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Dinesh K. Maheshwari
K. Annapurna *Editors*

Endophytes: Crop Productivity and Protection

Volume 2

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Volume 16

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Preface

A better understanding of endophytic microorganisms may help to elucidate their functions and potential role in developing sustainable systems of crop production and their protection against abiotic and biotic stresses. Endophytes play a vital role in growth and health promotion of plant. Endophytic bacteria are of agrobiological interests because they create host–endophyte relationship having exciting prospects for newer biotechnological applications. Endophytes proved beneficial alternative for sustainable solutions for agrochemicals due to their role in biological control of pests and diseases. They reduce the burden of excess use of agrochemicals. On the other hand, endophytes are potential source of several secondary metabolites and several useful other metabolites such as alkaloids, enzymes, biosurfactants, biocontrol agents, and plant growth promoters. It is imperative that these products have industrial applications in the field of biotechnology, pharmacy, and agriculture.

The 'Endophytes: Vol. II Crop productivity and protection' is an endeavor to review the current developments in the understanding of microbial endophytes and their potential applications in the enhancement of productivity and disease protection. This book contains various chapters presenting state of knowledge on involvement of endophytes in crop productivity and soil health because of beneficial for agricultural and forest ecosystem. Endophytes contribute in nonnative crops, volatile organic compound production, and a remarkable source of biologically active secondary metabolites and enzymes, as lignin degrading fungi, in bioremediation, phosphate solubilization, agricultural productivity, and plant disease control. The chapters describe the strategies for crop improvement and production of useful metabolites and aromatic compounds, enzymes, and other metabolites. These chapters are described with advance information on endophytes for productivity and protection in sustainable plant ecosystem.

We are sure the book will be useful to botanists, microbiologists, biotechnologists, molecular biologists, environmentalists, and those working for the protection of plant species of agricultural and medicinal importance. I am thankful to the contributors of these books for their cooperation and patience in the compilation of this task. I am also thankful to Springer team, particularly Drs. R. Valeria and Takeesha for their constant support in the publication of this work.

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Chapter 1
Endophytes as Contender of Plant Productivity and Protection: An Introduction

Dinesh K. Maheshwari, Shrivardhan Dheeman and K. Annapurna

Abstract Bacterial endophytes are versatile with impeccable mastery to occupy their niche in plant tissues, thus, experiences less competition than the other free-living rhizospheric inhabitants. These holds vast and extended scope of their utilization in plant health and growth promotion and contribution in sustainable agriculture as potent contender. This chapter introduces overview on the diverse role of endophytes for multidisciplinary benefits exclusively in plant productivity and protection.

Keywords Bioremediation · Bacterial metabolites · Invasive endophytes
Native plants · Non-native plants · Forest ecosystem

1.1 Introduction

There is a great deal of interest in understanding the role of endophyte diversity in plants and their ecology, evolutionary biology and applied sciences research ranging from crop productivity to protection against abiotic and biotic stresses. During last decade, maximum numbers of papers on beneficial endophytes have been published from the USA followed by narrow difference between China and India. Top nine countries have published on different aspects. Whereas subject-wise

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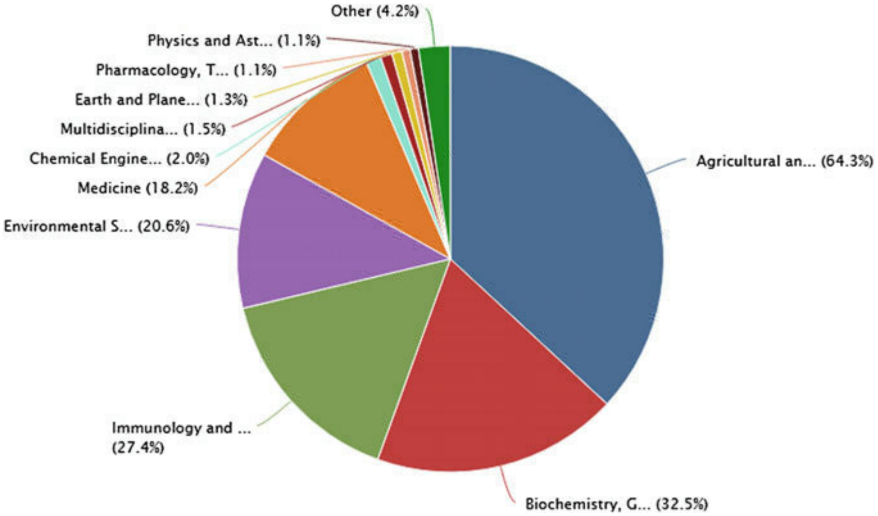

Fig. 1.1 Beneficial endophytes in different area (subject wise distribution). *Source* www.scopus.com/

maximum publications appeared on their beneficial role in both native and non-native crops and more particularly to that of agricultural benefits (Fig. 1.1).

With the growing need for increase food and bioenergy biomass but with a great understanding of the implications of conventional intensive agriculture, the time is right for a great emphasis on biological mechanisms for improvement of plant growth. Endophytes have an advantage since there would be less competition, when adding soil bacteria to the established rhizosphere communities. Endophytes with the ability to colonize internal host tissues has made them valuable microorganisms to improve crops performances as well as forest trees which are equally benefitted by using endophytes via seeds, seedlings, etc.

Almost whole plant, even the pollen and pistil are the sources of endophytic microorganisms but, present more in root than that of aerial plant tissues. Similarly, epiphyte microbial (leaf) populations (phyllosphere) are more numerous in comparison to that of endophytic populations (Beattie and Lindow 1999). It is interesting to note that fungal endophytes have bacteria and viruses make tritrophic endophytic interactions (Hoffman and Arnold 2010). Recently, Aeron et al. (2014) observed endophytic colonization of putative invasive non-rhizobia endophytes from *Clitoria ternatea* L. nodules; the bacteria that lack the ability to form nodules were also observed in the root nodules.

The majoring of reports deal with the culturable endophytes and for most of such nodule inhabiting bacteria, their endophytic nature is not yet proven. Since, they remain associated with plant adhering tissues, viz, nodules; these are now referred as putative endophytes. Various genera such as *Streptomyces*, *Agrobacterium*, *Bacillus*, *Paenibacillus*, *Pseudomonas*, *Enterobacter*, *Paracoccus*, *Lysinibacillus*, *Staphylococcus*, *Starkeya* and others exist or co-exist with or without a tree symbiont inside nodules.

Plant tissues colonized with diverse genera of microbes those persist as epiphytes and endophytes and historically, endophytes inherited from endotroph introduces concerns in relation with endomycorrhizal association (Frank 1885) and later used to define ferns colonized with algae as described by Campbell (1908). Endophytes have both beneficial and harmful effect to the associated plants. But more often, the endophytic microbes reduce herbivory (Koh and Hik 2007), induce plant growth and development (Hardoim et al. 2008), increase mineral uptake (Malinowski and Belesky 2000), fix nitrogen (Doty et al. 2009), suppress phytopathogens and diseases (Melnick et al. 2008) and induce plant defence Kloepper et al. 2004). As a matter of fact, their colonization in an ecological niche is similar to plant pathogens which might favour them as a potential biocontrol agent (Ramamorthy et al. 2001). The close association with plant tissues make them amicable and often a unique opportunity for their role in biological control. The endophytic microbes in biocontrol received lot of interest and suitably described in the present book.

Endophytes proved as a novel source of enzymes, antibiotics including other secondary metabolites of agro-biological and ecological significance. In addition, endophytes are often used in rhizoremedation. Reports on their ability and applications to degrade pollutants have now been possible (Doty 2008; Segura et al. 2009).

Next generation sequencing such as pyrosequencing, ROCHE sequencing, High throughput sequencing etc. can lead to discovery of new groups of microbes bioremediation of pollutants. Bacterial community from aerial part of plant bears plant growth promoting attribute to control diseases. The leaves harbour endophytic culturable bacteria beneficial to plant which can be used as bioinoculants for plant growth promotion thus for increasing their productivity (Malfanova 2013).

1.2 How Endophytes Are Beneficial for Agriculture System?

Similar to other bacteria endophytes are potential inhabitant in a wide variety of native and cultured crop plants. Their presence inside the host tissues undoubtedly exhibiting with diverse morphologies that ranges unicellular to filamentous forms. Their presence in both terrestrial and aquatic ecosystem, including marine environmental plants holds beneficial impacts via offering nutrient accumulation, secondary metabolite production, etc. Other than, rhizospheric benefits, actinobacteria are also involved in recycling of nutrients, decomposition of organic matter, degradation of agricultural and urban wastes, environmental pollutants, such as petroleum, dyes and other recalcitrant compounds which in turn corroborate the soil ecology and agro-ecosystem as discussed in Chap. 2.

1.3 Endophytes: A Part of Forest Ecosystem

Forest trees are providing unique ecological reservoir for bacterial endophytes. Of course, forests are important component to sustain environment and play significant role to keep integrity and sustainability of nature. Forests cover one-third of entire land on Earth, providing vital organic infrastructure for some of the planet's thickest and most diverse collections of life. Bacterial endophytes associated with tree species are rather limited but their importance should not be underrated. By virtue of beneficial endophytes associated with forest tree, wide range benefits can be harnessed in term raising potential future for forest trees so as to restore the density and sustainable existence of forest to keep earth green as reviewed in Chap. 3.

1.4 Endophytes in Native and Non-native Crops

The increasing introduction of non-native plants particularly improved germ-plasm of crops is utmost necessary for adequacy of food to human beings and feed to animals. Microbial invasion in plants has a considerable role to play in facilitating their growth and productivity besides biological control of deleterious phytopathogens causing diseases in non-native plants. To apply for beneficial relationships, endophyte-plant host interactions are suitable strategies that facilitates agricultural productivity. Beneficial endophytes of non-native crop host can be utilized in native or indigenous crop as reviewed in Chap. 4.

1.5 Endophytes Increase Microbial Activity in Tissues

The outer epidermal walls of plant cells are covered with mucilage and cuticle. The cell also secretes polysaccharides and their biopolymers. The organic and inorganic compounds in the cells cytoplasm are diffused out. This occurs probably due to unfavourable conditions and sometimes indirectly affect the aerial surface accumulate directly. In case of underground region, beneath the soil is root and loss of organic and inorganic compounds from its surface is known as root exudates. Inside the tissue, endophytes colonize and constitute a good base which is utilized by microorganism and release various metabolites multifarious in nature.

1.6 Endophyte as a Source of Potential Metabolites

These are member of volatile organic compounds as well as diffusible substances produces by endophytes. The low molecular weight hydrocarbons, aldehydes alcohol, lectones, peptides inorganic volatiles such as HCN are produced during primary and secondary metabolism of these endophytes. Some of these chemicals are the source of signalling that facilitates the activity of other microorganisms present is the ecological niche prove beneficial in both raising productivity and protecting plants. Even few of the endophytes act as agents triggering plant immunity and enhancing plant growth and health support. Thus, impact to understand the bioconversion of cellulosic domain into liquid fuel, role of volatile organic compounds in biocontrol, etc. cannot be ruled out. The characterization and elucidation of these compounds, with suitable strategy in agricultural practices has been elaborated in Chap. 5.

New discovery of molecule is a continuous process in pharmaceutical industry because of development of new races and genera of resistance in microorganisms. Various genera such as *Escherichia*, *Salmonella*, *Pseudomonas*, *Staphylococcus*, *Streptococcus*, *Micrococci,* etc. belong to multidrug resistance and some *Enterococcus* spp. proved vancomycin resistance. There is no proper drug available to combat infections cause by these genera. Suitable strategies still need to establish for isolating potent biomolecules both from microorganism as well as plants (Table 1.1). Endophytes are ubiquitous in nature associated with different genera and tissues of diversify nature cellulosic versus non-cellulosic, pectolytic versus

Table 1.1 Showing the similar product of both endophyte and plant origin

Name of the metabolite	Plant/plant part	Microorganisms	References
Azadirachtin A	*Azadirachta indica* A. Juss	*Eupenicillium parvum*by	Kusari et al. (2012)
Camptothecine (CPT)	*Miquelia dentata* Bedd.	Endophytic bacteria	Shweta et al. (2013a)
Rohitukine	*Dysoxylum binectariferum* Hook.f	*Fusarium proliferatum* (MTCC 9690)	Kumara et al. (2012)
Paclitaxel (taxol®)	*Taxus brevifolia*	*Taxomyces andreanae*	Stierle et al. (1993)
Plant-derived bioactive compounds	–	Endophytic fungi	Zhao et al. (2011)
CPT, 9-methoxy CPT (9-MeO-CPT) and 10-hydroxy CPT (10-OH-CPT)	*Miquelia dentata* (Icacinaceae)	*Fomitopsis* sp. P. *Karst* (MTCC 10177), *Alternaria alternata* (Fr.)	Shweta et al. (2013b)
		Keissl (MTCC 5477) and *Phomposis* sp. (Sacc.)	
Taxol	*Taxus brevifolia*	*Taxomyces andreanae*	Stierle et al. (1993)
Camptothecin	*Nothapodytes foetida*	*Entrophospora infrequens*	Puri et al. (2005)

(continued)

Table 1.1 (continued)

Name of the metabolite	Plant/plant part	Microorganisms	References
Camptothecin	*Apodytes dimidiate*	*Fusarium solani*	Shweta et al. (2010)
Podophyllotoxin	*Sinopodophyllum hexandrum*	*Alternaria* sp.	Trivedi et al. (1970)
Podophyllotoxin	*Sabina recurva*	*Fusarium oxysporum*	Kour et al. (2007)
Vinblastine	*Catharanthus roseus*	*Alternaria* sp.	Li et al. (2004)
Vincristine	*Catharanthus roseus*	*Fusarium oxysporum*	Wang et al. (2006)
Hypericin	*Hypericum perforatum*	*Chaetomium globosum*	Kusari et al. (2008)
Diosgenin	*Paris polyphylla var. yunnanensis*	*Cephalosporium* sp.	Jin et al. (2004)
Azadirachtin	*Azadirachta indica*	*Eupenicillium parvum*	Kusari et al. (2011)

non-pectolytic as well as in tissues having various deposits. Screening of endophytic microbes for biologically active metabolites with promising medicinal and agricultural application may provide a suitable outcome from endophytes association as discussed in present volume.

1.7 Are Endophytes Remediating Pollutants in Ecosystems?

Most studies of wood-decaying fungi are based on advanced stages of wood degradation. However, some endophytic fungi could be involved in triggering the development of early stages of wood decay. In nature, endophytes inhabit asymptomatic plant tissues, living in symbiosis with their hosts. Thus it becomes necessary to explore the role of wood-inhabiting fungi and study their ligninolytic mechanistic strategies so as to exploit as alternative for degrading lignin or other recalcitrant compounds hazardous to environment. Technological application of these fungi could improve current technological performance of bioconversion processes as reviewed in Chap. 7.

Although phyto-extraction process affect many advantage to remediate heavy metal contaminated soil but it has several demerits mainly the process is economically non-viable (Succuro et al. 2009). The addition of microorganisms in the plant rhizosphere is an established route to make the process more efficient. The microbial inducer improvement in the accumulation of the heavy metals in plant biomass are always coincident with enhances net phytoextraction (Pajuelo et al. 2007). Microbes in general and fungi in particular clean up environment and proved potential source for biodegradation of organic pollutant. Various genera of endophytic fungi developed a variety of tolerant mechanism toward host metabolites in order to increase their adaptability in environment and interconnection between different organisms further augment bioremediation potential of endophyte fungi in the management of toxic pollutant has suitably given in Chap. 8.

1.8 Factors Affecting Endophytic Colonization

Endophytic microbial colonization affecting by mass factors such as (a) temporary chilling of plant increases the release of amino acid from roots in sand soil (b) exudation induce under high intensity of light (capture by endophyte plant) and temperature (c) secondary metabolites of certain bacteria cause increase and in the presence of competitive synergative rhizobia; polygalactouronase is released from the roots resulting increase in polypeptide antibiotics thus increase the substantial leakage of both organic and inorganic compounds (Swamy et al. 2016). Root exudates are, therefore, bears induction of chemotaxis in bacteria towards the roots and the simultaneous conditioning of bacterial cells for host cell attachment. Thus, it is hypothesized that the capability of bacteria to condition for (plant) host cell attachment during chemotaxis is one of the most important factors for pathogenicity or colonization efficiency.

1.9 Conclusion and Suggestions

Endophytes in plants play significant role in microbial ecology, evolutionary biology, applied life sciences ranging from bioprospecting for genes and molecules to lead productivity enhancement and biocontrol for wide array of crop fungal pathogens. They are expected to control both endophytic fungi and epibiotic to other microorganisms of endophytic species as tools to manage plants disease, reproductive biology of plants. Biocatalysis and other biotechnological processes, new technologies and new crops with endophytes still have many areas open for future research. After consideration of all the chapters included in the present volume, some of the points have been summarized with few more interesting aspects being highlighted. More research on endophytes, yet to be cultivated on artificial culture media are required. This will be possible when a better knowledge of endophyte ecology and molecular interactions is attained.

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Chapter 2
Plant Growth Promotion by Endophytic Bacteria in Nonnative Crop Hosts

Akshit Puri, Kiran Preet Padda and Chris P. Chanway

Abstract Studies highlighting the colonization and plant growth-promoting ability of endophytic bacteria inoculated into nonnative plant hosts reviewed and presented in this chapter. Endophytic bacteria, especially those related to the genus *Bacillus*, *Burkholderia*, *Enterobacter*, *Gluconacetobacter*, *Herbaspirillum*, *Paenibacillus*, *Pseudomonas* have been reported to form endophytic colonies in roots and shoot of nonnative plant hosts. Marker genes like green fluorescent protein have also been used widely to view the sites of colonization in real time. Apart from colonizing a nonnative plant host, these endophytic bacteria are also involved in promoting host plant growth and acting as a biocontrol agent against pathogenic fungi. Such endophytes have a great potential in future for sustainable agriculture since they could be used in a range of environmental and biological conditions.

Keywords Endophytic bacteria · Nonnative crop hosts · Biological nitrogen fixation · Plant growth promoting bacteria · Diazotrophic endophytes

2.1 Introduction

When one considers both the expected worldwide population increase and the increasing environmental damage that is a result of ever-greater levels of industrialization, it is clear that in the next 10–20 years it will be a significant challenge to feed all of the world's people, a problem that will only increase with time. According to a report released by the United Nations in 2015, the world's population is set to rise to 9.7 billion by 2050 (United Nations 2015). Sadly, the threat of

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having inadequate food to feed all of the world's population in future is again in the news. At this point, our world is experiencing a variety of problems like climate change, food wastage, spoilage on an enormous scale, unequal distribution of food resources, and continuously growing population. There is certainly no time to lose and the world needs to act to feed this growing population. Although it is quite tempting to use chemical fertilizers to boost up the agricultural productivity, such a solution will have a detrimental effect on our environment. Agricultural scientists around the world are working round the clock to look for innovative ways to increase agricultural productivity sustainably, but it certainly represents a great challenge for them. The use of microorganisms with the objective of improving agricultural productivity is one of the most important sustainable practices (Freitas et al. 2007).

The soil is full of microscopic life including a diverse range of bacteria, fungi, protozoa, and algae. It is estimated that there are more than 94 million organisms in a single gram of soil, with most of them being bacteria (Glick 2015). The interaction between bacteria and plants could be beneficial, neutral, or detrimental to the plant. However, the effect that a particular bacterium has on a plant may change as the conditions change. For instance, a bacterium that facilitates plant growth by providing either fixed nitrogen (N) or phosphorus compounds that are often present in only limited amounts in many soils is unlikely to provide any benefit to plants when a significant amount of chemical fertilizer added to the soil (Glick 2012). This observed when a bacterial strain of *Paenibacillus polymyxa* (Bal et al. 2012) was inoculated into lodgepole pine (*Pinus contorta* var. *latifolia* Engelm. ex S. Watson). The bacterial strain fixed significant amounts of N directly from the atmosphere under N-limited conditions (Anand et al. 2013), but was unresponsive when sufficient amount of N was present in the soil (Yang et al. 2016, 2017).

2.2 Plant Growth-Promoting Bacteria (PGPB): Biofertilizers for Sustainable Agriculture

Bacteria that are able to provide a range of benefits to the plant also known as plant growth-promoting bacteria (PGPB). Bashan and Holguin (1998) proposed the term PGPB in the field of plant-microbe interactions. These bacteria are capable to affect plant growth via numerous independent or linked mechanisms for sustainable agriculture (Compant et al. 2010; Palacios et al. 2014). They counteract many stresses in plants (Kang et al. 2010; Kim et al. 2012), fighting against phytopathogens (Verhagen et al. 2004; Raaijmakers et al. 2009) and assisting in the recovery of damaged or degraded environments (Denton 2007; de Bashan et al. 2012). Nowadays, PGPBs are of great interest because of their applications in agriculture as biofertilizers, pesticides, and phytoremediation (Sturz et al. 2000; Berg 2009; Lugtenberg and Kamilova 2009; Weyens et al. 2009; Compant et al. 2010). Classification of PGPB based on their habitable niche presented in Fig. 2.1.

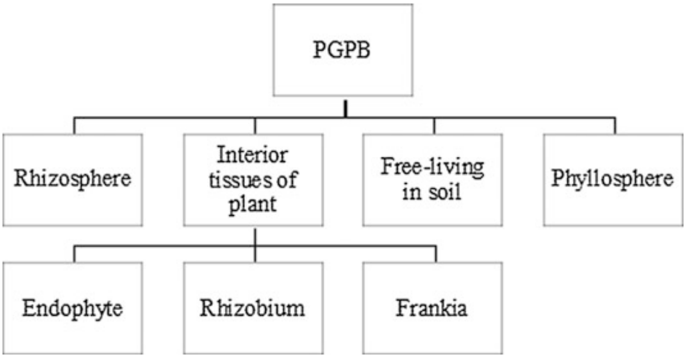

Fig. 2.1 Classification of plant growth-promoting bacteria (PGPB) based on their habitable niches

The rhizosphere is well explained and known to host a diversity of PGPB from more than 20 genera, including *Pseudomonas*, *Bacillus*, *Burkholderia*, *Enterobacter*, *Paenibacillus*, *Azospirillum*, *Agrobacterium*, and *Azotobacter*. Several bacteria deriving from the rhizosphere not only colonize the rhizoplane but can also enter plants and colonize internal tissues and many of them have shown plant growth-promoting effects (Hallmann 2001; Sessitsch et al. 2004; Compant et al. 2005, 2008, 2010; Hallmann and Berg 2006; Anand et al. 2013; Puri et al. 2015; Padda et al. 2016a, b). Often not considered as PGPB, cyanobacteria are also renowned for their ability to promote plant growth indirectly by fixing carbon through oxygen photosynthesis and N through biological nitrogen fixation. They can survive in diverse ecological niches including but not limited to phyllosphere (Fürnkranz et al. 2008; Hamisi et al. 2013), rhizosphere (Karthikeyan et al. 2009; Prasanna et al. 2009) and plant interior (Tyagi et al. 1980; Krings et al. 2009).

2.3 Endophytic Bacteria: Microbial Life Inside the Plant

About 150 years ago the term, “endophyte” was first coined by de Bary (1866) for pathogenic fungi entering inside leaves. Since then, many authors have been redefining this term, but taken literally, the word endophyte means “in the plant” (endon = within; phyton = plant). Galippe (1887) was the first scientist to postulate that various vegetable plants host microbes within their interior and these microbes are soil habitant. This was later confirmed by di Vestea (1888), but well-known scientists at that time such as Pasteur, Chamberland, Fernbach, Laurent, and others claimed that plants are normally free of microbes and they indeed demonstrated contradictory results to prove that Galippe’s hypothesis is wrong (Compant et al. 2010). However, it is now well accepted that plants generally host a wide range of phylogenetically distinct endophytes in various organs (Bacon and White 2000), and that almost all of these microbes are derived from the soil environment (Rosenblueth and Martínez-Romero 2006; Hardoim et al. 2008; Ryan et al. 2008; Compant et al. 2010).

Since this chapter has key focus on endophytic bacteria, the term needs to redefine before starting a new discussion. Numerous definitions of the term "Endophytic Bacteria" could be found in the literature (Kado 1992; Quispel 1992; Beattie and Lindow 1995; Hallmann et al. 1997), but each has its own restrictions. In this chapter, we use the term "Endophytic Bacteria" to describe "the bacteria that can be detected at a particular moment within the tissue of apparently healthy plant hosts without inducing disease or organogenesis" (Chanway et al. 2014). It is believed that via rhizosphere colonization, endophytic bacteria become colonize in various plant parts/tissues such as roots, stem, leaves, flowers, fruits, and seeds (James et al. 2002; Sessitsch et al. 2002; Berg et al. 2005; Compant et al. 2005, 2008, 2011; Okunishi et al. 2005; Bal et al. 2012; de Melo Pereira et al. 2012; Anand and Chanway 2013a; Trognitz et al. 2014; Puri et al. 2015, 2016a, b). Endophytic bacterial population is extremely variable in different plant organs and tissues shown to vary in from as low as hundreds to as high as 9×10^9 of bacteria per gram plant tissue (Jacobs et al. 1985; Misaghi and Donndelinger 1990; Sturz et al. 1997; Hallmann et al. 1997; Chi et al. 2005; Padda et al. 2016a, b). In contrast to free-living, rhizosphere or phyllosphere microorganisms, bacterial endophytes are better protected from abiotic stresses such as extreme variations in temperature, pH, nutrient, and water availability as well as biotic stresses such as competition (Loper et al. 1985; Cocking 2003; Rosenblueth and Martinez-Romero 2006). In addition, endophytic bacteria colonize niches that are more conducive to forming mutualistic relationships with plants (Richardson et al. 2009), for example providing fixed N to the plant and getting photosynthate in return (Hallman et al. 1997; Reinhold-Hurek and Hurek 1998a, b; Santi et al. 2013). Primary mechanisms by which endophytic bacteria promotes plant growth are highlighted in Fig. 2.2.

2.3.1 *Diazotrophic Endophytes: Biological N-Fixers Living Inside the Plant*

For plants, N is an essential mineral required to survive and grow. It is a primary constituent of nucleotides, proteins, and chlorophyll (Robertson and Vitousek 2009). The availability of fixed N (nitrate or ammonium converted from dinitrogen) is seen by many as the most yield-limiting factor related to crop production (Muthukumarasamy et al. 2002). Although N is found in high abundance in the atmosphere, biologically available N in terrestrial ecosystems is in short supply. Root-nodulating bacteria, such as well-known rhizobia form a symbiotic association and provide biologically fixed N directly to leguminous plants. However, nonleguminous plants, including economically important crop species belonging to Poaceae family like sugarcane (*Saccharum officinarum* L.), corn (*Zea mays* L.),

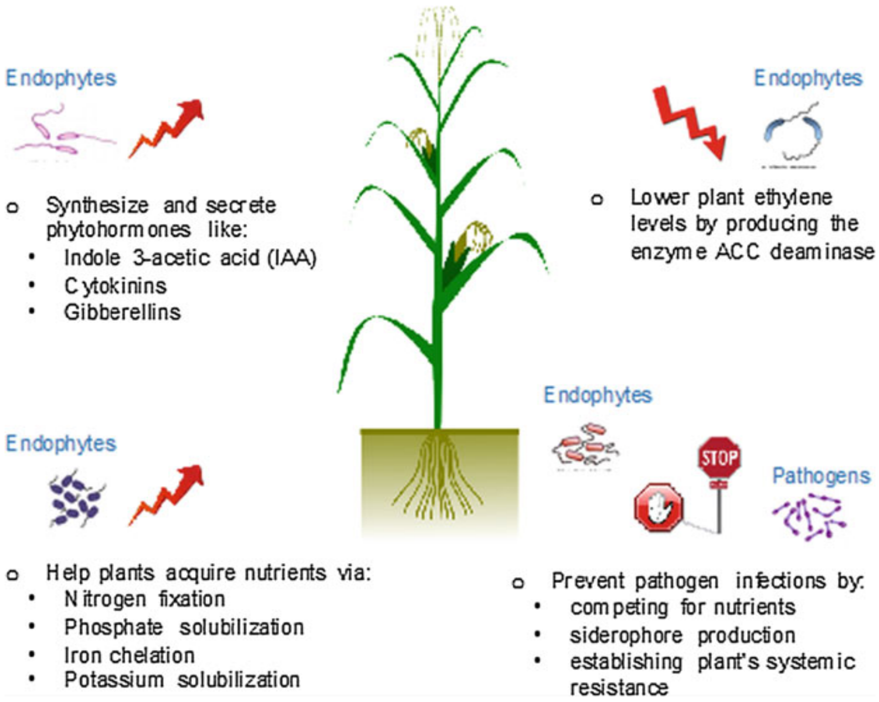

Fig. 2.2 Principal mechanisms of plant growth promotion exhibited by endophytic bacteria

wheat (*Triticum* spp.), and rice (*Oryza sativa*), do not have this type of symbiosis. Brazilian researchers were the first to report the presence of N-fixing bacteria (diazotrophs) in the rhizosphere and rhizoplane of a nonleguminous plant, sugarcane (Döbereiner and Alvahydo 1959; Döbereiner 1961). Initially, it was postulated that nitrogenase activity occurs in the rhizosphere soil but not in roots (Döbereiner et al. 1972; Ruschel 1981). In subsequent studies, various diazotrophs like *Azospirillum lipoferum*, *Azospirillum amazonense*, *Bacillus azotofixans*, *Enterobacter cloacae*, *Erwinia herbicola*, *Bacillus polymyxa* (Rennie et al. 1982; Magalhaes et al. 1983; Seldin et al. 1984; Baldani et al. 1986) were isolated from the rhizosphere of sugarcane. Later, it was determined that rhizospheric N-fixation does not occur at sufficient rates to facilitate high sugarcane yields. Cavalcante and Döbereiner (1988) reported the isolation of a diazotrophic bacterium from the stem and root tissues of sugarcane and postulated that this bacterium might be involved in fixing high amounts of N biologically. The isolated diazotroph was initially named as *Saccharobacter nitrocaptans* (Cavalcante and Döbereiner 1988) but was later changed to *Acetobacter diazotrophicus* (Gillis et al. 1989) and then renamed as *Gluconacetobacter diazotrophicus* (Yamada et al. 1997). This bacterium was able to form high endophytic populations and fix N at high sucrose concentrations (Boddey et al. 1991) and in low pH conditions (Boddey et al. 1991; Stephan et al.

1991) and these conditions are typically found in sugarcane tissues. This led to the suggestion that it can satisfy almost all of the sugarcane N requirements while living inside the sugarcane tissues. The term “endophytic diazotrophic bacteria“ was then coined by Döbereiner (1992) to designate all diazotrophs able to colonize primarily the root interior of graminaceous plants, survive very poorly in soil and fix N in association with these plants (Baldani et al. 1998). Since the discovery of endophytic diazotrophic bacteria in sugarcane, other agronomically important crop species including rice (Baldani et al. 2000; Gyaneshwar et al. 2001; Hurek et al. 2002), corn (Olivares et al. 1996; Riggs et al. 2001; Roesch et al. 2008; Montañez et al. 2009; Puri et al. 2015, 2016b), canola (*Brassica napus* L.) (Germida and de Freitas 1998; Puri et al. 2016a; Padda et al. 2016a, b) and wheat (Sabry et al. 1997) have been postulated to receive significant amounts of fixed N in this way. Table 2.1 presents a brief list of prominent diazotrophic endophytes isolated from key agricultural crops.

Table 2.1 Prominent diazotrophic bacteria isolated from different crop species

Crop	Diazotrophic endophytes	References
Canola	*Bacillus polymyxa*	Germida and de Freitas (1998)
	Paenibacillus polymxa	Padda et al. (2016a, b), Puri et al. (2016a)
Corn	*Burkholderia tropica* sp.	Reis et al. (2004)
	Burkholderia silvatlantica sp.	Perin et al. (2006)
	Gluconacetobacter diazotrophicus	Eskin (2012)
	Herbaspirillum spp.	Olivares et al. (1996), Roesch et al. (2008)
	Ideonella spp.	Roesch et al. (2008)
	Klebsiella pneumoniae	Palus et al. (1996), Chelius and Triplett (2000)
	Paenibacillus polymyxa	Puri et al. (2015, 2016b)
	Pseudomonas spp.	Montañez et al. (2009)
Rice	*Alcaligenes faecalis* [now known as *Pseudomonas stutzeri* (Vermeiren et al. 1999)]	You and Zhou (1989)
	Azoarcus spp.	Egener et al. (1999), Engelhard et al. (2000), Hurek et al. (2002)
	Burkholderia spp.	Baldani et al. (2000), Rangjaroen et al. (2015)
	Herbaspirillum spp.	Baldani et al. (2000), Elbeltagy et al. (2001)
	Klebsiella sp.	Rangjaroen et al. (2015)
	Serratia marcescens	Gyaneshwar et al. (2001)
Sugarcane	*Azoarcus* spp.	Reinhold-Hurek et al. (1993)
	Azospirillum brasilense	Carrizo de Bellone and Bellone (2006)
	Burkholderia tropica sp.	Reis et al. (2004)

(continued)

Table 2.1 (continued)

Crop	Diazotrophic endophytes	References
	Burkholderia silvatlantica sp.	Perin et al. (2006)
	Herbaspirillum spp.	Baldani et al. (1992, 1996, 2002), Cavalcante and Dobereiner (1988), Muthukumarsamy et al. (1999)
	Gluconacetobacter diazotrophicus	Gillis et al. (1989), Boddey et al. (1991), Stephan et al. (1991), Cavalcante and Dobereiner (1988), Sevilla et al. (2001)
Wheat	*Azorhizobium caulinodans*	Sabry et al. (1997)
	Azospirillum brasilense	Schloter and Hartmann (1998), Rothballer et al. (2003)
	Klebsiella pneumoniae	Iniguez et al. (2004)
	Herbaspirillum hiltneri	Rothballer et al. (2006)

2.4 Foreign Associations: Endophytic Bacteria Promoting the Growth of Nonnative Crop Species

Plants are a complex micro-ecosystem which can only be colonized by foreign microbes having metabolic diversity. Foreign associations of endophytes are not unfamiliar to the scientific community and numerous studies have highlighted the ability of these microbes to associate with a diversity of hosts. Endophytic bacteria can colonize and provide benefits to a variety of foreign plant hosts ranging from monocots to dicots, gymnosperms to angiosperms and woody trees to herbaceous plants. Although the list of these endophytes is very long and include genera such as *Acetobacter, Arthrobacter*, *Azoarcus*, *Azospirillum*, *Bacillus*, *Bradyrhizobium*, *Burkholderia*, *Enterobacter*, *Flavobacterium*, *Frankia*, *Gluconacetobacter*, *Herbaspirillum*, *Paenibacillus*, *Pseudomonas*, *Rhizobacter*, *Rhizobium*, *Sinorhizobium*, *Streptomyces*, and *Xanthomonas*, only a few important ones have been discussed in this chapter. A brief informative list of key endophytes that have been reported to play an important role in growth promotion of nonnative hosts through direct or indirect mechanisms has been compiled in Table 2.2. In the sub-sections to follow, studies relating to endophytic colonization and plant growth promotion by six of the most important bacterial endophytes reported in foreign plant host species have been reviewed in detail.

2.4.1 *Arthrobacter*

In 1947, Conn and Dimmick established a new genus "*Arthrobacter*" in the world of Microbiology (Conn and Dimmick 1947). By far more than 70 species have been included in this genus (Fu et al. 2014). Bacterial species belonging to this genus are

Table 2.2 List of important endophytic bacteria reported to colonize and promote growth of nonnative plant hosts

Genus	Strain	Isolated from	Inoculated into	Benefits provided to the nonnative host
Arthrobacter	*A. humicola* YC6002	Korean turf grass (Chung et al. 2010)	Radish (Chung et al. 2010)	Weed management
Azoarcus	*A.* sp. BH72	Kallar grass (Reinhold-Hurek et al. 1993)	Rice (Hurek et al. 1994)	Increases biomass and total protein
Bacillus	*B. subtilis* EDR4	Wheat (Qiao et al. 2006)	Rapeseed (Chen et al. 2014)	Biocontrol against pathogenic fungus
	B. licheniformis CHM1	Rice (Wang et al. 2009a)	Cole (Wang et al. 2009a)	Increases fresh weight and chlorophyll content
	B. subtilis FL and *B. atrophaeus* NRRLNRS-213	Japanese honeysuckle (Zhao et al. 2015)	Wheat (Zhao et al. 2015)	Increases seedling biomass and length
	B. subtilis EPC8	Coconut (Rajendran et al. 2008)	Tomato (Prabhukarthikeyan et al. 2014)	Increases plant length and fruit yield
Burkholderia	*B. gladioli* 3A12	Corn (Shehata et al. 2016)	Creeping bentgrass (Shehata et al. 2016)	Biocontrol against common crop pathogens
	B. cenocepacia 869T2	Vetiver grass (Ho et al. 2015)	Banana (Ho et al. 2015)	Biocontrol against fungus that causes Panama disease of Banana
	B. phytofirmans PsJN	Onion (Frommel et al. 1991)	Potato (Frommel et al. 1991)	Enhances root growth and plant lignin content
			Potato (Frommel et al. 1993)	Enhances root growth and overall yields
			Grapevine (Compant et al. 2005, 2008)	Increases seedling length and fresh weight

(continued)

Table 2.2 (continued)

Genus	Strain	Isolated from	Inoculated into	Benefits provided to the nonnative host
Enterobacter	*E. asburiae* JM22	Cotton (McInroy and Kloepper 1995)	Cucumber and bean (Quadt-Hallmann and Kloepper 1996)	–
	E. sp. strain 35	Sugarcane (Tanaka et al. 2006)	Cultivated rice and wild rice (Zakria et al. 2008)	Nitrogen fixation
	E. cloacae 344	Cacao tree (Leite et al. 2013)	Cucumber, corn, common beans (Moreira et al. 2015)	–
Gluconacetobacter	*G. diazotrophicus* spp.	Sugarcane (Youssef et al. 2004)	Wheat (Youssef et al. 2004)	Nitrogen fixation
	G. diazotrophicus PAL5	Sugarcane (Bertalan et al. 2009)	Rice (Alquéres et al. 2013)	–
			Rice (Rouws et al. 2010)	–
			Arabidopsis thaliana (Rangel de Souza et al. 2016)	Increases photosynthetic rate and water-use efficiency
	Acetobacter diazotrophicus (now known as *G. diazotrophicus*) PA15	Sugarcane (Gillis et al. 1989)	Rice (Sevilla and Kennedy 2000)	Increases plant height in N-limited conditions
Herbaspirillum	*H. seropedicae* strains ZAE94 and ZAE67	Sorghum (Baldani et al. 1986)	Rice (Baldani et al. 2000)	Fixes nitrogen and increases biomass
	H. seropedicae strain LR15	Corn (Baldani et al. 1986)	Corn, sorghum, rice (Roncato-Maccari et al. 2003)	Nitrogen fixation
	H. frisingense strain GSF30^T	*Miscanthus sacchariflorus* (Kirchhof et al. 2001)	Barley (Rothballer et al. 2008)	IAA production and ACC utilization

(continued)