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Editorial

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Recruitment of bacterial endophytes by host plants

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Introduction

Plants coupled with endophytic bacteria hold great potential for the remediation of polluted environments. The colonization patterns and activities of inoculated endophytes in the rhizosphere and endosphere of host plant are among the primary factors that may influence the phytoremediation process. However, these patterns and activities are in turn controlled by none other than the host plant itself.

The plant endosphere contains diverse groups of microbial communities. There is general consensus that these communities make significant contributions to plant health. Endophytes are microbial symbionts residing within the plant for the majority of their life cycle without any detrimental impact on the host plant. The use of these natural symbionts however, offers an opportunity to maximize crop productivity. Endophytes promote plant growth through; nitrogen fixation, phytohormone production, nutrient acquisition, and by conferring tolerance to abiotic and biotic stresses. Colonization by these endophytes is crucial for providing their benefits to the host plants. Endophytic colonization refers to the entry; growth and multiplication of endophytic populations within the host plant. Although, plant microbiome research has gained considerable attention lately; however, the mechanism that allows plants to recruit endophytes is largely unknown.

Endophytic strains of *Bacillus*, *Burkholderia*, *Enterobacter*, *Pseudomonads*, and *Serratia* were found to be effective in suppressing the growth of pathogenic microorganisms under *in vitro* and *in vivo* conditions (Kandel *et al*., 2015). Moreover, endophytic strains in the genera *Bacillus*, *Enterobacter*, *Pseudomonas*, *Azotobacter*, *Arthrobacter*, *Streptomyces*, and *Isoptericola* were successful also in alleviating drought, heat, and salt stresses in different crop plants. More importantly, endophytes were not only capable of relieving the different stresses on their symbiotic plants, but also significantly increased their biomass and heights (Ali *et al*., 2014). However, the mechanisms used by these bacterial endophytes to mitigate abiotic stresses remain unclear.

The rhizosphere serves as a hub for plant-endophyte communication during the early stages of the colonization process; and is likely to facilitate access of the endophyte to the inside of the host plant tissues through openings in this plant. Root exudates including organic acids, amino acids, and proteins may be involved in recruiting bacterial endophytes from the rhizosphere. According to Kawasaki *et al*., (2016), root exudates likely contain substrates that initiate early communication between host plants and bacterial endophytes, and consequently steer the colonization process.

The attachment or adhesion of bacterial cells to the plant surface is considered as the first step of the colonization process. Bacteria in the vicinity of plant roots most likely swim toward these roots; using chemotactic affinities for root exudates. This is followed by attachment to the root surface; which is likely important in getting access at lateral root emergence areas, or other openings caused by wounds or mechanical injuries.

The exopolysaccharides (EPS) produced by bacterial cells may facilitate their attachment onto the root surface; and may be important in the early stages of endophytic colonization. Meneses *et al*., (2011) reported that EPS produced by endophytic bacterium *Gluconacetobacter diazotrophicus* was an essential factor for rice root surface attachment and colonization (Fig. 1).

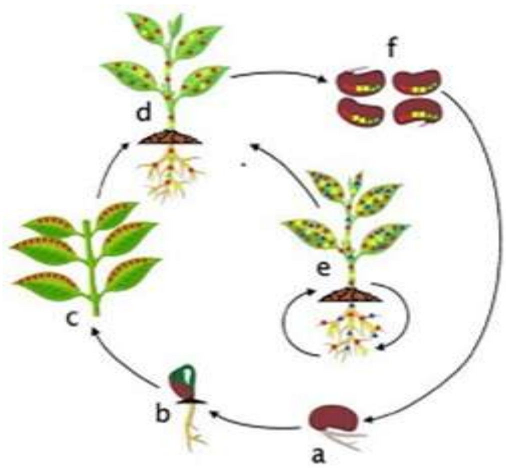

Fig. 1. Hypothesized colonization cycle of bacterial endophytes in their host plant: (a) Mobilization of seed endophytes in germinating seedlings; (b) Recruitment of alien endophytes from the soil in developing seedlings; (c) Colonization by alien and inherited endophytes; (d) Whole plant colonization by various endophytes; (e) Variation of endophytic communities in the host plant in response to different biotic and abiotic stresses; (f) Vertical transfer of endophytes into seeds.

In leaves, bacterial endophytes have been observed in the intercellular spaces of mesophyll, xylem tissues and in substomatal areas. Using green fluorescent protein (GFP) labeling and β-glucuronidase (GUS) staining, *Burkholderia* sp. strain PsJN was observed in xylem and substomatal chambers of inoculated leaves of grape vine plants. Interestingly, bacterial cells leaving through the stomatal aperture were also observed in grapevine leaves (Compant *et al*., 2005). Moreover, bacterial microcolonies have been detected in leaf veins, trichomes; and in cut sections of leaf pieces. Therefore, colonization was strong in various layers of the leaf tissues (Lo Piccolo *et al*., 2010).

One relatively new area of research that remains poorly studied is the intracellular colonization of plant cells by endophytes. Endophytes are known to typically colonize the intercellular spaces of plants but several examples of intracellular colonization of plants by bacteria have been reported recently (Frank *et al*., 2017). These examples include; the presence of intracellular bacteria in shoot-tips of banana, shoot meristem of Scotch pine, seedling roots of switch grass; and in micro propagated peach palm (Thomas *et al*., 2013).

Several hypotheses exist as to the potential colonization pathways that intracellular endophytes use. Root hairs offer a logical point of entry for these endophytes; as many cases begin with intracellular access of microbes through these root hairs. This is the case with the well-studied legume-rhizobium symbioses; and was reported to be used by many other endophytes (Perrine-Walker *et al*., 2007; Prieto *et al*., 2011). Choudhury *et al*., (2017) added that endophytes may be capable of gaining access to the intracellular spaces directly by secreting cell wall degrading enzymes; or through a phenomenon known as rhizophagy. According to Paungfoo-lonhienne *et al*., (2013), rhizophagy is a process in which roots of certain plants actively bring microbes in the soil into their cells, possibly in order to digest them and acquire essential nutrients from them.

One possible advantage of this intracellular colonization is the bombardment of the colonizing endophytes by intracellular hydrogen peroxide; which represents a potential advantage for the plant (White *et al*., 2014). Briefly, increasing intracellular reactive oxygen species (ROS) concentrations in the plant; could acclimate it to several stresses such as; drought, heat and salt stress (Choudhury *et al*., 2017). In addition, survival in the intracellular environment could provide the endophyte with a niche with low competition. White *et al*., (2014) revealed that specificity of this adaptation was supported by changes in the shapes of the intracellular endophytes of Switch grass to an L-form, which were lacking a cell wall; moreover, many of these endophytes were not culturable. Although this phenomenon seems widespread, the inability of culturing these intracellular endophytes makes them very difficult to be studied (Thomas *et al*., 2013). However, it is possible that stronger reliance on next generation sequencing and metagenomics; may be necessary for further studies of the life cycle and ecology of these endophytes.

The exchange of signaling molecules between the endophytic strains and their host plants; as well as temporal and spatial dimensions of the colonization process at the biochemical and molecular levels; should be investigated. The aim of this review is to summarize the recruitment process of the bacterial endophytes by the plant; from colonization (attachment and entry), to the distribution patterns of these endophytes in the plant endosphere.

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