

Original Research Article

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Multiple Roles of Endophytes in Modern Agriculture

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ABSTRACT

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Endophyte biology is an emerging field for practical use of beneficial microorganisms to control plant diseases and to sustain and assist crop production under non stress and stress conditions. Endophytes are microorganisms (fungi and bacteria) that colonize inside the plant tissues. The exact biological and biochemical roles of endophytes and their interactions with host plants in improving plant health and crop productivity is under investigation in many laboratories around the world. However, this has not stopped investigators in exploring the direct utility of endophytes in boosting crop production. Endophytes produce a myriad of biologically active compounds which includes plant growth promoting agents, antimicrobial agents, phytohormones, antibiotics, antioxidants, anticancer agents, immunosuppressive compounds and compounds with insecticide properties. This review is intended to provide background information on aspects of developments in endophyte biology and more importantly the roles of endophytes in modern agriculture.

Introduction

The existence of endophytes has been known for over one hundred years. They live as imperfect fungi most of the time and have been described as benign parasites or true symbionts. They can influence the distribution, ecology, physiology and biochemistry of the host plants (Sridhar and Raviraja, 1995). Endophytes were intensively studied during the past decades for the great potential of novel valuable metabolites which have medicinal, agricultural and industrial applications (Owen and Hundley, 2004). Endophytes are bacterial or fungal

microorganisms that colonize healthy plant tissue intercellularly (apoplasts) and/or intracellularly (symplast) without causing any apparent symptoms of disease (Wilson, 1995). All plant species that exist on the earth, is host to one or more endophytes (Strobel *et al.*, 2004). Only a few of these plants have been completely studied relative to their endophytic biology, endophytes are ubiquitous, colonize in all plants and have been isolated from almost all plants. Endophytic fungi represent an important and quantifiable component of fungal biodiversity and are known to affect plant community diversity and structure (Krings *et al.*, 2007).

Many endophytes are members of common soil bacterial genera, such as *Pseudomonas*, *Burkholderia* and *Bacillus* (Lodewyckx *et al.*, 2002). These genera are well known for producing diverse range of secondary metabolic products including antibiotics, anticancer compounds, volatile organic compounds, antifungal, antiviral, insecticidal and immunosuppressant agents. Endophytes can be beneficial to their host by producing a range of natural products that could be harnessed for potential use in medicine and agriculture industry. It has been shown that they have the potential to remove soil contaminants by enhancing phytoremediation and may play a role in soil fertility through phosphate solubilization and nitrogen fixation. Plants strictly limit the growth of endophytes and these endophytes use many mechanisms to gradually adapt to their living environments (Dudeja *et al.*, 2012). Endophytic population varies from plants to plants and from species to species. There is increasing evidence showing the presence of ubiquitous endophyte species in tropical and temperate forests. Different endophytes have been identified from different plant tissues. The biodiversity of endophytes can be judged by the potential of microbes to colonize the tissues and persist in the plant (Rosenblueth and Martinez-Romero, 2006).

They can infect plants from the soil and are competent root colonizers. The variation in the endophytic communities can be attributed to bacterial species, plant genotype, plant developmental stage, colonizing tissue type, soil type and environmental conditions (Kobayashi and Palumbo, 2000). Endophytic bacteria have been isolated from both monocotyledonous and dicotyledonous plants, ranging from woody tree species, such as oak and pear, to herbaceous crop plants such as sugar beet and maize. These organisms generally colonize the intercellular spaces, and they have been isolated from all plant

compartments including seeds (Posada and Vega, 2005). Investigation of the biodiversity of endophytic strains for novel metabolites may identify new drugs for effective treatment of diseases in humans, plants and animals (Strobel *et al.*, 2004). Dual culture has been successfully used in studying the physiological and morphological interactions between fungal endophytes and plant cells (Huang *et al.*, 2017). Banana trees have more endophytes in the roots (67%) than in the cortex (23%) or central cylinder (10%) (Pocasangre *et al.*, 2000).

To date, few endophytic bacterial genome sequences have been published; however, genome sequencing of a number of endophytes including *Enterobacter* sp.638, *Stenotrophomonas maltophilia* R551-3, *Pseudomonas putida* W619, *Serratia proteamaculans* 568 and *Methylobacterium populi* BJ001 is underway at the United States Department of Energy Joint Genome Institute (www.jgi.doe.gov). Improvement of endophyte resources could bring us a variety of benefits, such as novel and effective bioactive compounds that cannot be synthesized by chemical reactions. The metabolic impacts of endophytes on host plant may employ pathways of i) endophytes self-metabolizing ii) endophytes and host co-metabolizing and iii) Signalling (Ludwig-MuÈller, 2015).

Endophytes – Role in nutrient acquisition by plants

Endophytes may produce overabundance of substances of potential use to agriculture, industry and modern medicine such as novel antibiotics, antimycotics, immunosuppressant and anticancer compounds (Mitchell *et al.*, 2008). Endophytic bacteria show more plant growth promoting effects than bacteria found in the rhizosphere (Dawwam *et al.*, 2013). Endophytes are well known for their potential

to improve plant growth by direct and indirect mechanisms. Direct mechanisms involve the microbial synthesis of phytohormones for example, production of Indole-3-acetic acid (IAA), ethylene like, Cytokinin like and gibberellins like substances. In addition, these endophytic bacteria also have the ability of nitrogen fixation (Latif *et al.*, 2013). Indirect mechanisms include assisting plants in acquiring nutrients via phosphate solubilisation, nitrogen fixation and siderophores production. Besides these mechanisms, plant-associated microorganisms improve nutrient acquisition by supplying minerals and other micro/macro nutrients from the soil (Barrow, 2003).

Endophytes promote plant growth, by adopting various mechanisms which includes phosphate solubilisation activity (Wakelin *et al.*, 2004). Abid Ullah *et al.*, 2018 reported that, endophytic *Enterobacter* sp solubilize phosphate on a large scale. Ahemad and Khan, 2010; Lopez *et al.*, 2011 have reported that *E. asburiae* a potential plant growth promoting bacteria has ability to solubilize large amount of phosphates. It is reported that endophytes solubilize the inorganic phosphorus by reducing the pH through the excretion of organic acid, while organic phosphorous is solubilized by production of various phosphatases, which results in a better plant development and improved yield (Rodriguez and Fraga, 1999).

Nutrient acquisition for plants via nitrogen fixation is another mechanism behind plant growth promotion. Many species of endophytic nitrogen fixing bacteria have been isolated from sugarcane (Loiret *et al.*, 2004) and other plants, e.g., rice, kallar grass and maize, and these bacteria supply fixed nitrogen (N) to their hosts (Baldani *et al.*, 2002). Symbiotic associations between sugarcane and its endophytic nitrogen fixing bacteria provide mutual benefits such as a

combined N (NH₃) supply to the plant and photosynthates to the bacteria. Many genera of endophytic nitrogen fixing bacteria were generally Gram-negative (Loiret *et al.*, 2004).

Endophyte – Role in Phytohormone production

Phytohormone production by endophytes is probably the best-studied mechanism of plant growth promotion, leading to morphological and architectural changes in plant hosts. Endophytic bacteria produce a wide range of phytohormones, such as auxins, Cytokinins, and gibberellic acids. *Burkholderia vietnamiensis*, a diazotrophic endophytic bacterium isolated from wild cottonwood (*Populus trichocarpa*), produced indole acetic acid (IAA), which promotes the growth of the plants (Xin *et al.*, 2009). A new strain of fungus *Cladosporium sphaerospermum* isolated from the roots of *Glycine max* (L) Merr. showed the presence of higher amounts of bioactive GA₃, GA₄, and GA₇, which induced maximum plant growth in both rice and soybean varieties (Hamayum *et al.*, 2009). The beneficial effects of bacterial endophytes on their host plant appear to occur through similar mechanisms as of rhizosphere-associated bacteria. These mechanisms have been reviewed in great detail by Kloepper *et al.*, (1999) or, more recently, by Compant *et al.*, (2005).

A different mechanism for plant growth promotion by endophytes exists in addition to production of plant growth hormones. Adenine and adenine ribosides have been identified as growth-promoting compounds in endophytes of Scots pine (Pirttilä 2004). Volatile compounds, such as acetoin and 2, 3-butanediol, can stimulate plant growth (Ryu *et al.*, 2005). Many of the bacterial endophytes promote plant growth indirectly by inhibiting the growth and activities of phytopathogens by the production of antimicrobial substances

like HCN through a variety of different mechanisms.

Indole acetic acid (IAA) production (Lee *et al.*, 2004) by endophytes is another valuable trait that influences plant growth directly (Shi *et al.*, 2009). It has been reported that many endophytes including *Enterobacter*, *Azotobacter*, *Serratia*, *Klebsiella* spp. produced IAA which stimulated plant growth (Spaepen *et al.*, 2007). In addition to IAA, ammonia production is another plant growth promotion (PGP) trait which has a signalling role between plant and bacterial interactions (Ahemad and Khan, 2010). Ammonia produced by endophytes is used as a source of nitrogen (Deepa *et al.*, 2010). The production of siderophore by endophytes have been reported by Costa and Loper, 1994. Siderophores are biologically active compound with function of chelating iron ions in living organisms. They have found extensive applications in the field of agriculture and medicine.

Endophytic organisms can also supply essential vitamins to plants (Pirttila *et al.*, 2004). Besides, a number of other beneficial effects on plant growth have been attributed to endophytes which include osmotic adjustment, stomatal regulation, modification of root morphology (Compant *et al.*, 2005). In a few cases, endophytes were shown to accelerate seedling emergence and promote plant establishment under adverse conditions (Bent and Chanway, 1998).

Endophytes – Role in secondary metabolite production

Nowadays interest is growing in exploring the endophyte potential for their plant growth promoting attributes and their usage as a biological control agent of plant pathogens. Most of the endophytes isolated from plants are known for their antimicrobial activity.

They help in controlling microbial pathogens in plants and animals. Traditionally endophytes have been considered an important component of plant defence mechanisms against herbivores and stress tolerance. Plant endophytes protect their host by producing bioactive compounds against phytopathogenic fungi and bacteria. Natural products from endophytic microbes have been observed to inhibit or kill a wide variety of harmful disease-causing organisms including, phyto-pathogens, bacteria, fungi, viruses, and protozoans that generally affects plants and animals. Certain endophyte bacteria trigger a phenomenon known as induced systemic resistance (ISR), which is phenotypically similar to systemic-acquired resistance (SAR). Bacterial endophytes and their role in ISR have been reviewed recently by Kloepper and Ryu (2006). Endophytes may induce plant defence reactions (ISR), leading to a higher tolerance of pathogens (Zamioudis and Pieterse 2012). Bacterial strains of the genera *Pseudomonas* and *Bacillus* can be considered the most common groups inducing ISR (Kloepper and Ryu, 2006), although ISR induction is not exclusive to these groups (Bordiec *et al.*, 2011). Bacterial chemical factors responsible for ISR induction were identified to include antibiotics, *N*-acylhomoserine lactones, salicylic acid, jasmonic acid, siderophores, volatiles (e.g., acetoin), and lipopolysaccharides (Bordiec *et al.*, 2011).

Abundant reports have shown that endophytic microorganisms can have the capacity to control plant pathogens (Krishnamurthy and Gnanamanickam, 1997), insects (Azevedo *et al.*, 2000) and nematodes (Hallmann *et al.*, 1998). Some entomopathogenic fungi can live like endophytes, colonizing plant tissues and providing long lasting protection. Schulz *et al.*, (2002) has shown that it is possible to inoculate entomopathogenic fungi in plants to control insect pests. *Beauveria bassiana*

(Bals.) Vuill and *Lecanillium dimorphum* (JD Chen) Zare and W. Gams can be inoculated in leaves of *Phoenix dactylifera* L. where they live in the plant tissue (Gomez-Vidal *et al.*, 2006). A comparable effect has been observed when conidia suspensions of this fungus were applied to *Zea mays* L.; some hyphae grew on the plant cuticle and others penetrated the leaf tissue through the apoplast, reaching the xylem and distributing the fungus internally throughout the rest of the plant, increasing its resistance to the lepidopteran *Ostrinia nubilalis* Hübner (Wagner and Lewis, 2000). Isolated endophytic strains from *Withania coagulans* Dunal and *Olea ferruginea* Royal, were shown secretion of growth promoting substances like IAA, ammonia, phosphate solubilization and also act as biocontrol agents because they produced HCN and can inhibit phytopathogens as it has antimicrobial activity (Abid Ullah *et al.*, 2018). Hydrolytic enzyme protease is involved in the suppression of pathogenic growth and subsequent reduction in damage to plants (Bashan and Bashan, 2005). Schulz *et al.*, (2002) isolated around 6500 endophytic fungi and tested their biological potential, they analysed 135 secondary metabolites and found that 51% of bioactive compounds (38% for soil isolates) isolated from endophytic fungi were new natural products.

Endophyte produced alkaloids in pastures are plant defences (Omacini *et al.*, 2001) in exchange; the endophyte obtaining nutrients and protection inside the plant tissues (Menendez and Bertoni, 1997). Endophytes are capable of synthesizing bioactive compounds that are used by plants for defence against pathogens and some of these compounds have proven to be useful for novel drug discovery. Recent studies have reported hundreds of natural products including alkaloids, terpenoids, flavonoids, and steroids, from endophytes. Most of the bioactive compounds isolated from endophytes are

known to have functions of antibiotics, immunosuppressants, anticancer agents, biological control agents, and so forth. A large number of secondary metabolites have been extracted and characterized from endophytic microbes and these are detailed with extensive references (Dreyfuss and Chapela, 1994 and Strobel *et al.*, 2004). Few reports have shown that endophytes can produce secondary compounds similar to those of their host plant, suggesting the possibility of an endophyte-plant genome transfer and expression (Zhang *et al.*, 2006). Dreyfuss and Chapela, 1994 reported that until 2003 approximately 4,000 secondary metabolites with biological activity had been described from fungi. Most of these metabolites are produced by so called “creative fungi” which include species of *Acremonium*, *Aspergillus*, *Fusarium* and *Penicillium*.

Cryptonectria parasitica, a plant pathogen responsible of chestnut blight, was inhibited by the *Epichlōe festucae* metabolites indole-3-acetic acid (IAA); indole-3-ethanol (IEtOH); methylindole-3-carboxylate; indole-3-carboxaldehyde; diacetamide and cyclonerodiol, isolated from its fermentation culture (Yue *et al.*, 2000). *Colletotrichum gloeosporides* (Penz.) Penz. and Sacc, a plant pathogen found in over 470 host plant genera, produced an antifungal compound (colletotric acid) active against the plant pathogen *Helminthosporium sativum* when isolated as an endophyte in *Artemisia mongolica* (Zou *et al.*, 2000). Endophytes can also induce host plant resistance to pathogens (Cavaglieri *et al.*, 2004). It has been modified and inoculated to crop plants to improve their resistance and yield (Kozyrovska *et al.*, 1996). Endophytic microorganisms are regarded as an effective biocontrol agent, alternative to chemical control. An endophytic fungi *Beauveria bassiana* known as an entomopathogen was found to control

the borer insects in coffee seedlings (Posada and Vega, 2006) and sorghum (Tefera and Vidal, 2009). The endophytic bacteria *Bacillus subtilis*, isolated from *Speranskia tuberculata* (Bge.) Baill, was found to be strongly antagonistic to the pathogen *B. cinerea* in *in vitro* studies (Wang *et al.*, 2009). Diseases of fungal, bacterial, viral origin and in some instances even damage caused by insects and nematodes can be reduced following prior inoculation with endophytes (Berg and Hallmann, 2006).

The possibility of enhancing plant defences by using their associated endophytes opens an interesting avenue for their use in the control of crop pests and diseases that will be compatible with biological control for use in ecological agriculture. Not all of the endophyte-plant associations make plants more resistant to pests or diseases and we therefore must approach the problem from the outset as a three-way interaction: endophyte-plant-organism. Few species of endophytic bacteria are important to crop production because they can be advantageous to infected plants (fixing of nitrogen, plant defences, etc.) and the number of species present in the root system and the relative abundance of each one may be conditioned and/or regulated by the presence of certain endophytes in the plant (Hallman *et al.*, 1998). Chinese cabbage plants whose roots were inoculated with *Heteroconium chaetosporae* were found resistant to the leaf pathogens *Pseudomonas syringae* pv. *Macricola* and *Alternaria alternata* (Fr.) Keissler (Hashiba and Narisawa, 2005).

Endophytes – Role in abiotic stress tolerance in plants

Endophytic bacteria and fungi that live within healthy plant tissues promote plant growth under extreme abiotic stress conditions (below or above the optimal levels) which

limit plant growth and development. Drought, low/high temperature, salt stress and acidic conditions, heavy metal stress, nutrient stress and starvation are the major abiotic stresses that harm plants. Endophytes employ mechanisms through which plants overcome abiotic stress; these include accumulation of stress-responsive molecules, secondary metabolites, and production of antioxidant enzymes. The root fungal endophyte *Piriformospora indica* was shown to induce salt tolerance in barley (Baltruschat *et al.*, 2008) and drought tolerance in Chinese cabbage plants (Sun 2010).

An increase in drought resistance has been observed for plants infected with *Neotyphodium* and barley roots colonized by *Piriformospora indica* (Waller *et al.*, 2005) and in some cases an increase in nitrogen deficiency tolerance has also been observed (Selosse *et al.*, 2004). Diazotrophic bacteria can positively influence plants by improving growth and root development, which increases plant tolerance to various environmental stresses (Ullah *et al.*, 2015). Abid Ullah *et al.*, (2018), reported that the maximum salt tolerance of endophytic bacteria was observed at 2.5% and 7.5% salt concentration. These properties may support host plants to survive under stress conditions by interaction of bacteria and plants.

In conclusion, the endophytes represent an eco-friendly option for the promotion of plant growth and for serving as sustainable resources of novel bioactive natural products. Numerous endophytes and their genes have now been identified, which provide understanding about their behaviour and mechanisms.

Endophytes are well established for their potential to improve plant growth by phosphate solubilisation, nitrogen fixation, and siderophores production. Secondly,

production of phytohormone like auxins, Cytokinins, gibberellic acids play vital role in plant growth promotions and their growth. Endophytes act as a biological control agent of plant pathogens by these antimicrobial activities and induced systemic resistance mechanisms. Most of endophytes are soil genera, and well recognized for plant growth promotion and production of natural compounds, secondary metabolites which have important role in biotic and abiotic stress tolerance.

The property of endophytes to induce stress tolerance in plants can be applied to increase crop yields. These information encourages use of endophytes in improving crop growth and productivity under non stress and abiotic and biotic stress conditions.

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