Paenibacillus polymyxa: A Prominent Biofertilizer and Biocontrol Agent for Sustainable Agriculture

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Abstract

Agricultural practice is currently moving from traditional chemical fertilizers and pesticides toward sustainable and environment-friendly biofertilizer and biocontrol agents. *Paenibacillus polymyxa* (previously *Bacillus polymyxa*) is an agriculturally important microbe widely studied for its plant growth-promoting abilities. *P. polymyxa* is an endospore-forming bacterium that could colonize a range of ecological niches. It is commonly found in the agricultural soils, especially in close association with plants, and has been isolated from diverse geographic locations. *P. polymyxa* is renowned for its ability to act as a biocontrol agent against a wide array of plant pathogens. It can produce antibiotic compounds like polymyxin and antifungal compounds like fusaricidin that can suppress the growth of pathogens in both lab and field conditions. Apart from being a potent biocontrol agent, *P. polymyxa* strains are also known widely for their ability to fix atmospheric nitrogen, solubilize phosphate, and produce phytohormones; thus they could be used as effectual biofertilizers in commercial agriculture. The aim of this chapter is to provide an overview about both direct and indirect plant growth promotion accomplished by *P. polymyxa* in a wide variety of agricultural crops, through extensive reviewing of old and recent studies.

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Contents

6.1 Introduction

There has been a dramatic expand in the world's population since the last 150–200 years. According to the United Nations, the world's population is set to reach ~9.7 billion by 2050, which is fourfold the population in 1950 (United Nations 2015). Such drastic increase in population has put a serious pressure on our food resources causing a threat to the food security of many developing countries. Moreover, the environmental crisis like air, water, and soil pollution caused by the growing rate of global industrialization is making things worse for us and our planet (Glick 2015). In agriculture, the overuse of energy-intensive chemical fertilizers to boost crop yield has destroyed our soil ecosystem. Now is the best time to switch from these harmful chemical fertilizers to harmless and sustainable biofertilizers. Biofertilizer is a contraction of the term biological fertilizer, and it is very different from the organic fertilizer. Organic fertilizers contain organic compounds, which directly or indirectly increase soil fertility, whereas biofertilizers contain living organisms that increase the nutrient status of the host plant through their ongoing association with the host plant (Vessey 2003). The biofertilizer is a substance which contains living microorganisms which, when applied to seed, plant surfaces, or soil, colonizes the rhizosphere or the interior of the plant and promotes growth by increasing the supply or availability of primary nutrients to the host plant (Vessey 2003; Meena et al. 2013a; Bahadur et al. 2014; Maurya et al. 2014; Jat et al. 2015; Kumar et al. 2016b).

Apart from chemical fertilizers, the use of chemical pesticides to control the plant pest population is not only destroying our soil and natural environment but also impacting the human health both directly and indirectly. Pesticide is often considered a quick, easy, and inexpensive solution for controlling the pest population, but these benefits are incurred at the cost of our environment (Aktar et al. 2009).

Research on the use of much safer, biological control agents against pests is gaining momentum. "Biocontrol" is a commonly used, abbreviated synonym of "biological control." As defined by Pal and McSpadden Gardener (2006), "Biocontrol refers to the purposeful utilization of introduced or resident living organisms, other than disease resistant host plants, to suppress the activities and populations of one or more plant pathogens." The organism that suppresses the pest or pathogens are referred to as the "biocontrol agent." In this chapter, the term biofertilizer and biocontrol agent are used to signify those bacteria that are involved in promoting plant growth and controlling plant pathogen population, respectively (Kumar et al. 2015, 2016a; Ahmad et al. 2016; Meena et al. 2016a, b; Parewa et al. 2014; Prakash and Verma 2016; Jha and Subramanian 2016).

Plant growth-promoting bacteria (PGPB), as their name signifies, are those bacteria that can promote plant growth either directly, by aiding in nutrient acquisition (biofertilization) and moderating the plant hormone levels, or indirectly by acting as biocontrol agents against harmful plant pathogens (Glick 1995). These PGPB include bacteria that are free-living in the rhizosphere, form symbiotic relationships with plants like *Rhizobia* and *Frankia*, and can colonize interior tissues of plants (known as bacterial endophytes) (Glick 2012). Among the myriads of PGPB thriving in close association with plants, some spore-forming PGPB, particularly the gram-positive bacilli and streptomycetes, have drawn special attention because of their advantages over nonspore formers in product formulation and stable maintenance (Emmert and Handelsman 1999).

Among these, an agriculturally important microbe vital for present and future sustainable agriculture is "*Paenibacillus polymyxa.*" *P. polymyxa* is widely known for its plant growth-promoting (PGP) traits and the ability to thrive in diverse ecological niches. In this chapter, studies are signifying huge potential of *P. polymyxa* as a biofertilizer and biocontrol agent in sustainable agriculture (Priyadharsini and Muthukumar 2016; Kumar et al. 2017; Meena et al. 2015a, b, f; Raghavendra et al. 2016; Zahedi 2016; Dotaniya et al. 2016; Jaiswal et al. 2016).

6.2 Brief History of *Paenibacillus polymyxa* (Formerly *Bacillus polymyxa*)

History of *P. polymyxa* dates back to the nineteenth century when Prażmowski (1880) described an organism that closely resembled *Clostridium butyricum* but was able to grow in the presence of air. Prażmowski reported that this organism is slimy, strongly attacks starch and cellulose, and turns some carbohydrates into carbon dioxide gas (Porter et al. 1937). He designated it as "*Clostridium polymyxa*." But, in 1889, Eugéne Macé proposed the species name "*Bacillus polymyxa*" for this bacterium due to its rod-shaped cells (Macé 1889). *Bacillus* means "a rod" and polymyxa means "much slime." Macé reported that these bacteria are rod-shaped, produce spores, and can develop on the cooked slices of beets and turnips when exposed to air, and when grown in liquid media, they form a thick, creamy membrane on the surface (Macé 1889). Since then, this bacterium has been isolated frequently from soil and various plant species (Porter et al. 1937; Nakamura 1987) and has been reported to provide a variety of benefits to plants, like fixed nitrogen (N) (Bredemann 1909; Grau and Wilson 1962; Kalininskaya 1968; Seldin et al. 1984); PGP enzymes, viz., β-amylase (Fogarty and Griffin 1975; Hensley et al. 1980) and 2,3-butanediol (Ledingham and Neish 1954); and pathogen protection by secreting antibiotic polymyxin (Porter et al. 1949, Gordon et al. 1973; Skerman et al. 1980). Nakamura (1987) regarded *B. polymyxa* an agriculturally, industrially, and medically important organism.

Although bacterial species belonging to the genus *Bacillus* have been extensively studied, but it was always acknowledged that the taxonomy of this genus is unsatisfactory. Ash et al. (1991) referring to Bergey's Manual of Systematic Bacteriology, Vol. 2 (Claus and Berkeley 1986), pointed out that genus *Bacillus* is phenotypically and phylogenetically heterogeneous with species showing an extremely wide range of nutritional requirements, growth conditions, metabolic diversity, and DNA base composition. Ash et al. (1991) reported this phylogenetic heterogeneity by comparing and analyzing the small-subunit rRNA sequences of all species (51 species) known at that time. They divided these 51 species into five phylogenetically distinct groups and placed *B. polymyxa* into group 3. Findings reported in this chapter formed the basis for the proposal to reclassify group 3 bacilli comprising of *B. polymyxa* and ten other close relatives into a new genus *Paenibacillus* (meaning: almost a *Bacillus*) under the same family Bacillaceae (Ash et al. 1993). This proposal to form a new genus was officially approved and announced by the International Committee on Systematic Bacteriology (1994) through their official journal. Eventually, genus *Paenibacillus* was reclassified into a separate family *Paenibacilliaceae* and was designated as the family's type genus (Priest 2009; Rawat et al. 2016; Yasin et al. 2016; Meena et al. 2016c; Saha et al. 2016a; Yadav and Sidhu 2016; Meena et al. 2016d; Das and Pradhan 2016; Dominguez-Nunez et al. 2016).

6.3 *P. polymyxa* Strains Isolated from Agricultural Crops

The *P. polymyxa* strains inhabit diverse ecological niches including but not limited to rhizosphere and internal tissues of agricultural crops (von der Weid et al. 2000; Gu et al. 2010) and forest trees (Shishido et al. 1995; Bal et al. 2012), fermented food (Piuri et al. 1998; He et al. 2007), and marine environment (Ravi et al. 2007; Ma et al. 2010). Its ability to survive in a range of environmental conditions can be related to its endospore-forming potential. Agriculturally important *P. polymyxa* strains that have been isolated from various agricultural sites over the years are listed in Table 6.1. N-fixing *P. polymyxa* strain B5 was isolated from the rhizosphere of spring wheat (*Triticum aestivum* L.) growing on a research field (Lindberg and Granhall 1984). Since DNA identification techniques were not available at that time, authors identified the isolates using standard biochemical tests and comparing the results with reference strain ATCC 842. Strain B5 reduced significant amounts of acetylene and exhibited nitrogenase activity in vitro, thus indicating that it is a

Table 6.1 List of important *Paenibacillus polymyxa* strains that have been isolated from agricultural sites

Strain	Origin	References
B1, B2	Wheat rhizosphere	Lindberg and Granhall (1984)
130 different strains	Wheat rhizosphere	Mavingui et al. (1992)
CF43	Wheat rhizosphere	Gouzou et al. (1993)
PMD216, PMD230, PMD112, PMD128, PMD66	Wheat rhizosphere, rhizoplane, and soil	Lebuhn et al. (1997)
CM5-5, CM5-6	Barley rhizosphere	Nielsen and Sørensen (1997)
E681	Winter barley rhizosphere	Ryu and Park (1997)
70 different strains	Corn rhizosphere	von der Weid et al. (2000) and da Mota et al. (2002)
GBR-1	Roots of Korean ginseng	Jeon et al. (2003)
BRF-1	Soybean rhizosphere	Wang et al. (2003)
B5, B6	Peanut rhizosphere	Haggag and Timmusk (2008)
BMP-11	Cucumber rhizosphere	Liu et al. (2008)
SQR-21	Watermelon rhizosphere	Raza et al. (2009)
EBL-06	Wheat phyllosphere	Gu et al. (2010)
JSa-9	Soil	Deng et al. (2011)
G-14	Muskmelon rhizosphere	Shi et al. (2012)
SC09-21, SR04-02, SR04-16	Soil	Xu and Kim (2014)
EG2, EG14	Soil	Górska et al. (2015)
APEC128, APEC136	Apple rhizosphere	Kim et al. (2016a, b)

potent N-fixing bacterial strain (Saha et al. 2016b; Verma et al. 2014, 2015b; Meena et al. 2014a, 2015e; Teotia et al. 2016; Bahadur et al. 2016b).

Another strain of *P. polymyxa* (CF43) was isolated from the rhizosphere of spring wheat (cv. Castan) growing in a field near Nemours, France (Gouzou et al. 1993). It was determined that population size of strain CF43 present in the wheat rhizosphere ranged from 1 × 10^5 to 5 × 10^5 cfu/g dry weight of rhizosphere soil. It was also reported that strain CF43 enhances soil aggregate stability and overall porosity. In another study, bacterial strains were isolated from barley (*Hordeum vulgare* L.) rhizosphere and screened for their ability to produce selected enzymes and antagonize plant pathogenic fungi (Nielsen and Sørensen 1997). Two strains of *P. polymyxa* (CM5-5 and CM5-6) were successful in these screening tests, and according to the authors, these strains could be promising biocontrol agents (Sharma et al. 2016; Verma et al. 2015a; Meena et al. 2013b; Shrivastava et al. 2016; Meena et al. 2016e).

The diversity of *P. polymyxa* strains colonizing the rhizosphere and the surrounding soil is huge. Mavingui et al. (1992) studied the diversity among 130 strains of *P. polymyxa* isolated from rhizosphere soil, non-rhizosphere soil, and rhizoplane of wheat. Phenotypic and genotypic characterization tests revealed that there is higher diversity within *P. polymyxa* strains isolated from non-rhizosphere and rhizosphere soil as compared to the strains isolated from the rhizoplane (Meena et al. 2017). In another study conducted with *Zea mays* plants growing in Cerrado soil, which is found commonly in tropical belts of the world, ~70 different isolates of *P. polymyxa* were harvested from the rhizosphere of corn plants (von der Weid et al. 2000; da Mota et al. 2002). Isolation of two strains designated as B5 and B6 from soil around the peanut (*Arachis hypogaea* L.) roots was performed, and by using genomic identification techniques, strains were identified as *P. polymyxa* (Haggag and Timmusk 2008).

The strains were able to suppress the activity of pathogenic fungus *Aspergillus niger* (causes crown rot disease of peanut) both in vitro and in vivo (greenhouse and field experiments). *P. polymyxa* strains have also been isolated from watermelon (*Citrullus lanatus*) and muskmelon (*Cucumis melo* L.). Fusaricidin-type compound-producing strain SQR-21, exhibiting antagonistic activity against pathogenic fungus, *Fusarium oxysporum* f. sp. *niveum*, was isolated from watermelon plants (Raza et al. 2009). On the other hand, a strain of *P. polymyxa* (G-14) was isolated from soil samples collected from muskmelon fields in Changji, Xinjiang, China (Shi et al. 2012). It was reported that strain G-14 can produce antibiotic compounds that can antagonize the activity of pathogenic bacteria, *Pseudomonas syringae* pv., *Lachrymans*, and *Acidovorax avenae* subsp. *citrulli*, that cause bacterial spot disease in muskmelon. Apart from living in the rhizosphere of a plant, *P. polymyxa* strain has also been reported to inhabit agricultural soils. *P. polymyxa* strain JSa-9 was isolated from soil collected from the farmland of Nanjing (Jiangsu province, China) and was reported to show antagonistic activity against local plant pathogens (Deng et al. 2011; Velazquez et al. 2016; Meena et al. 2014b, 2015c; Sindhu et al. 2016; Singh et al. 2016; Masood and Bano 2016).

Similarly, three strains of *P. polymyxa* (SC09-21, SR04-02, SR04-16) were isolated from soil samples collected from 30 different locations within fields (where Chinese cabbage, garlic, and orrice were cultivated) in Samcheok, Gangwon Province, Korea (Xu and Kim 2014). Isolated strains showed a range of PGP traits both in vitro and in vivo. In another study, two diazotrophic (N-fixing) strains EG2 and EG14 of *P. polymyxa* were isolated from agriculturally used land in Poland (Górska et al. 2015). *P. polymyxa* strain was also isolated from phyllosphere of wheat cultivated in a field located at Tongzhou near Beijing City, China (Gu et al. 2010). A study reviewed in this section clearly proves the potential of *P. polymyxa* strains to inhabit a range of agricultural crops and soil at a variety of locations all around the world (Meena et al. 2013c, 2015d; Singh et al. 2015; Bahadur et al. 2016a).

6.4 Complete Genome Sequencing of *P. polymyxa* Strains

Complete genome sequencing determines the complete DNA sequence of an organism's genome at a single time. This technique is crucial to identify the genes that are responsible for different traits of a PGPB. For instance, N-fixing trait of a PGPB is related to the presence of *nif* genes. Genome sequencing helps to link the field/lab observed characteristics of a PGPB with the genes responsible for exhibiting those PGP traits. Although complete genomes of a large number of PGPB have been sequenced, very few studies have reported the complete genome sequence of *P. polymyxa* strains. To date, complete genomes of only six strains of *P. polymyxa* are

Table 6.2 List of *Paenibacillus polymyxa* strains whose complete genomes have been sequenced to date

Strain	Origin	Genome size (Mbp)	References
E681	Winter barley rhizosphere	5.4 [1 chromosome, 0 plasmid]	Kim et al. (2010)
SC2	Pepper rhizosphere	5.7 [1 chromosome, 1 plasmid]	Ma et al. (2011)
M-1	Internal root tissues of wheat	5.8 [1 chromosome, 1 plasmid]	Niu et al. (2011)
CR1	Corn rhizosphere	6.0 [1 chromosome, 0 plasmid]	Eastman et al. (2014a)
SQR-21	Watermelon rhizosphere	5.8 [1 chromosome, 0 plasmid]	Li et al. (2014)
Sb3-1	Organically managed soil	5.6 [1 chromosome, 2 plasmids]	Rybakova et al. (2015)

available in the NCBI database (https://www.ncbi.nlm.nih.gov), and amazingly all six strains were isolated from agricultural sites and were reported to possess PGP abilities (Table 6.2). Korean researchers were the first to sequence and report the complete genome of a *P. polymyxa* strain (E681) (Kim et al. 2010). *P. polymyxa* E681 is an endospore-forming bacterium that was isolated from the rhizosphere of winter barley in South Korea (Ryu and Park 1997). Based on sequence investigations, Kim et al. (2010) reported that strain E681 possesses genes responsible for synthesizing antibiotic compound polymyxin, antifungal compound fusaricidin, and phytohormone auxin. Subsequently, the complete genome of another *P. polymyxa* strain (SC2) originally isolated from pepper (*Capsicum annuum* L.) (Zhu et al. 2008) was sequenced and reported (Ma et al. 2011). Genome sequencing revealed that this strain possesses genes that are involved in antibiotic biosynthesis like fusaricidin-synthetic gene, polymyxin-synthetic gene cluster, and antibiotic-synthetic gene cluster; thus, it can be concluded that this bacterial strain will exhibit a broad-spectrum antimicrobial activity (Ma et al. 2011). Till now, the one and only endophytic strain of *P. polymyxa* (M-1) whose complete genome has been sequenced (Niu et al. 2011) was isolated from internal tissues of wheat roots (Yao et al. 2008).

In another report, the complete genome of a PGPB (*P. polymyxa* CR1), isolated from corn rhizosphere, was sequenced (Eastman et al. 2014a). Genome sequencing revealed that this strain possesses genes responsible for N fixation (*nif* genes), indole-3-acetic acid (IAA) synthesize, biomass degradation, and antimicrobial production, thus confirming their previous infield observations. Li et al. (2014) and Rybakova et al. (2015) have also reported complete genomes of *P. polymyxa* strains SQR-21 and Sb3-1, respectively. These strains also possess a variety of PGP traits. Eastman et al. (2014b) was the first to conduct a comparative genomic analysis of *P. polymyxa* strains. Their work highlighted that plant growth promotion by *P. polymyxa* is mediated largely through phytohormone production, increased nutrient availability, and biocontrol mechanisms. Similar study comparing the genomes of nine *P. polymyxa* strains and five other *Paenibacillus* spp. isolated from diverse ecological niches and geographic regions was conducted recently (Xie et al. 2016).

Authors concluded that genes relevant to PGP traits, i.e., phosphate solubilization, N fixation, IAA production, and antibiotic synthesis, are well conserved or have evolved with diversity in *P. polymyxa* and its closely related species.

6.5 Plant Growth Promotion by *Paenibacillus polymyxa* Strains

Generally, *P. polymyxa* strains promote plant growth either directly by helping in nutrient acquisition (like biological N fixation), producing plant growth regulators (like auxin, cytokinins, gibberellins), controlling plant ethylene levels, and enhancing root permeability and soil porosity or indirectly through biocontrol of major plant pathogens. Primary PGP characteristics of *P. polymyxa* strains have been presented in Fig. 6.1. Various reports about the direct and indirect benefits provided by prominent *P. polymyxa* strains to agricultural crops have been listed in Table 6.3.

6.5.1 Biofertilization : Direct Plant Growth Promotion

P. polymyxa strains possess many PGP characteristics through which direct plant growth promotion is achieved (Fig. 6.1). This includes biological N fixation by either living in the rhizosphere or internal tissues of the plant; positively affecting the physical structure of rhizosphere soil; enhancing nutrient uptake from the soil, thus increasing the plant length and biomass along with the overall crop yield; and secreting plant growth hormones. Lindberg et al. (1985) observed the N fixation activity of two *P. polymyxa* strains B1 and B2 isolated from field-grown wheat (Lindberg and Granhall 1984) by using acetylene reduction assay (ARA). Results of ARA indicated that strains B1 and B2 can produce 10.6 and 3.3 nmol C_2H_4plant^{-1} h^{-1}, respectively, thus establishing their N-fixing ability. Besides fixing N, these strains were involved in increasing the seedling biomass and shoot length. To observe the endophytic colonization by these strains in wheat roots, authors used transmission electron microscopy technique and found that these strains can colonize intercellular and intracellular spaces of root epidermal cells. In later studies, production of cytokinin by strain B2 was also assessed using the chromatography techniques (Timmusk et al. 1999). Strains B1 was tagged with GFP to analyze the endophytic colonization ability and pathway through which it enters the plant tissues (Timmusk et al. 2005). Fluorescence microscopy and electron scanning microscopy revealed that this strain colonizes predominantly the root tip, where it forms biofilms and then invade the plant roots. This was the first study in which invasion and colonization of plant roots by a *P. polymyxa* strain were reported in detail. Some studies have implied the physical and microbial approach to analyze the effects of *P. polymyxa* inoculation on soil aggregation. In one such study, *P. polymyxa* strain CF43, isolated from wheat rhizosphere, increased the mass of soil adhering to the wheat roots by 57% when grown in a glasshouse (Gouzou et al. 1993). When aggregate size distribution was compared, it was observed that inoculated rhizosphere soil has a

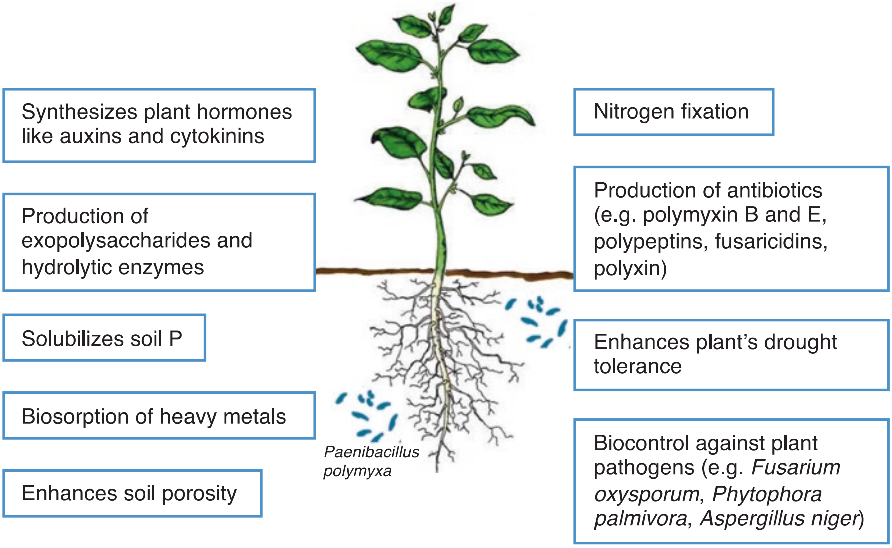

Fig. 6.1 Primary plant growth-promoting (PGP) characteristics of *Paenibacillus polymyxa* strains

more porous structure as compared to the uninoculated control. Increased aggregation of rhizosphere soil by CF43 was also confirmed by Bezzate et al. (2000) using molecular techniques. Bezzate et al. (2000) hypothesized that levan, which is a fructosyl polymer produced by strain CF43, is responsible for enhanced soil aggregation. A mutant strain, SB03, was constructed by silencing the *sacB* gene (responsible for encoding levan) of strain CF43. Inoculation with CF43 significantly increased the wheat root dry mass and root-adhering soil dry mass as compared to inoculation with SB03 strain, thus signifying the importance of levan produced by the strain CF43 in increasing the soil aggregation. In a recent study, N-fixing ability of two *P. polymyxa* strains (EG2 and EG14) isolated from agricultural soils was assessed (Górska et al. 2015). The genome of these strains was found to carry *nif* genes which encode individual components of the nitrogenase complex. In vitro tests of nitrogenase activity by using ARA revealed that EG2 and EG14 can produce 2.9 and 0.4 nM $C_2H_4ml^{-1}$ h^{-1}.

Diazotrophic (N-fixing) strains have immense potential as biofertilizers since N is believed to be the most important mineral nutrient required for plant growth and maintenance (Robertson and Vitousek 2009). Bal et al. (2012) isolated an endophytic diazotroph, *P. polymyxa* P2b-2R , from stem tissues of lodgepole pine (*Pinus contorta*). Strain P2b-2R was able to grow on N-free medium [combined carbon medium (CCM; Rennie 1981)] and consistently reduced significant amounts of acetylene in ARA (Bal et al. 2012). By using a more accurate method of determining the amount of N fixed (^{15}N foliar dilution assay), Bal and Chanway (2012a), Anand et al. (2013), and Yang et al. (2016) reported P2b-2R's remarkable ability to derive up to 79% of

Table 6.3 List of prominent *Paenibacillus polymyxa* strains reported to provide a variety of benefits to agricultural crops

Strain	Host	Benefits	References
B1, B2, B3, B4	Wheat and *Arabidopsis thaliana*	Nitrogen fixation, cytokinin production, improves abiotic and biotic stress tolerance and antagonizes oomycete plant pathogens	Lindberg et al. (1985), Timmusk and Wagner (1999) and Timmusk et al. (1999, 2009)
CF43	Wheat	Enhance soil porosity	Gouzou et al. (1993) and Bezzate et al. (2000)
PMD216, PMD230, PMD112, PMD128, PMD66	Wheat	Production of auxin and other indolic and phenolic compounds	Lebuhn et al. (1997)
CM5-5, CM5-6	–	Antagonism against pathogenic microfungi	Nielsen and Sorensen (1997)
E681	*Arabidopsis thaliana*, cucumber, red pepper, sesame, and tobacco	Plant growth promotion and suppress the activity of a variety of plant pathogenic fungi both in vitro and in vivo	Ryu and Park (1997), Ryu et al. (2005a, b, 2006), and Lee et al. (2013)
Nb	Sugar beet and barley	Plant growth promotion and increase in overall yield	Çakmakçi et al. (1999, 2006)
PKB-1	–	Produce fusaricidin-type antifungal peptides active against *Leptosphaeria maculans* (causative agent of canola blackleg disease)	Beatty and Jensen (2002)
B5, B6	Peanut and *Arabidopsis thaliana*	Inhibitory effect against crown rot disease caused by *Aspergillus niger* pathogen and antagonizes oomycete plant pathogens	Haggag (2007), Haggag and Timmusk (2008), and Timmusk et al. (2009)
BRF-1	Soybean	Control brown stem rot disease caused by the pathogenic fungus *Phialophora gregata* and in vitro antifungal activity against *Rhizoctonia solani*	Zhou et al. (2008) and Chen et al. (2010)
SQR-21	Watermelon	Biocontrol against *Fusarium oxysporum* cause of Fusarium wilt disease and increase plant dry weight	Raza et al. (2009, 2015a) and Ling et al. (2011)
JSa-9	–	Antimicrobial activity	Deng et al. (2011)
HKA-15	Soybean	Antagonism against the phytopathogen *Xanthomonas campestris* pv. phaseoli M-5	Mageshwaran et al. (2012)

(continued)

Table 6.3 (continued)

Strain	Host	Benefits	References
G-14	Muskmelon	Suppress the incidence of bacterial spot diseases	Shi et al. (2012)
CF05	Tomato	Suppress Fusarium wilt disease	Mei et al. (2014)
SC09-21, SR04-02, SR04-16	Tomato	Suppress Fusarium crown and root rot disease, enhances a range of plant growth parameters, solubilize phosphate, produce IAA, siderophore, and other phytohormones	Xu and Kim (2014)
EBL-06	Tea	Enhanced tea yield, quantity of water extract, and tea polyphenol levels	Xu et al. (2014)
EG2, EG14	–	Nitrogen fixation	Górska et al. (2015)
HT16	Table grapes	Reduce white rot disease caused by *Coniella diplodiella*	Han et al. (2015)
GBR-1	Korean ginseng	Antagonistic activity against fungal and bacterial pathogens	Kim et al. (2015)
P2b-2R, P2b-2R*gfp*	Canola, Corn and Tomato	Nitrogen fixation, increases seedling length, and biomass	Puri et al. (2015, 2016a, b), Padda (2015) and Padda et al. (2016a, b)
WR-2	–	Antifungal compounds that inhibit the growth of *Fusarium oxysporum*	Raza et al. (2015a, b)
APEC128, APEC136	Apple	Biocontrol of anthracnose and white rot diseases in apples	Kim et al. (2016a, b)
SC09-21	Pepper	Induces defensive response against Phytophthora blight (caused by *Phytophthora capsici*) and promotes plant growth	Xu and Kim (2014, 2016)
1465	Wheat	Increase total root and shoot length, total root, and shoot weight	Yegorenkova et al. (2016)
BFKC01	*Arabidopsis thaliana*	Promote plant Fe assimilation	Zhou et al. (2016)

N from the atmospheric pool when inoculated into lodgepole pine. In a subsequent report, it was observed that strain possesses *nif* genes required to encode the nitrogenase enzyme (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).

P2b-2R was able to colonize internal tissues of stem and root of another gymnosperm tree species, western red cedar (*Thuja plicata*), and significantly enhance seedling length and biomass along with fixing considerable amounts of N from the atmosphere (Bal and Chanway 2012b; Anand and Chanway 2013b; Tang et al. 2017; Yang et al. 2017). Puri et al. (2015) hypothesized that strain P2b-2R can provide similar benefits to agricultural crops through rhizospheric and endophytic colonization. Puri et al. (2015) used corn as the model crop to test this hypothesis. P2b-2R colonized rhizosphere and internal root tissues of corn seedlings with a population size of 10^5 cfu/g dry root or fresh tissue in just 10 days. P2b-2R also fixed up to ~20% of N from the atmosphere and increased seedling length by ~35% and biomass by 30% in 30-day long trials (Puri et al. 2015). P2b-2R successfully colonized 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 and provide benefits to a broad range of hosts (Table 6.4). Padda (2015) reported an astonishing discovery with the GFP-tagged P2b-2R (P2b-2R*gfp*) constructed by Anand and Chanway (2013a). Padda (2015) compared the GFP-tagged strain with the wild-type strain of P2b-2R in terms of their ability to fix N and enhance seedling length and biomass.

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. 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 *P. polymyxa* 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). In Fig. 6.2, a clear difference can be seen in canola plant growth when seeds were, either inoculated with P2b-2R*gfp* or P2b-2R or not inoculated (controls) (reproduced from Padda et al. 2016b). The increased PGP efficiency of P2b-2R after GFP-tagging is still a mystery, although in an unpublished study, it has been determined that GFP-tagging of P2b-2R leads to overexpression of *nifH*, *nifD*, and *nifK* genes, which play a major role in N fixation activity of a bacterial strain.

Plant hormones, like cytokinins, gibberellins, IAA, ethylene, etc., play a vital role in plant growth and development and in the response of plants to their environment (Glick 2012). PGPB can produce or modulate plant hormone levels, thereby affecting the plant's hormonal balance and its response to abiotic and biotic stress. *P. polymyxa* strains isolated from different proximity to wheat roots were evaluated for production of indolic and phenolic compounds like IAA, indole-3-ethanol, indole-3-lactic acid, indole-3-carboxylic, and benzoic acid (Lebuhn et al. 1997). Authors concluded that the presence of *P. polymyxa* strains at different proximities to roots indicates distinct potentials to produce indolic and phenolic compounds. Phi et al. (2008) reported that a number of genes are involved in the regulation of IAA biosynthesis by *P. polymyxa*, and a change in IAA regulation directly affects

Table 6.4 Plant growth promotion (seedling length, seedling biomass, and foliar N concentration enhancement) and nitrogen fixation (% nitrogen derived from the atmosphere) by *Paenibacillus polymyxa* strain P2b-2R when inoculated into important agricultural crops

Host plant	Days after sowing and inoculation	%Ndfa[a]	Foliar nitrogen concentration enhancement[b]	%Seedling length enhancement[c]	%Seedling biomass enhancement[d]	References
Corn	30	19.6	10.2	35.3	30.9	Puri et al. (2015)
	40	15.7	17.1	24.7	28.4	Padda (2015)
	90	30.2	27.3	51.9	52.7	Puri et al. (2016b)
Canola	40	16.2	20.0	28.4	37.1	Padda et al. (2016a)
	60	21.8	40.3	24.9	30.1	Puri et al. (2016a)
	90	27.1	11.7	70.7	100.8	Padda et al. (2016b)
Tomato	40	18.1	30.0	24.9	93.0	Padda et al. (2016a)

[a] Percent nitrogen derived from the atmosphere (%Ndfa) by strain P2b-2R
[b] Percent increase of foliar nitrogen concentration after inoculation with strain P2b-2R
[c] Percent increase of seedling length after inoculation with strain P2b-2R
[d] Percent increase of seedling biomass after inoculation with strain P2b-2R

the growth of inoculated plants. In another study, in vitro production of IAA, siderophore, and other phytohormones and phosphate solubilization by *P. polymyxa* strains SC09-21, SR04-02, and SR04-16 isolated from agricultural soil was reported (Xu and Kim 2014). Greenhouse pot trials revealed that inoculation with these *P. polymyxa* strains can enhance tomato shoot and root length, shoot and root fresh weight, shoot and root dry weight, and chlorophyll content. In vitro production of phytohormones like ammonia, cellulase, indole-3-acetic acid, protease, and siderophores and phosphate solubilization by *P. polymyxa* strain SC09-21 was confirmed in a subsequent study (Xu and Kim 2016). Xu and Kim (2016) also inoculated pepper with strain SC09-21 in a 2-week-long greenhouse trial and found that inoculated pepper plants were longer and had more fresh weight, biomass, and chlorophyll content, thus establishing that *P. polymyxa* strain SC09-21 could be an effective biofertilizer which can associate with a variety of agricultural crops. Although regarded as a micronutrient, iron is a major limiting factor in plant growth and development. Microbe-induced iron assimilation in a plant by *P. polymyxa* strain BFKC01 was recently reported (Zhou et al. 2016). Based on their findings, authors proposed a model: "productions of IAA by strain BFKC01 activates auxin-mediated signaling pathways and promotes lateral root formation in Arabidopsis plants, thus plants efficiently absorb iron from the rhizosphere. Strain BFKC01 also regulates plant iron uptake by integrating the mechanisms of both enhancement of iron deficiency responses and increased secretion of iron-mobilizing phenolic compounds."

Fig. 6.2 *Paenibacillus polymyxa* strain P2b-2R*gfp* inoculated seedling (*left*), *P. polymyxa* strain P2b-2R inoculated seedling (*center*), and uninoculated control seedling (*right*) of canola (*Brassica napus* L.) harvested 3 months after sowing and inoculation. Obvious differences in length, biomass, number of floral buds and pods, and plant health can be seen (Reproduced from Padda et al. 2016b)

6.5.2 Biocontrol: Indirect Plant Growth Promotion

Biocontrol of plant pathogens is an effective and environmentally safe alternative to chemical pesticides. *P. polymyxa* can produce two types of peptide antibiotics, one type is only active against bacteria and the other is active against fungi, gram-positive bacteria, and actinomycetes (Beatty and Jensen 2002). This antagonistic potential is the base for effective applications of *P. polymyxa* strains against a wide set of fungal and bacterial plant pathogens. The possible mechanisms that enable *P. polymyxa* strains to control a variety of plant pathogens have been reviewed extensively (Raza et al. 2008). Timmusk and Wagner (1999) used a known PGPB, *P.*

polymyxa strain B2, along with other *P. polymyxa* strains (B3 and B4) isolated by Lindberg and Granhall (1984) to assess their abiotic and biotic stress response when tested in *Arabidopsis thaliana*. Challenges by either the pathogenic bacteria, *Erwinia carotovora* (biotic stress), or induction of drought (abiotic stress) revealed that *P. polymyxa* inoculated plants were more resistant than control plants.

Authors also suggested that genes and/or gene classes associated with plant defenses against abiotic and biotic stress may be co-regulated. In another study, strains of *P. polymyxa* (B5 and B6), isolated from peanut rhizosphere, were reported to show in vitro antagonism against pathogenic fungus, *Aspergillus niger* (Haggag 2007; Haggag and Timmusk 2008). *A. niger* causes crown rot disease of peanut, which is the most important disease in Egypt and several other temperate countries (Haggag and AboSedera 2000). Strains B5 and B6 densely colonized the roots of peanut as visualized by scanning electron microscopy and suppressed the activity of *A. niger* in peanut, thereby decreasing the crown rot disease development. It was also reported that these strains increase the activity of plant defense enzymes including β-1,3-glucanase and chitinase, which might be the reason behind the suppression of pathogen activity (Haggag 2007). The results of two field trials indicated that these strains significantly reduce the incidence rate of crown rot disease in peanut; thus, they could be used as an effective biocontrol agent against *A. niger* at farm level (Haggag and Timmusk 2008).

The effectiveness of strains B5 and B6 along with strain B2 was tested against common oomycete plant pathogens, *Phytophthora palmivora* and *Pythium aphanidermatum* (Timmusk et al. 2009). These oomycete pathogens cause one of the most devastating groups of diseases. Almost all plants are susceptible to root rot disease caused by these pathogens, and the disease is difficult to control once the rot has begun. Strains B2, B5, and B6 showed clear antagonism against oomycete pathogens in the in vitro experiment (using agar plates and liquid medium). Using *Arabidopsis thaliana* as the model plant system antagonism against oomycete pathogens was also studied in a soil medium, and it was found that the survival rate of *P. polymyxa* inoculated plants was significantly higher than the control plants. *P. polymyxa* strain E681 isolated from barley in South Korea showed in vitro antagonism against *Rhizoctonia solani*, *P. ultimum*, and *F. oxysporum* f. sp. *Cucumerinum* (Ryu et al. 2005a). When E681 strain was inoculated into cucumber (*Cucumis sativus* cv. Shinpung), incidence of damping-off disease caused by the abovementioned pathogens was significantly reduced (Ryu et al. 2005a).

In another study, Ryu et al. (2006) reported that strain E681 shows in vitro antagonism against nine different pathogens, viz., *P. debaryanum*, *R. solani*, *F. oxysporum*, *Botrytis cinerea*, *B. allii*, *Cladosporium fulvum*, *P. ultimum*, *P. capsici*, and *Aspergillus* sp. Ryu et al. (2006) also established that E681 is an effective biocontrol against damping-off disease caused by pathogens in a month-long field trial conducted with sesame (*Sesamum indicum* L.). In a subsequent study, strain E681 was screened for fusaricidin compounds (Lee et al. 2013). Pre- and posttreatment of a 3-week-old red pepper (*Capsicum annuum* L.) with fusaricidin compound through soil drench or foliar spray application greatly reduced the disease severity caused by

P. capsici. Similar effects were reported in tobacco (*Nicotiana tabacum*) and *Arabidopsis thaliana* (Lee et al. 2013).

Brown stem rot disease of soybean (*Glycine max* L.) caused by the soilborne fungus, *Phialophora gregata*, is one of the most disastrous soybean diseases in the USA and Japan (Bachman and Nickell 2000). Biocontrol effectiveness of *P. polymyxa* strain BRF-1 isolated from the rhizosphere of diseased soybean seedlings was tested (Zhou et al. 2008). The severity of brown rot disease in BRF-1 inoculated and control soybean plants was significantly decreased after 62 days of fungal inoculation, thus establishing its biocontrol efficacy against the *P. gregata* fungus. In vitro antifungal activity by BRF-1 against a range of fungal pathogens was also reported by Chen et al. (2010). Authors also isolated and identified the antifungal peptide of this strain, which is active against a range of pathogens. Raza et al. (2009) isolated *P. polymyxa* strain SQR-21 from the rhizosphere of healthy watermelon plants growing in a heavily wilt-diseased field and evaluated its biocontrol potential against *F. Oxysporum* (the causative agent of *Fusarium* wilt disease of watermelon) in a greenhouse experiment.

Strain SQR-21 combined with organic fertilizer significantly decreased the disease incidence (by 70%) and increased the plant biomass by ~113%. Subsequently, Ling et al. (2011) attempted to understand the plant-microbe communications that take place when watermelon plants are inoculated with either SQR-21 strain or pathogenic fungi *F. oxysporum* f. sp. *niveum*. When treated with SQR-21 watermelon plants produced root exudates that significantly reduced the conidial germination of *F. oxysporum*. Another strain of *P. polymyxa* (WR-2) showed a similar antagonistic effect against *F. oxysporum* f. sp. *niveum* (Raza et al. 2015b). Strain WR-2 inhibited the growth fungal pathogen by ~40% in three different media (agar, sterilized soil, and natural soil), and this inhibitory effect was increased to about 60% when organic fertilizer was added. Raza et al. (2015b) also reported that strain WR-2 produces seven different volatile organic compounds, viz., benzothiazole, benzaldehyde, undecanal, dodecanal, hexadecanal, 2-tridecanone, and phenol that inhibit the growth of *F. oxysporum*. In another study, *P. polymyxa* strain CF05 showed in vitro antagonism against *F. oxysporum* f. sp. *lycopersici* (the causative agent of Fusarium wilt of tomato).

Greenhouse experiment confirmed this finding, where CF05 suppressed the Fusarium wilt disease by ~78% in tomato. It was also reported that strain CF05 induces systemic resistance in the tomato plant, thereby stimulating the release of plant defense enzymes and protecting the plant from the pathogen.

6.6 Field Studies and Commercial Availability of *Paenibacillus polymyxa* Strains

The PGPB inoculated crops signify a minor segment of current global agricultural practice, but lately the interest in the infield usage of PGPB that promotes plant growth and yield has increased. A number of these bacteria are now being used commercially as aides to promote sustainable agriculture. Numerous studies underlining the plant growth-promoting effects of various *P. polymyxa* strains under field conditions have been reported. Ryu et al. (2006) conducted experiments under field conditions to evaluate the antagonistic effect of *P. polymyxa* strain E681 in two types of soilborne diseases: preemergence and postemergence damping-off in sesame seeds. Seed pelleting technique was used in this study to improve the ability of strain E681 as a biocontrol agent. Experiments were conducted at GSNU Research Farm, Daegok, Jinju, where sesame had been cultivated for 2 successive years with serious yield loss. Seed pelleting with strain E681 enhanced emergence rate by ~92%, whereas emergence rate of untreated sesame seeds was less than 30%. Combined treatment of pelleting and strain E681 resulted in a greater percentage of healthy stand (92%) than pelleting alone (40%) or non-pelleted seeds treated with E681 (24%) when evaluated 2 months after sowing. These results suggest that pelleting combined with *P. polymyxa* strain E681 can be used to control damping-off disease caused by complex organisms in the field. The effect of *P. polymyxa* strains B5 and B6 on pod yield and control of crown rot disease in peanut caused by *A. niger* was investigated in two successive field experiments (Haggag 2007; Haggag and Timmusk 2008).

Peanut plants treated with *P. polymyxa* strains displayed decreased incidence of crown rot disease triggered by *A. niger*. Plant growth and yield of seeds treated with strain B5 were found to be significantly higher in comparison to seeds treated with strain B6 and untreated plants. Biocontrol activity of *P. polymyxa* strain G-14 against bacterial spot diseases of muskmelon caused by two pathogens, *Pseudomonas syringae* pv. *Lachrymans* and *Acidovorax avenae* subsp. *citrulli*, was examined under field conditions (Shi et al. 2012). G-14 strain significantly inhibited the development of pathogens and suppressed the incidence of bacterial spot diseases. Inoculation with an N-fixing*P. polymyxa* strain increased sugar beet (*Beta vulgaris* cv. *Loretta*) root yields by 12% and barley seed yields by 15% when evaluated by in-field studies conducted at two different sites in Turkey (Çakmakçi et al. 1999). These results were also confirmed by a subsequent field study (Çakmakçi et al. 2006).

A yearlong field investigation (for three seasons—autumn, spring, and summer) was conducted to determine the effects of *P. polymyxa* strain EBL-06 on the growth of tea (*Camellia sinensis*) plantations (4 years old) in semitropical uplands, Hunan, China (Xu et al. 2014). Inoculation with EBL-06 increased tea plant yield (~17%) and tea quality by enhancing the level of green tea extracts by about 6% and tea polyphenols by ~10%. Thus, it was concluded that this strain could be a successful biofertilizer for tea plants that might be used for organic tea production in the future to enhance tea yield and quality. Field studies play an important role in determining the effects of a particular bacterial strain in actual conditions and open the doors for their use as commercial biological inoculants. Due to numerous field studies that have reported rigorous testing by scientists, many *P. polymyxa* strains are now available commercially in several countries.

6.7 Concluding Remark and Future Prospective

Since the first isolation and characterization more than a century ago, significant advances have been made in understanding how *P. polymyxa* affects plant growth. *P. polymyxa* is now known to fix nitrogen, secrete phytohormones, and produce antibiotic and antifungal compounds. The most common antifungal compound produced by *P. polymyxa* is fusaricidin which has been reported to suppress many strains of *Fusaricidin oxysporum* in a variety of plants species both in vitro and in vivo. It is believed that microorganisms with two or more PGP traits which are able to colonize and provide benefits to a wide range of crops may be effectively used for commercial and large-scale agriculture. It is an effective biocontrol agent against a wide range of plant pathogens like *Aspergillus* sp., *B. allii*, *B. cinerea*, *C. fulvum*, *F. oxysporum*, *P. capsici*, *P. debaryanum*, *P. ultimum*, and *R. solani*. Complete genome sequencing indicated that *P. polymyxa* E681 could produce antibiotic polymyxin and antifungal fusaricidin compounds, revealing the genetic evidence behind its ability to antagonize plant pathogens. Another example is *P. polymyxa* P2b-2R, which was reported to fix significant amounts of N directly from the atmosphere in crop species like corn, canola, and tomato. Possibly through N fixation and some other linked mechanisms, strain P2b-2R also promoted plant growth (length and biomass) and crop yield. These PGP properties together with its endospore-forming potential enable it to thrive in a wide range of environmental conditions, making it an important and promising biofertilizer and biocontrol agent for current and future sustainable agriculture. Through continuing research, agricultural scientists are making important inroads to understand the biology and ecology of *P. polymyxa* strains that could ultimately result in more commercially viable and environmentally friendly bio-inoculants for use in agriculture.

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