# Endophytic Bacteria: Application Against Biotic and Abiotic Stresses and Plant Health Improvements for Sustainable Agriculture

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## Abstract

Endophytes are an endosymbiotic group of microorganisms that colonize in plants and microbes that can be readily isolated from any microbial or plant growth medium. They act as reservoirs of novel bioactive secondary metabolites, such as alkaloids, phenolic acids, quinones, steroids, saponins, tannins, and terpenoids, that serve as a potential candidate for antimicrobial, anti-insect, anticancer, and many more properties. Endophytes are known to produce metabolites of utility value for various applications. Endophytes can also be beneficial to their host by producing a range of natural products that could be harnessed for potential use in medicine, agriculture, or industry. In addition, 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. In the present chapter we briefly summarize the importance of endophytic bacteria and their role in abiotic and biotic stresses.

## Keywords

Phytopathogenic activity · Growth promotion · Antioxidant · Plant health

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## 1.1 Introduction

Endophytes are found in plants of most ecosystems and are of agricultural importance since they help to improve crops yields, by stimulating plant growth and immune response, excluding plant pathogens by niche competition, and actively participating in phenylpropanoid metabolism and antioxidant activities (Pandey et al. 2018). Endophytes are bacteria or fungi that live within a plant within intercellular spaces, tissue cavities, or vascular bundles without harming the host and often benefit the host. The endophytic bacteria can be found in most plant species and can be recovered from roots, leaves, stems, and a few from flowers, fruits, and seeds (Lodewyckx et al. 2002); they have the potential to produce a variety of secondary metabolites with application in agriculture and pharmaceutical and industrial biotechnology. It is known that endophytic bacteria are located in the apoplast, and plant roots are proposed to be the entry point (Paungfoo-Lonhienne et al. 2013). It is also suggested that they are transmitted using an alternative vertical strategy due to their presence in flowers and seeds (Tamosiune et al. 2017). Endophytes are facultative or obligate symbiotic microorganisms, mainly bacterial and fungal species that live in apparently healthy internal plant tissues, without causing disease (Schulz and Boyle 2006).

The use of chemical fungicides against fungal pathogens adversely affects soil and plant health thereby resulting in overall environmental hazards. Therefore, biological source for obtaining antifungal agents is considered as an environment-friendly alternative for controlling fungal pathogens. Fungal phytopathogens are challenging to control because of their diverse host spectra and their soil-borne nature. Chemical fungicides are commonly used in higher doses to manage the phytopathogens. However, the increasing use of chemical fungicides results in several undesirable effects, such as development of resistance in pathogens and non-targeted environmental impacts. Therefore, alternative measures are essential for long-term and environment-friendly control of the fungal phytopathogens. The use of antagonistic microbes in biological control not only will provide an efficient control of the plant pathogens but is also harmless to the environment.

Endophytes are an endosymbiotic group of microorganisms that colonize in plants and microbes that can be readily isolated from any microbial or plant growth medium. They act as reservoirs of novel bioactive secondary metabolites such as alkaloids, phenolic acids, quinones, steroids, saponins, tannins, and terpenoids that serve as a potential candidate for antimicrobial, anti-insect, anticancer, and many more properties. While plant sources are being extensively explored for new chemical entities for therapeutic purposes, endophytic microbes also constitute an important source for drug discovery.

The endophytic bacteria play important roles in plant growth, such as a plant growth promoter with the production of plant growth regulators such as IAA and GA3, and they can supply the nutrients that are essential for the growth and development of plants. Endophytic bacteria have been found in virtually every plant studied, where they colonize the internal tissues of their host plant and can form a range of different relationships including symbiotic, mutualistic, commensalistic, and trophobiotic. Most endophytes appear to originate from the rhizosphere or phyllosphere; however, some may be transmitted through seeds. Endophytic bacteria can promote plant growth and yield and can also act as a biocontrol agent.

Endophytic actinomycetes act as a promising resource of biotechnologically valuable bioactive compounds and secondary metabolites. Endophytic Streptomyces sp. produce some novel antibiotics which are effective against multi-drug-resistant bacteria. Antimicrobial agents produced by endophytes are eco-friendly, toxic to pathogens, and do not harm humans. Endophytic inoculation of the plants modulates the synthesis of bioactive compounds with high pharmaceutical properties besides promoting growth of the plants. Hydrolases, the extracellular enzymes produced by endophytic bacteria, help the plants to establish systemic resistance against pathogen invasion. Phytohormones produced by endophytes play an essential role in plant development and drought resistance management. The high diversity of endophytes and their adaptation to various environmental stresses seem to be an untapped source of new secondary metabolites.

Endophytes can also be beneficial to their host by producing a range of natural products that could be harnessed for potential use in medicine, agriculture, or industry. In addition, 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. There is increasing interest in developing the potential biotechnological applications of endophytes for improving phytoremediation and the sustainable production of non-food crops for biomass and biofuel production.

Plants have served as a source of medicinal bioactive compounds against numerous forms of ailments for centuries. Ironically, in recent years, microorganisms associated with plants rather than plants themselves have proved to offer materials and products with high therapeutic potential (Subbulakshmi et al. 2012). Endophytes are an endosymbiotic group of microorganisms—often bacteria or fungi—that colonize the intercellular and/or intracellular locations of plants (Pimentel et al. 2011; Singh and Dubey 2015). For these organisms, whole or a part of their life cycle occurs within their hosts, without causing any apparent symptoms of disease. They are ubiquitous in nature and exhibit complex interactions with their hosts, which involve mutualism, antagonism, and rarely parasitism (Nair and Padmavathy 2014).

Endophytic bacteria form a large proportion of the indigenous microbial communities in plants. Their internal colonization is often assisted by a wide array of enzymes, which are also present in plant pathogenic bacteria. Endophytic bacteria have become adapted to the plant's selective environment and can be beneficial, neutral, or deleterious for the plant by affecting plant growth and or the defense of the plant against pathogens. In contrast to pathogenic bacteria they do not produce visual symptoms.

Pleban et al. (1995), reported the inhibition of plant pathogens *Rhizoctonia solani* (46–56%, in bean), *Pythium ultimum*, and *Sclerotium rolfsii* (26–79%) by using *Pseudomonas* and *Bacillus* sp. as introduced endophytes, comes from studies conducted on crops such as cotton, oilseed rape, tomato, cucumber, and peas

(Alstrom 2001). In some of these studies, the introduced endophytic bacterium caused both growth promotion and biological control.

## 1.2 Importance of Endophyte

Endophytes are known to enhance host growth and nutrient gain. They may enhance the plant's resistance to insects and pests along with tolerance to various abiotic and biotic stresses. They produce phytohormones and other bioactive compounds of biotechnological interest (enzymes and pharmaceutical drugs) (Joseph and Priya 2011). In recent past, researchers defined endophytes as 'endo-symbionts' which inhabit the inner parts of plant tissues and do not damage or inflict diseases which could be isolated through adherence of aseptic methods (Arnold and Lutzoni 2007; Khan et al. 2015). Plant interiors are occupied by a large variety of microorganisms, which interact towards the development of a relatively stable microbial community. The number of reports on bacteria being isolated from healthy plant tissues is increasing fast, and several reviews have been published recently (Kobayashi and Palumbo 2000). Fisher et al. (1992) studied the distribution of bacterial endophytes in fieldgrown *Zea mays* plants and found that the plant parts closer to the soil were more heavily colonized by bacteria than those near the top of the plants. In general the basal part of the stem and the root contain the largest numbers and biodiversity of endophytic bacterial species. Several groups known as plant growth promoting rhizobacteria have been isolated also as endophytes, including the nodulating and nonnodulating diazotrophs.

Endophyte populations usually range from $10^3$ to $10^6$ and rarely exceed $10^7$ cfu/g plant matter, as have been reported for tissues of various plant species (Chanway 1998). The high biodiversity among these bacterial endophytes is evident from the studies made by Mundt and Hinkle (1976) and McInroy and Kloepper (1995). The endophytic bacteria most commonly isolated from various plant parts of different crops are summarized by Hallmann et al. (1997) and Kobayashi and Palumbo (2000). The study of Tjamos et al. (1999) with two effective root-tip *Bacillus* isolates provided evidence that their ability to colonize both epiphytically and endophytically can be an important factor determining their effectiveness in controlling *Verticillium* wilt in planta.

Redman et al. (1999) studied the biochemical analysis of plant protection afforded by a nonpathogenic endophytic mutant of *Colletotrichum magna*. Studies had shown previously to protect watermelon (*Citrullus lanatus*) and cucumber (*Cucumis sativus*) seedlings from anthracnose disease elicited by wild-type *C. magna*. Plant biochemical indicators of a localized and systemic (peroxidase, phenylalanine ammonia-lyase, lignin and salicylic acid) "plant-defense" response were investigated in anthracnose-resistant and susceptible cultivars of cucurbit seedlings. Results indicated disease protection in path-1- colonized plants were correlated with the ability of inducing plant defense mechanism in the host.

Strobel et al. (2007) discovered a novel endophytic fungus *Muscodor vitigenus* from the liana *Paullinia paullinioides* that produced naphthalene, an insect repellant. The extracted naphthalene has chromatographic and mass spectral properties that are identical to authentic naphthalene. In a preferred embodiment the naphthalene in the gas phase of *M. vitigenus* is useful in the repellency of unwanted insect pests. This unique biological activity of this novel endophyte suggests a wide range of potential practical applications particularly in the area of insect repellents, insecticides, antimicrobials, anti helminthics, and vermicides.

Pimentel et al. (2011) reviewed on the use of endophytes for the production of bioactive compounds and their use in biotransformation process. The role of endophytes on the production of anticancer, antimicrobial, and antioxidant compounds illustrating their potential for human use was inferred. It also describes biotransformation as an auspicious method to obtain novel bioactive compounds from microbes. Biotransformation allows the production of regio and stereo selective compounds under mild conditions and that using endophytic fungi have been reviewed for e.g. biotransformation of grandisin by the endophytic fungus *Phomopsis sp*. to a tetrahydrofuran which showed trypanocidal activity.

## 1.3 Isolation of Endophytes from Plants

Lodewyckx et al. (2002) elaborated the methods used for the isolation and characterization of bacteria and reported at least 81 bacterial species which were found to be associated with crop plants. Moore et al. (2006) isolated endophytic bacteria from the popular tree grown on contaminated site and studied the effectiveness of these bacteria in phytoremediation. Ryan et al. (2008) indicated that endophytic bacteria can be isolated from all kinds of plants in the plant kingdom irrespective of the nature of plants like trees, herbs, and shrubs.

Taghavi et al. (2010) analyzed the bacterial species in different parts of plants and observed that *Azoarcus*, *Acetobacter* (renamed as *Gluconobacter*), *Bacillus*, *Enterobacter*, *Burkholderia*, *Herbaspirillum*, *Pseudomonas*, *Serratia*, *Stenotrophomonas*, and *Streptomyces* were the predominant bacterial endophytes colonized in plant tissues. Malfanova (2013) reviewed in depth the diversity of endophytic bacteria and reported that three major phyla were studied predominantly by the researchers, namely, *Actinobacteria*, *Proteobacteria*, and *Firmicutes.* Hallmann and Berg (2006) reported that the species of the above genera were found to form colonies in most of the soil and rhizosphere of the plants, whereas Compant et al. (2010) confirmed the presence of endophytes above the root zone, flowers, and also seeds. Jesus and Lugtenberg (2014) reported the presence of bacterial endophytes and their identification from various parts of the plant sap. Endophytes populations are always greater in the roots than any other organ of plants. In the root the average density is 105 cfu per g fresh weight, whereas average values of 104 and 103 are reported for stem and for leaf, respectively.

Endophytes can be easily isolated on any microbial or plant growth, such as agar, potato dextrose agar, and any nitrogen- or carbon-containing media. The most frequent method used to detect and enumerate endophytes involves isolation from surface-sterilized host plant tissue. The main factors that may regulate entophyte colonization within a plant or microbial species, include the genotype of the plant, the growth stage of the plant, the physiological status of the plant, the type of plant tissues, the environmental condition of the soil in which it is grown, the sampling season, the surface sterility, selective media, and culture conditions as well as different agricultural practices (Gaiero et al. 2013; Golinska et al. 2015) Ecological awareness on the role of endophytes in nature can also provide the best clues for targeting a particular type of endophytic bioactivity with the greatest potential for bioprospecting (Strobel and Daisy 2003).

Das et al. (2017) reported the antimicrobial potentials of endophytic bacteria isolated from leaf tissues of *Hyptis suaveolens* against some clinically significant pathogens. The results indicated that 60% of the isolates showed antimicrobial activity inhibiting at least one of the test pathogens in preliminary screening. Among them two isolates showed considerable antimicrobial activity against the test pathogens. The isolates were identified as Bacillus and Pseudomonas species by morphological and biochemical characterization.

Sharma and Roy (2015) reported a total number of 536 bacterial and fungal endophytes isolated from root, stem, and leaves of the plant *Amaranthus spinosus*. Roots supported more number of bacterial endophytes than stem or leaves, whereas stem supported more number of fungal endophytes than either roots or leaves. The plant harboured more of gram negative compared to gram positive bacterial endophytes. The fungal endophytes isolated from root, stem, and leaves of the plant *A. spinosus* revealed the presence of *Penincillum*, *Aspergillus Cladosporium*, *Phoma*, *Bipolaris*, and *Fusarium* spps.

Etminani and Harighi (2018) demonstrated the production of plant growth hormone auxin and gibberellins by the strains isolated from leaves and stems healthy wild Pistachio trees (*Pistacia atlantica* L.). The isolated strains belong to the genus *Pantoea*, *Bacillus*, *Pseudomonas*, *Serratia*, and *Stenotrophomonas* and also showed biocontrol activity.

Endophytes can either be fungal or bacterial in nature and are capable of producing biologically active compounds, some of which are used by the plant as part of its arsenal in its defense against pathogens, while some promote plant growth (González-Teuber et al. 2014). Most of the bioactive compounds extracted from endophytes have shown a plethora of bioactivities including but not limited to antimicrobial, immunosuppressant, and anticancer (Nair and Padmavathy 2014).

## 1.4 Application of Endophytes Microorganism in Biotic and Abiotic Stresses

### 1.4.1 Anti-Fungal Activity of Endophytes

Hazarika et al. (2019) reported that seven endophytic bacteria were isolated from sugarcane leaves and screened for its antifungal activity against 10 fungal isolates belonging to the genera *Alternaria*, *Cochliobolus*, *Curvularia*, *Fusarium*, *Neodeightonia*, *Phomopsis*, and *Saccharicola* isolated from diseased leaves of sugarcane. They concluded that the antifungal potential of isolate *Bacillus subtilis* SCB-1 was established against taxonomically diverse fungal pathogens including the genera *Saccharicola*, *Cochliobolus*, *Alternaria*, and *Fusarium*, and the potent antifungal compound surfactin as well as volatiles produced by the bacterial isolate which could be responsible for its bio-control activity against fungal infections.

Abdallah et al. (2018) studied that *Fusarium graminearum* can cause Giberella Ear Rot (GER) and seedling blight in maize, resulting in major yield losses. Besides GER, the infected grains are consequently contaminated with multiple mycotoxins of *F. graminearum*. They explored the effect of the endophytic fungal genera of *Epicoccum* and *Sordaria* to control *F. graminearum* infection in comparative trials with *Piriformospora* spp., an elusive endophytic genus. The results showed a considerable variability in the antifungal activity, both among species and among isolates within one species.

Endophytic fungi (EF) are an important source for novel, potential, and active metabolites. Plant–endophyte interaction and endophyte–endophyte interactions study provide insights into mutualism and metabolite production by fungi. Bioactive compounds produced by endophytes main function are helping the host plants to resist external biotic and abiotic stress, which benefit the host survival in return. Plants lack immune response to certain pathogens, but the endophytes that reside inside the plant tissue enhance the immune response of the plants to fight against invading pathogens (Melotto et al. 2008). Endophytes commonly increase plant biomass under stressful conditions but the cellular mechanisms involved in stress tolerance and growth enhancement are poorly characterized. The "balanced antagonism" hypothesis was initially proposed to address how an endophyte controls host defense mechanisms to be activated against it, ensures self-resistance before being incapacitated by the toxic metabolites of the host, and manages to grow within its host without causing visible manifestations of infection or disease (Arnold and Lutzoni 2007).

Liang et al. (2014) reported a total of 83 endophytic fungi strains isolated from the root, stem, leaf, and fruit of *Brucea javanica*. About 34 strains were obtained from the stem, 32 strains were obtained from the leaf, 15 strains were isolated from the root, and 2 strains came from the fruit, and it was concluded that 14 strains had antifungal activities against at least one pathogenic fungi and 9 strains showed antibacterial activities against one or more bacteria.

Tashi-Oshnoei et al. (2017) demonstrated the samples of roots, leaves, and stems of healthy oak trees collected from various locations in the Baneh and Marivan regions, Iran. In total, 63 endophytic bacteria were isolated and grouped according to phenotypic properties. The isolates have the ability to produce plant hormone such as auxin and gibberellin along with siderophore production, phosphate solubilization, atmospheric nitrogen fixation, and protease and hydrogen cyanide production.

Premjanu et al. (2017) explained the isolation of endophytic fungi from *Lannea coromandelica* having antifungal activity potential and the isolation of the secondary metabolite from the dominant fungi and predict the probable mechanism behind its activity. They have isolated *Aspergillus flavus*, *Aspergillus niger*, *Alternaria alternata, and Colletotrichum gloeosporioides* identified based on their morphological features as endophytic fungi and concluded that among the four dominant fungi, the antifungal activity of *Aspergillus flavus* showed the maximum activity with an inhibitory zone of 26.22 mm against *Candida albicans* and 16.72 mm against *Malassezia pachydermis*.

The endophytic bacteria were isolated from the root tissues of *Talinum triangulare* by surface sterilization method. The isolates were cultured in Trypticase Soybean agar (TSA) and antagonist activities were evaluated by dual culture assay against *Fusarium oxysporum*, *Trichoderma reesei*, and *Candida albicans.* The result reveals that 4 of 23 endophytic bacterial isolates demonstrated great antifungal potentiality against many tested fungi. Ali and Rante (2018) isolated and identified bacteria with antifungal properties on the basis of morphological, physiological, biochemical and 16S rRNA analysis as member of genus *Bacillus* and *Brevibacillus*.

Osama et al. (2018) isolated endophytic bacteria from Chinese traditional medicinal plant *Glycyrrhiza uralensis* (licorice) and evaluated their in vitro antimicrobial activities against common fungal pathogens of tomato (*Fusarium oxysporum* f. sp., *Fulvia fulva, Alternaria solani*), cotton (*Fusarium oxysporum* f. sp. *vasinfectum, Verticillium dahliae*), pomegranate (*Ceratocystis fimbriata*), Cymbidium (*Colletotrichum gloeosporioides*), and Tsao-ko (*Pestalotiopsis microspora* and *Fusarium graminearum*). And, they reported that the antimicrobial activities of natural endophytes, particularly *Bacillus atrophaeus*, suggest this species may be a promising candidate as a biocontrol agent to confer resistance to *Verticillium* wilt disease and other phytopathogens in cotton and other crops.

Wild-type *Arabidopsis* used to test the effect of the endophytic bacterium on inhibition of seed surface mycoflora. The seeds were treated with a bacterial suspension and allowed to germinate. The bacterium-treated seedlings were healthy without disease symptoms while a majority of the untreated *A. thaliana* seedlings showed evidence of overgrowth by fungi and necrosis. The bacteria either antagonized fungal spores and mycelia on the seed surface directly or they released antifungal lipopeptides that suppressed fungal growth. An endophytic *Bacillus* species isolated from a paddy field showed similar activity in protecting maize and horsebean from infection of *Bipolaris maydis* and *R. solani*, respectively (Wang et al. 2009).

Bacon and Hinton (2002) characterized two strains of *B. subtilis* (ATCC55422 and ATCC55614) as endophytic to maize plants having in vitro inhibition activity of *F. moniliforme*. Endophytic fungi of maize have also been shown to have antagonistic activity against fungal pathogens including *Aspergillus flavus* and *Fusarium verticillioides* (Wicklow et al. 2005).

### 1.4.2 Antibacterial Activity of Endophytes

Manganyi et al. (2019) determined the antimicrobial properties and identified the chemical compounds of secondary metabolites produced by endophytic fungi isolated from *Sceletium tortuosum*. A total of 60 endophytic fungi produced secondary metabolites that were detected after fermentation and extraction. Antibacterial properties of the secondary metabolites were determined using the disc diffusion assay against pathogenic environmental Gram-positive and Gram-negative bacteria as well as control stain. They found that 15% of fungal extracts displayed a narrow spectrum of activity against the bacteria strains. Despite this, none of the fungal extracts inhibited growth of *Enterococcus faecalis* (ATCC S1299) and *Enterococcus gallinarum* (ATCC 700425) while *Bacillus cereus* (ATCC 10876) was the most susceptible against the fungal extracts. *Fusarium oxysporum* (GG 008) with accession no. KJ774041.1 displayed significant antibacterial activity that was linked to high levels of 5-hydroxymethylfurfural (HMF) and octadecanoic acid as revealed by GC-MS and concluded that endophytic fungi from *S. tortuosum* L. produced secondary metabolites that exhibited highly effective antibacterial activity against multi-drug-resistant bacterial strains, and these isolates could serve as potential sources for the isolation of novel antimicrobial agents that may contribute in the fight against antibiotic strains.

Beiranvand et al. (2017) demonstrated the molecular identification and measuring the antimicrobial activity of endophytic actinomycetes isolated from medicinal plants of Iran. About 16 out of 23 bacterial isolates (69%) exhibited antimicrobial activity against the selected pathogenic bacteria *Bacillus cereus*, *Staphylococcus aureus*, *Bacillus subtilis*, *Klebsiella pneumoniae*, *Citrobacter freundii*, *Proteus mirabilis*, *Shigella flexneri*, and *Escherichia coli*. About 2 out of 23 endophytic bacterial isolates, EB4 and EB7, showed inhibitory activity against *Bacillus cereus*. In addition, EB9 showed inhibitory activity against *Staphylococcus aureus*, *Citrobacter freundii*, and *Shigella flexneri*. About 16 isolates (69%) obtained by hot method showed strong activity against selected pathogenic organisms and two of them (EB7 and EB69) had broad spectrum antibacterial activity. Ultrasonic method showed that 13 out of 23 isolates (46%) inhibited microbial growth. Among the 5 endophytic bacteria only 4, except *Staphylococcus* spp. LCP, showed antimicrobial activity. *Pseudomonas* spp. SSRN1 and *Enterobacter* spp. SSRP1 were considered as the most active strains as they both had a moderate activity against *S. aureus*. High zone of inhibition was by *Pseudomonas* spp. SSRN1 and *Enterobacter* spp. SSRP1, followed by *Lysinibacillus* spp. HSRN, then lastly *Bacillus* spp. Endophytic bacteria have the potential to produce novel natural compounds with antibacterial and antifungal activity (Christina et al. 2013). Bacterial endophytes (*Pseudomonas* spp. and *Bacillus* spp.) isolated from *Plectranthus tenuiflorus* have shown great antimicrobial activity against some human pathogenic strains such as *Salmonella typhi*, *S. aureus*, *E. coli*, *Klebsiella pneumoniae*, *Streptococcus agalactiae, Proteus mirabilis*, and *Candida albicans* (EI-Deeb et al. 2013).

*Enterobacter* spp. isolated from *Raphanus sativus* L. also showed antibacterial activity against a few human pathogenic bacteria including *E. coli*, *Salmonella enteritidis*, *Shigella sonnei*, *Salmonella typhimurium*, *P. aeruginosa*, *Shigella flexneri*, and *B. cereus* (Seo et al. 2010). *Pseudomonas* spp. has been proven to possess antimicrobial compounds called ecomycins and pseudomycins (Christina et al. 2013). Secondary metabolites from *C. molle* were also reported to possess antimicrobial activity (Kaleab et al. 2006; Fankam et al. 2015).

Marcellano et al. (2017) reported the antibacterial activity of endophytic fungi associated with the bark of *Cinnamomum mercadoi*. The pure isolates were identified through their morphological characteristics. Agar plug diffusion assay was employed in the primary screening of their antibacterial activity against *Staphylococcus aureus*, *Bacillus cereus*, *Escherichia coli*, and *Pseudomonas aeruginosa*. Twelve (12) endophytes were isolated from the bark of *C. mercadoi*. All endophytes exhibited antibacterial activity on at least one of the test pathogens. However, only 2 of the 4 endophytes subjected to the secondary screening showed wide-spectrum activity and inhibited the growth of all test bacteria. *Fusarium* sp. 2 was identified to have the most promising activity with MIC values ranging from 2.1 to 4.2 mg/mL. They concluded that *C. mercadoi* harbours endophytes, particularly *Fusarium* sp. 2, which possess antibacterial activity and thus a potential source of antibacterial compounds.

Indrawati et al. (2018) reported that the bacterial endophytes from the tropical plant *Syzygium polycephalum* (Kupa) can be used as an alternative solution to reduce the utilization of synthetic antibiotics. A total of 9 isolates of bacterial endophytes have been successfully obtained. From these isolates, a total of 4 species of endophytic bacteria were identified: Bacillus sp. (1), Bacillus sp. (2), *Bacillus pumilus*, and *Bacillus amyloliquefaciens*. Antibacterial tests revealed that *Bacillus* sp. (2) derived from the leaves appeared to be the most potent antibacterial isolates against pathogenic bacteria with 22 and 9 mm of inhibitory zone to methicillin-resistant *Staphylococcus aureus* (MRSA) and to *Bacillus cereus*, respectively. On the other hand, endophytic isolate Bacillus sp. (1) derived from stem was able to inhibit *Klebsiella pneumoniae* and *B. cereus* with inhibitory zones as much as 10 and 7 mm. They concluded that the results strongly indicated that the antibacterial effect of bacterial endophytes from the study was species-specific and indeed the bacterial endophytes in this study could serve as a potential source of novel natural antibiotics.

Francielly et al. (2017) analyzed the antimicrobial potential of 10 actinomycetes isolated from the medicinal plant *Vochysia divergens* located in the Pantanal sul-mato-grossense, an unexplored wetland in Brazil. Strains were classified as belonging to the *Aeromicrobium*, *Actinomadura*, *Microbacterium*, *Microbispora*, *Micrococcus*, *Sphaeris Sporangium*, *Streptomyces*, and *Williamsia* genera, through morphological and 16S rRNA phylogenetic analysis. All conditions were analyzed for active metabolites, and the best antibacterial activity was observed from metabolites produced with SG medium at 36 °C. They concluded that LGMB491 (closely related to *Aeromicrobium ponti*) extract showed the highest activity against methicillin-resistant *Staphylococcus aureus* (MRSA), with an MIC of 0.04 mg/mL, and it was selected for SM identification. Strain LGMB491 produced 1-acetyl-β-carboline (1), indole-3-carbaldehyde (2), 3-(hydroxyacetyl)-indole (4), brevianamide F (5), and cyclo-(L-Pro-L-Phe) (6) as major compounds with antibacterial activity.

### 1.4.3 Plant Growth Promoters (PGPR)

A growing body of literature indicated an array of advantages of endophytes. Kang et al. (2007) detailed the growth-promoting characteristics of endophytes, while

Kloepper et al. (2004) demonstrated the disease- inhibiting traits of endophytes. The nature of endophytes in strengthens the defense mechanism of crops to various plant diseases. Anti-herbivory products were found to be instigated by endophytes (Sullivan et al. 2007). Backman et al. (1997) discussed various factors influencing endophytes as biocontrol agents against various plant diseases like specific bacterial species colonizing in a particular crop species, the changing population in different seasons, the pattern with which they have been colonizing and their capacity to mobilize inside the tissues and to stimulate systemic resistance.

Endophytic bacteria seem to be distributed in most plant species and have been isolated from roots, leaves, and stems, and a few from flowers, fruits, and seeds (Lodewyckx et al. 2002). Endophytic bacteria may accompany certain metabolic properties, such as promoting plant growth, controlling soil-borne pathogens, or helping host plants to defeat stress responses to environmental abuse (Mastretta et al. 2006; Taghavi et al. 2007; Ryan et al. 2008). Furthermore, the interactions between plants and bacteria help plants to settle in ecosystem restoration processes (Glick et al. 1995). These interactions may increase the ability of plants to utilize nutrients from the soil by increasing root development, nitrate uptake or solubilizing phosphorus, and to control soil-borne pathogens (Whipps 2001).

The improvement of the growth and health of the plants cannot be separated from the role of endophytic bacteria. They supply nutrient elements through the process of fixing the nutrient elements from the air (Hirano and Upper 2000), improve the mobilization of P, trapped Fe (Ryan et al. 2008), fight against plant pathogens through the induction of systemic resistance and produce secondary metabolic compounds that are antagonists (Kloepper and Ryu 2006; Sturz and Nowak 2000), as well as reduce plants' biotic or abiotic stress without pathogenicity (Lugtenberg and Kamilova 2009).

Shen et al. (2019) demonstrated the seedlings of rice (*Oryza sativa*) planted in soil with 1, 5, or 10 times as the recommended rates of the fungicides etridiazole, metalaxyl, and tricyclazole. Endophytic Bacteria were isolated from roots of rice seedlings. The bacterial 16S rDNA sequences and related PGP characteristics including potential nitrogen fixation, phosphorus-solubilizing and indole acetic acid (IAA) production ability were examined. They found that 17 different strains were obtained from rice seedling roots; five strains with both nitrogen fixation potential and IAA production ability included *Rhizobium larrymoorei* E2, *Bacillus aryabhattai* E7, *Bacillus aryabhattai* MN1, *Pseudomonas granadensis* T6, and *Bacillus fortis* T9. With further test, they concluded that *Bacillus aryabhattai* MN1 showed high tryptophan dose-dependent IAA production ability, tolerance towards etridiazole and metalaxyl application and should be considered a potential bacterial biofertilizer.

Microorganisms play a key role in the health and development of crops (Tikhonovich and Provorov 2011; Cory and Franklin 2012) and the relationship between rhizobacteria and endophytes with their plant hosts has been reviewed extensively (Ryan et al. 2008; Hayat et al. 2010; Blanco and Lugtenberg 2014). Such plant growth promoting rhizobacteria (PGPR) have considerable potential as biological inoculants in sustainable agriculture (Saharan and Nehra 2011; Glick

2012; Sivasakthi et al. 2014). Plants that are inoculated with PGPR benefit from the resulting plant–microbe interaction as the bacteria contribute to plant growth and health by multiple mechanisms including nitrogen fixation, synthesis of phytohormones, modulation of plant ethylene levels, solubilization of unavailable soil phosphate and suppression of pathogens through niche exclusion, and the production of anti-microbial metabolites (Fuentes-Ramirez and Caballero-Mellado 2005; Franche et al. 2009; Babalola 2010; Compant et al. 2010).

A collection of plant-associated bacteria from various plant hosts (*Miscanthus giganteus*, *B. napus*, and *Iris pseudacorus*) have been isolated and partially characterized (Otieno et al. 2013). Strains were isolated following standard procedures from rhizosphere and internal plant tissues including root, leaves, and stem (Germaine et al. 2004; Otieno et al. 2013). Many of these strains have multiple plant growth promotion (PGP) characteristics including siderophore production, 1-aminocyclopropane-1-carboxylic acid (ACC) deaminase activity (for the regulation of plant stress hormone ethylene caused by abiotic stress conditions), phosphate solubilization, and in some cases biocontrol against fungal plant pathogens.

Khan et al. (2020) explained that *Paenibacillus polymyxa* is a plant growth-promoting rhizobacterium that has immense potential to be used as an environmentally friendly replacement of chemical fertilizers and pesticides. *Paenibacillus polymyxa* SK1 was isolated from bulbs of *Lilium lancifolium*. The isolated endophytic strain showed antifungal activities against important plant pathogens like *Botryosphaeria dothidea*, *Fusarium oxysporum*, *Botrytis cinerea*, and *Fusarium fujikuroi*. The highest percentage of growth inhibition, i.e., 66.67 ± 2.23%, was observed for SK1 against *Botryosphaeria dothidea* followed by 61.19 ± 3.12%, 60.71 ± 3.53%, and 55.54 ± 2.89% against *Botrytis cinerea*, *Fusarium fujikuroi*, and *Fusarium oxysporum* respectively. They concluded that the isolated strain SK1 showed plant growth-promoting traits such as the production of organic acids, ACC deaminase, indole-3-acetic acid (IAA), siderophores, nitrogen fixation, and phosphate solubilization. IAA production was strongly correlated with the application of exogenous tryptophan concentrations in the medium and revealed that *P. polymyxa* SK1 may be utilized as a source of plant growth promotion and disease control in sustainable agriculture.

### 1.4.4 Applications of Endophytes in Soil pH Stress

Ngwene et al. (2016) studied endophytic Sebacinales member *Piriformospora indica*, which was isolated a decade ago from an Indian desert, and which is known for increasing plant resistance and tolerance to stress and for promoting plant growth. The authors hypothesized its ability to support plant nutrition and showed that *P. indica* growth was higher in the presence of inorganic phosphate than in organic phosphate sources. The related genes were all repressed by higher amounts of inorganic phosphate, but mostly expressed when the fungus received phytate. Interestingly, a pH decrease was observed in the presence of *P. indica* irrespective of the phosphate source. Ngwene et al. (2016) indicated that *P. indica* is able to solubilize phosphate from inorganic, but not from organic sources, and that phosphate solubilization could not be due to enzymatic activities, but rather to the lowering of the medium pH.

Postma et al. (2007) demonstrated colonization by root endophytes that can be beneficial to plants growing on acid, nutrient-poor soils. Arbuscular mycorrhizal (AM) fungi can supply herbs with nutrients and may give protection against aluminium toxicity. AM fungi are the most prevalent symbionts in herbs at neutral to acidic soil pH. At extremely low pH, fungal growth can be limited and AM colonization is usually rare. They investigated root colonization by AM, FE and DSE in *Maianthemum bifolium*, *Galium odoratum*, *Mercurialis perennis* and *Stellaria nemorum*, from a range of acidic beech forests to relate endophyte colonization to a gradient in soil pH. With decreasing pH, colonization by AM decreased, whereas the other two endophytes increased. AM and FE colonization were inversely correlated in *Maianthemum bifolium*. They concluded with the compared changes in root colonization with those in chemical composition of soil and leaf samples and found a positive correlation between leaf magnesium concentrations and the presence of DSE in *Galium odoratum* and found aluminium concentration in *Maianthemum bifolium* tended to be lower when FE colonization was high, suggesting a possible role for the fungi in plant protection against Al. They suggested that FE and DSE may replace AM fungi in herbaceous vegetation at extremely low pH, counteracting some of the negative effects of high soil acidity on plants.

Tall fescue is grown on soils where low pH and limited nutrient supply restrict plant productivity, caused by interactions among prior land use practices, relatively high rainfall amounts, and soil geochemistry. Plants that are adapted to acidic soils possess a variety of mechanisms that enable them to tolerate or overcome adverse soil chemical conditions. Soil acidity affects plant growth through a complex of chemical changes in the rhizosphere involving increased $H'$, $Al''$, and Mn 2. These include inhibition of metal cation ($Ca2'$, Mg2) uptake, a decrease in P and Mo solubility and increased efflux of nutrients and metabolites from roots. Root morphology and function also change when soil chemical conditions are less than ideal for plant growth, when soil water is scarce, some species can explore large areas of soil, and, in other instances, mineral challenges can elicit or suppress the production of fine root structure (Huang 2001).

### 1.4.5 Applications of Endophytes in Drought Tolerance

Ullah et al. (2019) demonstrated that endophytic bacteria which survive within plant tissues are among the most appropriate technologies improving plant growth and yield under drought conditions. These endophytic bacteria live within plant tissues and release various phytochemicals that assist plants to withstand harsh environmental conditions, i.e., drought stress. Their plant growth-promoting characteristics include nitrogen fixation, phosphate solubilization, mineral uptake, and the production of siderophore, 1-aminocyclopropane-1-carboxylate (ACC) deaminase, and various phytohormones. These plant growth promoting characteristics of endophytic bacteria improve root length and density, which leads to enhanced drought tolerance. The plant-endophytic bacteria assist plants to withstand drought stress by producing drought-tolerant substances, for instance, abscisic acid, indole-3-acetic acid, ACC deaminase, and various volatile compounds. Indirectly, endophytic bacteria also improve osmotic adjustment, relative water content, and antioxidant activity of inoculated plants. Altogether, these bacterial-mediated drought tolerance and plant growth-promoting processes continue even under severe drought conditions which lead to enhanced plant growth promotion and yield.

Vigani et al. (2018) determined the two endophytic bacteria endowed with an array of in vitro plant growth promoting traits. Their genome sequences confirmed the presence of traits previously shown to confer drought resistance to plants, such as the synthesis of nitric oxide and of organic volatile organic compounds. The two strains of pepper (*Capsicuum annuum* L.) were used because of their high sensitivity to drought. Under drought conditions, both strains stimulated a larger root system and enhanced the leaves' photosynthetic activity. By testing the expression and activity of the vacuolar proton pumps, H+ -ATPase (V-ATPase) and H+ -PPase (V-PPase), they found that bacterial colonization enhanced V-PPase only and, therefore, concluded that the enhanced expression and activity of V-PPase can be favoured by the colonization of drought-tolerance-inducing bacterial endophytes.

Dastogeer et al. (2018) reported that the fungal endophytes and a virus confer drought tolerance to *Nicotiana benthamiana* plants through modulating osmolytes, antioxidant enzymes, and expression of host drought responsive genes. They evaluated how the colonization of two fungal endophytes isolated from wild *Nicotiana* species from areas of drought-prone northern Australia, and a plant virus, yellowtail flower mild mottle virus (genus *Tobamovirus*), improved water stress tolerance in *N. benthamiana* plants. Inoculation with both of the two fungal strains used and the virus significantly increased plants tolerance to water stress as manifested by their significant delay in wilting of shoot tips. The water stress tolerance of fungus-inoculated plants was correlated with increases in plant biomass, relative water content, soluble sugar, soluble protein, proline content, increased activities of the antioxidant enzymes catalase, peroxidase and polyphenol oxidase, decreased production of reactive oxygen species, and decreased electrical conductivity. They concluded that the influence of the virus was similar to the fungi in terms of increasing the plant osmolytes, antioxidant enzyme activity, and gene expression. Although separate infection of fungi and virus increased plant water stress tolerance responses, their co-infection in plants did not have an additive effect on water stress responses.

Hubbard et al. (2013) demonstrated the impact of fungal endophyte symbiosis on the growth, eco-physiological and reproductive success of wheat exposed to heat and drought. The resistance of pot-grown wheat to heat or drought stress was measured by quantifying efficiency of photosystem II (Fv/Fm), plant height, average seed weight (ASW), total seed weight (TSW), water-use efficiency (WUE) as well as time to 50% germination and percentage germination of second-generation seeds produced under heat stress, drought stress or well-watered conditions. The endophytic fungi tested increased wheat tolerance for drought and heat. They found out that Endophyte SMCD 2206 was the most beneficial, followed by SMCD 2210 and 2215. The second-generation seeds produced by drought-stressed wheat colonized by SMCD 2206, 2210, or 2215 had decreased WUE relative to those produced by endophyte-free, drought-stressed plants.

Hubbard et al. (2013) reported that fungal endophytes can improve plant tolerance to abiotic stresses such as heat and drought. He hypothesized that six endophytic fungi, SMCD 2204, 2206, 2208, 2210, 2214, and 2215, would promote heat and drought tolerance in wheat during both seed germination and at later developmental stages as well as assessed mycomediated enhancement of seed germination (mycovitality) including seedling performance, in vitro in terms of percent germination, seedling fresh weight, energy of germination (EG), and hydrothermal time (HTT) of germination. He concluded that Endophytes SMCD 2206, 2210, and 2215 improved seedling heat or drought resistance, while SMCD 2204, 2208, and 2214 did not. He demonstrated that fungal endophytes SMCD 2206, 2210, and 2215 improve wheat tolerance for heat and drought both in vitro and in pot studies.

### 1.4.6 Applications of Endophytes in Soil Salinity Tolerance

Salinity affects 20% of agriculture lands worldwide and is a major cause of reductions in plant productivity and the degradation of land (Siddikee et al. 2010; Ramadoss et al. 2013). Soil salinity can be caused by the interaction of natural factors including geological processes, climate change, and water management. Salinity can also be induced by anthropogenic activity, e.g., the inappropriate use of fertilizers and improper irrigation practices (Bianco and Defez 2011; Paul and Lade 2014). Osmotic stress and associated imbalances in ions and nutrients adversely affect plant growth and function (Evelin et al. 2009). Ramaiah et al. (2020) demonstrated that a salt-tolerant endophyte isolated from salt-adapted Pokkali rice, a *Fusarium* sp., colonizes the salt-sensitive rice variety IR-64, promotes its growth under salt stress and confers salinity stress tolerance to its host.

*Piriformospora indica*, has been reported to promote growth in a number of plant systems under abiotic stresses including salinity stress (Varma et al. 2012). In Arabidopsis, *P. indica* maintains the Na + and K+ homeostasis under salt stress (Arshad et al. 2017). Two bacterial endophytes, *Bacillus subtilis* and *Mesorhizobium ciceri,* confer salt tolerance to chickpea by decreasing $H_2O_2$ concentrations and increasing proline content (Egamberdieva et al. 2017). *Pseudomonesa fluorescens* and *P. migulae* ameliorate salinity stress in tomato plants by increasing the 1-aminocyclopropane-1-carboxylate deaminase activity, the key enzyme for ethylene biosynthesis. (Ali et al. 2014).

Asaf et al. (2018) demonstrated *Aspergillus flavus* CHS1-mediated salinity tolerance in *Glycine max*. L. through the stimulation of the antioxidative system and endogenous hormone levels in the host. Bajaj et al. (2018) showed that colonization of soybean plants by *P. indica* resulted in the stimulation of genes associated with the phenylpropanoid and lignin pathways, both of which are known to play an important role in oxidative stress tolerance. Kearl et al. (2019) explained that the salt-tolerant halophyte rhizosphere bacteria stimulate the growth of Alfalfa in salty soil. Bacteria were isolated from the rhizosphere and as root endophytes of *Salicornia rubra*, *Sarcocornia utahensis*, and *Allenrolfea occidentalis* and a total of 41 independent isolates were identified by 16S rRNA gene sequencing analysis. Isolates were tested for maximum salt tolerance, and some were able to grow in the presence of up to 4 M NaCl. *Halomonas*, *Bacillus*, and *Kushneria* species were consistently isolated both from the soil and as endophytes from roots of all three plant species at all collection times. The most commonly identified bacteria were from several phyla commonly found in soil or extreme environments: *Acidobacteria*, *Actinobacteria*, *Bacteroidetes*, *Chloroflexi*, and Gamma- and Delta-Proteobacteria. Isolates were tested for the ability to stimulate growth of alfalfa under saline conditions. This screening led to the identification of one Halomonas and one Bacillus isolate that, when used to inoculate young alfalfa seedlings, stimulate plant growth in the presence of 1% NaCl, a level that significantly inhibits growth of uninoculated plants. The same bacteria used in the inoculation were recovered from surface sterilized alfalfa roots, indicating the ability of the inoculum to become established as an endophyte. They concluded that the results with these isolates have exciting promise for enhancing the growth of inoculated alfalfa in salty soil.

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