van Overbeek, L.S., Berg, G., Pirttilä, A.M., Compant, S., Campisano, A., Döring, M., Sessitsch, A., 2015. The hidden world within plants: ecological and evolutionary considerations for defining functioning of microbial endophytes. *Microbiol Mol Biol Rev.* 79(3), 293-320.
- Hardoim, P.R., van Overbeek, L.S., van Elsas, J.D., 2008. Properties of bacterial endophytes and their proposed role in plant growth. *Trends Microbiol.* 16(10), 463-471.
- Hassan, S.E.D., 2017. Plant growth-promoting activities for bacterial and fungal endophytes isolated from medicinal plant of *Teucrium polium* L. *Journal of advanced research*, 8(6), pp.687-695.
- Henning, K., Villforth F., 1940. Experimentelle untersuchungen zur frage der bacteriesymbiose in höheren pflanzen und ihre beeinflussung durch 'Leitemente'. *Biochemische Zeitschrift*, 305: 299–309.
- Herre, E.A., Knowlton, N., Mueller, U.G., Rehner, S.A., 1999. The evolution of mutualisms: exploring the paths between conflict and cooperation. *Trends Ecol Evol.* 14(2), 49-53.

- Huang, W.Y., Cai, Y.Z., Hyde, K.D., Corke, H., Sun, M., 2007. Endophytic fungi from *Nerium oleander* L (Apocynaceae): main constituents and antioxidant activity. *World J Microbiol Biotechnol.* 23(9), 253-1263.
- Iniguez, A.L., Dong, Y., Carter, H.D., Ahmer, B.M., Stone, J.M., Triplett, E.W., 2005. Regulation of enteric endophytic bacterial colonization by plant defenses. *Mol Plant Microbe Interact.* 18(2), 169-178.
- Iwai, H., Usui, M., Hoshino, H., Kamada, H., Matsunaga, T., Kakegawa, K., Ishii, T., Satoh, S., 2003. Analysis of sugars in squash xylem sap. *Plant Cell Physiol.* 44(6), 582-587.
- James, E.K., Gyaneshwar, P., Mathan, N., Barraquio, W.L., Reddy, P.M., Iannetta, P.P., Olivares, F.L., Ladha, J.K., 2002. Infection and colonization of rice seedlings by the plant growth-promoting bacterium *Herbaspirillum seropedicae* Z67. *Mol Plant Microbe Interact.* 15(9), 894-906.
- James, E.K., Olivares, F.L., de Oliveira, A.L., dos Reis Jr, F.B., da Silva, L.G., Reis, V.M., 2001. Further observations on the interaction between sugar cane and *Gluconacetobacter diazotrophicus* under laboratory and greenhouse conditions. *J Exp Bot.* 52(357), 747-760.
- Janczarek, M., Rachwał, K., Cieśla, J., Ginalska, G., Bieganowski, A., 2015. Production of exopolysaccharide by *Rhizobium leguminosarum* bv. trifolii and its role in bacterial attachment and surface properties. *Plant and soil.* 388(1-2), 211-227.
- Jasim, B., Jimtha, C.J., Jyothis, M. and Radhakrishnan, E.K., 2013. Plant growth promoting potential of endophytic bacteria isolated from *Piper nigrum*. *Plant Growth Regulation*, 71(1), pp.1-11.
- Jasim, B., Jimtha, C.J., Jyothis, M. and Radhakrishnan, E.K., 2013. Plant growth promoting potential of endophytic bacteria isolated from *Piper nigrum*. *Plant Growth Regulation*, 71(1), pp.1-11.
- Jasim, B., Joseph, A.A., John, C.J., Mathew, J. and Radhakrishnan, E.K., 2014. Isolation and characterization of plant growth promoting endophytic bacteria from the rhizome of *Zingiber officinale*. *3 Biotech*, 4(2), pp.197-204.
- Joe, M.M., Devaraj, S., Benson, A. and Sa, T., 2016. Isolation of phosphate solubilizing endophytic bacteria from *Phyllanthus amarus* Schum & Thonn: Evaluation of plant

growth promotion and antioxidant activity under salt stress. *Journal of applied research on medicinal and aromatic plants*, 3(2), pp.71-77.

Johnston-Monje, D., Raizada, M.N., 2011. Conservation and diversity of seed associated endophytes in *Zea* across boundaries of evolution, ethnography and ecology. *PLoS One*. 6(6), p.e20396.

Jones, J.D., Dangl, J.L., 2006. The plant immune system. *Nat.* 444:323–29.

Kaga, H., Mano, H., Tanaka, F., Watanabe, A., Kaneko, S., Morisaki, H., 2009. Rice seeds as sources of endophytic bacteria. *Microbes Environ.* 0904220080-0904220080.

Kaneko, T., Nakamura, Y., Sato, S., Minamisawa, K., Uchiumi, T., Sasamoto, S., Watanabe, A., Idesawa, K., Iriguchi, M., Kawashima, K., Kohara, M., 2002. Complete genomic sequence of nitrogen-fixing symbiotic bacterium *Bradyrhizobium japonicum* USDA110. *DNA research*. 9(6), 189-197.

Karthikeyan, B., Joe, M.M., Islam, M.R. and Sa, T., 2012. ACC deaminase containing diazotrophic endophytic bacteria ameliorate salt stress in *Catharanthus roseus* through reduced ethylene levels and induction of antioxidative defense systems. *Symbiosis*, 56(2), pp.77-86.

Khan, Z. and Doty, S.L., 2009. Characterization of bacterial endophytes of sweet potato plants. *Plant and soil*, 322(1-2), pp.197-207.

Khan, Z., Guelich, G., Phan, H., Redman, R., Doty, S., 2012. Bacterial and yeast endophytes from poplar and willow promote growth in crop plants and grasses. *ISRN Agronomy*.

Khandual, S., 2007. Flavonoids as signaling molecules and regulators of root nodule development. *Dynamic soil, Dynamic plant*. 1(2), 83-94.

Khare, E., Mishra, J., Arora, N.K., 2018. Multifaceted interactions between endophytes and plant: Developments and Prospects. *Front Microbiol.* 9.

Kost, T., Stopnisek, N., Agnoli, K., Eberl, L., Weiskopf, L., 2014. Oxalotrophy, a widespread trait of plant-associated *Burkholderia* species, is involved in successful root colonization of lupin and maize by *Burkholderia phytofirmans*. *Front Microbiol.* 4, 421.

- Krause, A., Ramakumar, A., Bartels, D., Battistoni, F., Bekel, T., Boch, J., Böhm, M., Friedrich, F., Hurek, T., Krause, L., Linke, B., 2006. Complete genome of the mutualistic, N₂-fixing grass endophyte *Azoarcus* sp. strain BH72. *Nature Biotechnol.* 24(11), 1384.
- Kumar, A., Singh, R., Yadav, A., Giri, D.D., Singh, P.K. and Pandey, K.D., 2016. Isolation and characterization of bacterial endophytes of *Curcuma longa* L. *3 Biotech*, 6(1), p.60.
- Kumar, V., Kumar, A., Pandey, K.D. and Roy, B.K., 2015. Isolation and characterization of bacterial endophytes from the roots of *Cassia tora* L. *Annals of microbiology*, 65(3), pp.1391-1399.
- Latif Khan, A., Ahmed Halo, B., Elyassi, A., Ali, S., Al-Hosni, K., Hussain, J., Al-Harrasi, A. and Lee, I.J., 2016. Indole acetic acid and ACC deaminase from endophytic bacteria improves the growth of *Solanum lycopersicum*. *Electronic Journal of Biotechnology*, 19(3), pp.58-64.
- Liu, H., Carvalhais, L.C., Crawford, M., Singh, E., Dennis, P.G., Pieterse, C.M. and Schenk, P.M., 2017. Inner plant values: diversity, colonization and benefits from endophytic bacteria. *Frontiers in microbiology*, 8, p.2552.
- Liu, Y., Zuo, S., Xu, L., Zou, Y., Song, W., 2012. Study on diversity of endophytic bacterial communities in seeds of hybrid maize and their parental lines. *Arch Microbiol.* 194(12), 1001-1012.
- Liu, Y., Zuo, S., Zou, Y., Wang, J., Song, W., 2013. Investigation on diversity and population succession dynamics of endophytic bacteria from seeds of maize (*Zea mays* L., Nongda108) at different growth stages. *Ann Microbiol.* 63(1), 71-79.
- Lopez-de-Victoria, G., Lovell, C.R., 1993. Chemotaxis of *Azospirillum* species to aromatic compounds. *Appl Environ Microbiol.* 59(9), 2951-2955.
- Lòpez-Fernàndez, S., Sonego, P., Moretto, M., Pancher, M., Engelen, K., Pertot, I., Campisano, A., 2015. Whole-genome comparative analysis of virulence genes unveils similarities and differences between endophytes and other symbiotic bacteria. *Front Microbiol.* 6, p.419.

- López-López, A., Rogel, M.A., Ormeno-Orrillo, E., Martínez-Romero, J., artínez-Romero, E., 2010. Phaseolus vulgaris seed-borne endophytic community with novel bacterial species such as *Rhizobium endophyticum* sp. nov. Syst Appl Microbiol. 33(6), 322-327.
- López-Ráez, J.A., Shirasu, K., Foo, E., 2017. Strigolactones in plant interactions with beneficial and detrimental organisms: the Yin and Yang. Trends Plant Sci. 22(6), 527-537.
- Lundberg, D.S., Lebeis, S.L., Paredes, S.H., Yourstone, S., Gehring, J., Malfatti, S., Tremblay, J., Engelbrekton, A., Kunin, V., Del Rio, T.G., Edgar, R.C., 2012. Defining the core *Arabidopsis thaliana* root microbiome. Nat. 488(7409), 86.
- Ma, Y., Rajkumar, M., Luo, Y., Freitas, H., 2011. Inoculation of endophytic bacteria on host and non-host plants—effects on plant growth and Ni uptake. J Hazard Mater. 195, 230-237.
- Madore, M., Webb, J.A., 1981. Leaf free space analysis and vein loading in *Cucurbita pepo*. Can J Bot. 59(12), 2550-2557.
- Majeed, A., Abbasi, M.K., Hameed, S., Imran, A. and Rahim, N., 2015. Isolation and characterization of plant growth-promoting rhizobacteria from wheat rhizosphere and their effect on plant growth promotion. Frontiers in microbiology, 6, p.198.
- Malfanova, N., Lugtenberg, B.J. and Berg, G., 2013. Bacterial endophytes: who and where, and what are they doing there. Molecular microbial ecology of the rhizosphere, 1, p.2.
- Malfanova, N., Lugtenberg, B.J., Berg, G., 2013. Bacterial endophytes: who and where, and what are they doing there. Molecular microbial ecology of the rhizosphere. 1, p.2.
- Marczak, M., Mazur, A., Koper, P., Żebracki, K., Skorupska, A., 2017. Synthesis of rhizobial exopolysaccharides and their importance for symbiosis with legume plants. Genes. 8(12), 360.
- Marques, A.C., Santos, L., Costa, M.N., Dantas, J.M., Duarte, P., Gonçalves, A., Martins, R., Salgueiro, C.A. and Fortunato, E., 2015. Office paper platform for bioelectrochromic detection of electrochemically active bacteria using tungsten trioxide nanopores. Scientific reports, 5, p.9910.

- Mastretta, C., Taghavi, S., Van Der Lelie, D., Mengoni, A., Galardi, F., Gonnelli, C., Barac, T., Boulet, J., Weyens, N., Vangronsveld, J., 2009. Endophytic bacteria from seeds of *Nicotiana tabacum* can reduce cadmium phytotoxicity. *Int J Phytoremediat.* 11(3), 251-267.
- Matos, A.D., Gomes, I.C., Nietsche, S., Xavier, A.A., Gomes, W.S., Dos Santos Neto, J.A. and Pereira, M.C., 2017. Phosphate solubilization by endophytic bacteria isolated from banana trees. *Anais da Academia Brasileira de Ciências*, 89(4), pp.2945-2954.
- Mattinen, L., Somervuo, P., Nykyri, J., Nissinen, R., Kouvonen, P., Corthals, G., Auvinen, P., Aittamaa, M., Valkonen, J.P., Pirhonen, M., 2008. Microarray profiling of host-extract-induced genes and characterization of the type VI secretion cluster in the potato pathogen *Pectobacterium atrosepticum*. *Microbiol.* 154(8), 2387-2396.
- Mendes, R., Pizzirani-Kleiner, A.A., Araujo, W.L. and Raaijmakers, J.M., 2007. Diversity of cultivated endophytic bacteria from sugarcane: genetic and biochemical characterization of *Burkholderia cepacia* complex isolates. *Appl. Environ. Microbiol.*, 73(22), pp.7259-7267.
- Meneses, C.H., Rouws, L.F., Simões-Araújo, J.L., Vidal, M.S., Baldani, J.I., 2011. Exopolysaccharide production is required for biofilm formation and plant colonization by the nitrogen-fixing endophyte *Gluconacetobacter diazotrophicus*. *Mol Plant Microbe Interact.* 24(12), 1448-1458.
- Mitter, B., Petric, A., SG Chain, P., Trognitz, F., Nowak, J., Compant, S., Sessitsch, A., 2013. Genome analysis, ecology, and plant growth promotion of the endophyte *Burkholderia phytofirmans* strain PsJN. *Molecular microbial ecology of the rhizosphere.* 1, 865-874.
- Mitter, B., Pfaffenbichler, N., Flavell, R., Compant, S., Antonielli, L., Petric, A., Berninger, T., Naveed, M., Sheibani-Tezerji, R., von Maltzahn, G., Sessitsch, A., 2017. A new approach to modify plant microbiomes and traits by introducing beneficial bacteria at flowering into progeny seeds. *Front Microbiol.* 8, p.11.
- Moran, N.A. 2006. Symbiosis. *Curr Biol.* 16, R866–R871.
- Moulin, L., James, E.K., Klonowska, A., Miana de Faria, S., Simon, M.F., 2015. Phylogeny, diversity, geographical distribution, and host range of legume-nodulating

- betaproteobacteria: what is the role of plant taxonomy. de Bruijn FJ. Biol. nitrogen Fixat. Chichester: Wiley, 177-190.
- Mukhopadhyay, K., Garrison, N.K., Hinton, D.M., Bacon, C.W., Khush, G.S., Peck, H.D., Datta, N., 1996. Identification and characterization of bacterial endophytes of rice. *Mycopathologia*. 134(3), 151-159.
- Mundt, J.O., Hinkle, N.F., 1976. Bacteria within ovules and seeds. *Appl Environ Microbiol*. 32(5), 694-698.
- Naveed, M., Mitter, B., Yousaf, S., Pastar, M., Afzal, M., Sessitsch, A., 2014. The endophyte *Enterobacter* sp. FD17: A maize growth enhancer selected based on rigorous testing of plant beneficial traits and colonization characteristics. *Biol Fertil Soils*. 50, 249–262.
- Nguema-Ona, E., Vicré-Gibouin, M., Cannesan, M.A., Driouich, A., 2013. Arabinogalactan proteins in root–microbe interactions. *Trends Plant Sci*. 18(8), 440-449.
- Normand, P., Lapierre, P., Tisa, L.S., Gogarten, J.P., Alloisio, N., Bagnarol, E., Bassi, C.A., Berry, A.M., Bickhart, D.M., Choisne, N., Couloux, A., 2007. Genome characteristics of facultatively symbiotic *Frankia* sp. strains reflect host range and host plant biogeography. *Genome Res*. 17(1), 7-15.
- Oku, S., Komatsu, A., Tajima, T., Nakashimada, Y., Kato, J., 2012. Identification of chemotaxis sensory proteins for amino acids in *Pseudomonas fluorescens* Pf0-1 and their involvement in chemotaxis to tomato root exudate and root colonization. *Microbes and Environ*. p.ME12005.
- Okunishi, S., Sako, K., Mano, H., Imamura, A., Morisaki, H., 2005. Bacterial flora of endophytes in the maturing seed of cultivated rice (*Oryza sativa*). *Microbes Environ*. 20(3), 168-177.
- Pandey, P.K., Yadav, S.K., Singh, A., Sarma, B.K., Mishra, A. and Singh, H.B., 2012. Cross-species alleviation of biotic and abiotic stresses by the endophyte *Pseudomonas aeruginosa* PW09. *Journal of Phytopathology*, 160(10), pp.532-539.
- Pandey, S.S., Singh, S., Babu, C.V., Shanker, K., Srivastava, N.K. and Kalra, A., 2016. Endophytes of opium poppy differentially modulate host plant productivity and genes

- for the biosynthetic pathway of benzyloisoquinoline alkaloids. *Planta*, 243(5), pp.1097-1114.
- Partida-Martinez, L.P.P., Heil, M., 2011. The microbe-free plant: fact or artifact? *Front. Plant Sci.* 2, 100
- Paungfoo-Lonhienne C, Rentsch D, Robatzrk S, Webb RI, Sagulenko E, Nasholm T, Schmidt S, Lonhienne TGA. 2010. Turning the table: plants consume microbes as a source of nutrients. *PLOS ONE* 5(7): e11915. doi: 10:1371/journal.pone.0011915.
- Paungfoo-Lonhienne, C., Schmidt, S., Webb, R. and Lonhienne, T. 2013. Rhizophagy- A new dimension of plant-microbe interactions, in de Briujn, F.J. (Ed.) *Molecular Microbial Ecology of the Rhizosphere*. Wiley-Blackwell. Pub John Wiley & Sons, Inc.
- Peiffer, J.A., Spor, A., Koren, O., Jin, Z., Tringe, S.G., Dangl, J.L., Buckler, E.S., Ley, R.E., 2013. Diversity and heritability of the maize rhizosphere microbiome under field conditions. *Proc Natl Acad Sci.* 110(16), 6548-6553.
- Philipson, M.N., Blair, I.D., 1957. Bacteria in clover root tissue. *C J Microbiol.* 3(2), 125-129.
- Pitzschke, A., 2016. Developmental peculiarities and seed-borne endophytes in quinoa: omnipresent, robust bacilli contribute to plant fitness. *Front Microbiol.* 7, p.2.
- Preston, G.M., Bertrand, N., Rainey, P.B., 2001. Type III secretion in plant growth-promoting *Pseudomonas fluorescens* SBW25. *Mol Microbiol.* 41(5), 999-1014.
- Prieto, P., Schilirò, E., Maldonado-González, M.M., Valderrama, R., Barroso-Albarracín, J.B., Mercado-Blanco, J., 2011. Root hairs play a key role in the endophytic colonization of olive roots by *Pseudomonas* spp. with biocontrol activity. *Microb Eco.* 62(2), 435-445.
- Rajendran, L., Karthikeyan, G., Raguchander, T. and Samiyappan, R., 2010. Cloning and sequencing of novel endophytic *Bacillus subtilis* from coconut for the management of Basal Stem Rot disease. *Asian Journal of Plant Pathology*, 4(1), pp.20-33.
- Rasche, F., Lueders, T., Schloter, M., Schaefer, S., Buegger, F., Gattinger, A., Hood-Nowotny, R.C., Sessitsch, A., 2009. DNA-based stable isotope probing enables the

- identification of active bacterial endophytes in potatoes. *New Phytologist*. 181(4), 802-807.
- Rashid, S., Charles, T.C., Glick, B.R., 2012. Isolation and characterization of new plant growthpromoting bacterial endophytes. *Appl. Soil Ecol.* 61, 217-224
- Reinhold-Hurek, B., Hurek, T., 2011. Living inside plants: bacterial endophytes. *Curr Opin Plant Biol.* 14:435–43.
- Reinhold-Hurek, B., Maes, T., Gemmer, S., Van Montagu, M., Hurek, T., 2006. An endoglucanase is involved in infection of rice roots by the not-cellulose-metabolizing endophyte *Azoarcus* sp. strain BH72. *Mol Plant Microbe Interact.* 19, 181–188.
- Ren, H., Xiong, S., Gao, G., Song, Y., Cao, G., Zhao, L. and Zhang, X., 2015. Bacteria in the injection water differently impacts the bacterial communities of production wells in high-temperature petroleum reservoirs. *Frontiers in microbiology*, 6, p.505.
- Ringelberg, D., Foley, K., Reynolds, C.M., 2012. Bacterial endophyte communities of two wheatgrass varieties following propagation in different growing media. *Can J Microbiol.* 58(1), 67-80.
- Rodríguez-Navarro, D.N., Dardanelli, M.S., Ruíz-Sáinz, J.E., 2007. Attachment of bacteria to the roots of higher plants. *FEMS Microbiol Lett.* 272(2), 127-136.
- Roncato-Maccari, L.D., Ramos, H.J., Pedrosa, F.O., Alquini, Y., Chubatsu, L.S., Yates, M.G., Rigo, L.U., Steffens, M.B.R., Souza, E.M., 2003. Endophytic *Herbaspirillum seropedicae* expresses nif genes in gramineous plants. *FEMS Microbiol Ecol.* 45(1), 39-47.
- Rosenblueth, M., Martínez-Romero, E., 2006. Bacterial endophytes and their interactions with hosts. *Mol Plant Microbe Interact.* 19(8), 827-837.
- Rossi, F.A., Medeot, D.B., Liaudat, J.P., Pistorio, M., Jofré, E., 2016. In *Azospirillum brasilense*, mutations in flmA or flmB genes affect polar flagellum assembly, surface polysaccharides, and attachment to maize roots. *Microbiol Res.* 190, 55-62.
- Rozpądek, P., Domka, A.M., Nosek, M., Ważny, R., Jędrzejczyk, R.J., Wiciarz, M., Turnau, K., 2018. The Role of Strigolactone in the Cross-Talk Between *Arabidopsis thaliana* and the Endophytic *Fungus Mucor* sp. *Front Microbiol.* 9, 441.

- S Zawoznik, M., C Vázquez, S., Díaz Herrera, S.M., D Groppa, M., 2014. Search for endophytic diazotrophs in barley seeds. *Braz J Microbiol.* 45(2), 621-625.
- Samish, Z., Etinger-Tulczynska, R., Bick, M., 1961. Microflora within healthy tomatoes. *Appl Microbiol.* 9(1), p.20.
- Sattelmacher, B., 2001. The apoplast and its significance for plant mineral nutrition. *New Phytologist.* 149(2), 167-192.
- Sauer, K., Camper, A.K., 2001. Characterization of phenotypic changes in *Pseudomonas putida* in response to surface-associated growth. *J Bacteriol.* 183(22), 6579-6589.
- Scervino, J.M., Ponce, M.A., Erra-Bassells, R., Bompadre, M.J., Vierheilig, H., Ocampo, J.A., Godeas, A., 2006. Glycosidation of apigenin results in a loss of its activity on different growth parameters of arbuscular mycorrhizal fungi from the genus *Glomus* and *Gigaspora*. *Soil Biol Biochem.* 38(9), 2919-2922.
- Schardl, C.L., 2001. *Epichloë festucae* and related mutualistic symbionts of grasses. *Fungal Genet Biol.* 33(2), 69-82.
- Schell, M.A., Ulrich, R.L., Ribot, W.J., Brueggemann, E.E., Hines, H.B., Chen, D., Lipscomb, L., Kim, H.S., Mrázek, J., Nierman, W.C., DeShazer, D., 2007. Type VI secretion is a major virulence determinant in *Burkholderia mallei*. *Mol Microbiol.* 64(6), 1466-1485.
- Schlaeppli, K., Bulgarelli, D., 2015. The plant microbiome at work. *Mol Plant-Microbe Interact.* 28(3), 212-217.
- Schlaeppli, K., Dombrowski, N., Oter, R.G., van Themaat, E.V.L., Schulze-Lefert, P., 2014. Quantitative divergence of the bacterial root microbiota in *Arabidopsis thaliana* relatives. *Proc Natl Acad Sci.* 111(2), 585-592.
- Sharrock, K.R., Parkes, S.L., Jack, H.K., Rees-George, J., Hawthorne, B.T., 1991. Involvement of bacterial endophytes in storage rots of buttercup squash (*Cucurbita maxima* D. hybrid 'Delica'). *New Zeal J Crop Hort Sci.* 19(2), 157-165.
- Sheibani-Tezerji, R., Naveed, M., Jehl, M.A., Sessitsch, A., Rattei, T., Mitter, B., 2015. The genomes of closely related *Pantoea ananatis* maize seed endophytes having different effects on the host plant differ in secretion system genes and mobile genetic elements. *Front Microbiol.* 6, p.440.

- Sheng, X.F., Xia, J.J., Jiang, C.Y., He, L.Y. and Qian, M., 2008. Characterization of heavy metal-resistant endophytic bacteria from rape (*Brassica napus*) roots and their potential in promoting the growth and lead accumulation of rape. *Environmental pollution*, 156(3), pp.1164-1170.
- Shi, Y., Yang, H., Zhang, T., Sun, J. and Lou, K., 2014. Illumina-based analysis of endophytic bacterial diversity and space-time dynamics in sugar beet on the north slope of Tianshan mountain. *Applied microbiology and biotechnology*, 98(14), pp.6375-6385.
- Siciliano, S.D., Fortin, N., Mihoc, A., Wisse, G., Labelle, S., Beaumier, D., Ouellette, D., Roy, R., Whyte, L.G., Banks, M.K., 2001. Selection of specific endophytic bacterial genotypes by plants in response to soil contamination. *Appl. Environ. Microbiol.* 67, 2469-2475.
- Singh, V.K., Singh, A.K., Kumar, A., 2017. Disease management of tomato through PGPB: current trends and future perspective. *3 Biotech*, 7(4), p.255.
- Singh, V.K., Singh, A.K., Singh, P.P. and Kumar, A., 2018. Interaction of plant growth promoting bacteria with tomato under abiotic stress: A review. *Agr. Ecosyst. Environ.* 267, pp.129-140.
- Sona Janarthine, S.R., Eganathan, P., Balasubramanian, T. and Vijayalakshmi, S., 2011. Endophytic bacteria isolated from the pneumatophores of *Avicennia marina*. *African Journal of Microbiology Research*, 5(26), pp.4455-4466.
- Sprent, J.I., De Faria, S.M., 1989. Mechanisms of infection of plants by nitrogen fixing organisms. In *Nitrogen Fixation with Non-Legumes* (3-11). Springer, Dordrecht.
- Steinkellner, S., Lenzemo, V., Langer, I., Schweiger, P., Khaosaad, T., Toussaint, J.P., Vierheilig, H., 2007. Flavonoids and strigolactones in root exudates as signals in symbiotic and pathogenic plant-fungus interactions. *Molecules*. 12(7), 1290-1306.
- Strobel, G., Daisy, B., 2003. Bioprospecting for microbial endophytes and their natural products. *Microbiol Mol Biol Rev.* 67(4), 491-502.

- Suárez-Moreno, Z.R., Devescovi, G., Myers, M., Hallack, L., Mendonça-Previato, L., Caballero-Mellado, J., Venturi, V., 2010. Commonalities and differences in regulation of N-acyl homoserine lactone quorum sensing in the beneficial plant-associated *Burkholderia* species cluster. *Appl Environ Microbiol.* 76(13), 4302-4317.
- Sun, K., Liu, J., Gao, Y., Jin, L., Gu, Y. and Wang, W., 2014. Isolation, plant colonization potential, and phenanthrene degradation performance of the endophytic bacterium *Pseudomonas* sp. Ph6-gfp. *Scientific reports*, 4, p.5462.
- Sun, L., Lu, Z., Bie, X., Lu, F. and Yang, S., 2006. Isolation and characterization of a co-producer of fengycins and surfactins, endophytic *Bacillus amyloliquefaciens* ES-2, from *Scutellaria baicalensis* Georgi. *World Journal of Microbiology and Biotechnology*, 22(12), pp.1259-1266.
- Sun, L., Qiu, F., Zhang, X., Dai, X., Dong, X. and Song, W., 2008. Endophytic bacterial diversity in rice (*Oryza sativa* L.) roots estimated by 16S rDNA sequence analysis. *Microbial ecology*, 55(3), pp.415-424.
- Sunkar, S., Akshaya, A., Aarthi, B., Nachiyar, V.C. and Prakash, P., 2018. Phytochemical analysis and isolation of endophytic bacteria from *Bauhinia purpurea*. *Research Journal of Pharmacy and Technology*, 11(5), pp.1867-1876.
- Suzuki, T., Shimizu, M., Meguro, A., Hasegawa, S., Nishimura, T., Kunoh, H., 2005. Visualization of infection of an endophytic actinomycete *Streptomyces galbus* in leaves of tissue-cultured rhododendron. *Actinomycetologica.* 19(1), 7-12.
- Taghavi, S., Garafola, C., Monchy, S., Newman, L., Hoffman, A., Weyens, N., Barac, T., Vangronsveld, J. and van der Lelie, D., 2009. Genome survey and characterization of endophytic bacteria exhibiting a beneficial effect on growth and development of poplar trees. *Appl. Environ. Microbiol.*, 75(3), pp.748-757.
- Taghavi, S., Van Der Lelie, D., Hoffman, A., Zhang, Y.B., Walla, M.D., Vangronsveld, J., Newman, L. and Monchy, S., 2010. Genome sequence of the plant growth promoting endophytic bacterium *Enterobacter* sp. 638. *PLoS genetics*, 6(5), p.e1000943.

- Timmusk, S., Grantcharova, N., Wagner, E.G.H., 2005. *Paenibacillus polymyxa* invades plant roots and forms biofilms. *Appl Environ Microbiol.* 71(11), 7292-7300.
- Tiwari, R., Kalra, A., Darokar, M.P., Chandra, M., Aggarwal, N., Singh, A.K. and Khanuja, S.P.S., 2010. Endophytic bacteria from *Ocimum sanctum* and their yield enhancing capabilities. *Current microbiology*, 60(3), pp.167-171.
- Trevet, I.W., 1948. Bacteria in the storage organs of healthy plants. *Phytopathol.* 38, 960-967.
- Trivedi, P., Spann, T. and Wang, N., 2011. Isolation and characterization of beneficial bacteria associated with citrus roots in Florida. *Microbial ecology*, 62(2), pp.324-336.
- Vega, F.E., Pava-Ripoll, M., Posada, F., Buyer, J.S., 2005. Endophytic bacteria in *Coffea arabica* L. *Journal of Basic Microbiology: An International Journal on Biochemistry, Physiology, Genetics, Morphology, and Ecology of Microorganisms.* 45(5), 371-380.
- Verma, S.K., Kingsley, K., Irizarry, I., Bergen, M., Kharwar, R.N. and White Jr, J.F., 2017. Seed-vectored endophytic bacteria modulate development of rice seedlings. *J Appl Microbiol.* 122(6), 1680-1691.
- Verma, S.K., White Jr, J.F., (editors). 2019. *Seed Endophytes: Biology and Biotechnology.* Springer Nature, Switzerland. 507 pages; ISBN 978-3-030-10503-7.
- Wang, X.M., Yang, B., Ren, C.G., Wang, H.W., Wang, J.Y. and Dai, C.C., 2015. Involvement of abscisic acid and salicylic acid in signal cascade regulating bacterial endophyte-induced volatile oil biosynthesis in plantlets of *Atractylodes lancea*. *Physiologia plantarum*, 153(1), pp.30-42.
- Webster, G., Jain, V., Davey, M.R., Gough, C., Vasse, J., Denarie, J., Cocking, E.C., 1998. The flavonoid naringenin stimulates the intercellular colonization of wheat roots by *Azorhizobium caulinodans*. *Plant Cell Environ.* 21(4), 373-383.
- Weilharter, A., Mitter, B., Shin, M.V., Chain, P.S., Nowak, J. and Sessitsch, A., 2011. Complete genome sequence of the plant growth-promoting endophyte *Burkholderia phytofirmans* strain PsJN.
- White JF, Chen Q, Torres MS, Mattera R, Irizarry I, Tadych M, Bergen M. 2015. Collaboration between grass seedlings and rhizobacteria to scavenge organic nitrogen in soils. *AoB PLANTS* 7: plu093. doi:10.1093/aobpla/plu093.

- White JG, Kingsley KL, Verma SK, Kowalski K. 2018. Rhizophagy Cycle: An Oxidative Process in Plants for Nutrient Extraction from Symbiotic Microbes. *Microorganisms*, 6(3),95. <https://doi.org/10.3390/microorganisms6030095>.
- Wilkinson, D.M., Sherratt, T.N., 2001. Horizontally acquired mutualisms, an unsolved problem in ecology? *Oikos*. 92(2), 377-384.
- Xu, M., Sheng, J., Chen, L., Men, Y., Gan, L., Guo, S. and Shen, L., 2014. Bacterial community compositions of tomato (*Lycopersicon esculentum* Mill.) seeds and plant growth promoting activity of ACC deaminase producing *Bacillus subtilis* (HYT-12-1) on tomato seedlings. *World Journal of Microbiology and Biotechnology*, 30(3), pp.835-845.
- Yaish, M.W., Antony, I. and Glick, B.R., 2015. Isolation and characterization of endophytic plant growth-promoting bacteria from date palm tree (*Phoenix dactylifera* L.) and their potential role in salinity tolerance. *Antonie Van Leeuwenhoek*, 107(6), pp.1519-1532.
- Yaron, S., Römling, U., 2014. Biofilm formation by enteric pathogens and its role in plant colonization and persistence. *Microb Biotechnol*. 7(6), 496-516.
- Zachow, C., Fatehi, J., Cardinale, M., Tilcher, R., Berg, G., 2010. Strain-specific colonization pattern of *Rhizoctonia* antagonists in the root system of sugar beet. *FEMS Microbiol Eco*. 74(1), 124-135.
- Zheng, H., Mao, Y., Teng, J., Zhu, Q., Ling, J., Zhong, Z., 2015. Flagellar-dependent motility in *Mesorhizobium tianshanense* is involved in the early stage of plant host interaction: study of an flgE mutant. *Curr Microbiol*. 70(2), 219-227.
- Zinniel, D.K., Lambrecht, P., Harris, N.B., Feng, Z., Kuczmariski, D., Higley, P., Ishimaru, C.A., Arunakumari, A., Barletta, R.G., Vidaver, A.K., 2002. Isolation and characterization of endophytic colonizing bacteria from agronomic crops and prairie plants. *Appl Environ Microbiol*. 68(5), 2198-2208.

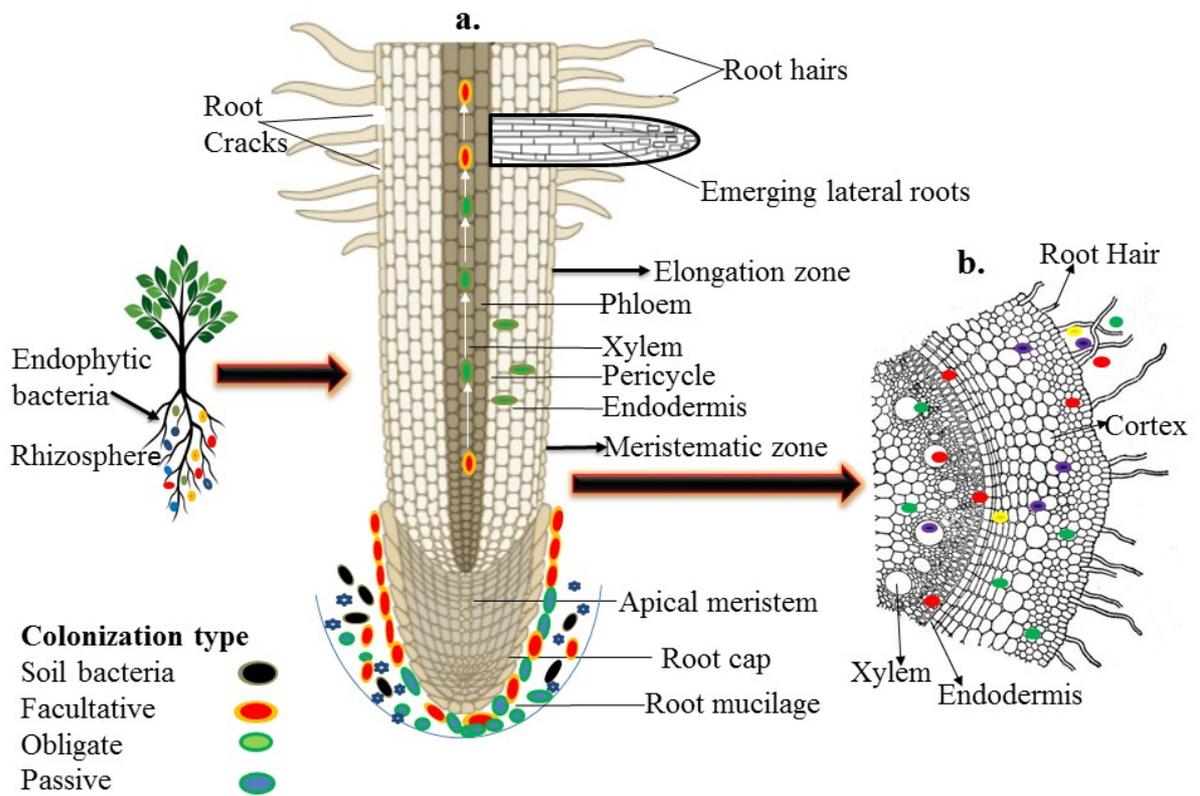


Fig. 1. Schematic representation of endophytic bacterial colonization and distribution in the endosphere of a plant root. **(a.)** Invasion of bacteria into a plant using several root zones. White arrows shows translocation of bacteria in to the phloem and xylem and colonization type represented by different colored ovals. **(b.)** occurrence of endophytes either at the site of entry (indicated in blue) or in the intercellular space of the cortex and xylem vessels (indicated in green). Red and yellow sphere represents rhizospheric bacteria which are unable to colonize inner plant tissues

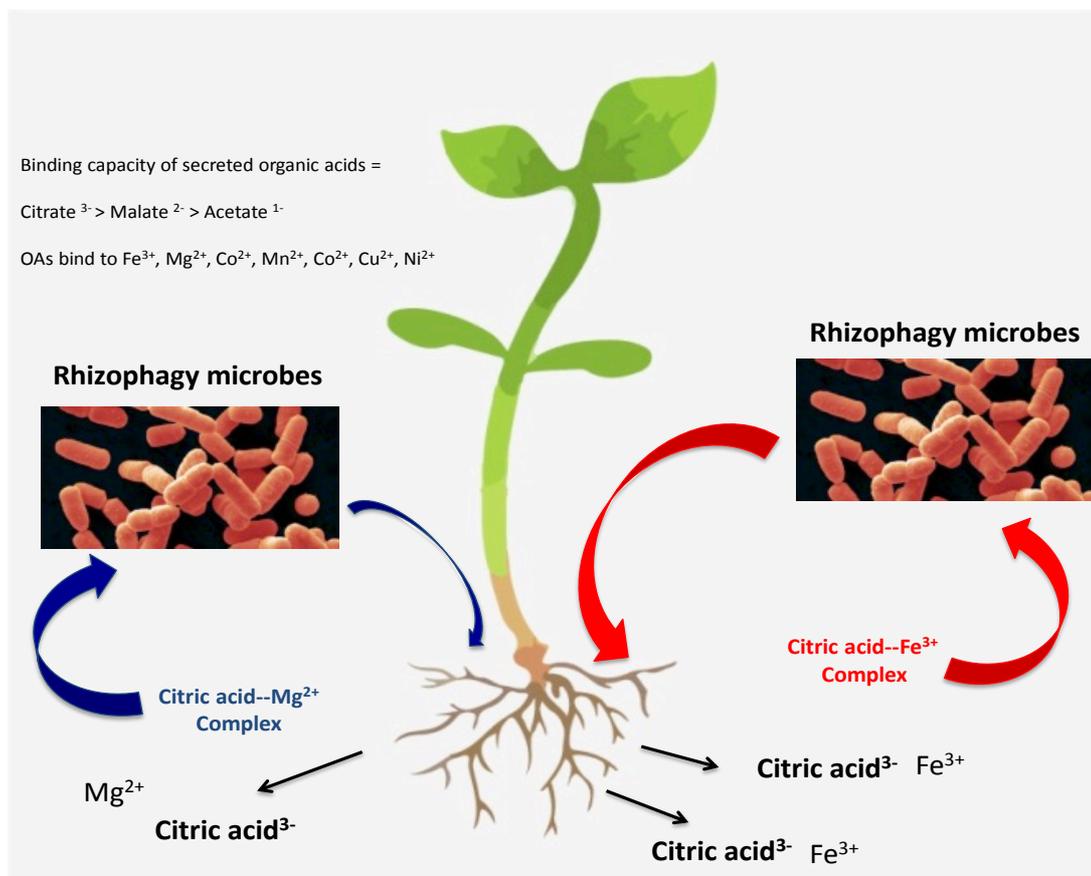


Fig. 2. Diagrammatic representation of nutrient mining by rhizophagy microbes. Plant roots secrete organic acids (citric, malic, and acetic acids) into the soil. Organic acids complex with metals in the soil (Fe^{3+} , Mg^{2+} , Co^{2+} , Mn^{2+} , Cu^{2+} , Ni^{2+} , etc...). Rhizophagy cycle microbes possess transporters that bind to these organic acid-metal complexes and absorb them into the microbe cells. Microbes then return to the plant root and enter into root cells where nutrients are extracted from microbes oxidatively.