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.

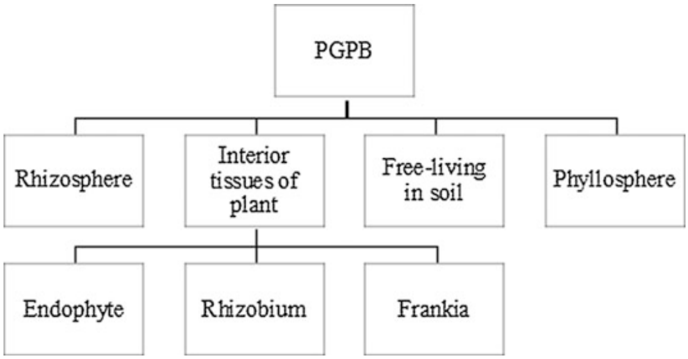

Fig. 2.1 Classification of plant growth-promoting bacteria (PGPB) based on their habitable niches

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.),

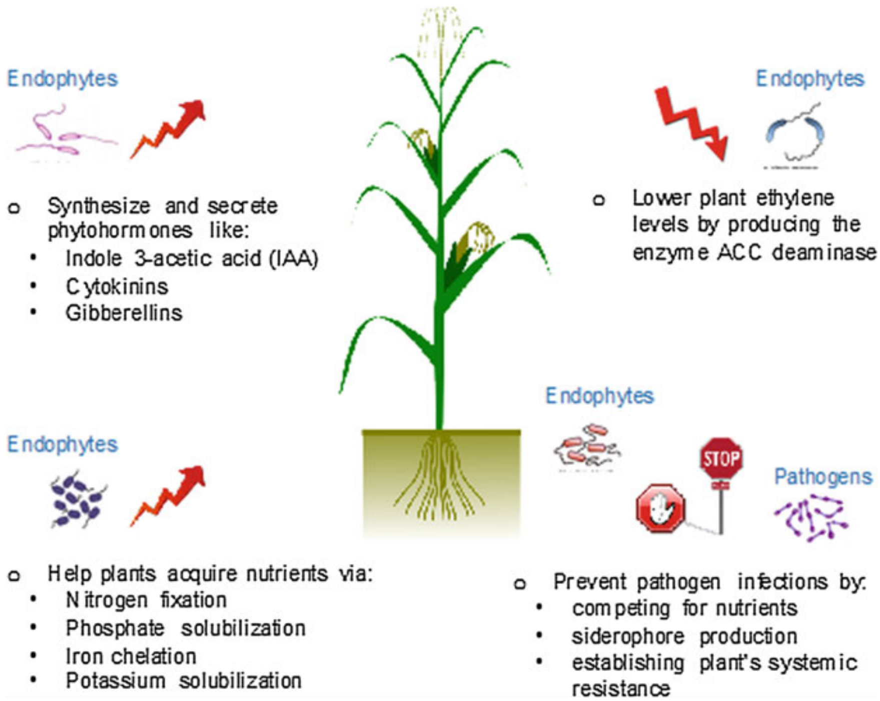

Fig. 2.2 Principal mechanisms of plant growth promotion exhibited by endophytic bacteria

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)

Table 2.2 (continued)

Genus	Strain	Isolated from	Inoculated into	Benefits provided to the nonnative host
Paenibacillus	*P. polymyxa* strains 1D6, 4G12 and 4G4	Wild maize (teosinte) (Johnston-Monje and Raizada 2011)	Modern maize (corn) hybrid (P35F40) (Mousa et al. 2015)	Reduce Gibberella ear rot disease severity
	P. polymyxa IAM 13419 and *P. ehimensis* IFO15659	Japanese honeysuckle (Zhao et al. 2015)	Wheat (Zhao et al. 2015)	Increase seedling length, biomass and chlorophyll content
	P. polymyxa P2b-2R	Lodgepole pine (Bal et al. 2012)	Corn (Puri et al. 2015, 2016b)	Fixes nitrogen and increases seedling length and biomass
			Canola (Puri et al. 2016a; Padda et al. 2016a, b)	
			Tomato (Padda et al. 2016a)	
Pseudomonas	*P.* sp. Ph6	Clover (Sun et al. 2014)	Ryegrass (Sun et al. 2014)	Degrades phenanthrene, a toxic metabolite that enters plant
	P. aeruginosa PM389	Pearl millet (Gupta et al. 2013)	Wheat (Gupta et al. 2013)	Increases root and shoot length and vigor index
	P. brassicacearum YC5480	*Artemisia* sp. (Chung et al. 2008)	Radish (Chung et al. 2008)	Counteracts inhibitory effect of a pathogenic fungus on seed germination and shoot growth
	P. aeruginosa PW09	Wheat (Pandey et al. 2012)	Cucumber (Pandey et al. 2012)	Increases seedling biomass under biotic and abiotic stresses

Gram-positive obligate aerobes commonly found in soils. They are rod-shaped during the stationary growth phase and cocci-shaped during stationary phase. Members of *Arthrobacter* genus can survive in a variety of environmental conditions, including but not limited to water, air, human skin, oil, sludge, tobacco leaves, soil (Ding et al. 2013; Fu et al. 2014). Studies have shown that members of this genus can be helpful in many ways in agriculture. For instance, they fix atmospheric N, solubilize sulfur and phosphorous in soil and degrade heavy metals in polluted sites (Singer et al. 2000; Jiang et al. 2004; Postma et al. 2010). One of the most important aspects of plant growth promotion is deriving N from the atmosphere. *Arthrobacter* sp. HS-G8 was isolated from compost in Japan's Okinawa prefecture that possessed N-fixing ability (Jiang et al. 2004). In another study, two endophytic strains, *Arthrobacter nitroguajacolicus* A18 and A34, originally isolated from corn leaves possess nitrogenase reductase gene *nif*H indicating that these strains could fix atmospheric N (Pisarska and Pietr 2012). These strains successfully colonized and fixed N in different cultivars of corn thereby promoting the growth of a nonnative host (Pisarska and Pietr 2012). An endophytic bacterial strain, *Arthrobacter humicola* YC6002, from surface-sterilized root tissues of Korean turf grass (*Zoysia japonica*) reported by Chung et al. (2010). This bacterial endophyte successfully colonized internal tissues of a nonnative host, radish (*Raphanus sativus*), and could be used in future for weed management due to its ability to produce phytotoxic compounds like 3-phenylpropionic acid (Chung et al. 2010).

2.4.2 *Bacillus*

The history of genus *Bacillus* dates back to 1835 when Christian Gottfried Ehrenberg isolated a bacterium (*Vibrio subtilis*, now known as *Bacillus subtilis*) belonging to this genus (Ehrenberg 1835). Later, in 1872, Ferdinand Cohn proposed a new genus "*Bacillus*" and renamed *Vibrio subtilis* to *Bacillus subtilis* (Cohn 1872). Bacteria of this genus are Gram-positive, endospore-forming and rod-shaped that could be either obligate aerobes or facultative anaerobes. Genus *Bacillus* is one of the most diverse group of bacteria that is well known for its many agricultural and industrial applications. In agriculture, bacteria of this genus are widely used as an effective biocontrol agent for numerous crop species. The commercial success of *Bacillus thuringiensis* exemplified as a biocontrol agent worldwide. Other bacterial isolates of this genus having biocontrol and plant growth-promoting (PGP) properties have also been widely studied and successfully used commercially in agriculture. Endophytic colonization in plant species by bacteria has also been reported (Wang et al. 2009b; Lee et al. 2012; Liu et al. 2014; Khalifa and Almalki 2015). Biocontrol of pathogens like *Sclerotinia sclerotiorum*, *Fusarium oxysporum*, *Rhizoctonia solani*, *Botrytis cinereapers*, *Gibberella zeae*, *Dothiorella gregaria*, *Colletotrichum gossypii*, *Phytophthora capsici*, *Pythium myriotylum*, *Athelia rolfsii*, *Magnaporthe oryzae*, *Ralstonia solanacearum, and*

Xanthomonas axonopodis pv. *punicae* by *Bacillus* in non-native plants has been reported over the years (Maheshwari 2013).

Stem rot disease of rapeseed (*Brassica napus* L.), caused by a pathogenic fungus *Sclerotinia sclerotiorum*, is a major problem faced worldwide by many countries. Chen et al. (2014) tested the ability of an endophyte, *B. subtilis* EDR4, to inhibit the growth of this pathogen in vitro and in vivo in rapeseed under greenhouse and field conditions. *B. subtilis* EDR4 was initially isolated from root tissues of wheat (Qiao et al. 2006) and subsequently reported to inhibit the growth of the fungal pathogen, *Gaeumannomyces graminis* var. *tritici*, of wheat (Liu et al. 2007). In the in vitro experiments, germination rate and hyphal growth of *S. sclerotiorum* were significantly inhibited by *B. subtilis* EDR4 and the results of in vivo experiment conducted under greenhouse and field conditions were no different. Scanning electron microscopy revealed that EDR4 causes leakage in the cytoplasm, shrinking of hyphae and irregular swelling of tips of the fungus. In another study related to *Brassica napus*, an endophytic strain *B. licheniformis* CHM1 was isolated from stem tissues of rice and tested for biocontrol activity and plant growth promotion in cole (*Brassica napus*) (Wang et al. 2009a). Strain CHM1 colonized stem/leaf tissues and significantly promoted the growth of cole seedlings (increasing the fresh weight of seedlings by 72% and chlorophyll content by 61%). This bacterial strain also inhibited the growth of common fungal pathogens like *F. oxysporum*, *R. solani*, *B. cinereapers*, *D. gregaria*, *G. zeae* and *C. gossypii* in in vitro experiments. In in vivo experiments, it provided 60% protection against *R. solani* in horse bean (*Vicia faba*) and 70% protection against *Bipolaris maydis* in corn. In a more recent study, wheat plant growth was significantly promoted by two endophytic strains (135 and 170) belonging to the genus *Bacillus*, isolated from stem and root tissues of a medicinal plant, *Lonicera japonica*, native to eastern China (Zhao et al. 2015). In in vitro experiments, it was found that these two strains possess many PGP traits that could increase wheat growth. Results of in vivo experiment were consistent with results of in vitro experiment since inoculation with these strains significantly increases fresh weight, dry weight and length of wheat seedlings along with the chlorophyll content. These strains also showed in vitro antifungal activity against common pathogenic fungi like *Magnaporthe grisea* (rice blast fungus), *F. oxysporum* (usually affects wheat and rice crops) and *Alternaria alternate* (causes leaf spot disease). Based on the results of physiological and biochemical tests, and the sequencing of 16S rRNA gene and phylogeny analysis, it was revealed that strains *Bacillus* spp. 135 and 170 are very closely related to *B. subtilis* FL and *B. atrophaeus* NRRLNRS-213^{T}, respectively. This study was also important in establishing the fact that strains belonging to genus *Bacillus* are potentially capable of colonizing and promoting the growth of a completely distinct host (wheat, a monocot) as compared to the host species from which it was isolated (*Lonicera japonica*, a eudicot).

In a completely different approach to combat with pathogens and increase plant yield, Prabhukarthikeyan et al. (2014) used a bioformulation containing a mixture of an entomopathogenic fungus, *Beauveria bassiana* B2, known for its ability to control a wide range of agriculturally important insect pests and an endophytic strain of *B. subtilis* (EPC8) against *Fusarium* wilt (*F. oxysporum* f. sp. *lycopersici*) and fruit borer (*Helicoverpa armigera*) disease in tomato (*Solanum lycopersicum* Mill.). It should be noted that *B. subtilis* EPC8 was initially isolated from root tissues of coconut (*Cocos nucifera*) (Rajendran et al. 2008). Bioformulation of B2 and EPC8 suppressed these pathogens in in vitro experiments and under glasshouse and field conditions when tomato plants were treated with this mixture. The combination of B2 and EPC8 was better than the pesticide control (carbendazim + quinalphos) against both *Fusarium* wilt and fruit borer in glasshouse study and was equally good in field conditions. Interestingly, it was also observed that such bioformulation promotes tomato growth by increasing the plant height and fruit yield under both glasshouse and field conditions. Recently, Munjal et al. (2016) reported that an endophytic biocontrol agent, *Bacillus megaterium* BP17, initially isolated from root tissues of black pepper (*Piper nigrum*) (Aravind et al. 2009) can colonize ginger plant (*Zingiber officinale*). Ginger roots were successfully colonized by this bacterial strain with population size ranging from 2.5 to 2.8 $\log_{10}$ cfu/g. It was also reported that this bacterial strain is capable of releasing antimicrobial chemical compounds. In an interesting study, colonization pattern of three nonnative host species by an endophytic *Bacillus* strain under sterile and non-sterile conditions was reported by Moreira et al. (2015). *Bacillus amyloliquefaciens* 629 was initially isolated from *Theobroma cacao* (Leite et al. 2013) and was inoculated into three distinct host species namely, cucumber (*Cucumis sativus* cv. Marketmore 76), corn (cv. BRS Caatingueiro) and common bean (*Phaseolus vulgaris* cv. BRS Notável). Strain 629 successfully colonized stem and leaf tissues of cucumber, root and stem tissues of common bean, and root, stem and leaf tissues of corn plant under both sterile and non-sterile conditions significantly. It is important to note that the population size of endophytic bacteria was 3 times lower under non-sterile conditions in all plant species as compared to the sterile conditions. It could be concluded that indigenous endophytic bacteria and fungi pose a competition to the nonindigenous endophytes. Thus, the foreign association and establishment of an endophyte within a nonnative host is a formidable task.

2.4.3 Burkholderia

The genus '*Burkholderia*' was first proposed by Yabuuchi et al. (1992) for the RNA homology group II of *Pseudomonas* genus. Seven species of this group were transferred to the new genus *Burkholderia* and renamed as *B. caryophylli*, *B. cepacia*, *B. gladioli*, *B. mallei*, *B. pickettii*, *B. pseudomallei,* and *B. solanacearum*. Currently, there are close to 100 species in this genus that are known to inhabit diverse ecological niches, ranging from contaminated soils to the respiratory tract of humans. *Burkholderia* species are renowned for their ability to promote plant growth through various mechanisms including, N-fixation (Gillis et al. 1995; Cruz et al. 2001; Estrada-De Los Santos et al. 2001) and biocontrol of pathogens (Hebbar et al. 1998; Heungens and Parke 2000; Parke and Gurian-Sherman 2001). The majority of species are soil bacteria that are generally found in the rhizosphere or as free-living microbes in the soil but there are some species that can colonize internal tissues of plants and form beneficial interactions (Caballero-Mellado et al. 2004; Pandey et al. 2005; Park et al. 2005; Mendes et al. 2007; Ho et al. 2015). The interactions of some endophytic species of *Burkholderia* genus seem to be restricted to only one type of host, whereas other species have a diverse host range (Coenye and Vandamme 2003).

In a recent study, three strains belonging to the *B. gladioli* species were isolated from roots and seeds of ancient and wild maize plants (Shehata et al. 2016). In vitro studies revealed that these strains can inhibit fungal pathogen *Sclerotinia homoeocarpa* and their interaction was also visualized on microscope slides by staining with Evans blue. These strains were also successful in inhibiting the growth of other common crop pathogens. The ability of these strains to act as a biocontrol against *S. homoeocarpa* was also tested in vivo with creeping bentgrass (*Agrostis stolonifera*) in two greenhouse trials and the results were no different from the in vitro studies. The endophytic ability of one of the strains, *B. gladioli* 3A12, was also tested in a nonnative host, creeping bentgrass, by tagging the strain with green fluorescent protein (GFP) and examining under a confocal microscope. It was found that GFP-tagged 3A12 strain successfully colonized shoots of creeping bentgrass. The authors concluded that wild cultivars of agricultural crops might possess an unexplored reservoir of bacterial endophytes having biocontrol traits against a wide range of pathogens. In a study conducted a few years back, an endophyte, *B. cenocepacia* 869T2, was isolated from root tissues of vetiver grass (*Chrysopogon zizanioides*) (Ho et al. 2015). In vitro, strain 869T2 was able to inhibit the mycelial growth of *Fusarium oxysporum* f. sp. *cubense* tropical race 4 (Foc TR4), a pathogenic fungus that causes Panama disease in banana (*Musa acuminata*), showing 44% antifungal efficiency. When this endophytic strain was inoculated into banana plantlets (Cavendish cv. Pei-Chiao), it developed stable endophytic population in pseudostem tissues, thus showing endophytism in a distinct host. The in-field experiment revealed that inoculation of banana plantlets with strain 869T2 not only reduces the disease symptoms of Foc TR4 but also promotes growth by increasing the plant height and pseudostem girth significantly. This strain of *B. cenocepacia* can be used as an effective biocontrol agent in susceptible banana cultivars. Species of *Burkholderia* MSSP inhabit root nodule of *Mimosa pudica* capable for N fixation along with antagonism against *Rhizoctonia solani,* and *Sclerotinia sclerotiorum* has been reported by Pandey et al. (2005).

A remarkable endophytic bacterial strain (PsJN) was isolated by Dr. Jerzy Nowak as a contaminant from surface-sterilized onion (*Allium cepa* L.) roots infected with fungal pathogen *Glomus vesiculiferum* (Frommel et al. 1991; Sessitsch et al. 2005). This strain has shown outstanding ability over the years to endophytically colonize a wide range of plant hosts. The strain PsJN was initially classified as a *Pseudomonas* sp. (Frommel et al. 1991), but was later reclassified as a *B. phytofirmans* sp. (Sessitsch et al. 2005). Endophytic colonization by PsJN in a nonnative host was first reported in potato (*Solanum tuberosum*) (Frommel et al. 1991). By using light and electron microscopy Frommel et al. also reported that endophytic population of PsJN strain is present in the epidermal layers of root and in the xylem tissues of the stem. They also found that inoculation significantly promotes the growth of potato plantlets by increasing root dry weight, secondary root branching, root number, haulm dry weight, stem length, leaf hair formation, and total lignin content of the plant. They also laid out a preliminary hypothesis that growth promotion by the strain PsJN is due to the production of phytohormones. In a subsequent study (Frommel et al. 1993), the ability of this strain to colonize internal root tissues and promote plant growth in field conditions was reported with the same cultivar of potato as was used in Frommel et al. (1991). In-field, it stimulated plant emergence, root development, and overall yields of the potato plant. Another report about the endophytic colonization of a nonnative host by strain PsJN was published in 1997, in which the effect of inoculum density, temperature, and genotype on colonization and growth promotion of tomato (*Lycopersicon esculentum* L.) seedlings was evaluated (Pillay and Nowak 1997). In this study, the inoculum range that promoted shoot and root interior colonization also best-promoted plant growth of tomato cultivars. Endophytic colonization patterns of strain PsJN were reported for the first time by Compant et al. (2005) inside grapevine (*Vitis Vinifer* L.). The strain PsJN was tagged with GFP or *gusA* and visualized under the desired microscope to examine internal tissue colonization. Colonization of grapevine plantlet started with the bacterial strain gaining entry through the sites of the emergence of lateral root or through the root tips, then accumulating near the cell wall of the rhizodermis cells followed by intercellular colonization of cortical cells. PsJN bacterial cells moved up through the xylem vessels colonizing the fifth internode and leaf internal tissues. It was also observed that the strain PsJN secretes cell wall-degrading enzymes, endoglucanase, and endopolygalacturonase thus supporting the findings of microscopy studies. In a subsequent study with grapevine, GFP-tagged PsJN strain could also be visualized as an endophyte inside young berries (Compant et al. 2008) and was able to thrive inside and outside the plantlet even when grown under non-sterile conditions (with the presence of other microorganisms). Analysis of the complete genome of a microorganism can reveal a lot about its properties and behavior in diverse ecological niches. Although, the complete genome of *B. phytofirmans* PsJN was sequenced and reported earlier (Weilharter et al. 2011), the analysis of the genome was carried out by Mitter et al. (2013). As reported by Mitter et al. PsJN strain in many aspects is outstanding because it has a large genome which is well-equipped with genes that can degrade complex organic compounds (plant cell walls). It also possesses a high number of cell surface signaling and secretion systems and has a 3-OH-PAME quorum-sensing system that might be helping this bacterium to switch from free-living to symbiotic lifestyle. In another interesting study, the ability to fix N was successfully transferred from a known N-fixing bacterium, *B. phymatum* STM 815, to *B. phytofirmans* PsJN through horizontal gene transfer (Lowman et al. 2015). The new strain was named PsJN+, which outperformed the wild-type strain PsJN in terms of promoting the growth of switchgrass plant even under low N conditions. *B. phytofirmans* PsJN is a unique and completely outstanding endophyte that has been shown wide spectrum of endophytic lifestyles in diverse host species ranging from monocots to dicots since its isolation from onion roots (Frommel et al. 1991, 1993; Liu et al. 1995; Pillay and Nowak 1997; Sharma and Nowak 1998; Nowak et al. 2004; Compant et al. 2005, 2008; Sun et al. 2009; Poupin et al. 2013; Naveed et al. 2014a, b) and could be used as an effective commercial biofertilizer in agriculture production.

2.4.4 Gluconacetobacter

The genus *Gluconacetobacter* was proposed by Yamada et al. (1997) in an attempt to reclassify and include the bacterial species *Acetobacter diazotrophicus* into a new genus. Although there are currently 24 species in this genus but the most widely studied species is *Gluconacetobacter diazotrophicus*. *G. diazotrophicus* is a renowned diazotrophic endophyte found frequently in tissues of sugarcane and other grasses, known for its ability to provide significant amounts of N to the plant directly from the atmosphere. Studies about this bacterial species, including earliest isolation, endophytism, and N-fixing trait have already been discussed in Sect. 2.3.1. The studies highlighting the association of this bacteria with diverse host species are discussed here. *A. diazotrophicus* (now known as *G. diazotrophicus*) strain PA15 isolated from sugarcane roots (Gillis et al. 1989) was tagged with three different reporter genes, *uidA*, GFP and *cobA* to evaluate the colonizing ability of this bacterial strain in three different crops namely wheat, corn and rice (Sevilla and Kennedy 2000). Strain PA15 heavily colonized corn kernels, primary root, and root hairs in just two days after inoculation. Rice seeds were not as heavily colonized as corn but lateral roots and root hairs of rice were colonized heavily. Colonization pattern in wheat was similar to rice. Plant growth promotion by strain PA15 was observed only in rice seedlings and was thought to be due to the bacteria's N-fixing ability since mutants of PA15 with *nif* gene removed were not able to promote rice growth. In another study, diazotrophic isolates belonging to the genus *Gluconacetobacter* were isolated from internal tissues of sugarcane growing in ancient agricultural fields of the Nile Delta (Giza) (Youssef et al. 2004). It was observed that these *Gluconacetobacter* spp. were able to form colonies in the stem (xylem vessels) and roots (cortex and vascular cylinder) of 21-day-old wheat seedlings when studied by using scanning electron microscopy. Apart from endophytically colonizing a diverse host species (wheat) these isolates were able to increase the stem and root dry weight significantly, thus increasing the overall plant biomass of wheat. Another study, *G. diazotrophicus* strain PAL5 (Bertalan et al. 2009) isolated from sugarcane was shown to colonize rice shoot and root endophytically with a population size of 10^4 cfu/gm fresh tissue. To visualize the endophytic colonies in rice, this strain was tagged with GFP and observed by using confocal laser microscopy. Microscopy experiment revealed that bacterial cells of PAL5 initially gather near the sites of lateral root emergence and at junctions between root cap and root axis in the vicinity of the apex and then enter the roots through these different openings (Rouws et al. 2010). In a subsequent study, Alquéres et al. (2013) also indicated the endophytic colonization of rice roots by strain PAL5 through GFP-tagging. Secretion of reactive oxygen species (ROS) is a typical defense response activated by the plants in response to a pathogen attack. This study also established that strain PAL5 secrets ROS-scavenging enzymes that play a key role in the endophytic colonization of rice. Further, endophytic colonization pattern of strain PAL5 in *A. thaliana* root was studied by tagging it with a red-fluorescent protein (Rangel de Souza et al. 2016). Inoculation by this strain significantly promoted shoot and root fresh weight, shoot and root dry weight, total leaf area, the number of leaves. Whole canopy gas exchange was also evaluated in this study by using a portable photosynthesis system and the results revealed that inoculation by PAL5 significantly increases net photosynthetic rates, lowers transpiration rate and increases water-use efficiency in *A. thaliana*. These studies clearly establish the ability of *G. diazotrophicus* PAL5 to endophytically colonize a range of plant hosts and promote plant growth through different mechanisms. Although, *G. diazotrophicus* bacterium grows well in high sucrose environments like internal tissues of sugarcane and has been associated most of the time with sugarcane either as an endophyte or as a beneficial rhizospheric microbe, but this bacterium can also endophytically colonize a variety of plant species and promote their growth mainly through N-fixation.

2.4.5 Paenibacillus

The genus *Bacillus* was very heterogeneous containing phylogenetically diverse bacterial species. To reclassify some facultative anaerobes into a new genus (particularly *B. polymyxa* and some of its close relatives; rRNA group 3 of Ash et al. (1991, 1993) created the genus *Paenibacillus* (meaning: almost a *Bacillus*). Bacterial species belonging to this genus are low (mol% G + C contants) in DNA, Gram-positive, neutrophilic, peri-flagellated heterotrophic, endospore-forming facultative anaerobes. There are currently more than 180 species in this genus, most of them discovered within the last decade (http://www.bacterio.net/paenibacillus.html). The type species of this genus, *Paenibacillus polymyxa*, is well known for its ability to fix N (Guemouri-Athmani et al. 2000; Anand et al. 2013; Anand and Chanway 2013b; Bal and Chanway 2012a, b), promote plant growth (Timmusk et al. 1999; Puri et al. 2015; Puri et al. 2016a, b; Padda et al. 2016a, b) and suppress plant pathogens (Dijksterhuis et al. 1999; Ryu et al. 2006; Choi et al. 2007; Haggag and Timmusk 2008; Timmusk et al. 2009). *P. polymyxa* is known to colonize diverse ecological niches like soil, rhizosphere, intercellular and intracellular spaces of plant tissues, marine environments, fermented food products (Lal and Tabacchioni 2009). Endophytic colonization of plant tissues by this bacterial species has been reported time and again by various scientists (Bent and Chanway 1998; Shishido et al. 1999; Chanway et al. 2000; Bal et al. 2012; Pu et al. 2015; Yang et al. 2016; Tang et al. 2017).

An interesting study about the invasion of plant roots and endophytic colonization by *P. polymyxa* suggests that it form biofilms on the surface of the roots to gain entrance into the plant (Timmusk et al. 2009). Biofilms are communities of bacterial cells covered in a self-produced extracellular matrix, that are surface-attached and highly structured (Costerton 1995). GFP-tagging of *P. polymyxa* and visualization under confocal laser microscope has revealed that this bacterium can colonize both intercellular and intracellular spaces of stem and root tissues, which was significant in establishing its endophytic nature (Timmusk et al. 2009; Anand and Chanway 2013a). Zhao et al. (2015) isolated several endophytic strains from a medicinal plant, *Lonicera japonica*, generally grown in eastern china. Two of the isolated strains belonged to genus *Paenibacillus* (*P. polymyxa* and *P. ehimensis)* and possessed many plant growth-promoting characteristics including siderophore production, phosphate solubilization, IAA production, aminocyclopropane-1-carboxylic acid (ACC) deaminase activity, and cellulase and pectinase activity. Apart from that, these strains were able to suppress the growth of common crop pathogens. These *Paenibacillus* strains endophytically colonized a nonnative host, wheat, and promoted its growth by significantly increasing shoot and root length, seedling fresh and dry weight, and chlorophyll content. In another recent study, several endophytic strains were isolated from wild maize (teosinte) believed to harbor beneficial endophytes that could provide resistance to common crop pathogens (Mousa et al. 2015). After initial in vitro screening against fungal pathogen, *Fusarium graminearum*, causative agent of Gibberella Ear Rot (GER) in modern corn, three antifungal endophytes identified as *P. polymyxa* were tested for their ability to suppress GER in modern corn seedlings. GFP-tagged *P. polymyxa* endophytic strains colonized internal tissues of modern corn plants and suppressed the growth of *F. graminearum* pathogen in vivo. It was concluded that wild relatives of modern crops might have a reservoir of endophytes that could be used as biocontrol against pathogens that lead to extensive crop loss.

Chris P Chanway and his group have been working with *P. polymyxa* since 1988 and have published significant reports about the role of this bacterium in promoting plant growth and health in both agricultural and forest ecosystems. In 2012, the group reported the existence of an endophytic diazotroph, *P. polymyxa* P2b-2R, living in stem tissues of a gymnosperm, lodgepole pine (*Pinus contorta*), naturally regenerating at a site located in Williams Lake, BC, Canada (Bal et al. 2012). P2b-2R was able to grow on N-free media, combined carbon medium (CCM; Rennie 1981), and consistently reduced significant amounts of acetylene in the acetylene reduction assay (ARA) (Bal et al. 2012). By using a more accurate method of determining the amount of N fixed (^{15}N foliar dilution assay), Anand et al. (2013) discovered this bacterial strain's remarkable ability to derive up to 79% of N from the atmospheric pool. In a subsequent report, it was observed that strain possesses *nif* genes, required to fix atmospheric N (Anand and Chanway 2013c). GFP-tagged P2b-2R strain was constructed to evaluate the endophytic colonization sites in lodgepole pine and it was reported to colonize both intercellular and intracellular spaces of lodgepole pine interior tissues (Anand and Chanway 2013a). First reports about P2b-2R's ability to colonize a nonnative host came out in 2012 and 2013 when this bacterial strain was found to colonize internal tissues of stem and root of another gymnosperm tree species, western red cedar (*Thuja plicata*) (Bal and Chanway 2012b; Anand and Chanway 2013b). P2b-2R significantly enhanced seedling length and biomass of western red cedar and also fixed considerable amounts of N from the atmosphere (Anand and Chanway 2013b). Subsequently, Puri et al. (2015) hypothesized that this bacterial strain could provide similar benefits to angiosperms, especially the crop species, by colonizing them endophytically. Their hypothesis was evidenced and P2b-2R colonized internal root tissues of corn seedlings with a population size of 10^5 cfu/g fresh tissue weight in just 10 days. P2b-2R also fixed up to 20% of N from the atmosphere, increased seedling length by 35% and biomass by 30% in 30-day long trials (Puri et al. 2015). P2b-2R's ability to colonize diverse host species was ascertained, when it successfully colonized interior tissues of an important oilseed crop species, canola (Puri et al. 2016a) and vegetable crop species, tomato (Padda et al. 2016a). Similar benefits were provided by P2b-2R to these crop species indicating that P2b-2R can symbiotically associate with a broad range of hosts (see Table 2.3). Padda et al. (2017) reported an astonishing discovery with the GFP-tagged P2b-2R (P2b-2R*gfp*) constructed by Anand and Chanway (2013a), where P2b-2R*gfp* inoculation significantly enhanced corn seedling growth (length and biomass) as compared to the wild-type P2b-2R inoculation. This was the first report in literature where GFP-tagging of a bacterial strain related to the *Bacillus* (and *Paenibacillus*) genus enhanced its growth-promoting abilities. A similar discovery about the enhancement of PGP abilities by GFP-tagging was reported in *Azospirillum brasilense* a

Table 2.3 Nitrogen fixation and plant growth promotion of important agricultural crops by *Paenibacillus polymyxa* P2b-2R

	Days after inoculation	Corn	Canola	Tomato
%Ndfa[a]	20	6.52	8.08	10.0
	30	10.9	12.9	12.3
	40	15.7	16.2	18.1
	90	30.2	27.1	–
% seedling length promotion[b]	20	28.4	17.8	40.6
	30	24.1	20.5	36.5
	40	24.7	28.4	24.9
	90	51.9	70.7	–
% seedling biomass promotion[c]	20	17.2	57.0	56.1
	30	34.1	53.7	69.0
	40	28.4	37.1	93.0
	90	52.7	100.9	–

[a]Percent nitrogen derived from the atmosphere (%Ndfa)
[b]Percent seedling length promoted by inoculation with *P. polymyxa* P2b-2R
[c]Percent seedling biomass promoted by inoculation with *P. polymyxa* P2b-2R. These parameters were calculated using the formulas described in Puri et al. (2016b). [Data provided in the table has been compiled from [Padda et al. (2016a, b, 2017); Puri et al. (2016b)]

decade ago (Rodriguez et al. 2006). The ability of P2b-2R*gfp* to perform better than the wild-type strain was also confirmed in canola and tomato (Padda et al. 2016a). Benefits of inoculating this PGP endophytic strain and its GFP-tagged counterpart in a long-term trial were also evaluated and the results were even better than the previous studies which were of shorter duration (Puri et al. 2016b; Padda et al. 2016b). Thus, it can be concluded that *P. polymyxa* strain P2b-2R is an ideal endophytic strain that is able to colonize a variety of host species that are completely different physiologically and botanically.

2.4.6 *Pseudomonas*

Pseudomonas genus was first identified and described in the late nineteenth century (Migula 1894). The history of this genus from the time when it was first discovered till now has been described in great detail by Palleroni (2010). It is a diverse genus containing more than 230 species (http://www.bacterio.net/pseudomonas.html). Most of these species have a wide range of metabolic and catabolic capabilities. Bacterial species can be found in diverse ecological niches and could be plant growth and health-promoting bacteria, plant pathogens, or disease-causing human and animal pathogens (Preston 2004; Miller et al. 2008). *Pseudomonas* spp. are known to promote plant growth through a variety of mechanisms like biocontrol of pathogens, stimulating induced systemic resistance, N-fixation, phosphorus solubilization, and secreting phytohormones like auxins and cytokinins (Miller et al. 2008). Many studies have reported the ability of *Pseudomonas* spp. to associate endophytically with a variety of plant hosts, such as Peanut (Gupta et al. 2006), Sesame (*Sesamum indicum* L.) (Kumar et al. 2009), Mustard (Aeron et al. 2011), potato (Andreote et al. 2009), olive (*Olea europaea*) (Prieto et al. 2009; Maldonado-González et al. 2013), poplar (*Populus deltoides*) (Weyens et al. 2010, 2012), and wheat and cucumber (Pandey et al. 2012). Due to the diversity of *Pseudomonas* spp., many scientists have reported about their ability to colonize a range of nonindigenous plant hosts.

A diazotrophic endophyte, *P. aeruginosa* PM389, was isolated from an important forage crop, pearl millet (*Pennisetum glaucum*), widely grown in the Indian subcontinent, South America, USA and Australia (Gupta et al. 2013). It was observed that PM 389 has the ability to fix N, solubilize mineral phosphate, produce siderophores, inhibit the growth of bacterial and fungal pathogens. Looking at its plant growth-promoting abilities, Gupta et al. (2013) inoculated this bacterial strain into wheat and observed that it successfully colonizes the wheat seedlings and significantly enhance root and shoot length, and vigor index. In another study, another strain of *P. aeruginosa* originally isolated from wheat stem successfully shielded cucumber seedlings from various biotic and abiotic stresses (Pandey et al. 2012). Biomass of *P. aeruginosa* PW09-inoculated cucumber seedlings increased significantly as compared to the controls when grown under biotic stress (treated with pathogenic fungus, *Sclerotium rolfsii*) and abiotic stress (NaCl treatment). In a subsequent study, another strain PaBP35, belonging to this bacterial species, isolated from stem tissues of black pepper and tagged with GFP to visualize the endophytic colonization sites in a nonnative host, tomato (Kumar et al. 2013). GFP-tagged PaBP35 colonized interior tissues of the root, stem, and leaves of a 14-day-old tomato with high population densities, thus confirming its ability to form endophytic colonies in a nonnative host. Effective root colonization is a prerequisite attribute for the success of PGPR in plant growth and yield promotion. Colonization by fluoresent *Pseudomonas* in sesame rhizosphere promotes growth and proved effective as indigenous microflora over nonindigenous microflora (Aeron et al. 2010). Recently, a phenanthrene-degrading endophytic *Pseudomonas* strain was isolated from clover (*Trifolium pratense* L.) (Sun et al. 2014). Phenanthrene is a polycyclic aromatic hydrocarbon, which is a toxic metabolite found in some soils and can be taken up by the plants through roots. It can enter the food chain and cause serious harm to human health. Sun et al. (2014) investigated the ability of *Pseudomonas* strain Ph6 to colonize ryegrass (*Lolium multiflorum* Lam.) and degrade phenanthrene. GFP-tagged Ph6 colonized root, stem, and leaf tissues internally when visualized under fluorescence microscope. Heavy colonization of root and shoot tissues by GFP-tagged Ph6 was observed with population density ranging from 10^3 to 10^5 cfu/g fresh tissue weight. Inoculation of ryegrass with Ph6 led to a significant decrease in the concentration of phenanthrene in shoot and roots. Along with that the overall accumulation of phenanthrene in roots and shoot was also significantly reduced with inoculation, possibly due to the degrading mechanism of Ph6 strain (Sun et al. 2014).

P. fluorescens and *P. putida* are the most commonly studied PGPB known to associate with many different plant host species and colonize them both internally and externally. In a study conducted on phosphate solubilizing *P. fluorescens* strains, L132 and L321, isolated from *Miscanthus giganteus* leaf tissues (Keogh 2009) were tested for their ability to promote pea (*Pisum sativum* L.) growth (Oteino et al. 2015). It was observed that inoculation with these endophytic strains significantly increased fresh weight as well as the dry weight of the pea seedlings possibly due to the phosphate solubilizing abilities of these endophytes since mean soluble phosphorous levels were also observed to be higher in inoculated plants as compared to the controls. Another endophyte related to *Pseudomonas* genus was isolated from internal root tissues of *Artemisia* sp. (Chung et al. 2008). The strain was identified as *P. brassicacearum* YC5480 and was observed to demonstrate antifungal activity against common pathogens like *Colletotrichum gloeosporioides*, *Fusarium oxysporum*, and *Phytophthora capsici*. When colonized into a different host, radish, treated with *C. gloeosporioides*, the bacterial strain YC5480 counteracted the inhibitory effects of this pathogenic fungus. Therefore, it can be concluded that *Pseudomonas* spp. have the ability to cross-infect plant species other than their native host and have a broad application as a PGP agent in the agricultural industry.

2.5 Conclusion

Since their discovery, endophytic bacteria have been considered to play a crucial role in survival and growth of plants. By living inside the plant they are better protected from various biotic and abiotic stresses as compared to the rhizobacteria and free-living bacteria in soil. They have been reported to occupy almost every part of the plant, including intracellular and intercellular spaces. Due to the unique metabolic diversity of selected endophytes, they have been reported to colonize many nonindigenous plant host species and promote growth through direct or indirect mechanisms. Special mentioning deserves the endophytic bacteria belonging to the genus *Burkholderia* and *Paenibacillus*. Species belonging to these two genera have been frequently reported to endophytically colonize a variety of important agricultural crops, promote their growth in greenhouse and field conditions, and inhibit the growth of common crop pathogens in vitro as well as in vivo. These endophytic bacteria could potentially be the future commercial biofertilizers and biocontrol agents that can be used with many different crops and in various growing conditions, thus promoting sustainable agriculture.

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