

A Renaissance in Plant Growth-Promoting and Biocontrol Agents by Endophytes

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Abstract

Endophytes are the microorganisms which colonize the internal tissue of host plants without causing any damage to the colonized plant. The beneficial role of endophytic organisms has dramatically documented worldwide in recent years. Endophytes promote plant growth and yield, remove contaminants from soil, and provide soil nutrients via phosphate solubilization/nitrogen fixation. The capacity of endophytes on abundant production of bioactive compounds against array of phytopathogens makes them a suitable platform for biocontrol explorations. Endophytes have unique interaction with their host plants and play an important role in induced systemic resistance or biological control of phytopathogens. This trait also benefits in promoting plant growth either directly or indirectly. Plant growth promotion and biocontrol are the two sturdy areas for sustainable agriculture where endophytes are the key players with their broad range of beneficial activities. The coexistence of endophytes and plants has been exploited recently in both of these arenas which are explored in this chapter.

Keywords

Endophytes • PGP • Biocontrol • *Bacillus* • *Piriformospora* • *Streptomyces*

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3.1 Introduction

Plants have their life in soil and are required for soil development. They are naturally associated with microbes in various ways. They cannot live alone and hence they release signal to interact with microbes. Interaction can be of either beneficial

or pathogenic. The pathogenic interaction where the bacteria inject the effector protein to suppress the host defense response leads to plant diseases. Agricultural productivity suffers a heavy loss due to this pathogenic interaction. There is an immediate need to find and establish an ideal strategy for sustainable agriculture and improvement in crop growth. Agriculture being the world's largest economic sector, the demand should be addressed seriously. Environmental pollution is the biggest problem and a public concern today, and that is caused either directly or indirectly by use of fertilizers, pesticides, and herbicides. This has turned to seek alternative for the established chemical strategy to facilitate plant growth in agriculture and horticulture (Glick et al. 2007a). Many approaches have been taken to control plant pathogens. Several investigations have aimed at improving the understanding of plant defense systems and plant pathogen interactions (Dodds and Rathjen 2010). For a sustainable agriculture, new ways are in line to develop either to control the plant diseases or to promote the plant growth. Plant growth-promoting rhizobacteria (PGPR) plays an important role in sustainable agriculture as it functions as both plant growth promotion and disease suppression (Shoebitz et al. 2009; Beneduzi et al. 2012).

3.2 Endophytes: The Origin and Dwelling

Symbiosis refers to “living together of dissimilar organism” (De Bary 1879). There are more life that lives in symbiotic relation based on macroscopic hosts and microscopic creatures. The plant root system mainly anchors in nutrient and water uptake. Apart from that, it mediates numerous underground interactions with beneficial microbes such as rhizobia, mycorrhiza, endophytes, and rhizobacteria. The word endophyte came from two Greek words, “endon” means within and “phyton” means plant. Endophytes are microorganisms that can asymptotically grow within plant tissues without causing any damage or eliciting any disease to the host. Endophytic bacteria and fungi are ubiquitously

found in all plant species and evolve with higher plants from the day they are derived. Since the endophyte may be of both beneficial and harmful, the changes in the environment might affect the host or be neutral to the plant (Lacava et al. 2004; Ardanov et al. 2012).

The plant and the endophytic microbes have symbiotic relationship where both species benefit from the interaction. The diversity of endophytes is surprising as each and every plant species harbors one or more endophytes and they are driven by symbiotic forces in the ecosystem (Faeth and Fagan 2002). Woody plants were found to have more than one hundred different species of endophytes (Saikkonen et al. 1998; Arnold et al. 2000). They are found to be a promising candidate to increase crop yields, remove contaminants, inhibit pathogens, and able to also produce novel metabolites and fixed nitrogen.

Endophytic colonization occurs in several ways in plants. The route of colonization seems to be the rhizosphere where the microbes reach by chemotaxis and attach to the plant tissues either by pili, lipopolysaccharide, or exopolysaccharide in their cell wall (Lugtenberg and Kamilova 2009; Malfanova et al. 2013). The endophytes which are rhizosphere colonizers attach to the cell elongation zone or root hair zone of the apical roots and enter through a crack or damage. Preferably the colonization takes place in differentiation zone and intercellular spaces in the epidermis (Raven et al. 2009). When bacteria enter the exodermal barrier, there are three places where they can reside, viz., the site of entry, deep inside the cortex, and at the intercellular space of the cortex. Only few penetrate the endodermal barrier and invade xylem vessels. They are influenced by abiotic and biotic factors. But comparative to rhizospheric microbes, the endophytes are more protected from the abiotic and biotic stresses (Seghers et al. 2004). The true endophytes should be isolated after surface sterilization and confirmed with tagged studies in microscope. The endophytes which are validated in microscope are named to be putative endophytes. Endophytes mediate plant defense by two ways: (i) the innate endophytic community that should contain resistance-

competent traits and (ii) reviving of innate endophytic bacterial subpopulations by an incoming bacterium (e.g., a biocontrol agent) (Podolich et al. 2014). Endophytes have attracted the attention of researchers to evaluate them to be a potential and more effective option for use as plant growth promotion (PGP)/biological control agents in agricultural system. Understanding the interactions among endophytic microbes and their plant hosts will hopefully prove them to be alternative control measures for diseases. Gaining knowledge of the way they enter their plant hosts, the interactions that occur, and the influence that can be made for biocontrol purposes all relate to control the agricultural diseases. This chapter walks in detail over the endophytes and its types which would give a new eye on PGP and biocontrol agents.

3.3 Beneficial Traits of Endophytes and Its Mechanism

On colonization of the microbe in the plant, they can positively influence the growth and disease resistance. Several groups report the mechanism of PGP and biocontrol to be similar as rhizobacteria, but only few mechanisms have been proven to occur *in planta*. Still this chapter will review on all the expected mechanism for PGP and biocontrol (Fig. 3.1).

3.3.1 Plant Growth Promotion

PGP can take place by two ways, viz., direct or indirect mechanism. Endophytic microbes can stimulate the PGP by providing the essential nutrients, directly producing phytohormones and growth regulators, or regulating phytohormone levels.

3.3.1.1 Nitrogen Fixation

Nitrogen is a major limiting nutrient for the growth of the plant. Plants uptake nitrogen from the atmosphere and make available by the help of symbionts in the root nodules of legumes, and the

process is said to be biological nitrogen fixation. Rhizobia and nitrogen-fixing bacteria share *nod* and *nif* genes which encodes for nodulation and nitrogen fixation, respectively (Zehr and Turner 2001). Studies reveal that endophytes associate themselves in the same process in other agriculturally important crops. The nitrogen fixation is done by the nitrogenase enzyme produced by the bacteria (You et al. 2005). Nitrogen fixation is regulated by oxygen concentration and availability of nitrogen. Nitrogen-limited condition also interferes in plant hormone production, and hence some diazotrophs are able to produce phytohormones in addition to nitrogen fixation.

3.3.1.2 Phosphate Solubilization

Phosphorus is the next limited compound available for plants. They play a role in cell metabolism and signaling (Vance et al. 2003). Phosphorus in $H_2PO_4^-$ and HPO_4^{2-} can be absorbed by plants, but unfortunately they are present in bound form with organic or inorganic molecules which are unavailable to plants (Smyth 2011). Though phosphorus is used as a chemical fertilizer, excessive and unmanaged application has a negative impact on the environment. Endophytes are phosphate-solubilizing bacteria which solubilize the bound form thereby making available to plants. The production of organic acid like gluconic acid is a major factor in the release of phosphorus from a bound form (Rodriguez et al. 2006). In addition, enzymes including phosphonates, phytases, and C-P lyases also play a role in converting insoluble phosphorus to available phosphorus.

3.3.1.3 Siderophore Formation

Iron is a vital nutrient and occurs as Fe^{3+} in the aerobic environment and forms insoluble hydroxides and oxyhydroxides. These insoluble forms are not accessible to both plants and microbes. Generally, endophytes synthesize low molecular weight compounds termed as siderophores that sequester Fe^{3+} since they have high Fe^{3+} affinity constants and mobilize the irons present (Zhang et al. 2008; Vendan et al. 2010). Some endophytes produce hydroxamate type and other produce catechol type of sidero-

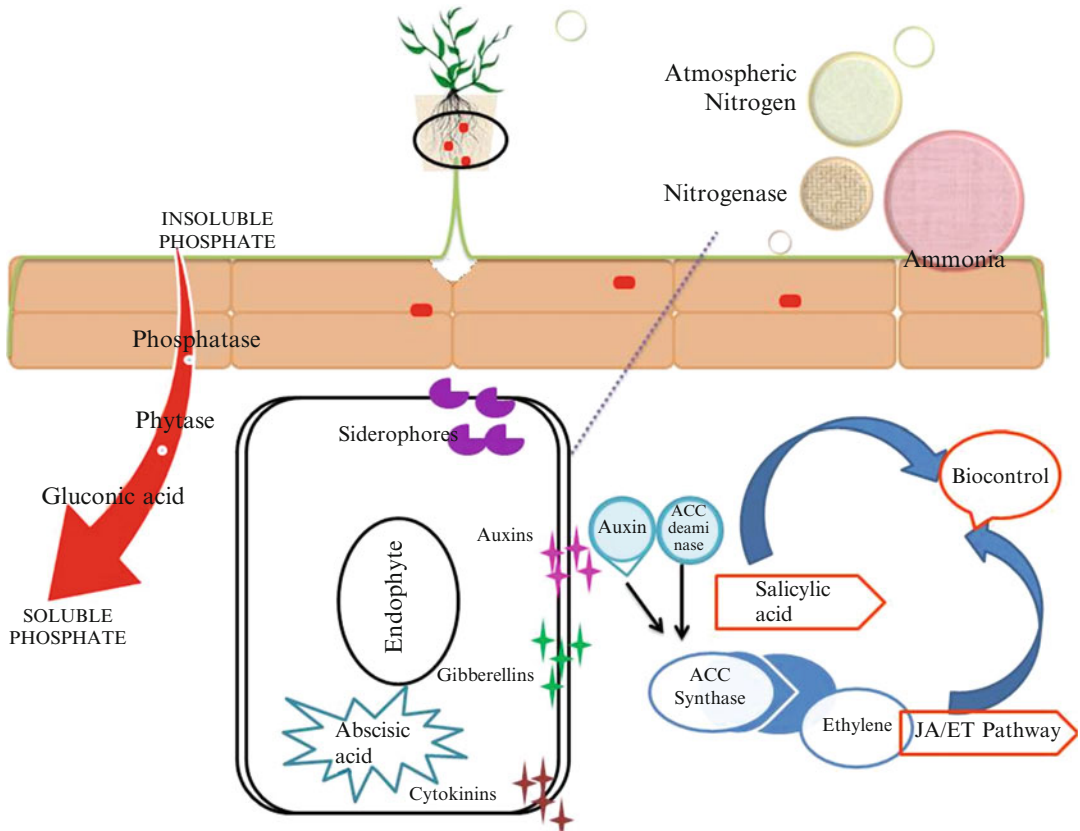


Fig. 3.1 A proposed schematic representation of PGP and defense response by endophytes

phores (Neilands and Nakamura 1991). The siderophores are water soluble and of two types, viz., extracellular and intracellular, i.e., secreted as iron-free siderophores for cellular iron uptake and located within the cell for intracellular iron storage, respectively (Johnson et al. 2013). Specific proteins are involved in transport of iron siderophore complex in iron-limited conditions. PGP and disease suppression are achieved by siderophore formation (Hayat et al. 2010). Many plant species absorb bacterial Fe^{3+} siderophore complexes, but the role of siderophores in PGP is yet to be proved.

3.3.1.4 Growth Regulators

Plants produce hormones such as auxins, cytokinins, gibberellins, ethylene, and abscisic acid. Endophytic microbes have the potent to produce these hormones which influence plant growth and development.

Auxins Auxin is the crucial plant hormone and fundamental component that modulates plant growth and development (Halliday et al. 2009; Grossmann 2010). Indole-3-acetic acid (IAA) is a member of auxin family produced by bacteria, fungi, and plants. IAA induces lateral root formation in dicots and adventitious root formation in monocots (McSteen 2010). IAA combines cambial growth and vascular development. Auxins promote secondary wall thickness and increase xylem cells (Uggla et al. 1996). They are transported via phloem by forming concentration gradients and accumulate in different tissues (Eklund et al. 2010; Tromas and Perrot-Rechenmann 2010). IAA concentrations vary depending on the tissues of the plant and organ (Reid et al. 2011). IAA pathway is a robust network which was identified by the enzymes that catalyze each reaction and the intermediates involved in each step (Lehmann et al. 2010). Several recent studies are

being proposed with IAA biosynthesis pathway. Detailed study of the IAA pathway is reviewed by Duca et al. (2014).

Cytokinins Zeatin is a member of cytokinin family. They play a role in division of plant cell in the presence of auxin. They involve in callus growth (Salome et al. 2001). Auxin and cytokinins help in root differentiation and shoot differentiation, respectively.

Gibberellins Terpenoid groups come under this category. They are mainly involved in cell division, cell elongation, and internode elongation. The mechanism by which plant growth is promoted through gibberellins is still unclear. Fulchieri et al. (1993) reported that they increase root hair density in root zones involved in uptake of nutrient and water.

Abscisic Acid It is a stress hormone which regulates the plant development and physiological process. They play an important role in seed germination, stomatal closure, and abiotic stress tolerance (Lee and Luan 2012). It is an abiotic elicitor for plant biosynthesis of bioactive compounds (Sun et al. 2012).

ACC Deaminase Ethylene is produced from ACC synthase (Giovannelli et al. 1980) which inhibits primary root elongation and lateral root formation but promotes root hair formation (Dodd et al. 2010), thus having a positive and negative role. Ethylene increases at a higher rate when the plant is in stressed conditions (Glick 2005). Hence, it is also known as stress hormone. The enzyme ACC deaminase is produced by many endophytes which converts ACC into α -ketobutyrate and ammonia (Glick et al. 2007b). Reduction in ACC level reduces ethylene levels and thus decreases the plant stress.

3.3.2 Biocontrol

The use of agrochemicals to control plant diseases can be minimized by means of biological process such as the use of endophytes which

inhibit or antagonize the phytopathogens. Though the chemical products kill the plant pathogen, workers and consumers are at high risk. Biocontrol agents communicate with other pathogens/organisms through a variety of signal molecules. These signal molecules play a role in the defense against disease. They include jasmonic acid, salicylic acid, abscisic acid, etc., which are induced during abiotic stress conditions.

Defense-related proteins and secondary metabolites are produced by induction of jasmonic acid (Brodersen et al. 2006; Balbi and Devoto 2008). Salicylic acid gets involved in flowering, growth and development, ethylene biosynthesis, stomatal behavior, etc. Abscisic acid in defense signaling is found to promote seed dormancy (Asselbergh et al. 2008). Mechanisms of biocontrol by the endophytes may be either one of the following:

1. Antibiosis – many bacteria are potent in producing antibiotics which are the best known class of biocontrol agents. Limitation on using antibiotic-producing bacteria might be the cross-resistance, and also the genes encoding might be transferable (Zhang et al. 1993).
2. Predation and parasitism – control agents produce exoenzymes that can degrade the fungal cell and use them as food for their survival.
3. Induced systemic resistance (ISR) – ISR is the plant immune response that is activated by beneficial microbes (Kloepper et al. 2004, Van Wees et al. 2008). Upon immunization, the plant becomes more potent in producing infection-induced immune response which might result in enhanced protection. ISR is also a systemic response which is similar to systemic acquired resistance (SAR) and protects from many pathogens (Van Loon 2007). They induce innate immunity and use toll-like receptors (De Weert et al. 2007). The signal transduction pathway and the molecular basis underlying are different. In SAR, the signals include hypersensitive response, salicylic acid biosynthesis, or induction of pathogenesis-related proteins, whereas the hormone jasmonic acid and ethylene play a main role in ISR (Sena et al. 2013). Hence, in any of the

above means, the natural microbes, i.e., endophytes, can be potent in controlling diseases thereby reducing the usage of chemical products.

3.4 Bacterial Endophytes

The origination of bacterial endophytes is of 120 years older where they were initially identified from seeds and surrounding environment. Endophytic bacteria are reported to be present in roots, stems, leaves, seeds, fruits, tubers, ovules, and also inside legume nodules (Compant et al. 2011) in which more preferably in roots (Rosenblueth and Martinez-Romero 2006). The endophytic population varies depending on the bacteria and the host, host developmental stage, inoculum density, and environmental conditions (Tan et al. 2006). The endophytes that are dominating in the plants are intensively reviewed in many reports (Rosenblueth and Martinez-Romero 2006). Though, the community composition is non-determinable but can be determined by colonization process. Factors such as nature and stage of the host, physiological status, type of plant tissue, soil conditions, and agriculture practices determine colonization (Hardoim et al. 2008).

Endophytes are host specific, for example, a group of clostridia is found to be only in grass species, i.e., *Miscanthus sinensis*, but not in the soil (Miyamoto et al. 2004). Endophytic bacteria are seen in legume nodules as co-occupants (Benhizia et al. 2004). They are reported to be isolated from different vascular and nonvascular plants denoting the wide spectrum of endophytic bacteria (Hardoim et al. 2012; Rosenblueth and Martinez-Romero 2006). Metagenomic approach is the recent hot spots in endophytes due to the unculturable nature of certain groups of endophytes (Manter et al. 2010; Sessitsch et al. 2012; Bulgarelli et al. 2012; Bodenhausen et al. 2013). This approach exploits a deeper understanding of the functions of the endophytes and the mechanism used to reside inside the endosphere.

Based on the lifestyle, they are classified as obligate and facultative endophytes. Obligate

endophytes depend on the host plant for their growth and survival and transmit to other vertical plants or through vectors, whereas facultative bacteria exist outside of the plant for a part of its lifetime, and for the rest, they dwell inside the plants. Bacterial phytopathogens also can be considered as facultative endophytes because they are present in avirulent forms. *Ralstonia solanacearum* can survive in water and occurs as an endophyte in tomato plants as avirulent bacteria (Van Overbeek et al. 2004). Endophytes include both Gram-positive and Gram-negative bacteria, and they are classified as *Alpha*-, *Beta*-, and *Gammaproteobacteria*, *Bacteroidetes*, *Actinobacteria*, and *Firmicutes* (Lodewyckx et al. 2002; Bacon and Hinton 2006). The higher percentage of rhizosphere community is *Acidobacteria* (31 %) and *Alphaproteobacteria* (30 %), whereas most endophytes were associated to *Gammaproteobacteria* (54 %) and *Alphaproteobacteria* (23 %) (Gottel et al. 2011).

3.4.1 Role in PGP and Biocontrol

PGP can be induced at higher rate by the bacteria. Most mechanistic pathway of either direct or induced PGP is more or less similar to rhizosphere bacteria. Direct PGP is caused by the inducing availability of nutrients or by hormone production. Indirect PGP might be taken place at three conditions: (1) in the presence of a pathogen, the beneficial bacteria inactivate/kill the pathogen; (2) when a remediation occurs, the bacterium inactivates a pollutant which stops the growth of the plant; (3) during stress conditions' excess of ethylene, heavy metal, drought, etc., ACC deaminase is produced which can tolerate stress conditions.

Bacterial endophytes are reported to produce auxins (Vendan et al. 2010, Shcherbakov et al. 2013) using tryptophan as a precursor (Rosenblueth and Martinez-Romero 2006), whereas gibberellins are reported to be produced by rhizosphere bacteria. IAA production by *P. putida* CR₃ and *Rahnella aquatilis* HC₂ stimulates growth in cereals and radish (Malfanova 2013). *Bacillus subtilis* HC-8 induced plant growth by

gibberellin production. Ethylene is a stress hormone for which ACC is the precursor. The bacteria convert ACC into α -ketobutyrate and ammonia which can tolerate the stress conditions caused by ethylene, salination, and heavy metals (Malfanova et al. 2011). A total of 174 endophytes isolated from interior tissues of tomato plants were collected from various countries in the world. The bacteria that are able to utilize ACC as sole carbon source were selected further and tested for IAA synthesis, siderophore formation, phosphate solubilization, optimal growth temperature, salt tolerance, and antibiotic sensitivity. Of the 174 endophytes, 25 isolates were potent in all the parameters tested, and they were found to be the genera of *Pseudomonas* spp., *Microbacterium* spp., *Agrobacterium* spp., *Bacillus* spp., and few unculturable (Rashid et al. 2012). Plants which prefer the endophytes with high ACC deaminase activity will confer benefits for both plant and bacteria (Hardoim et al. 2008).

Nitrogen fixation is involved in growth stimulation (Iniguez et al. 2004). Some endophytic bacteria are able to fix atmospheric nitrogen and convert them into ammonia which can be taken by the plant (Krause et al. 2006; Vendan et al. 2010; Shcherbakov et al. 2013). Endophytes such as *A. diazotrophicus* PA15 and *Herbaspirillum* sp. B5D when inoculated on sugarcane and rice, respectively, enhanced 0.6 % and 0.14 % total nitrogen in 24 h (Sevilla et al. 2001; Wu et al. 2009). Bacteria producing enzymes that can solubilize the phosphorus are agriculturally important. Some endophytic bacteria which cannot enter the interior layers of the plant cell are found to be potent in mobilizing the phosphorus (Sturz et al. 2000). Endophytic bacteria are potent antagonist in controlling the fungal pathogens. *Pseudomonas* species as an endophyte was reported to be an antagonist for different phytopathogens on various hosts (Adhikari et al. 2001; Grosch et al. 2005; Prieto et al. 2009). Similarly, plant defense mechanism is also activated by ISR. This ISR can be done by various metabolites, molecules, or volatiles produced by the bacteria inside plant tissues. For instance, *B. amyloliquefaciens*, *B. subtilis*, *P. fluorescens*, and

Serratia marcescens were reported to induce ISR (Kloepper and Ryu 2006). Reiter et al. (2002) demonstrated many genera of endophytic bacteria such as *P. fluorescens*, *P. alcaligenes*, *P. putida*, *Flavobacterium* spp., and *B. megaterium* inhibiting plant pathogens. Other endophytes that inhibit pathogens include *Alcaligenes* spp., *Kluyvera* sp., *Microbacterium* sp., and *Curtobacterium* sp. (Zinniel et al. 2002). Ramesh et al. (2009) reported 28 isolates of endophytic bacteria inhibiting bacterial wilt pathogen *Ralstonia solanacearum*.

Endophytic bacteria might follow a predation and parasitism mechanism. This might be due to production of cell wall-degrading enzymes such as cellulase, chitinase, and glucanase (Krechel et al. 2002; Berg and Hallmann 2006). They are also potent in suppressing the proliferation of nematode in host plants (Sturz and Kimpinski 2004). *Curtobacterium flaccumfaciens*, an endophyte isolated from citrus plant, was reported to inhibit the pathogen *Xylella fastidiosa* (Araujo et al. 2002). Similarly, endophytes from potato act as antagonist against bacteria and fungi (Sessitsch et al. 2004; Berg et al. 2005). Recent interest is on genetically engineered endophytes. For instance, *Herbaspirillum seropedicae* and *Clavibacter xyli* are genetically engineered endophytes that produce endotoxin of *B. thuringiensis* in order to control insect pests (Downing et al. 2000). Another endophyte *Burkholderia cepacia* has modified to tolerate toluene (Barac et al. 2004). Hence, with the detailed study of the mechanism in colonization, these can be implemented in promoting plant growth and as biocontrol agents. Recently studied endophytes with plant host are tabulated (Table 3.1).

3.5 Fungal Endophytes

More than 100 years of research suggests that most, if not all, plants in natural ecosystem are symbiotic with mycorrhizal fungi. Among all endophytes, fungal endophytes are studied more till date. Fungal endophytes are of increasing interest due to growing list of benefits that they can confer on their hosts, including both biotic

Table 3.1 PGP and biocontrol properties of bacterial endophytes

Endophytes	Host plant		PGP/biocontrol	References
	Common name	Scientific name		
<i>Bacillus megaterium</i> LNL6, <i>Methylobacterium oryzae</i> CBMB 205	Rice	<i>Oryza sativa</i>	IAA, ACC deaminase, N fixation	Subramanian et al. (2014)
<i>Gluconobacter diazotrophicus</i>	Sugarcane	<i>Saccharum officinarum</i>	Systemic defense	Idogawa et al. (2014)
<i>Burkholderia</i> , <i>Azospirillum</i> , <i>Ideonella</i> , <i>Pseudacidovorax</i> , <i>Bradyrhizobium</i>	Potatoes	<i>Solanum tuberosum</i> L.	N fixation, phytohormone production, biocontrol of <i>Fusarium</i> , <i>Koribacter</i> , <i>Pectobacterium</i>	Pageni et al. (2014)
<i>Paenibacillus</i> , <i>Bacillus</i> , <i>Microbacterium</i> , <i>Klebsiella</i>	Rice cultivars	<i>O. sativa</i>	IAA, P solubilization, siderophore	Ji et al. (2014)
<i>Burkholderia</i> , <i>Klebsiella</i> , <i>Novosphingobium</i> , <i>Sphingomonas</i>	Rice	<i>O. sativa</i>	IAA, P solubilization, siderophore	Rangjaroen et al. (2014)
<i>Bacillus subtilis</i> var. <i>amyloliquefaciens</i> 72β24	Rice	<i>O. sativa</i>	Biocontrol of <i>Rhizoctonia solani</i>	Nagendran et al. (2014)
<i>Bacillus</i> sp., <i>Enterobacter</i> sp.	Corn	<i>Zea mays</i>	N fixation, IAA, siderophore	Szilagyi-Zecchin et al. (2014)
<i>Pantoea dispersa</i>	Cassava	<i>Manihot esculenta</i> Crantz	P solubilization	Chen et al. (2014)
<i>Bacillus pumilus</i>	Thulasi	<i>Ocimum sanctum</i>	P solubilization, IAA, siderophore, HCN	Murugappan et al. (2013)
<i>Acinetobacter johnsonii</i> strain 3-1	Beet	<i>Beta vulgaris</i>	IAA, P solubilization	Yingwu et al. (2011)
<i>Martellella mediterranea</i> , <i>Hoeflea alexandrii</i>	Japanese rose and annual sea blite	<i>Rosa rugosa</i> , <i>Suaeda maritime</i>	P solubilization, IAA, nitrate reduction, biocontrol of <i>Phytophthora capsici</i> , <i>Pythium ultimum</i>	Bibi et al. (2012)
<i>Bacillus thuringiensis</i> GDB-1	Scots pine	<i>Pinus sylvestris</i>	ACC, IAA, P solubilization, siderophore	Babu et al. (2013)
<i>Bacillus</i> , <i>Paenibacillus</i> , <i>Klebsiella</i> , <i>Acinetobacter</i>	Wheat	<i>Triticum</i> spp.	IAA, P solubilization, siderophore, biocontrol of <i>Gaeumannomyces graminis</i>	Duran et al. (2014)
<i>Enterobacter</i> sp. strain FD17	Maize	<i>Z. mays</i>	IAA, ACC, P solubilization, siderophore	Naveed et al. (2014)
<i>Pseudomonas fluorescens</i> PICF7	Olive	<i>Olea europaea</i>	Biocontrol of <i>Verticillium</i> wilt	Cabans et al. (2014)
<i>B. subtilis</i> NA-108, <i>B. subtilis</i> NA-120, <i>Enterobacter</i> sp. EMB-79	Strawberry	<i>Fragaria ananassa</i>	IAA, siderophore, N fixation	de Melo Pereira et al. (2012)
<i>Bacillus</i> spp.	Rose gum	<i>E. urophylla</i> x <i>E. grandis</i>	IAA, P solubilization, N fixation	Paz et al. (2012)

(continued)

Table 3.1 (continued)

Endophytes	Host plant		PGP/biocontrol	References
	Common name	Scientific name		
<i>Stenotrophomonas maltophilia</i> , <i>Pseudomonas putida</i> , <i>S. maltophilia</i> , <i>Achromobacter xylosoxidans</i> , <i>Achromobacter</i> sp.	Amaranth, tomato, calabaza	<i>Amaranthus hybridus</i> , <i>Solanum lycopersicum</i> , <i>Cucurbita maxima</i>	IAA, P solubilization, ammonia	Ngoma et al. (2013)
<i>Escherichia fergusonii</i> , <i>Acinetobacter calcoaceticus</i> , <i>Salmonella enterica</i>	Coffee	<i>Coffea arabica</i> , <i>C. robusta</i>	Phosphatase, siderophore, IAA	Silva et al. (2012)
<i>Methylobacterium</i> spp., <i>Micrococcus luteus</i> , <i>Lysinibacillus fusiformis</i> , <i>Stenotrophomonas maltophilia</i>	Citrus, Ginseng	<i>Citrus</i> sp., <i>Ginseng</i> sp.	Siderophore, IAA, P solubilization, N fixation	Vendan et al. (2010)

and abiotic. They have the ability to provide resistance against herbivores (Brem and Leuchtmann 2001), pathogens (Gond et al. 2010), temperature and salinity (Redman et al. 2002) and also stresses and heavy metals (Li et al. 2012). Fungal endophytes unlike mycorrhizal fungi colonize plant root and grow into rhizosphere. Plant tissue is the residence of the fungal endophytes which may grow in all or any part of the plants. There are numerous reports documenting the presence of fungal endophytes in distinct phyla. Petrini et al. (1992) reported that more than one type of fungal endophytes is found in single plant. Kharwar et al. (2008) evidence 13 isolates in leaf, stem, and root tissues of *Catharanthus roseus*. Fungal endophytes are predominantly found to be present in tropical, subtropical, and terrestrial ecosystems. Kharwar et al. (2011) also reported the isolation of total 149 fungal endophytic isolates belonging to 17 fungal genera in leaf, stem, and petiole. Among all tissues studied, leaves showed about 72 % endomycobiota compared to stem and petiole which are 68 % and 25.54 %, respectively. The predominant genera include *Cryptosporiopsis lunata* (4.18 %), *F. roseum* (4.07 %), *A. niger* (5.93 %), *Stenella agalis* (5.20 %), *Fusarium oxysporum* (5.18 %), and *Aspergillus alternata* (6.30 %).

3.5.1 Classification

A detailed study in the classification of the fungal endophytes has been reviewed by Rodriguez et al. (2009). Endophytes are broadly classified into two groups, viz., clavicipitaceous endophytes (class I) and nonclavicipitaceous endophytes (class II), based on evolution, taxonomy, ecology, and nature of the host. Depending upon the host range, the way they colonize, the pattern of transmission, tissue specificities, and symbiotically conferred benefits, they are of two more classes (III, IV).

3.5.1.1 Class I (Clavicipitaceous) Endophytes

These endophytes are defensive mutualism of host grasses. They include free-living and symbiotic species associated with insects and fungi (*Cordyceps* sp.) or grasses, rushes, and sedges (*Balansia* sp., *Epichloe* sp., and *Claviceps* sp.) (Bacon and White 2000). This class of endophytes is believed to begun from insect-parasitic ancestors and diversified through an interkingdom. The evolution of endophyte is thought to have begun with free-living insect parasite and then progressed to epibiotic plant gaining access to plant nutrients (Spatafora et al. 2007; Torres et al. 2007). These endophytes descend-

ing from insects do not possess enzymes or toxins for killing or degrading plant tissues but produce toxins that affect insects and other animals. The life history states that *Epichloe* spp. are endophytes present in grass which is present in intercellular spaces of leaf sheaths, rhizomes, and surface of leaf blades (Moy et al. 2000; Tadych et al. 2007). During flowering stage, fungus grows over to form a stroma, where inflorescence primordium remains at arrested stage preventing seed development. Some species exhibit stromata allowing partial seed production and vertical transmission. Inoculation of *E. festucae* in turf grasses showed significant resistance over uninoculated turf to two major leaf spot pathogens: dollar spot disease caused by *Sclerotinia homeocarpa* (Clarke et al. 2006) and red thread disease caused by *Laetisaria fuciformis* (Bonos et al. 2005).

3.5.1.2 Class II (Nonclavicipitaceous) Endophytes

They are a single group with diverse fungi and can be provisionally classified into at least three functional groups on life history, ecological intern, and traits. It comprises of diversified species, which are a member of Dikarya, most belonging to *Ascomycota* and minority of *Basidiomycota*. These fungi colonize plants via infection structures such as sporulation or by direct penetration of plant tissue via hyphae growth through plant tissue which is dominantly intracellular with little or no impact on host cells. These fungi rapidly emerge and sporulate during host senescence (Weber et al. 2004). Many endophytes protect host to some extent against fungal pathogens. Endophytic isolates of *F. oxysporum* and *Cryptosporiopsis* sp. conferred disease resistance against virulent pathogens in barley (*Hordeum vulgare*) and larch (*Larix decidua*), and resistance was correlated to an increase concentration of phenolic metabolites (Schulz et al. 1999). The uniqueness lies in the ability of the individual isolates to asymptotically colonize and confer habitat-adapted fitness benefits on genetically distant host species representing monocots and eudicots (Rodriguez et al. 2009).

3.5.1.3 Class III Endophytes

These include the hyperdiverse endophytic fungi associated within leaves of tropical trees as well as ground tissues of nonvascular plants, seedless vascular plants, conifers, woody, and herbaceous angiosperm. Fungi with similar life histories of class III endophytes also occur with asymptomatic lichens and in that case are known as endolichenic fungi (Arnold 2008). Members of *Basidiomycota* belonging to *Agaricomycotina*, *Pucciniomycotina*, and *Ustilaginomycotina* also are class III endophytes. Reproduction is by spore formation which is released passively. Spores might be sexual or asexual.

3.5.1.4 Class IV Endophytes

The dark pigmented endophytes called as “mycelium radialis atrovirens” or dark septate endophytes are grouped as class IV endophytes. They are ascomycetous fungi that are either conidial or sterile and that form melanized structures such as inter- and intracellular hyphae and microsclerotia in the roots. These groups are less specific toward the host and have been reported about 600 plants including plants that are non-mycorrhizal, from Arctic, Antarctic, alpine, subalpine, tropic zones, temperate zones, coastal plains, and lowlands (Jumpponen 2001).

3.5.2 Role in PGP and Biocontrol

Fungal endophytes are valued more for its PGP traits and biocontrol potency (Azevedo and Araújo 2007; Suryanarayanan et al. 2012). Several investigations have performed to improve the plant growth and protect the plant. The endophytic fungi are beneficial to the host plants by inducing higher nutrient uptake (Lekberg and Koide 2005). Endophytic fungi are present right from the seed germination. At this stage, they degrade the cellulose of the cuticle and make carbon available for the plant germination and establishment. They colonize in the root of the host and result in promotion of growth and higher yield. They produce plant growth regulators, thereby promoting seed germination in crops (Bhagobaty and Joshi 2009).

Fungi are potent in producing wide variety of growth hormones, viz., gibberellins, auxins, and abscisic acid (You et al. 2012). Many endophytes have reported in vitro production of IAA and its effect on PGP (Govindarajan et al. 2008). IAA production further enhances plant growth under salinity, drought, and temperature stress (Redman et al. 2011). The sand flora of Korean coastal region showed a majority of 80.7 % growth promotion of Waito-C rice, thus indicating the induction of PGP hormones by fungal endophytes (Khan et al. 2012). A review by Mei and Flinn (2010) has listed US patents showing the significance of fungal and bacterial endophytes for plant growth promotion and stress tolerance.

Fungal endophytes have higher resistance toward insect herbivores, nematodes, and plant pathogens which is an important factor favoring crop protection. The defense against insects is enhanced by secreting growth-regulating compounds or metabolites. These in turn influence plant development and help in crop protection (Marina et al. 2011). The endophytes against crop diseases by fungus were reported by Webber (1981) for the first time where *Phomopsis oblonga* protects from *Physocnemum brevilineum*, a pest of elm trees. Plant hormones that act as defense signaling molecule include salicylic acid, jasmonic acid, etc. (Shinozaki and Yamaguchi-Shinozaki 2007). Endophytic genera of *Neotyphodium* and *Fusarium* suppress *Triticum* diseases and nematodes, respectively (Tunali et al. 2000). Several studies demonstrated that endophytic fungi can resist the plants against *Phytophthora palmivora*, *Moniliophthora roreri*, and *M. perniciosa* (Mejia et al. 2008) in which one of the endophytes *Gliocladium catenulatum* can reduce up to 70 % incidence of witches' broom disease (Rubini et al. 2005). *Piriformospora indica* induces systemic resistance in *Arabidopsis* against powdery mildew pathogen *Golovinomyces orontii* by activating the jasmonate signaling pathways (Stein et al. 2008). More examples of endophytic fungi controlling plant diseases caused by pathogenic fungi, nematodes, and bacteria are reviewed by Azevedo and Araújo (2007).

Inoculation with *P. indica* isolated from *Prosopis juliflora* and *Ziziphus nummularia* increased the plant growth in diverse host plants (Varma et al. 1999). Improved plant nutrition and increased tolerance to abiotic and biotic stress elucidate the plant growth stimulation mediated by endophytes. *Epichloe festucae* is a fungal endophyte that increases uptake of phosphorus on inoculation with *Festuca rubra*, by solubilizing rock phosphate from soil (Zabalgogezcoa et al. 2006).

Many endophytes like *F. fujikuroi*, *Sphaceloma manihoticola*, *Phaeosphaeria* sp., *Neurospora crassa*, *Cladosporium* sp., *Penicillium* sp., *Gliomastix murorum*, *Arthrinium phaeospermum*, and *Aspergillus fumigatus* have been reported as growth promoters. Under extreme environmental conditions, these phytohormones producing endophytic fungi affect the production of several secondary metabolites like flavonoids to help the plant to tolerate/avoid stress (Schulz 2002; Waller et al. 2005; Khan et al. 2011). Representative fungal endophytes with PGP and biocontrol traits were tabulated (Table 3.2). Today's interest is toward the endophytic fungi which have residence in root tissues and secrete plant growth-regulating compounds to increase the crop yield and quality. On controlling the plant diseases and increasing the yield, the ideal strategy of sustainable agriculture can be reached. Though the molecular mechanism of the endophytic fungi in PGP and defense is not clearly known, several studies confirm that they play a key role in the crop protection and yield enhancement. The culturable and unculturable techniques are involved to explore still on the endophytes. Fungal endophytes have attracted the researchers and hence they are researched globally to combat crisis and demands in agriculture (Rai et al. 2014).

3.6 Endophytic Actinomycetes

Actinomycetes are Gram-positive filamentous bacteria belonging to the phylum *Actinobacteria* with 6 classes, 5 subclasses, 25 orders, 14 suborders, 52 families, and 232 genera. It is one of the

Table 3.2 PGP and biocontrol properties of fungal endophytes

Endophytes	Host plant		PGP/biocontrol	References
	Common name	Scientific name		
<i>P. indica</i>	Barley	<i>Hordeum vulgare</i> L.	Ethylene/phytohormone production	Schafer et al. (2009)
<i>P. indica</i>	Arabidopsis	<i>Arabidopsis thaliana</i>	Cytokinins, abscisic acid, gibberellins	Vadassery et al. (2009)
<i>Cladosporium</i> sp.	Cucumber	<i>Cucumis sativus</i>	Gibberellins	Hamayun et al. (2010)
<i>Scolecobasidium humicolas</i>	Tomato	<i>Solanum lycopersicum</i>	N fixation	Mahmoud and Narisawa (2013)
<i>Penicillium</i> sp., <i>Phoma glomerata</i>	Cucumber	<i>Cucumis sativus</i>	IAA, gibberellins, jasmonic acid	Waqas et al. (2012)
<i>Pestalotiopsis</i> sp.	Tomato	<i>Solanum lycopersicum</i>	IAA	Hoffman et al. (2013)
<i>Aspergillus flavipes</i> CanS-34A, <i>Chaetomium globosum</i> CanS-73, <i>Clonostachys rosea</i> CanS-43, <i>Leptosphaeria biglobosa</i> CanS-51	Oilseed rape	<i>Brassica napus</i>	Biocontrol of <i>Sclerotinia sclerotiorum</i> , <i>Botrytis cinerea</i>	Zhang et al. (2014)
<i>Paraconiothyrium</i> sp.	Taxus	<i>Taxus baccata</i>	Salicylic acid, benzoic acid	Soliman and Raizada (2013)
<i>Penicillium verruculosum</i>	Cinquefoils	<i>Potentilla fulgens</i>	IAA	Bhagobaty and Joshi (2009)
<i>Curvularia</i> , <i>Fusarium</i> , <i>Pestalotiopsis</i> , <i>Tolyposcladium</i>	Cacao	<i>Theobroma cacao</i>	Biocontrol of <i>Phytophthora palmivora</i>	Hanada et al. (2010)
<i>Penicillium</i> sp.	Wheat	<i>Triticum</i> spp.	P solubilization	Wakelin et al. (2004)
<i>Fusarium oxysporum</i>	Banana	<i>Musa paradisiaca</i>	ISR against <i>Radopholus similis</i>	Vu et al. (2006)
<i>Penicillium copticola</i>	Cannabis	<i>Cannabis sativa</i> L.	Biocontrol of <i>Botrytis cinerea</i> , <i>Trichothecium roseum</i>	Kusari et al. (2013)
<i>Aureobasidium pullulans</i> , <i>Paraconiothyrium sporulosum</i>	Frailejón	<i>Espeletia grandiflora</i> and <i>Espeletia corymbosa</i>	Biocontrol of <i>Rhizoctonia solani</i>	Miles et al. (2012)
<i>Paecilomyces formosus</i>	Cucumber	<i>Cucumis sativus</i>	Gibberellin	Khan et al. (2012)
<i>Trichoderma gamsii</i>	Lentil	<i>Lens esculenta</i>	P solubilization, chitinase, ammonia, salicylic acid	Rinu et al. (2014)

largest taxonomic groups among the 18 known lineages within the bacterial domain (Stackebrandt and Schumann 2000). They are found in the internal tissue of the plant without harming the plant either as damage or in morphological change (Kunoh 2002; Hasegawa et al. 2006). Plant ecosystem is diversified and it is a

rich reservoir of novel taxa actinomycetes (Inbar et al. 2005; Zin et al. 2007; Qin et al. 2009). They have wide range of host and found to be residing in many plants, viz., barley, rye, oats, and soybean (Sardi et al. 1992), rice (Tian et al. 2004), banana (Cao et al. 2005), cowpea (Dimkpa et al. 2008), medicinal plants (Qin et al. 2009), blue

lupin (Trujillo et al. 2010), tomato (de Oliveira et al. 2010), chickpea (Misk and Franco 2011), neem tree (Verma et al. 2011), and wheat (Sadeghi et al. 2012).

Among actinomycetes identified as endophytes, *Streptomyces* sp. is the predominant, and *Microbispora*, *Micromonospora*, *Nocardioides*, *Nocardia*, and *Streptosporangium* are the common genera. According to the study performed in roots and leaves of maize plants (*Zea mays* L.), *Microbispora* sp. was found to be the most common *Actinobacteria* (De Araujo et al. 2000), although *Streptomyces* and *Streptosporangium* spp. were also present. But a number of 619 actinomycetes were isolated from different cultivars of tomato, and all of them were *Streptomyces* spp. (Tan et al. 2006). Similarly Taechowisan et al. (2003) isolated 330 strains belonging to four different genera (*Streptomyces*, *Microbispora*, *Nocardia*, and *Micromonospora*) in 330 medicinal plants. Lee et al. (2008) reported 81 endophytic *Actinobacteria* including eight genera from Chinese cabbage roots, and *Microbispora* spp. were the most common isolates, followed by *Streptomyces* sp. and *Micromonospora* sp. Colonization takes place at higher rate in roots of the host. To date, more than 40 new taxa have been found by polyphasic taxonomic approaches, including four new genera, *Plantactinospora*, *Actinophytocola*, *Phytohabitans*, and *Jishengella*. The greatest diversity of endophytes occurs in the tropical and temperate regions. Janso and Carter (2010) reported a total of 123 endophytic actinomycetes isolated from plants collected from several locations in Mborokua Island, Papua New Guinea, and Solomon Islands. Filamentous *Actinobacteria* was found to be present in surface-sterilized roots of wheat plants (Coombs and Franco 2003). Misk and Franco (2011) observed a physiologically different endophytic group in legumes such as lentil, chickpea, pea, etc. Strobel and Daisy (2003) have reported that a great diversity of endophytic *Actinobacteria* is found in tropical and temperate regions. Taechowisan et al. (2003) isolated about 330 strains from 36 medicinal plants in Thailand which showed that the genera *Streptomyces*, *Microbispora*, *Micromonospora*,

and *Nocardia* are predominant. *Actinobacteria* has attracted researchers in recent years where 50 new taxa have been identified from various plants in terrestrial environment. The identification and characterization is done by polyphasic approach which includes morphological, chemotaxonomical, and molecular techniques (Bruseti et al. 2008; Yuan et al. 2008). The next-generation sequencing, a high-throughput study, is another upcoming technique which is used in diversity and taxonomy studies (Mardis 2008, Lauber et al. 2010, Robinson et al. 2010).

3.6.1 Role in PGP and Biocontrol

Recently, actinomycetes have attracted the researchers' interest because of its potent biocontrol nature and significant role in plant promotion. However, the *Streptomyces* strain had the smallest population size (10^2 – 10^5 cfu/g) in a wheat rhizosphere; they relatively lived for a longer duration (1 year) than other organisms under the conditions tested (Yuan and Crawford 1995). Several studies have proved that endophytic actinomycetes can control many fungal pathogens and plant diseases (Quecine et al. 2008). This antagonistic ability is due to the production of bioactive compounds, cell wall-degrading enzymes, and competent in nutrition (El-Tarabily and Sivasithamparam 2006). They can also trigger ISR. The endophytic strain *S. galbus* R-5 released cellulose and pectinase and produced actinomycin X₂ and fungichromin to induce resistance in the rhododendron seedlings and triggered plant jasmonate-associated defense responses (Shimizu et al. 2005). Conn et al. (2008) observed that *Streptomyces* sp. EN27 and *Micromonospora* sp. strain EN43 led to increased resistance in *A. thaliana* leaves against pathogens such as *Erwinia carotovora* and *F. oxysporum* and triggered the expression of defense genes related to salicylic acid- or jasmonic acid-/ethylene-dependent signaling pathways in the absence of a pathogen. *Streptomyces* isolated from banana plant was found to have antibiosis property and was also capable in siderophore production (Cao et al. 2004). Similarly,

Micromonospora and *Streptomyces* from mango plants in China were potent to inhibit protein synthesis with antibiosis property (Hong et al. 2009). They promote plant growth by inducing the production of phytohormone production of siderophores to scavenge ferric iron from the environment, solubilization of inorganic phosphate, nitrogen fixation, and suppression of stress ethylene in plant by the production of ACC deaminase (Dimkpa et al. 2008; Kannan and Surendar 2008; Trujillo et al. 2010; de Oliveira et al. 2010; Verma et al. 2011; Sadeghi et al. 2012). A wide range of pathogens can be controlled by actinomycetes including *Rhizoctonia solani*, *Verticillium dahliae*, *Plectosporium tabacinum*, *F. oxysporum*, *Pythium aphanidermatum*, and *Colletotrichum orbiculare* (Krechel et al. 2002; Shimizu et al. 2009). Several endophytic *Actinobacteria* isolated from winter rye produced IAA (Merzaeva and Shirokikh 2010). *Frankia* strains are symbionts in certain nonleguminous plants and can induce N₂-fixing root nodules (Benson and Silvester 1993). Tomato plants from Algerian Sahara were found to have many *Streptomyces* genera which were screened for the ability of IAA production and also potent in controlling *R. solani* (Goudjal et al. 2013, 2014). Endophytic actinomycetes isolated from various plants with PGP and biocontrol properties were summarized in Table 3.3.

Recently, our research group at ICRISAT has isolated from various rhizospheric soil and collected about 1500 microbes (bacteria and actinomycetes) in which many have documented agriculturally favorable traits. Actinomycetes such as *Streptomyces* spp., *S. griseorubens*, *S. caviscabies*, and *S. globisporus* subsp. *caucasicus* isolates have potency in in vitro PGP traits with upregulation of PGP genes such as IAA and siderophore-producing genes (Gopalakrishnan et al. 2012, 2013, 2014a). Apart from the PGP traits, they also have the capacity to act as biocontrol agents. The PGP actinomycetes were found to have inhibitory activity against *Fusarium oxysporum* f. sp. *ciceri* (FOC) and *Sclerotium rolfsii* Sacc., which causes *Fusarium* wilt and collar rot in chickpea, respectively (Gopalakrishnan et al. 2011a), and also against

Macrophomina phaseolina, which causes charcoal rot in sorghum (Gopalakrishnan et al. 2011b). PGP bacteria such as *B. megaterium*, *B. subtilis*, *Serratia marcescens*, and *Pseudomonas geniculata* (Gopalakrishnan et al. 2014b), a fungus *Metarhizium anisopliae*, and actinomycetes such as *S. cavourensis* sup sp. *cavourensis*, *S. cyaneofuscatus*, *S. bacillaris*, *S. antibioticus*, *S. albolongus*, *S. hydrogenans*, and *S. carpaticus* were found to have broad-spectrum insecticide against lepidopteran pests such as *Helicoverpa armigera*, *Spodoptera litura*, and *Chilo partellus* (Gopalakrishnan et al. 2011c; Vijayabharathi et al. 2014). Recently, five strains of *Streptomyces* sp. isolated from chickpea have been found to inhibit charcoal rot of sorghum and induce PGP of sorghum and rice. They have been found to have IAA and siderophore-producing genes (Gopalakrishnan et al. 2015). All these bacteria and actinomycetes with PGP and biocontrol ability need to be further evaluated for its endophytic ability by addressing the query of survival inside the endodermal layer. Plant growth-promoting properties of endophytic *Actinobacteria* and the recent increased understanding of some of the mechanisms suggest that this promising source merits further investigations for potential application in agriculture.

3.7 Future Prospects

The endophytic population is the gut population of the plants. They might be of bacteria, fungi, or actinomycetes. Majority of these are not identified yet. Endophytes make a renaissance in using microbes for biological control of plant pathogens for a sustainable agriculture where the emphasis mainly is on hazards associated with chemical pesticides and transgenic plants. They colonize inside and outside the host tissues and make a long-term friendship, actually a lifelong relation without making any harm to the host (Rodriguez et al. 2009). Though several decades of research has underwent in the field of symbiosis and their associations, there is a gap to know about the things needed for association and the way they maintain the association. The future

Table 3.3 PGP and biocontrol properties of actinomycete endophytes

Endophytes	Host plant		PGP/biocontrol	References
	Common name	Scientific name		
<i>Streptomyces albosporus</i> R13	Rice	<i>O. sativa</i>	Siderophore	Gangwar et al. (2012)
<i>S. griseus</i>	Wheat	<i>Triticum</i> spp.	IAA	Hamdali et al. (2008)
<i>S. olivochromogenes</i> , <i>Microbispora rosea</i> subsp. <i>rosea</i>	Chinese cabbage	<i>Brassica rapa</i>	Biocontrol of <i>Plasmodiophora brassicae</i>	Lee et al. (2008)
<i>Streptomyces</i> MBR-5, AOK-30	Alpenrose	<i>Rhododendron ferrugineum</i>	<i>Phytophthora cinnamomi</i> , <i>Rhizoctonia</i> sp.	Hasegawa et al. (2006)
<i>Streptomyces</i> sp. EN27 and EN28, <i>Micromonospora</i> sp. EN43, <i>Nocardioides albus</i> EN46	Arabidopsis	<i>Arabidopsis thaliana</i>	Systemic acquired resistance	Conn et al. (2008)
<i>Streptomyces</i> sp. MBCu-56	Cucumber	<i>Cucumis sativus</i>	<i>Colletotrichum orbiculare</i>	Shimizu et al. (2009)
<i>Micromonospora</i> sp., <i>Streptomyces</i> sp., <i>Actinoplanes</i> sp.	Lucerne	<i>Medicago sativa</i>	N fixation	Solans et al. (2009)
<i>Streptomyces</i> sp.	Neem	<i>Azadirachta indica</i>	IAA, siderophore, biocontrol of <i>Alternaria alternata</i>	Verma et al. (2011)
<i>Streptomyces</i> sp., <i>Nonomuraea</i> sp., <i>Actinomadura</i> sp., <i>Nocardia</i> sp.	Eaglewood	<i>Aquilaria malaccensis</i>	IAA, ammonia	Nimnoi et al. (2010)
<i>S. griseorubiginosus</i>	Banana	<i>Musa paradisiaca</i>	Biocontrol of <i>F. oxysporum</i> f. sp. <i>cubense</i>	Cao et al. (2005)
<i>Streptomyces</i> sp. PT2	Spiderflower	<i>Cleome arabica</i>	Biocontrol of <i>Rhizoctonia solani</i>	Goudjal et al. (2013)
<i>Streptomyces</i> sp.	Wheat	<i>Triticum</i> spp.	P solubilization, IAA, phytase, chitinase, siderophore	Jog et al. (2014)
<i>Streptomyces</i> sp. En-1	Chinese yew	<i>Taxus chinensis</i>	IAA	Lin and Xu (2013)
<i>Streptomyces</i> sp., <i>Nocardia</i> sp., <i>Nocardiosis</i> sp., <i>Spirillospora</i> sp., <i>Microbispora</i> sp., <i>Micromonospora</i> sp.	Mandarin	<i>Citrus reticulata</i>	IAA	Shutsrirung et al. (2013)
<i>Streptomyces</i> sp. BSA25, <i>Streptomyces</i> sp. WRA1	Wheat, Faba bean	<i>Triticum</i> spp., <i>Vicia faba</i>	Siderophore, biocontrol of <i>Phytophthora medicaginis</i>	Misk and Franco (2011)
<i>Streptomyces</i> sp.	Maize	<i>Z. mays</i>	Biocontrol of <i>Pythium aphanidermatum</i>	Costa et al. (2013)

studies are queries lying in line to be solved. These include genomics of endophytes, signaling and dwelling in the same host, nutrient availability and sharing, etc. The diversity of the endophytes is very vast (Klitgord and Segre 2010), and with this nature assessing the common attribute in each and every endophyte is not possible. This complex environment in turn limits the uses of the endophytes. Next is that the use of the endophytes *in vitro* and *in vivo* has some limitations. Many metabolites are produced by these endophytes which sometimes are novel compounds also (Yu et al. 2010). These compounds are not the same when produced *in vitro* condition. High-throughput studies are carried to conduct screening strategies for increased production. In such cases with cultural modifications, the genetic and molecular level modifications are performed. The challenge here is picking out the specific genes that make such modification. Using the endophytes *in planta* is another big challenge where it should address the mechanism of action for protection and PGP which has not developed with higher success rate till date. Overall, isolating the unculturable and identifying them has brought molecular approaches and next-generation sequencing into the field (Draper et al. 2011). Thus, it is expected that many more endophytes will be identified, analyzed, and utilized. The future challenges are dependent on identifying, delineating, dissecting, and defining the mechanisms of the relation they have. A basement-level success in this research which is reached and further answers the above challenges might ensure the present and future successful technological applications of microbial endophytes mainly in growth promotion and in control of plant diseases.

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