



# Role of Endophytes in Plant Health and Abiotic Stress Management

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## Abstract

Microbial endophytes are symbionts dwelling within plant tissues without appearance of disease symptoms on host plant and have been recently investigated for their plant growth-promoting properties and their beneficial functions associated with plant responses under abiotic stress conditions. This study focuses on the critical role of endophytic microbes in plant health and their stimulatory different mechanisms to tolerance against abiotic stress in plants. Endophytic microbial community can enhance plant growth through producing secondary active compounds which protect the plant from pathogens such as insect and fungi; also endophytes can produce extracellular enzymes which play critical roles in colonization of endophytes within the plant host. Microbial endophytes have the ability to act as plant growth-promoting agents through producing phytohormones and also enable plants to grow in contaminated soils through breakdown of hazardous compounds. Endophytes manage plant growth under adverse conditions such as salinity, drought, temperature, heavy metal stress, and nutrient stress through different mechanisms. This chapter may introduce new approaches for the use of endophytic inoculants to combat abiotic stresses in agricultural fields, which increases global crop production.

## Keywords

Endophyte · Plant · Abiotic stress · Management

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## 6.1 Introduction

Endophytes are microbial communities that currently dwell in the healthy plant tissues such as stems, roots, leaves, and seeds without affecting physiological plant functions and not causing any disease symptoms to the plant tissues. Under normal conditions, endophytes have important roles in host plant growth either by secondary metabolite or nutrient assimilation or by preventing induction of plant disease symptoms by different pathogens. Endophytic microbes including bacteria, actinomycetes, and fungi tend to form a network closely to their host plants and are additionally sheltered from unfavorable climatic and other unwanted change in the environment (Zhao et al. 2011; Passari et al. 2017).

Recent research work suggests that about 300,000 species of plants are present, the unmistakable dominant part of which contains endophytes (Smith et al. 2008). In fact, microbial endophytes especially bacteria and fungi have originated in most plant species that have been investigated. According to Partida-Martínez and Heil (2011), endophyte-free plant is an unusual state to what is typically obtained in nature; a plant without endophytes would be susceptible to environmental stress conditions and lose their ability to resist the pathogens (Timmusk et al. 2011).

The origin of endophytes is still not clear because of the multiplicity of the host's living environment and the complex association between the endophyte and its host plant. Two hypotheses explaining the origin of endophytes were exogenous and endogenous. It was believed that in the last decade, endophytes are gaged from the chloroplast and mitochondria of the plant, and so it has comparable genetic backgrounds to the host (Wen 2004); this is the endogenous hypothesis, while the latter believes that endophytes arrive from outside of the plant and insert into the host from root wound, induced channels, or surface (Li 2005); this is exogenous hypothesis.

Different parts of plants were used for isolation of microbial endophytes as meristem, scale primordia, resin ducts (Pirttilä et al. 2003), leaf segments with midrib and roots (Hata et al. 2002), leaf blade, stem, petiole, bark, and buds (Pirttilä et al. 2008).

Endophytic fungi insert through the hyphae and enter the kernels in the seeds of plant cells that come below vertical transmission. A variant was detected in horizontal and vertical transmission of the endophyte species invading the host plant cells (Tintjer et al. 2008). The procedures of endophytic microbial growth in plants and methods of propagation were paid more attention to know their role in transmission. The endophytic fungal species transmits horizontally by sexual spores or asexually between different plants in community or a population (Tadych et al. 2014).

The microbial community such as bacteria, algae, fungi, and actinomycetes colonizes the host plant roots (Saharan and Nehra 2011; Prashar et al. 2014). Among microbial population found in the rhizosphere, actinobacteria are considered the second most abundant microorganisms, and they comprise more than 30% of the total microorganisms in the soil (Glick 2014). Endophytes are transmitted between the soil rhizosphere across the seeds. They spread quickly between

endo-rhizosphere through the lateral root junction instigated through microbial phyto-pathogens or nematode (Chi et al. 2005). Also, bacterial endophytes can enter their host plant roots through spaces between root hairs and epidermal cells (Hardoim et al. 2008).

The most common endophytic fungi isolated and identified from numerous plants are *Alternaria infectoria*, *Aspergillus* sp., *Penicillium* sp., *Colletotrichum musae*, *Colletotrichum gloeosporioides*, *Nigrospora oryzae*, *Phomopsis* sp., *Nigrospora sphaerica*, *Guignardia* sp., *Cordana musae*, *Rhizoctonia* sp., species of *Phialocephala sphaeroides*, *Xylaria* (Wilson et al. 2004), *P. chrysogenum* Pc\_25, *A. alternata* Aa\_27, and Sterile hyphae Sh\_26 (Fouda et al. 2015). On the other hand, endophytic *P. chrysogenum* Pc\_25 was mediated biosynthesis of ZnO nanoparticles (Fouda et al. 2019a).

In addition, various endophytic bacterial strains were isolated from economically important plant species. Several of the novel endophytic bacterial species belong to the *Arthrobacter* spp., *Actinobacter* spp., *Aeromonas* spp., *Enterobacter* spp., *Agrobacterium* spp., *Alcaligenes* spp., *Bacillus* spp., *Flavobacterium* spp., *Azospirillum* spp., *Azotobacter* spp., *Pseudomonas* spp., *Burkholderia* spp., *Beijerinckia* spp., *Enterobacter* spp., *Flavobacterium* spp., *Erwinia* spp., *Rhizobium* spp., and *Serratia* spp. were characterized and identified (Gray and Smith 2005). In the last periods, other endophytic actinobacteria such as *Streptomyces*, *Amycolatopsis*, *Nocardia*, *Microbispora*, *Micromonospora*, and *Streptomyces capillispiralis* Ca-1 have been positively isolated from different plant species (Shi et al. 2009; Ruanpanun et al. 2010; Hassan et al. 2018).

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## 6.2 Role of Endophytes in Plant Health

Great effort has been made to study the diversity of endophytic species in plants and their evolutionary biology, ecology, and their roles in defense mechanism against abiotic and biotic stress via production of different metabolites. Endophytic biotechnology can be expended for the efficient production of economically, agriculturally, and industrially significant plants and their crops. The reasonable application for different endophytic species associated with plants can help in improvement of the agricultural products, increasing metabolite productivity in different plants, as well as adjustment tolerance to numerous abiotic and biotic conditions (Wani et al. 2015).

Endophytic species have recently generated important new bioactive substances. It has been suggested that the relationship between different endophytic species and their host plant in the production of a great amount and diversity of biologically active molecules are related together, and this contrasted to epiphytes or soil-related microorganisms (Strobel 2003).

New biotechnology applications for endophytic species such as bioremediation and phytoremediation are gaining considerable impetus (Li et al. 2012a). Endophytes play critical roles in healthy plants through three different mechanisms known as biofertilization, phytostimulation, and biocontrol (Bloemberg and Lugtenberg 2001).

### 6.2.1 Endophytes as Source for Bioactive and Novel Compounds

Endophytic microbes release specialized biologically active compounds or metabolites without any observable damage to their host tissues (Liarzi et al. 2016). The bioactive compounds synthesized by different endophytic microbes that increase plant resistance against pathogenic microorganisms are too used in the pharmaceutical fields as anticancer, antimicrobial, antiviral, antidiabetic, and other biologically active compounds (Guo et al. 2008). Other biologically active compounds synthesized by endophytic microbes as alkaloids, terpenoids, steroids, peptides, poly-ketones, quinols, flavonoids, phenols, and insecticide azadirachtin are also investigated for their medical, agricultural, and industrial applications (Kusari et al. 2012a; Molina et al. 2012; Zinniel et al. 2002). Numerous of these bioactive compounds showed antioxidant, antimicrobial (antibacterial, antifungal, and antiviral activities), antineoplastic, antiproliferative, anti-leishmanial, cytotoxicity, and fuel production activities (Shankar Naik and Krishnamurthy 2010; Wang and Dai 2011). Examples of antifungal compounds produced by endophytes include cryptocandin, pestalocide, cryptocin, ecomycins, pestalopyrone, and pseudomycins (Yu, et al. 2010).

Naturally, different seasons, locations, environmental conditions, soil, age, and tissue of the host plant, all influence the endophyte biology and thus considerable variants in the synthesis of bioactive metabolites (Strobel and Daisy 2003). Also, cultivation conditions and separation methods can affect the type and variety of metabolites (Gunatilaka 2006). Aly et al. (2011) and Kusari et al. (2012b) reported that sampling, type, and size of the plant tissue used for isolation, composition, and culture conditions for media such as pH, incubation temperature, incubation period, agitation, and culture, all of these factors are controlling the productivity of bioactive compounds in the laboratory.

The productivity of bioactive compounds by endophytic microorganisms can be influenced both genetically and physicochemically (Kharwar et al. 2011). Separation and identification methods of bioactive metabolites from microbes, especially fungal and bacterial endophytic species, are fast growing, as can be detected from numbers of patents, reviews, and original articles available each year in the drug discovery field (Tejesvi and Pirttilä 2011). Fungal endophytic species are a native source for flavonoids, terpenoids, phenols, saponin, alkaloids, carbohydrates tannins, and nematode antagonistic compounds (Liu et al. 2016; Bogner et al. 2017). Endophytic actinomycetes are promising tool for synthesis of bioactive compounds, which can be used as therapeutic agents against different pathogens (Prashith-Kekuda 2016). On the other hand, endophytic bacteria have useful effects as enhancement of nitrogen fixation, phosphate solubilization, production of phytohormones, and reduction of ethylene biosynthesis as response to abiotic (pH, temperature, and osmotic pressure) and biotic (from fungi, bacteria, nematodes, and insects) stresses and have biocontrol activities. Supplementary than 300 endophytic bacteria and actinobacteria belonging to the genera *Streptomyces*, *Rhodococcus*, *Nocardiopsis*, *Microbacterium*, *Brevibacterium*, *Arthrobacter*, *Nocardia*,

*Brachy bacterium*, *Tsukamurella*, *Kocuria*, *Pseudonocardia*, and *Nocardioidea* were isolated from *Dracaena cochinchinensis* Lour. plant. Of these, 17 endophytic strains have antimicrobial, anthracyclines-producing activities, antifungal properties, and anticancer activities against Hep G2 and MCF-7 as cancer cells (Salam et al. 2017). Endophytic microorganisms have already a bulk for the discovery of biologically active compounds, but still innovative methods are demanded to natural product-based drug discovery.

### 6.2.2 Extracellular Enzyme Production

Endophytes play an important role in plant health via extracellular enzyme production which have been counted as the most significant and important mechanisms for endophyte colonization in plants. Among enzymes, extracellular enzymes or exoenzymes have industrial importance in different fields such as fermentation process, food, and other biotechnological applications. Microorganisms including fungi and bacteria produce different types of extracellular enzymes, which are oxidoreductases, hydrolases, transferases, and lyases (Traving et al. 2015). Extracellular enzymes breakdown numerous macromolecules such as lignin, sugar-based polymers, proteins, organic phosphate, and carbohydrates to micromolecules and are transported throughout the cells; they are continuously metabolized and help to instruct the host symbiosis process (Strong and Claus 2011; Wingender et al. 1999). Also, extracellular hydro-lyase enzymes increase plant responses to pathogenic infection (Leo et al. 2016).

Different extracellular enzymes such as  $\beta$ -1,3-glucanase, protease, lipase, and chitinase associated with endophytic microbes lyse the cell walls of pathogenic bacteria and fungi and hence can be used as biocontrol agents (Fouda et al. 2015, Wang et al. 2014).

On the other hand, improvement in endophytic microbial growth within host plant tissues and then reduction in the pathogens are influenced by production of various enzymes such as xylanases, cellulases, pectinases, lipases, proteases, phosphatases, amylase, and glucosidases (Kannan et al. 2015; Pereira et al. 2016; Khan et al. 2016; Ayob and Simarani 2016).

Chathurdevi and Gowrie (2016) reported that the endophytic fungi isolated from medicinal plants can support plant growth to overcome the adverse conditions through producing different extracellular enzymes. Also, approximately 50 endophytic fungal strains having amylase, laccase, cellulase, pectinase, lipase, and protease were isolated and identified according to Sunitha et al. (2013). In addition, bacterial endophytes have been investigated to produce 1-aminocyclopropane-1-carboxylate (ACC) deaminase, amylase, cellulases, esterase, pectinase, protease, lipase, asparaginase, phytase, and xylanase (Carrim et al. 2006; Gupta et al. 2013; Fouda et al. 2015; Akinsanya et al. 2016). Vijayalakshmi et al. (2016) isolated bacterial endophytes from medicinally significant plants producing various extracellular enzymes as cellulase, amylase, and protease.

### 6.2.3 Plant Growth-Promoting Activity

Endophytic microbes play a critical role in plants' adaptation to stress conditions and varying environments which can limit their development and growth. To contract with extreme environments, plants may form network with microorganisms in symbiotic relationship, which confer helpful effects on evolution to both partners and appropriateness (Rodriguez et al. 2009). Extreme environment conditions such as low water and nutrient availability, high radiation, strong winds, and low temperatures affect plant survival and organization (Convey 2011).

A practical strategy to reducing stress without cooperating plant growth is the use of plant growth-promoting microbe relationship. Widespread varieties of metabolite substances produced by endophytic fungi are used to improve plant growth (Waqas et al. 2015).

Endophytic microbes enhance plant growth through their ability to synthesize enzymes and various bioactive metabolites. Endophytic microorganisms, especially fungi such as *Sebacina vermifera*, *Piriformospora indica* and numerous species of *Colletotrichum* and *Penicillium*, are distinguished to have better plant growth-promoting effects under unfavorable conditions (Waller et al. 2005; Redman et al. 2011; Hamilton and Bauerle 2012). Plant growth-promoting microbes (PGPM) associated with many species of plants tend to have useful effects such as intensified plant growth and decreased sensitivity to diseases instigated by plant pathogenic viruses, fungi, bacteria, and nematodes. Main activities of PGPM are accompanied with plant hormone synthesis such as indole-3-acetic acid (IAA), cytokinins, gibberellins, siderophores, phosphate solubilization, nutrient uptake, and antagonism to phytopathogens. Also, PGPM can induce chemical or physical changes related to plant protection, a process signified as induced systemic resistance (ISR). PGPM have developed to be beneficial for plants constantly under many abiotic stresses. Several reports confirmed the critical roles of plant growth-promoting fungi (PGPF) in increasing tolerance against different stresses such as heat, drought, salinity, cold, and heavy metals (Khan et al. 2012). On the other hand, stresses like salinity and drought induce osmotic stress, which is conveyed through abscisic acid (ABA)-independent or ABA-dependent pathways (Cao et al. 2014), and low levels of ABA productions were achieved under fungal action (Jahromi et al. 2008; Khan et al. 2014). Miransari (2012) reported that plants needed low attempt to synthesize ABA and hence protect cell progress under stress, as the water equilibrium in plant was achieved by treatment with endophytic *Penicillium* spp.

Plant growth-promoting bacteria (PGPB) are proficient to enhance plant growth through independent or linked mechanisms for maintainable agriculture (Compant et al. 2010; Palacios et al. 2014). PGPB showed different responses against numerous stresses in plants (Kim et al. 2012), fighting against plant pathogens (Raaijmakers et al. 2009) and supplementary in the recovery of damaged cells or degraded constituents (de Bashan et al. 2012). Colonization of host plant tissues by endophytic bacterial species has been reported by Yang et al. (2016) and Tang et al. (2017), and its capability to promote growth, fix nitrogen, and repress phytopathogens with induced systemic resistance (ISR) of this pathogen was reported by Pieterse et al.

(2014), Puri et al. (2016), and Padda et al. (2016). Endophytic actinobacteria can improve plant growth via one or more plant growth-promoting mechanisms including nitrogen fixation, solubilization of inorganic nutrients, excretion of phytohormones, and siderophores (Dudeja et al. 2012).

Indoleacetic acid (IAA) is fundamental plant growth hormone used for the development and growth of shoot and root cells of plants; many microorganisms including plant growth-promoting rhizobacteria (PGPR) produce IAA (Hassan 2017). Soil microorganisms such as bacteria and fungi synthesize plant growth-promoting compounds such as gibberellins and IAA (Radhakrishnan et al. 2013; Limtong et al. 2014).

Several reports proved that endophytic actinobacteria synthesize plant growth regulators such as auxins, cytokinins, gibberellins (gibberellic acid), and IAA in vitro (Ghodhbane-Gtari et al. 2010; Fouda et al. 2019b).

Siderophores are small compounds with high-affinity iron chelators (soluble  $\text{Fe}^{3+}$ -binding agents) synthesized by microbes such as fungi, bacteria, and actinobacteria growing under low iron stress. Several endophytic microbes have been explored to synthesize siderophores, with a molecular weight ranging between 400 and 1500 daltons (Kannahi and Senbagam 2014). There are four types of siderophores synthesized by bacteria, viz., catecholate, salicylate, hydroxamate, and carboxylate. Endophytic actinobacteria including the genera *Pseudonocardia*, *Streptomyces*, *Nocardia*, *Actinopolyspora*, *Micromonospora*, *Salinispora*, *Actinomadura*, and *Kibdelosporangium* are recognized as siderophore producers (Gangwar et al. 2011; Kannahi and Senbagam 2014; Bhosale and Kadam 2015). Endophytic actinobacteria synthesize siderophores as an extramechanism, which act as plant growth regulators and in defense against pathogens (Rungin et al. 2012).

Moreover salicylic acid (SA), as a phytohormone, is a significant plant hormone concerned in many processes such as root initiation, seed germination, floral induction, stomatal closure, and increased tolerance of plant to abiotic and biotic stresses. Bacterial endophytes synthesize SA, which enhance the growth of plant seedlings under water stress and reduce the growth of plant pathogens such as fungi (Klessig et al. 2016).

#### 6.2.4 Biocontrol Agents

Endophytic microorganisms are defined as a functional biocontrol agent, instead of chemical control. Endophytic fungi play a critical role in controlling insect herbivores not only in grasses but also in conifers (Parker 1995). Tefera and Vidal (2009) reported that *Beauveria bassiana*, an endophytic fungi known as an entomopathogen, was used to control the borer insects in sorghum. Also, acute rotting caused by fungal pathogens in tomato fruits can be achieved during storage and shelf life. Different bacterial endophytic strains such as *Bacillus subtilis* isolated from *Speranskia tuberculata* (Bge.) Baill has an antagonistic effect in vitro against the pathogen *Botrytis cinerea*, which cause rotting of tomato fruits during storage (Wang et al. 2009). New endophytes, such as *Burkholderia pyrrocinia* JK-SH007 and *Bacillus cepacia*, were used in biocontrol study against poplar canker (Ren et al. 2011). New approaches in biocontrol studies induced genetically engineered

gene expression into an endophytic microorganism to synthesize anti-pest proteins like lectins for insect control.

On the other hand, endophytic strains such as *Chaetomium globosum* YY-11 isolated from rape seedlings, *Enterobacter* sp., and *Bacillus subtilis* isolated from seedlings of rice were utilized for the expression of *Pinellia ternate* agglutinin (*PtA*) gene (Zhao et al. 2010). The previous endophytic recombinant fungal and bacterial strains which express the *PtA* gene were used successfully to control sap-sucking pests in numerous crop seedlings. Similarly, in another study, *Enterobacter cloacae*, as a recombinant endophytic bacterial strain expressing the *PtA* gene, was proved as a bio-insecticidal agent against the white backed plant hopper *Sogatella furcifera* (Zhang et al. 2011). The recombinant endophytic strains which easily dwell within several plants can be used as a new strategy to control different plant pests through expression of different anti-pest proteins. Also, Hassan et al. (2018) reported that copper nanoparticles synthesized using the endophyte *Streptomyces capillispiralis* Ca-1 have the ability to biocontrol *Culex pipiens* (Mosquito) and *Musca domestica* (housefly). On the other hand, copper oxide nanoparticles synthesized by two endophytic actinomycetes, *Streptomyces zaomycticus* Oc-5 and *Streptomyces pseudogriseolus* Acv-11, isolated from *Oxalis corniculata* L. plant have antimicrobial activity against four phytopathogenic fungi, namely, *Phoma destructiva*, *Fusarium oxysporum*, *Alternaria alternata*, and *Curvularia lunata* (Hassan et al. 2019).

### 6.2.5 Bioremediation/Biodegradation Activity

Endophytic microorganisms have a powerful ability to enhance plant growth in contaminated soil through breakdown of hazard compounds. Bioremediation is defined as elimination of pollutants and hazardous wastes from contaminated environments by breakdown of these wastes using biological processes. This is due to the major microbial diversity. Mastretta et al. (2009) reported the ability of *Nicotiana tabacum* plants in bioremediation through inoculation of their seeds with endophytes. They have showed enhanced plant biomass production under Cadmium (Cd) as heavy metal stress, and the Cd concentration in plant tissue was higher compared to noninoculated plants. These results proved the useful effects of endophytic inoculated seeds on accumulation and assimilation of heavy metals.

To discover the role of endophytic microbes in the breakdown of contaminants such as plastics, different endophytic fungal strains were subjected to growth in agar and broth media containing polyester polyurethane (PUR) as a sole carbon source (Russell et al. 2011). Among fungal endophytic strains, two *Pestalotiopsis microspora* isolates have the ability to use PUR as the sole carbon source under aerobic and anaerobic conditions and using serine hydrolase enzyme for the degradation of PUR.



### 6.2.6 Induced Systemic Resistance (ISR)

Endophytic microorganisms increase plant resistance to pathogen through induce defense mechanisms, so-called induced systematic resistance (ISR) (Zamioudis and Pieterse 2012). At an initial stage, there is increasing evidence that interactions between endophytic microorganisms and their hosts stimulate immune response in host plants; this is similar to those happening against pathogens; later on, endophytic microorganisms colonize plants through escaping from defense responses as occurring in the bacterial genera *Bacillus* and *Pseudomonas* (Kloepper and Ryu 2006). Different bacterial factors such as antibiotics, salicylic acid, N-acyl-homoserine lactones, siderophores, jasmonic acid, lipopolysaccharides, and volatiles (e.g., acetoin) are responsible for induction of ISR (Bordiec et al. 2011). The defense mechanisms and protections of plants against herbivorous insects and pathogens were related to ISR. Although several endophytic bacteria have increased ISR via salicylic acid induction, ethylene (ET) and jasmonic acid (JA) as plant hormones have important regulatory roles in signaling pathways implicated in ISR induction (Pieterse et al. 2012). The endophytic bacterium *Pseudomonas fluorescens* 89B-61 was the first reported, explaining the ISR induction to protect cucumber plants against cucumber anthracnose (Kloepper and Ryu 2006). The resistance of potato plant against the pathogen *Pectobacterium atrosepticum* was increased in the presence of the endophyte *Methylobacterium* sp. IMBG290. The resistance manner was related to changes in composition of the native endophytic community. Changes in endophytic community were linked to disease resistance, which means the endophytic community has a critical role in disease repressions (Ardanov et al. 2011). Also, endophytic fungi have been involved in protection mechanisms via ISR induction but less than endophytic bacteria (Bae et al. 2011). The potentiality of endophytic fungi in producing metabolites has inhibitory activities against herbivores, and plant pathogens were recorded. These metabolites comprise steroids, alkaloids, peptides, terpenoids, flavonoids, polyketones, phenols, chlorinated compounds, and quinols (Higginbotham et al. 2013; Tejesvi et al. 2013). On the other hand, metabolites having antibacterial, antiviral, insecticidal, and antifungal activities were reported by fungal endophytes, which transmitted horizontally, forming local disease in their hosts (Gunatilaka 2006; Tejesvi et al. 2011).

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### 6.3 Alleviation of Abiotic Stresses via Microbial Endophytes

Plant growth and development are restricted by different extreme conditions which include environmental stresses as well as stresses caused by living communities.

Plants can tolerate abiotic stress by two mechanisms: (i) plants can avoid negative effects of stress via activation of response systems directly after exposure to stress (Meena et al. 2017), and (ii) biochemical compounds are synthesized by

endophytes and act as anti-stress agents (Schulz et al. 2002). The up- and downregulation for some stress-inducible genes in pepper plant were reduced after inoculation with the endophyte *Arthrobacter* sp. and *Bacillus* sp. when compared with gene expression in uninoculated plants. Assimilation of nutrients, such as magnesium, potassium, and calcium, plant biomass, growth parameters, and decreased sodium toxicity were significantly increased in cucumber plants under sodium chloride and drought stress after inoculation with *Phoma glomerata* and *Penicillium* sp. when compared with uninoculated plants (Waqas et al. 2012). Bailey et al. (2006) revealed that *Trichoderma* sp. isolated from *Theobroma cacao* increases tolerance in *cacao* plant against abiotic stress especially drought via gene expression change.

The resistance of tissue cultured *Kalmia latifolia* L. to drought stress was increased after seedling inoculation with *Streptomyces padanus* AOK-30 as endophytic actinomycetes as reported by Hasegawa et al. (2004).

Bae et al. (2009) reported that sugars and amino acids showed significant increase in endophyte-colonized plants due to drought stress. Increase in sugar and amino acid production (as indicators for increased osmolytic activity) is due to intricate symbiotic relationship in plants possessing a drought-tolerant phenotype (Shinozaki and Yamaguchi-Shinozaki 2007). Significantly producing biomass is one response to drought, temperature, and salt stress in endophyte-colonized plants than their non-colonized one (Redman et al. 2011). Zhang and Nan (2010) revealed that increased seedling growth as drought response was due to higher antioxidant activity. Also, Zhang and Nan (2007) showed that increase in biomass, proline concentrations, and relative water content as a result of endophyte colonization under low water conditions was investigated. Inoculation of wheat with *Burkholderia phytofirmans* PsJN increased CO<sub>2</sub> assimilation, photosynthetic rate, water use efficiency, and chlorophyll content under drought conditions (Naveed et al. 2014).

*The following are examples for abiotic stresses that have a negative effect on plant growth and development, and alleviate via endophytes.*

### 6.3.1 Drought Stress

Drought is one of the most important abiotic stresses that suppress plant growth, development, and productivity. Plants undergo drought conditions through either limiting water supply to the roots or very high transpiration (Anjum et al., 2011). It has been concluded that diurnal water stress normally occurs in most plant species during noon and afternoon hours in temperate climates, even though the soil water contents are normal. This temporary drought stress has a negative impact on the growth rate (Granier and Tardieu 1999). Drought causes reduced germination rates, membrane loss of its integrity, repression of photosynthesis, and increase in the productivity of reactive oxygen species (Greenberg et al. 2008). Furthermore, elevated drought and salinity were the main causes of osmotic stress to plants. While drought leads to osmotic stress, salinity shows both ionic or ion-toxicity, and osmotic stress impacts cells (Zhu 2002). The shoot system symptoms of osmotic

stress caused by salinity interfere with that of drought stress including stunted growth and leaf senescence (Munns 2002).

Plants harboring endophytes (rice, tomato, dune grass, and panic grass) consumed significantly less water and had enhanced biomass than nonsymbiotic plants. Increased accumulation of solutes in tissues of endophyte-associated plants comparable with noninfected plants, or because of thicker cuticle formation, or by decreased leaf conductance and a slower transpiration stream may explain the drought tolerance phenomenon (Malinowski and Beleskey 2000). The ability of plant to tolerate water stress may be related to morphological and genetic adaptation and biochemical responses. However, the central response to water deficits is the increase in the biosynthesis of plant hormone ABA and/or reduction in ABA breakdown (Bray 2002). In plants suffering from drought, it is supposed that ABA behaves like the signal that manages the plant's resistance to water deficit, principally by controlling water loss and stomata closure (Zhang and Outlaw 2001). Also, other evidence proposes that ABA has a role in root branching, enhancing the plant water absorption capacity (De Smet et al. 2006).

ABA was defined using full scan mass spectrometry as a by-product of chemically enhanced growth cultures of *Azospirillum brasilense* Sp 245. Adding NaCl to the culture medium led to increased bacterial ABA production, and ABA levels were improved in *Arabidopsis thaliana* seedlings inoculated with *Azospirillum brasilense* Sp 245 (Cohen et al. 2008).

### 6.3.2 Salinity Stress

Soil salinization happens when water-soluble salts accumulate in the soil to a level that affected environmental health, agricultural production, and economics. In the first stages, salinity has a negative impact on the metabolism of soil organisms and hence decreases soil productivity, but in advanced stages, it destroys all vegetation and other organisms living in the soil, consequently transforming fertile and productive land into barren and desertified lands (Jones et al. 2012). A saline soil is known to have an electrical conductivity (EC) of the saturation extract (EC<sub>e</sub>) in the root zone more than 4 dS m<sup>-1</sup> (nearly 40 mM NaCl) at 25 °C with exchangeable sodium of 15%. The yield of most crop plants is decreased at this EC<sub>e</sub>, and many crops showed reduced yield at lower EC<sub>e</sub>s (Jamil et al., 2011).

It is a key factor contributing to reduced productivity of cultivated soils. Although accurate estimation is difficult, the salinized soil area is increased, and this phenomenon is particularly dense in irrigated soils. It is estimated that about 20% (45 million hectares) of irrigated land, which produces one-third of global food, is affected by salinity (Shrivastava and Kumar 2015). Soil salinity impacts an estimated one million hectares in the European Union, particularly in the Mediterranean countries, a major cause of desertification. In Spain, about 3% of irrigated land (3.5 million hectares) is severely affected, significantly reducing their agricultural potential, while another 15% are at high risk (Stolte et al. 2015). In the Mediterranean area, soil alkalization associated with land degradation may deteriorate at increasing rates

in the coming decades due to the expected increase in irrigated regions and the increasing deficiency of good-quality water (Bowyer et al. 2009).

### 6.3.2.1 Effect of Soil Salinity on Plants

Salinity significantly affects agricultural crops, which reduces agricultural output and affects the physical and chemical properties of the soil and environmental balance of the region, as well as low economical findings and soil corrosions (Hu and Schmidhalter 2002).

Complex interactions led to salinity effects comprising biochemical, physiological, and morphological processes including vegetative growth, water uptake, seed germination, enzyme activity, seedling growth, protein synthesis, and mitosis of DNA and RNA (Akbarimoghaddam et al. 2011). It has deep impact on reproductive development by stamen filament elongation and inhibiting microsporogenesis, ovule abortion, and senescence of fertilized embryos and enhanced cell death in tissue types. Since many salts are also plant nutrients, increased salt concentrations in the soil can disturb the plant nutritional balance or interfere with the absorption of some nutrients (N, Ca, K, P, Fe, and Zn) leading to nutrient deficiency. Because P ions precipitate with Ca ions, P uptake is significantly reduced by soil salinity (Bano and Fatima 2009).

While  $K^+$  has a main role in biochemical reactions, acting as a cofactor for various enzymes and in protein synthesis, high concentrations of  $K^+$  mediates binding of tRNA to ribosomes. However, soil salinity leads to ion toxicity resulting from replacing  $K^+$  by  $Na^+$  in such reactions. Furthermore,  $Cl^-$  and  $Na^+$  induced conformational modifications in proteins (Zhu 2002). Soil salinity imposes osmotic stress, which leads to loss of turgidity, cell dehydration, and, finally, death of cells. Osmotic stress and ion toxicity lead to metabolic imbalance, which in turn causes oxidative stress (Ashraf 2004).

Photosynthesis is negatively affected by salinity of the soil through reducing photosystem II capacity, chlorophyll content, leaf area, and stomatal conductance (Netondo et al. 2004). Moreover, salinity may impede the supply of hormones or photosynthetic assimilates to growing tissue (Ashraf 2004). The cell cycle is transiently arrested by salinity stress which causes reduction in the activity and expression of cyclins that result in fewer cells in the meristem, consequently limiting growth. In addition, the posttranslational inhibition during salinity stress causes reduction in the activity of cyclin-dependent kinase (Seckin et al. 2009).

### 6.3.2.2 Salinity Stress Alleviation by Microbial Endophytes

Salinity problem threatens more than 20% of agricultural soil (Zhu 2000), and by 2050, about 50% of important agricultural land will be affected by salinity stress (Munns and Tester 2008). Endophytic microbes can enhance growth properties and modulate metabolism and phytohormone signaling. In addition, endophytic microbes improve adaptation to abiotic and biotic stress. Endophytes represent a particular concern for improved crop adaptation to stress as they are relatively protected from the harsh soil environment under high salt, drought, or other stress conditions (Sturz et al. 2000).

*The following are the major advantages of endophytes to minimize salinity impacts on plants.*

### **Plant Antioxidant Status**

Reactive oxygen species in plants are formed on the onset of salt and osmotic stress. Scavenging enzymes such as ascorbate peroxidase, catalase, and superoxide dismutase inhibit oxidation of DNA, membrane proteins, and lipids. Microorganisms use similar methods to deal with oxidative stress. Hamilton and colleagues in 2012 reported the fungal endophyte mediation of reactive oxygen species in plants (Hamilton et al. 2012). Previous studies have suggested the relationship between tolerance of plants to salt stress and the alleviation of antioxidant enzymes (Sekmen et al. 2007). Scavenging enzymes for ROS include glutathione reductases (GR), superoxide dismutases (SOD), catalases (CAT), dehydroascorbate reductases (DHAR), ascorbate or thiol-dependent peroxidases (APX), and mono-dehydroascorbate reductases (MDHAR), in addition to tocopherol and glutathione (Rouhier et al. 2008). These enzymes involved in the removal of ROS either directly (APX, SOD, CAT) or indirectly via regeneration of glutathione and ascorbate in the cell. On constant, when the nonsymbiotic plants *Leymus mollis* (dunegrass) subjected to 500 mmol l<sup>-1</sup> NaCl solution becomes severely wilted, desiccated within 7 days and ultimately dead after 14 days (Rodriguez et al. 2008). Plants infected with *Fusarium culmorum* did not show the symptoms of wilt until it was subjected to 500 mmol l<sup>-1</sup> NaCl for 14 days. The endophyte *Piriformospora indica* induces salt tolerance by improving the antioxidant status of barley (Baltruschat et al. 2008).

### **ACC Deaminase**

Although endophytic microbes might produce ACC deaminase enzyme and do not benefit from it, the enzyme has a role in promoting plant growth and enhances plant stress tolerance through cleaving ethylene, which acts as a precursor for the synthesis of ACC (Glick 2014). ACC deaminase can reduce plant ethylene levels by cleaving its precursor ACC (1-aminocyclopropane-1-carboxylate) to 2-oxobutanoate and ammonia, inhibiting ethylene signaling (Glick et al. 1998). Ethylene is a significant plant hormone that contributes in seed germination, in response to several stresses, and it is the main regulator for bacterial colonization of plant tissues (Iniguez et al. 2005). Ethylene accumulation in plants as a stress response is commonly detrimental to plant health and growth (Czarny et al. 2006). In addition to stress relief, ACC deaminase enzyme supports bacterial endophyte colonization of the plant. *Burkholderia phytofirmans* PsJN lost the capacity of root elongation in canola plant seedlings when the gene of ACC deaminase was inactivated (sun et al. 2009). A previous study on cut flowers reported the ability of endophytic bacteria to colonize shoot. Moreover, the ACC deaminase enzyme delayed flower senescence (Ali et al. 2012).

### **Phytohormone Production**

Endophytes capable of promoting plant growth considerably produce auxins, principally indole-3-acetic acid (IAA) (Witzel et al. 2012). Auxins act against ethylene and play a major role in promotion of root development and growth. So,

endophytic management of auxin production might be a significant tool in awarding salt tolerance in halophytic plants. IAA production was found in (i) species of *Serratia*, *Bacillus*, *Vibrio*, *Brevundimonas*, *Oceanobacillus Exiguobacterium*, *Staphylococcus*, and *Halobacillus* isolated from four samples of halotolerant plants grown in coastal sandbank of China (Bian et al. 2011) and (ii) salinity-tolerant rhizobacteria (*Halomonas* sp., *Arthrobacter* sp., *Pseudomonas mendocina*, *Bacillus pumilus*, and *Nitrinicola lacsaponensis*) originating from extremely saline habitats (Tiwari et al. 2011). It was suggested that IAA, one of the auxins, increases the efficiency of colonization (Suzuki et al. 2003), probably via interference with the host defense system (Navarro et al. 2006), and the production of such compounds or other related compounds might be a significant property for colonization of plant by endophytes. The halophytic plant *Prosopis strombulifera* also produced ABA, gibberellins, and IAA (Piccoli et al. 2011). ABA is a vital hormone for plant development and growth, and plants increase their ABA levels in stressed conditions. The main role of ABA is to regulate water balance of plant and tolerance of osmotic stress (Tuteja 2007). Wheat plants growing in saline soil showed increased fitness when inoculated with rhizobacteria having IAA producing and salt-tolerant capacity (Tiwari et al. 2011). The function of phytohormones for enhancing salt tolerance has not been analyzed for root fungi either mycorrhizal or endophytic (Ruppel et al. 2013).

### Nitrogen Fixation

Benefits of endophytes include pathogen suppression, phytohormone production, nutrient supply, and nitrogen fixation; these mechanisms also contribute to the mitigating effects of endophytes when the host plant faces unfavorable ecological conditions (Ruppel et al. 2013). Various root endophytes could fix nitrogen (e.g., *Azoarcus* spp., *Acetobacter diazotrophicus*, and *Herbaspirillum* spp.). Nitrogen fixation improves host plant fitness, mostly in poor nitrogen environments. Even if fixed nitrogen in single species is found in a low amount, it should be clarified whether fixed nitrogen is intended for the microbial demands and/or host plant demands. The endophytic strain *Paenibacillus* P22 isolated from poplar trees conferred the fixed nitrogen to the pool of total nitrogen of host plant, as well as induced changes in plant metabolism (Hardoim et al. 2015).

### Compatible Solutes

Sequestration of  $\text{Na}^+$  and  $\text{Cl}^-$  ions in the vacuole of plant cell causes osmotic pressure. To balance this pressure, metabolically compatible organic solutes must be accumulated (even at elevated concentrations) in organelles and cytosol. Sucrose, glycine betaine, and proline are the most prevalent accumulated solutes (Munns and Tester 2008).

Cumulating organic solutes consider a vital mechanism to counter osmotic pressure, and this was also found in halophytic plants (Flowers and Colmer 2008); proline amino acid was the topic of research to understand the increased salt tolerance in plants colonized with endophytes. Nevertheless, mycorrhizal fungi gave variable results and suggested that accumulation of proline is generally considered as the

effect, but it is not the reason for salinity tolerance (Ruiz-Lozano et al. 2012). Osmosis can also be regulated by betaines and sugars. Increased levels of sugars and betaines in mycorrhizal plants suggested that they have a role in salinity tolerance (Manchanda and Garg 2011). The endophyte *Pseudomonas pseudoalcaligenes* showed an improvement in salinity tolerance of rice by stimulating the accumulation of glycine betaine-like compounds in high concentrations (Jha et al. 2011).

### 6.3.3 Temperature Stress

Extreme temperature adversely affects plant growth, and high temperature leads to significant damage to cellular proteins that are widely denatured and aggregated, leading to cell death. On the other hand, low temperature causes impaired metabolism due to inhibition of enzyme reactions, interactions among macromolecules, changes in protein structure, and modulating the membrane properties (Andreas et al. 2012).

Only few reports have the detrimental effects of extreme temperatures, which are often related to water limitation. In this regard, *Burkholderia phytofirmans* enhance resistance of plants grown at low temperatures (Ait Barka et al. 2006). The grass *Dichanthelium lanuginosum* was able to survive, although soil temperatures ranged from 38 °C to 65 °C in the Yellowstone National Park due to *Curvularia protuberata* and its thermal tolerance mycovirus *Curvularia* (CThTV) (Redman et al. 2002). The fungal endophytes have increased wheat tolerance to temperature regarding grain weight and seed germination of the second generation (Hubbard et al. 2014).

High temperature, precipitation, and latitude can interact and influence the endophyte composition in plants. For example, in sweet root (*Osmorhiza depauperata*), the endophytes *Sinorhizobium meliloti* and *Agrobacterium tumefaciens* were more abundant in locations with higher precipitation and annual temperature, while *Paenibacillus* strains were more common at sites with lower precipitation and higher latitudes (Li et al. 2012b).

Matsouri et al. (2010) reported that enhanced tolerance of endophyte-colonized plants to temperature and salt stress arise from alterations in ratios of oxidized-to-reduced forms of ascorbate and glutathione as well as lipid peroxidation. Endophytes enhance the adaptation of plant with chilling temperatures. This results in reduced cellular damage, increased photosynthetic activity, and accumulation of various metabolites related to cold stress such as phenolic compounds, proline, and starch. Endophytes also have a positive effect on the metabolic balance, which also reduces the impact of drought stress on wheat growth in reduced watering conditions (Naveed et al. 2014).

### 6.3.4 Heavy Metal Stress

Toxicity by heavy metals is one of the most important abiotic stresses that cause the loss of about 25–80% of various cultivated crops. In acidic soils, low crop

productivity and reduced soil fertility are principally due to manganese and aluminum toxicities along with nutrient deficiencies (K, Mg, P, and Ca) (Singh et al. 2011). Heavy metals are very toxic to roots of cultivated plants and cause poor development of the root system (Singh et al. 2011). Heavy metal toxicity has become a serious problem that restricts crop productivity in acidic soils, in addition to overlapping with many physiological and biochemical processes including nutrient uptake, protein and nitrogen metabolism, photosynthesis, and respiration (Zhang et al. 2009).

It is recognized that bacterial endophytes participate in immobilization and mobilization of the metal cations, which affect availability of cations to plants (Pandey et al. 2016). In Cd-stressed soil, the dark septate endophyte (DSE) *Exophiala pisciphila* associated with *Zea mays* root showed improved activity of the antioxidant enzymes (Wang et al. 2016). Three major genes contributing to detoxification, transport, and uptake of Cd have been identified as PCS and MTP upregulation and ZIP downregulation when plants were inoculated with DSE and subsequently exposed to high concentrations of Cd. Changes in the content of 1-aminocyclopropane-1-carboxylate (ACC) by *Gigaspora* and *Pseudomonas* can change heavy metal tolerance directly by manipulating levels of plant ethylene (Friesen et al. 2011).

### 6.3.5 Nutrient Stress

Light, mineral nutrients, carbon, and water are essential prerequisites of plants for development, reproduction, and optimal growth. Starvation and nutrient stress are important abiotic stresses that harm plants (Chaves and Oliveira 2004).

Endophytes can provide their host with micronutrients and macronutrients. Bacteria that have nitrogen-fixing capacity can metabolize root exudates of plants and, in turn, supply nitrogen for the synthesis of plant amino acids. Endophytes can promote growth of plant by gibberellins (GAs), phosphate solubilization, cytokinins, IAA, and production of siderophore and supply essential vitamins to the plant (Jha et al. 2011). Choi et al. (2008) have reported that solubilization of phosphate in wheat and rice was mediated by gibberellic acid produced by *Pseudomonas* sp. The uptake of mineral nutrients (particularly Zn) in wheat plant has been improved by *Azotobacter chroococcum* and *Piriformospora indica* (Abadi and Sepehri 2015). Studies proved the function of endophytes in biological degradation of litter of the host plants. Endophytes initially colonize plants, facilitating the action of saprophytic microbes by antagonism, in that way increasing decomposition of litter (Terekhova and Semenova 2005). Another study explained the ability of all endophytes to decompose the organic components including cellulose lignin and hemicelluloses that facilitate nutrient cycling (He et al. 2012).



## 6.4 Conclusion

About 300,000 species of plants in the world harbor one or more endophytes. Each endophyte has its own function that helps to improve plant growth and protect it from diverse biotic and abiotic stresses. This benefit does not involve host specificity, so we can use endophytes as inoculants to alleviate abiotic stresses arising from changeful environmental conditions. With increasing interest on environmental protection, food security, and sustainable agriculture, exploiting useful endophytes is urgent. Endophytes may also be a good tool for enhancement of yield and quality of the plant products by producing various kinds of pioneer biologically active metabolites which may be able to positively regulate plant physiological disorders. They can protect plants from pathogens and remediate toxic residues of insecticides, herbicides, and various heavy metals. In addition, it has quick responses in stimulation of immune defense of the host.

Endophytes can be used as alternative strategies to plants that adapted to many stresses like drought, salinity, temperature, nutrient stress, and heavy metals. Further studies of endophytes will provide a better understanding of their relationship with host plant and maximize its utilization as promoters of plant growth as well as its ability to protect the plant from many harmful factors.

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