Chapter 11
New Insights in Plant-Associated *Paenibacillus* Species: Biocontrol and Plant Growth-Promoting Activity

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Abstract A wide number of new species have been included in recent years in the *Paenibacillus* genus, prompting to a new ecological and biotechnological appraisal of *Paenibacillus* bacteria. Several species are involved in plant growth promotion and biocontrol, and a few of them have also been reported to cause human infections. Some isolates of the genus *Paenibacillus* are among the most efficient microbial biocontrol agents, and some strains have been included in formulations that have been granted a patent to control plant pathogens. A strain belonging to the species *Paenibacillus lentimorbus* has recently been described as a potent plant growth-promoting and bioremediation agent in Cr-contaminated rhizosphere soil. Nitrogen fixation has been described in several species, and some of these bacteria are promising candidates for crop inoculation. Fourteen complete genome sequences are publicly available so far. Five of them belong to *Paenibacillus polymyxa* strains that have been isolated from crop rhizosphere and show traits related to plant growth promotion. Recently, the draft genome sequence of *Paenibacillus riograndensis* strain SBR5^T, which in addition to nitrogen fixation has shown several plant growth-promoting traits, has been published.

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11.1 Introduction

The microbial world is the largest not yet fully explored reservoir of biodiversity. Exploration of microbial diversity holds great promise because of the role of microbes in nutrient cycling, environmental detoxification, and novel metabolic abilities in pharmaceuticals and industrial processes (Satyanarayana 2005).

The *Paenibacillus* genus has attracted considerable interest because of its high biotechnological potential in sustainable agriculture and in different industrial processes (Govindasamy et al. 2011; Lal and Tabacchioni 2009). The genus *Paenibacillus* was created by Ash et al. (1993) to accommodate the former "group 3" of the genus *Bacillus* which comprises aerobic or facultative anaerobic endospore-forming bacterial species. Comparative 16S rRNA sequence analyses revealed that rRNA group 3 bacilli represents a phylogenetically distinct group and exhibits high intragroup sequence relatedness and is only remotely related to *Bacillus subtilis,* the type species of the genus *Bacillus*. The number of recognized member of this genus has been increased in the last few decades. At present, 174 species of the genus *Paenibacillus* with validly published names are available in the List of Prokaryotic Names with Standing in Nomenclature (LPSN), (http://www.bacterio.cict.fr/p/paenibacillus.html) database (Parte 2014). To date, a total of 152 finished and unfinished genomes of *Paenibacillus* are publicly available on NCBI (http://www.ncbi.nlm.nih.gov/) (Tatusova et al. 2014) and IMG-JGI (https://img.jgi.doe.gov/cgi-bin/er/main.cgi) (Markowitz et al. 2014). Species belonging to the genus *Paenibacillus* can be aerobic, anaerobic or facultatively anaerobic, mesophilic, psychrotolerant, or alkali tolerant and have the ability to degrade a variety of complex substrates such as xylan and cellulose (Rivas et al. 2005b). They have been isolated from a wide range of sources including soil, water, rhizosphere, vegetable matter, forage, and insect larvae (Daane et al. 2002), as well as from clinical samples such as blood samples (Noskin et al. 2001; Roux and Raoult 2004), cerebrospinal fluid shunt (Bosshard et al. 2002), human urine, and cerebrospinal fluid (Roux et al. 2008). *Paenibacillus polymyxa*, *Paenibacillus thiaminolyticus*, and *Paenibacillus hongkongensis* were reported as the cause of bacteremia and pseudobacteremia in a patient with cerebral infarction, in a patient on hemodialysis, and in a patient with neutropenic fever, respectively (Nasu et al. 2003; Ouyang et al. 2008; Teng et al. 2003). The highly diverse niche occupancy of *Paenibacillus* reflects the metabolic diversity of these bacteria. Indeed, fixation of atmospheric nitrogen, production of phytohormones, antibiotics, hydrolytic enzymes, and valuable chemical compounds such as 2.3-butanediol has been observed among isolates of the different *Paenibacillus* species (Govindasamy et al. 2011; Lal and Tabacchioni 2009). The majority of strains that are considered beneficial to plants have been isolated from soil and rhizosphere (McSpadden Gardener 2004; Govindasamy et al. 2011). Members of the genus *Paenibacillus* have also been recognized as important pathogens of insects. *Paenibacillus popilliae* and *Paenibacillus lentimorbus* are responsible of milky disease in the larvae of some beetles (order Coleoptera) including those that can cause crop diseases (Pettersson et al. 1999). *Paenibacillus larvae* is

the cause of the American foulbrood of honeybees (*Apis mellifera*) larvae, a disease that can significantly reduce pollination activity of fruit and vegetable crops (McSpadden Gardener 2004; Ashiralieva and Genersch 2006).

Over the past few years, sequencing of several genomes of *Paenibacillus* sp. bacteria isolated from the soil and rhizosphere has been carried out providing data on the genetic basis of determinants involved in plant growth promotion, nitrogen fixation, and biocontrol (Eastman et al. 2014).

In this chapter, highlights from recent studies on the taxonomy, genomics, ecology, plant growth promotion, and biocontrol of the different *Paenibacillus* species will be presented with the aim to evaluate their potential application in sustainable agriculture.

11.2 Taxonomy and Genomics

In the last few decades, a great number of prokaryotic genomes have been sequenced, and at present 32,525 bacterial genomes are available in the IMG database. Of these 32,525 genomes, 3998 genomes are finished, 3874 genomes are draft, and 24,753 genomes are permanent draft. As of January 2016, a total of 152 genomes belonging to species of the *Paenibacillus* genus are available in JGI-IMG (https://img.jgi.doe.gov/cgi-bin/er/main.cgi) (Markowitz et al. 2014) and in NCBI (http://www.ncbi.nlm.nih.gov/) (Tatusova et al. 2014). Out of 152 genomes, 28 are finished, 22 are draft, and 102 are permanent draft. In Table 11.1, a comprehensive view of the *Paenibacillus* species whose genomes have been or are being sequenced is given.

Autonomously replicating plasmids that do not integrate into the host genome were observed in only five *Paenibacillus* sp.: *Paenibacillus larvae larvae* 4-309, DSM 25430, *P. polymyxa* SC2, *P. polymyxa* M1, *Paenibacillus alvei* DSM 29, and *P. larvae larvae* 08-100, DSM 25719 (Table 11.1). Annotation of the *Paenibacillus* genome sequences showed that the genome size varies from 3.83 (*P. popilliae* ATCC 14706) to 8.82 Mb (*Paenibacillus mucilaginosus* K02) and % GC varies from 43 (*Paenibacillus assamensis* DSM 18201) to 67 (*Paenibacillus* sp. HW567) (Table 11.1).

Fifty-six *Paenibacillus* sp., well known to promote plant growth and to be involved in the biosynthesis of antibiotics and hydrolytic enzymes, were used to construct a phylogenetic tree (Table 11.2). The phylogenetic tree based on 16S rRNA nucleotide sequences of the 56 *Paenibacillus* sp. isolated from various habitats (Table 11.2) grouped into 13 clusters (Fig. 11.1). The 16S rRNA phylogenetic tree constructed in this study (Fig. 11.1) has shown almost similar topology to that of previously published trees on 16S rRNA phylogeny (Hong et al. 2009; Jin et al. 2011b).

Paenibacillus cellulositrophicus KCTC 13135, *Paenibacillus lactis* 154, *Paenibacillus lautus* Y412MC10, and *Paenibacillus vortex* V453 were grouped into Cluster 1 based on 16S RNA phylogenetic analysis (Fig. 11.1). *P. cellulositrophicus* KCTC 13135 is a thermophilic (50 °C) facultative anaerobe isolated from soil (Akaracharanya et al. 2009), whereas *P. lactis* 154, *P. lautus* Y412MC10, and *P.*

Table 11.1 Metadata of finished, draft and permanent draft genome of *Paenibacillus* species

Genomes	Sources of isolation	GenBank Accession no.	IMG Taxon ID	Genome status	Genome size (Mb)	% GC	Genes	Proteins
*P. lautus*Y412MC10	Obsidian Hot Spring (Yellowstone National Park, Montana, USA)	NC_013406	646311929	F	7.12	51	6444	6238
P. larvae larvae 4–309, DSM 25430	American foulbrood infected honey bee hive	NC_023134	2523231078	F	4.06	45	4133	3928
*P. lactis*154	Bioreactor	AGIP00000000	2506783046	F	6.84	52	6234	6149
*P. mucilaginosus*K02	Soil of maize-farming fields (Guizhou, China)	NC_017672.3	2513237182	F	8.82	58	7578	7354
*P. mucilaginosus*KNP414	Soil of Tianmu Mountain (Zhejiang, China)	NC_015690	650716070	F	8.66	58	7983	7811
*P. mucilaginosus*3016	Rhizosphere soil (Shandong, China)	NC_016935	2512564039	F	8.73	58	7528	7057
P. polymyxa E681	Rhizosphere of winter barley (Chonnam, South Korea)	NC_014483	648028048	F	5.39	46	4933	4805
*P. polymyxa*CR1	Corn rhizosphere	NC_023037	–	F	6.02	46	5510	5283
*P. polymyxa*SC2	Rhizosphere of pepper (Guizhou, China)	NC_014622	649633079	F	6.24	45	6286	6032
P. polymyxa M1	Surface-sterilized wheat root tissues	NC_017542	2517572207	F	6.23	45	5516	5364

*P. polymyxa*SQR-21	Rhizosphere of healthy watermelon plants	CP006872	–	F	5.83	46	5174	5024
*P. terrae*HPL-003	Soil of forest residue, Daejeon (Republic of Korea)	NC_016641	2511231079	F	6.08	47	5642	5525
Paenibacillus sp. JDR-2	Sweet gum stem wood buried in surface soil	NC_012914	644736396	F	7.18	50	6414	6213
Paenibacillus sp. J10	–	–	2505679063	F	4.7	52	4442	4328
P. alvei A6-6i-x	Leaf (tomato growing field - Virginia Eastern Shore	ATMS00000000	2541047089	D	6.48	47	5669	5584
*P. alvei*DSM 29	European foulbrood infected honey bee hive	AMBZ00000000	2561511085	D	6.83	46	6790	6605
P. alvei TS-15	Soil (tomato growing field – Virginia Eastern Shore)	ATMT00000000	2541048009	D	6.71	47	5867	5784
*P. azotofixans*ATCC 35681	Wheat roots (Parana state, Brazil)	ASQQ00000000	–	D	5.36	51	–	–
*P. barengoltzii*G22	–	ASSZ00000000	–	D	4.78	52	4394	4307
*P. curdlanolyticus*YK9	Soil (Kobe, Japan)	AEDD00000000	648276707	D	5.45	52	4957	4824
*P. dendritiformis*C454	Soil (Tel Aviv, Israel)	AHKH00000000	2513237294	D	6.37	54	5690	5660

(continued)

Table 11.1 (continued)

Genomes	Sources of isolation	GenBank Accession no.	IMG Taxon ID	Genome status	Genome size (Mb)	% GC	Genes	Proteins
*P. elgii*B69	Soil samples (Hangzhou, China)	AFHW00000000	2547132108	D	7.96	53	7828	7777
P. forsythiae T98	Rhizosphere soil of *Forsythia mira*, (Beijing, China)	ASSC00000000	–	D	5.08	53	–	–
P. graminis RSA19	Maize rhizosphere soil (Ramonville, France)	ASSG00000000	–	D	6.99	50	–	–
*P. larvae larvae*BRL-230010	Scales collected from a single severely diseased colony (Berkeley, CA, USA)	AARF00000000	641736255	D	4.01	44	5021	4955
P. larvae larvae B-3650	Lab culture	–	649989978	D	4.35	44	3630	3558
*P. lentimorbus*NRRL B-30488	Cows' milk	ANAT00000000	2554235229	D	3.91	46	4404	4292
*P. massiliensis*T7	Willow rhizosphere (Beijing, China)	ASSE00000000	–	D	6.3	48	–	–
P. peoriae KCTC 3763	Soil (Republic of Korea)	AGFX00000000	2547132140	D	5.77	46	5165	5073
P. polymyxa ATCC 842	Rhizosphere soil	AFOX00000000	2547132099	D	5.89	45	5468	5348
P. polymyxa ATCC 12321	Spoiled starch	ARYD00000000	2554235114	D	4.13	46	4201	4120
*P. polymyxa*OSY-DF	Fermented vegetables	AIPP00000000	2548876929	D	5.69	45	5069	5003

*P. polymyxa*1–43	Corn rhizosphere, (Shanxi China)	ASRZ00000000	–	D	5.97	45	–	–
P. polymyxa TD94	*Scutellaria* rhizosphere (Liaoning, China)	ASSA00000000	–	D	6.0	45	–	–
P. popilliae ATCC 14706	From commercial spore dust (CCEB 296) made with strain DeBryne 14F-D80 (H. Tashiro).	BALG00000000	2537561634	D	3.83	51	3934	3855
P. riograndensis SBR5	Wheat field (south of Brazil)	AGBD00000000	2548876532	D	7.41	51	7567	7494
P. senegalensis JC66	Fecal flora of a healthy patient	CAES00000000	2547132139	D	5.49	48	5134	5040
*P. sonchi*X19-5	Rhizosphere soil of *Sonchus oleraceus*	AJTY00000000	2548877040	D	7.51	50	7606	7511
P. sophorae S27	Rhizosphere of *Sophora japonica* (Beijing, China)	ASSF00000000	–	D	8.42	48	–	–
P. vortex V453	Rhizosphere (Tel Aviv, Israel)	ADHJ00000000	649989979	D	6.38	49	5993	5926
P. zanthoxyli JH29	Rhizosphere soils of *Zanthoxylum Simulans* (Beijing, China)	ASSD00000000	–	D	5.05	51	–	–
*Paenibacillus*sp. HGF5	Human intestinal microflora, USA	AEXS00000000	651324080	D	6.95	51	6578	6496

(continued)

Table 11.1 (continued)

Genomes	Sources of isolation	GenBank Accession no.	IMG Taxon ID	Genome status	Genome size (Mb)	% GC	Genes	Proteins
*Paenibacillus*sp. HGH0039	Human intestinal microflora, USA	AGEN00000000	2541046994	D	6.29	53	5758	5669
*Paenibacillus*sp. HW567	–	ARFI00000000	–	D	6.32	67	6047	5944
Paenibacillus sp. PAMC 26794	Tundra grasslands (Alaska)	ANHX00000000	2551306498	D	6.65	46	5969	5879
*Paenibacillus*sp. J14	–	JADQ00000000	2528768218	D	4.86	52	4552	4435
Paenibacillus sp. oral taxon 786 str. D14	Oral swab from female patient (USA)	ACIH00000000	647533191	D	5.09	52	4529	4460
Paenibacillus sp. HGF7	–	AFDH00000000	651324081	D	6.28	53	6075	5992
Paenibacillus sp. OSY-SE	Soil	ALKF00000000	2551306117	D	6.93	49	6337	6288
*Paenibacillus*sp. ICGEB2008	Gut of *Helicoverpa armigera*	AMQU00000000	2551306396	D	5.69	46	5147	4852
*Paenibacillus*sp. 1–18	Wheat rhizosphere, (Beijing, China)	ASSB00000000	–	D	5.4	46	–	–
Paenibacillus sp. 1–49	Corn rhizosphere (Shanxi, China)	ASRY00000000	–	D	5.62	47	–	–
Paenibacillus sp. JCM 10914	Gut of a soil-feeding termite	NZ_BAUO00000000	–	D	6.11	48	6149	6080
Paenibacillus sp. FSL H7-689	Milk	ASPU00000000	–	D	6.84	46	6008	5913
Paenibacillus sp. FSL H8-237	Milk	ASPV00000000	–	D	7.32	44	6563	6477

Paenibacillus sp. FSL H8-457	Milk	ASPW00000000	–	D	7.08	51	6415	6337
Paenibacillus sp. FSL R5-192	Milk	ASPW00000000	–	D	7.08	46	6275	6163
*Paenibacillus*sp. FSL R5-808	Milk	ASPT00000000	–	D	6.45	49	5922	5847
*Paenibacillus*sp. FSL R7-269	Milk	ASPS00000000	–	D	7.6	51	6816	6726
Paenibacillus sp. FSL R7-277	Milk	ASPX00000000	–	D	7.6	52	6523	6429
Paenibacillus sp. G1	–	CBVJ000000000	–	D	6.26	48	–	–
*Paenibacillus*sp. GD11	Human gut microbiota by culturomics	CBLK000000000	–	D	5.58	49	–	–
Paenibacillus sp. MAEPY1	Malaysian landfill leachate	AWUJ00000000	–	D	7.48	46	–	–
Paenibacillus sp. MAEPY2	Malaysian landfill leachate	AWUK00000000	–	D	7.48	46	–	–
Paenibacillus sp. WLY78	Bamboo rhizosphere (Beijing, China)	ALJV00000000	–	D	5.91	45	–	–
P. alginolyticus DSM 5050	Soil	AUGY00000000	2524614879	P	8.33	45	8232	8060
P. assamensis DSM 18201	Warm spring	AULU00000000	2524023086	P	5.03	43	4520	4415
P. barengoltzii J12	Spacecraft	–	2528768208	P	4.7	52	4414	4291
P. daejeonensis DSM 15491	Soil	ARKE00000000	2519103188	P	7.46	53	6524	6446
P. fonticola DSM 21315	Warm spring	ARMT00000000	2519899635	P	6.31	48	5753	5662

(continued)

Table 11.1 (continued)

Genomes	Sources of isolation	GenBank Accession no.	IMG Taxon ID	Genome status	Genome size (Mb)	% GC	Genes	Proteins
P. ginsengihumi DSM 21568	Soil of a ginseng field	ARKW00000000	2521172661	P	5.67	57	5245	5150
P. harenae DSM 16969	Desert sand	AULV00000000	2523533617	P	6.97	51	6377	6249
P. larvae larvae 08–100, DSM 25719	–	ADFW00000000	2524023248	P	4.57	44	5020	4843
P. massiliensis DSM 16942	Human blood	ARIL00000000	2517572189	P	6.39	49	5585	5475
P. pasadenensis DSM 19293	Clean room floor	AULW00000000	2524023087	P	5.71	63	4971	4870
P. panacisoli DSM 21345	Soil of a ginseng field	AUFO00000000	2524614514	P	6.32	48	5719	5591
P. pinihumi DSM 23905	Rhizosphere of the pine trees (Daejeon, Republic of Korea)	AULX00000000	2524023129	P	6.76	49	6170	6064
P. sanguinis DSM 16941	Human blood	ARGO00000000	2517572150	P	4.8	49	4501	4411
P. taiwanensis DSM 18679	Farmland soil	AULE00000000	2524614883	P	5.24	45	4780	4679
P. terrigena DSM 21567	Coastal soil (Chiba, Japan)	ARGP00000000	2517572151	P	6.36	46	5958	5865
P. uliginis N3/975	Fen peat soil of a nitrogen fertilization long-term experiment	–	2529292568	P	6.45	45	6136	6033
Paenibacillus sp. URHA0014	Mediterranean grassland soil	–	2556921041	P	7.37	45	6641	6504
*Paenibacillus*sp. J6	Rhizosphere	–	2528768219	P	4.83	52	4519	4406

– Genomes not available in the database, F Finished, D Draft, P Permanent draft

Table 11.2 *Paenibacillus* sp. used to construct 16S rRNA phylogenetic tree

Strain	NCBI Taxon ID	Genome Status	Genome Size (Mb)	16s rRNA (gi no.)[a]	Sources of isolation	References
P. lautus Y412MC10	481743	F	7.12	646360186[b]	Obsidian Hot Spring (Yellowstone National (Park, Montana, USA)	Mead et al. (2012)
P. polymyxa M1	1052684	F	6.23	2518127049[b]	Surface-sterilized wheat root tissues	Niu et al. (2011)
*P. polymyxa*SC2	886882	F	6.24	649679891[b]	Rhizosphere of pepper (Guizhou, China)	Ma et al. (2011)
P. lactis 154	743719	F	6.84	2507047847[b]	Bioreactor	Scheldeman et al. (2004)
*P. mucilaginosus*3016	997761	F	8.73	CP003235.1	Rhizosphere soil (Shandong, China)	Ma et al. (2012)
*P. mucilaginosus*KNP414	1036673	F	8.66	CP002869.1	Soil of Tianmu Mountain (Zhejiang, China)	Lu et al. (2013)
P. mucilaginosus K02	1116391	F	8.82	CP003422.2	Soil of maize-farming fields (Guizhou, China)	–
Paenibacillus sp. JDR-2	324057	F	7.18	644856946[b]	Sweet gum stem wood buried in surface soil	Chow et al. (2012)
P. polymyxa E681	349520	F	5.39	648168277[b]	Rhizosphere of winter barley (Chonnam, South Korea)	Kim et al. (2010)
*P. terrae*HPL-003	985665	F	6.08	2511570078[b]	Soil of forest residue (Daejeon, Republic of Korea)	Shin et al. (2012), Song et al. (2014)
*P. alvei*A6-6i-x	1117109	D	6.48	528200848	Leaf (tomato growing field – Virginia Eastern Shore)	Luo et al. (2013)
P. alvei TS-15	1117108	D	6.71	2545554562[b]	Soil (tomato growing field – Virginia Eastern Shore)	Luo et al. (2013)
P. azotofixans ATCC 35681	1333534	D	5.36	11342579	Wheat roots (Paranà State, Brazil)	Xie et al. (2012a), Hong et al. (2009)

(continued)

Table 11.2 (continued)

Strain	NCBI Taxon ID	Genome Status	Genome Size (Mb)	16s rRNA (gi no.)[a]	Sources of isolation	References
*P. elgii*B69	1007103	D	7.96	–	Soil samples (Hangzhou, China)	Teng et al. (2012), Ding et al. (2011)
P. forsythiae DSM17842	1333861	D	5.08	84798579	Rhizosphere soil of *Forsythia mira* (Beijing, China)	Xie et al. (2012a), Hong et al. (2009)
*P. graminis*RSA19	1333858	D	6.99	5701910	Maize rhizosphere soil (Ramonville, France)	Berge et al. (2002), Xie et al. (2012a), Hong et al. (2009)
*P. peoriae*KCTC 3763	1087481	D	5.77	359804172	Soil (Republic of Korea)	Jeong et al. (2012)
*P. pinihumi*DSM 23905	1122924	D	6.76	256807276	Rhizosphere of the pine trees (Daejeon, Republic of Korea)	Kim et al. (2009a)
*P. polymyxa*ATCC 842	1036171	D	5.89	2547356833[b]	Rhizosphere soil	Jeong et al. (2011), Hong et al. (2009)
P. polymyxa ATCC12321	1206104	D	4.13	2554737808[b]	Spoiled starch	Tong et al. (2013)
P. polymyxa OSY-DF	1156938	D	5.69	2550365550[b]	Fermented vegetables	Huang and Yousef (2012)
P. sophorae S27	682957	D	8.42	289623203	Rhizosphere of *Sophora japonica*(Beijing, China)	Jin et al. (2011a), Xie et al. (2012a)
*P. sonchi*X19-5	1173684	D	7.51	89033260	Rhizosphere soil of *Sonchus oleraceus*	Hong et al. (2009), Xie et al. (2012a)
P. terrigena DSM 21567	1122927	D	6.36	121308845	Coastal soil (Chiba, Japan)	Xie and Yokota (2007)
P. zanthoxyli JH29	1333860	D	5.05	94183943	Rhizosphere soils of *Zanthoxylum simulans* (Beijing, China)	Ma et al. (2007a), Hong et al. (2009)
Paenibacillus sp. A9	1284352	D	5.48	2554317331[b]	Soil	Jiang et al. (2013)
*P. curdlanolyticus*YK9	717606	D	5.45	648725777[b]	Soil (Kobe City, Japan)	–

P. vortex V453	58172	D	6.38	650065237[b]	Rhizosphere	Sirota-Madi et al. (2010)
*P. riograndensis*SBR5	1073571	D	7.41	2549005511[b]	Wheat field (Brazil)	Beneduzi et al. (2011)
P. beijingensis DSM24997	1126833	–	–	363498786	Jujube rhizosphere soil (Beijing, China)	Gao et al. (2012)
*P. brasilensis*PB172	128574	–	–	219857518	Rhizosphere of maize, (Cerrado, Brazil)	von der Weid et al. (2002)
*P. borealis*DSM13188	160799	–	–	219878160	Spruce forest humus (Finland)	Elo et al. (2001)
P. castaneae DSM 19417	474957	–	–	157787625	Phyllosphere of *Castanea sativa* (Spain)	Valverde et al. (2008)
P. catalpae DSM 24714	1045775	–	–	336283389[b]	Rhizosphere soil of *Catalpa speciosa*	Zhang et al. (2013)
*P. cellulositrophicus*KCTC 13135	562959	–	–	325672522	Soil (Thailand)	Akaracharanya et al. (2009)
P. donghaensis KCTC 13049	414771	–	–	118766593[b]	Deep-sea sediment	Choi et al. (2008a)
P. filicis JCM 16417	669464	–	–	256807274	Rhizosphere of ferns (Daejeon, Republic of Korea)	Kim et al. (2009b)
*P. frigoriresistens*JCM 18141	1143711	–	–	374923057	Peat bog sample (Mohe County, Heilongjiang Province, Northern China)	Ming et al. (2012)
*P. hordei*JCM 17570	980239	–	–	340780743	Naked barley (South Korea)	Kim et al. (2013)
*P. jilunlii*Be17	682956	–	–	289623202	Rhizosphere soil of *Begonia semperflorens*, (Beijing Botanical Garden, PR China)	Jin et al. (2011b), Xie et al. (2012a)
*P. macquariensis*JCM 14954	467974	–	–	157073843	Soil samples (Oblast Magadan, Russian Far East)	Hoshino et al. (2009)
*P. marinum*strain THE22	1033264	–	–	333756450	Sea hot spring “Ain Echefa” (Tunisia)	Bouraoui et al. (2013)

(continued)

Table 11.2 (continued)

Strain	NCBI Taxon ID	Genome Status	Genome Size (Mb)	16s rRNA (gi no.)[a]	Sources of isolation	References
*P. marinisediminis*17886	1031539	–	–	333123116	Marine sediment (south coast of the Republic of Korea)	Lee et al. (2013a)
*P. odorifer*TOD45	189426	–	–	265678582	Soil, plant rhizospheres, plant roots and pasteurized pureed vegetables	Hong et al. (2009), Berge et al. (2002)
P. phyllosphaerae CECT 5862	274593	–	–	47059737	Phyllosphere of *Phoenix dactylifera*	Rivas et al. (2005a)
*P. pini*JCM 16418	1236976	–	–	256807275	Rhizosphere of pine trees	Kim et al. (2009c)
P. prosopidis DSM 22405	630520	–	–	225696302	Root nodules of *Prosopis farcta* (Tunisia)	Valverde et al. (2010)
P. sabinae T27	1268072	–	–	84798580	Rhizosphere soils of plants of the species *Sabina squamata*, *Weigela florida* and *Zanthoxylum simulans*	Ma et al. (2007b), Xie et al. (2012a), Hong et al. (2009)
P. swuensis JCM 18491	1178515	–	–	385654395	Soil (South Korea)	Lee et al. (2014)
P. taohuashanense DSM25809	1184688	–	–	386785732	Rhizosphere soil sample of Caragana kansuensis Pojark	Xie et al. (2012b)
*P. taihuensis*NBRC 108766	1156355	–	–	378947806	Decomposing algal scum (eutrophic lake)	Wu et al. (2013)
*P. triticisoli*DSM 25425	1155956	–	–	378926930	Wheat rhizosphere soil	Wang et al. (2013), Wang et al. (2014)
*P. validus*DSM 3037	1349783	–	–	1089786	Contaminant from plates with germinating spores of *Glomus intraradices*	Hildebrandt et al. (2006)

*P. wynnii*LMG22176	268407	–	–	343201518	Soil from 12 different locations (Mars Oasis, Alexander Island, Antarctica)	Rodríguez-Díaz et al. (2005), Hong et al. (2009)
*P. wooponensis*WPCB018	554310	–	–	197091737	Fresh water sample collected from Woopo wetland (Korea)	Baik et al. (2011)
*P. xylanilyticus*XIL14	248903	–	–	37624893	Xylan-containing agar plates exposed to air	Rivas et al. (2005b)

F Finished, D Draft

[a]gi Gene ID or sequence identification numbers

[b]16s rRNA nucleotide sequences retrieved from JGI-IMG

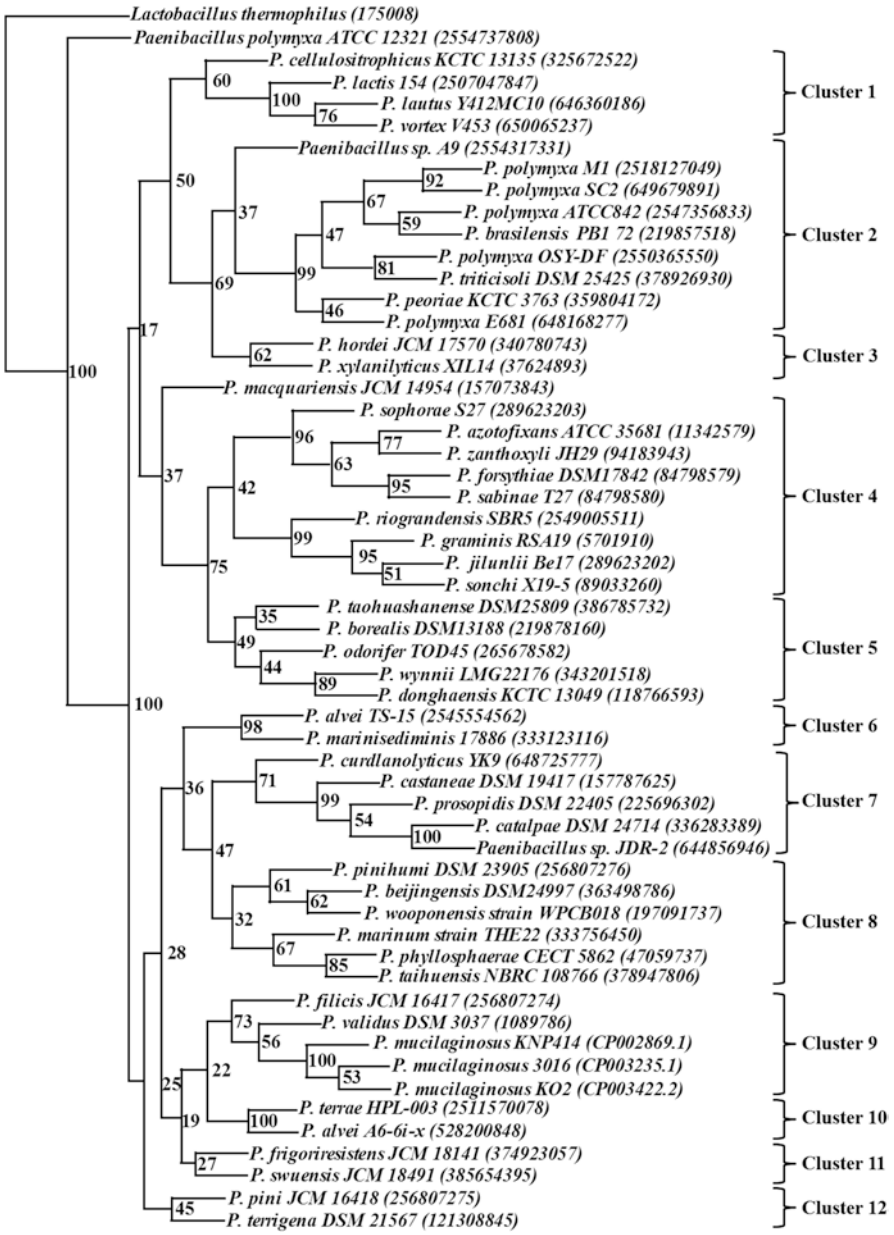

Fig. 11.1 16S rRNA phylogenetic tree of *Paenibacillus* species based on neighbour joining analysis was performed using PHYLIP software version 3.695. Bootstrap analyses were performed with 1000 cycles and values are given at nodes. Identification numbers (gi) of the respresentative sequences are given in parentheses. *Lactobacillus thermophillus* was used as an out group

vortex V453 are mesophiles isolated from a bioreactor, hot spring, and soil rhizosphere, respectively. *P. vortex* is the first sequenced genome providing the basis for the understanding of social organization and pattern formation within Gram-positive bacteria. *P. vortex* genome encodes an extensive set of transcription factors (TFs), two-component system (TCS), and defense-related genes which can support traits needed for thriving in heterogeneous, fluctuating, and highly competitive environment. Two other bacterial strains, *Paenibacillus* sp. JDR-2 and *P. lautus* Y412MC10, have more TCS genes in comparison to other Gram-positive bacteria (Sirota-Madi et al. 2010). Comparative genomic analysis of 500 complete bacterial genomes revealed that these bacteria can survive successfully in different environments if they possess extensive signal transduction and regulatory networks (Alon 2006; Galperin and Gomelsky 2005; Whitworth and Cock 2008). The analysis also revealed that *P. vortex* has many genes involved in the production of antimicrobial compounds and extracellular degrading enzymes (Sirota-Madi et al. 2010).

Except *P. polymyxa* ATCC 12321, all five *P. polymyxa* M1, *P. polymyxa* SC2, *P. polymyxa* E681, *P. polymyxa* ATCC842, and *P. polymyxa* OSY-DF are clustered together in Cluster 2 along with *Paenibacillus peoriae* KCTC 3763, *Paenibacillus brasiliensis* PB172, and *Paenibacillus triticisoli* DSM 25425 (Fig. 11.1). *P. polymyxa* M-1 produces polymyxin P encoded by the *pmxABCDE* gene cluster involved in suppressing phytopathogenic *Erwinia amylovora* and *Erwinia carotovora* (Gram-negative, facultative anaerobic, rod-shaped bacteria), the causative agents of the important plant diseases fire blight and soft rot, respectively. This finding suggested that *P. polymyxa* M-1 and antibiotic polymyxin P are a potential option to control fire blight, soft rot, and other plant diseases caused by Gram-negative bacteria (Niu et al. 2011). Polymyxin synthetase gene cluster from *P. polymyxa* M-1 consists of five open reading frames, *pmxA*, *pmxB*, *pmxE* involved in nonribosomal peptide synthesis and *pmxC* and *pmxD* and encoding ABC transporters (ATPase and permease components) (Shaheen et al. 2011). Similarly, *P. polymyxa* SC2 has also been widely used in biological control of soilborne plant diseases. It is known as an important plant growth-promoting rhizobacterium (PGPR) isolated from the rhizosphere of pepper in Guizhou, China (Zhu et al. 2008). Sequencing of the complete genome of *P. polymyxa* SC2 revealed that it consists of one circular chromosome (5.73 Mb) which possess many genes involved in antibiotic biosynthesis and one plasmid (510 kb) which carries many essential genes required for purine, pyrimidine, and lipid metabolism, as well as gene encoding for ribosomal proteins, translation elongation factors, and different types of DNA methyltransferase (Konz et al. 1997; Altena et al. 2000; Ma et al. 2011).

Complete genome sequence of *P. polymyxa* M-1 contains 41 kb gene cluster showing 96.41 % identity with polymyxin synthetase gene cluster of *P. polymyxa* E681 (Choi et al. 2009; Niu et al. 2013). Polymyxin produced by *P. polymyxa* E681 is a potent antimicrobial agent and can be used for the treatment of multidrug-resistant Gram-negative bacteria (Landman et al. 2008; Giamarellou and Poulakou 2009; Velkov et al. 2010). Genome analysis of *P. polymyxa* E681 revealed various genes encoding enzymes such as xylanases, pectic enzymes, cellulases, and amy-

lases that degrade plant-derived polysaccharides. It also has a gene cluster for lantibiotic production, but genes for nitrogen fixation were not detected (Kim et al. 2010). Genes cluster for lipopeptide antibiotics such as tridecaptin (58.5 kb) and fusaricidin (Li and Jensen 2008; Choi et al. 2008b) and the genes for biosynthesis of polymyxin (Choi et al. 2009), polyketides, lantibiotic, homoserine lactonase, and several extracellular carbohydrolases have been identified in the genome sequence of *P. polymyxa* ATCC 842. Comparative analysis of *P. polymyxa* genomes revealed the close relatedness between *P. polymyxa* ATCC 842 and *P. polymyxa* SC2 strains (Jeong et al. 2011) (Fig. 11.1). *P. polymyxa* OSY-DF also produces lantibiotic (paenibacillin) and polymyxin E1 (He et al. 2007). Draft genome sequence of *P. polymyxa* OSY-DF revealed two complete gene cluster of lantibiotic. One gene cluster (11.7 kb) was responsible for paenibacillin biosynthesis, and the other may encode a new kind of lantibiotic (de Jong et al. 2010). The analysis also identified many nonribosomal peptide synthetase (NRPS) genes (Huang and Yousef 2012). Phylogenetically, *P. peoriae* is closely related to *P. polymyxa* E681. Analysis of draft genome sequence of *P. peoriae* revealed gene clusters for the biosynthesis of tridecaptin, a heptapeptide antibiotic that is similar to hexapeptide fusaricidin antibiotics, and several NRPS genes encoding unknown products on different contigs. Many genes have been shown to encode for extracellular carbohydrases such as amylase, xylanase, cellulase, and several glucanases that may be responsible for the utilization of plant-derived polysaccharide in the rhizosphere (Jeong et al. 2012).

Phylogenetic analysis of 16S rRNA gene sequences of a novel nitrogen-fixing bacterium, BJ-18, isolated from wheat rhizosphere soil showed a close relation with *P. peoriae* DSM 8320 (99.05 %) and *P. brasiliensis* DSM13188 (98.55 %) (Wang et al. 2013). On the basis of phenotypic and genotypic characteristics, the BJ-18 strain was named *Paenibacillus beijingensis* BJ-18 (Wang et al. 2013). This name with a different type strain has been effectively published previously (Gao et al. 2012). Thus, *P. beijingensis* BJ-18 was renamed as *P. triticisoli* (triticum wheat; solum soil) (Wang et al. 2013, 2014). *Paenibacillus hordei* is closely related to *Paenibacillus xylanilyticus* XIL14T and grouped together in Cluster 3 (Fig. 11.1) (Kim et al. 2013).

Cluster 4 includes two distinct groups of *Paenibacillus* sp. In the first group, *Paenibacillus sophorae* S27 showed a close relation with *Paenibacillus azotofixans* ATCC35681, *Paenibacillus zanthoxyli* JH9, *Paenibacillus forsythiae* DSM 17842, and *Paenibacillus sabinae* T27 (Fig. 11.1). This was supported by phylogenetic analysis based on *nifH* gene sequences revealing that *P. sophorae* S27 is clustered with *P. forsythiae* (96.9 %), *P. zanthoxyli* (96.3 %), *Paenibacillus durus* (95.1 %), and *P. sabinae* (79.6 %) (Jin et al. 2011a).

In the second group, *P. riograndensis* SBR5 was grouped with *Paenibacillus graminis* RSA19, *Paenibacillus jilunlii* Be17, and *Paenibacillus sonchi* X19-5 (Fig. 11.1). Comparative analysis of N_2-fixing *Paenibacillus* strains revealed that a *nif* gene cluster (10.5–12 kb) comprising *nifB*, *nifH*, *nifD*, *nifK*, *nifE*, *nifN*, *nifX*, *hesA*, and *nifV* encoding Mo-nitrogenase is highly conserved. This analysis also identified two homologous alternative nitrogenases: V- and Fe-nitrogenase encoded by the *vnf* and *anf* genes, respectively, in some *Paenibacillus* species (Xie et al. 2014). The

draft genome of nitrogen-fixing bacteria *P. riograndensis* SBR5 showed 23 genes for nitrogen fixation and complete *nif* operon comprising the *nifBHDKENXV* genes. Several other copies of *nif* genes were identified along with the operon coding for alternative nitrogenase (*Anf*). Genome analysis also showed 46 sigma factors suggesting that it has a versatile transcriptional regulation and genes involved in antibiotics resistance such as ampicillin, tetracycline, erythromycin, fosfomycin, gentamicin, and bleomycin (Beneduzi et al. 2011). *Paenibacillus taohuashanense*, *Paenibacillus borealis* DSM 13188, *Paenibacillus odorifer* TDO45, *Paenibacillus wynnii* LMG22176, and *Paenibacillus donghaensis* KCTC 13049 were grouped together in Cluster 5 (Fig. 11.1). This topology was supported by 16S rRNA phylogenetic analysis performed by Xie et al. (2012b) revealing that nitrogen-fixing *P. taohuashanense* DSM25809 has close relation with *P. borealis* DSM 13188 (97.5 %), *P. odorifer* ATCC BAA-93 (97.3 %), *P. durus* DSM 1735 (97.0 %), and *P. sophorae* DSM23020T (96.9 %).

P. alvei and *Paenibacillus marinisediminis* were grouped together in Cluster 6 (Fig. 11.1). *P. alvei* is known to produce peptide antibiotics that affect a wide spectrum of Gram-positive and Gram-negative bacteria (Anandaraj et al. 2009). The genomes of the two strains, *P. alvei* A6-6i and TS-15, isolated from plant material and soil, respectively, were sequenced, and several genes involved in antimicrobial biosynthetic pathways were identified (Luo et al. 2013).

Paenibacillus curdlanolyticus YK9, *Paenibacillus castaneae* DSM 19417, *Paenibacillus prosopidis* DSM 22405, *Paenibacillus catalpae* DSM 24714, and *Paenibacillus* sp. JDR-2 are grouped together in Cluster 7. Only *Paenibacillus* sp. JDR-2 (finished) and *P. curdlanolyticus* YK9 (draft) genomes are sequenced.

Cluster 8 includes six *Paenibacillus* sp., out of which only *Paenibacillus pinihumi* DSM 23905 genome was sequenced. The remaining five strains, *P. beijingensis* DSM24997, *Paenibacillus wooponensis* WPCB018, *Paenibacillus marinum* strain THE22, *Paenibacillus phyllosphaerae* CECT 5862, and *Paenibacillus taihuensis* NBRC 108766, were identified on the basis of 16S RNA phylogenetic analysis (Fig. 11.1). Bouraoui et al. (2013) described in detail the xylanolytic, thermophilic, and facultatively halophilic species *P. marinum* (strain THE22) isolated from the water of thermal spring in the sea of Korbous, northeastern of Tunisia. 16S rRNA gene sequence analysis showed that strain THE22 is clustered with *P. phyllosphaerae* PALXIL04T (95.8 %).

Cluster 9 includes three species, *P. mucilaginosus* 3016, *P. mucilaginosus* KNP414, and *P. mucilaginosus* K02, whose genomes have been already sequenced, and two species, *P. filicis* JCM 16417 and *Paenibacillus validus* DSM 3037 which are not sequenced yet (Fig. 11.1).

P. mucilaginosus 3016 has been used as a microbial fertilizer in agricultural applications due to its growth-promoting properties (Liu et al. 2006; Hu et al. 2008). Many genes involved in the metabolism of nitrogen, phosphorus, and potassium, as well as nitrogen-fixing NifU domain-containing protein, potassium channel protein, and potassium-transporting ATPase subunit A were detected in the genome (Ma et al. 2012). In particular, the genome analysis of *P. mucilaginosus* KNP414 revealed eight genes related to nitrogen assimilation which help strain KNP414 to fix the

nitrogen and allow it to grow in a nitrogen-free environment even though the mechanisms to do so are still unknown (Lu et al. 2013).

Paenibacillus terrae HPL-003 and *P. alvei*A6-6i-x are clustered together in Cluster 10. *Paenibacillus terrae* HPL-003 is considered a very good xylanase producer (Hwang et al. 2011). *P. alvei* A6-6i-x is known to produce peptide antibiotics (Anandaraj et al. 2009; Luo et al. 2013).

Cluster 11 includes *Paenibacillus frigoriresistens* JCM 18141 and *Paenibacillus swuensis* JCM 18491. Genomes of these strains have not been sequenced yet, but strains were identified on the basis of 16S rRNA (Fig. 11.1).

Paenibacillus pini JCM 16418 is closely related to *Paenibacillus terrigena* DSM 21567 and they are clustered together in Cluster 12. Permanent draft genome sequence of *P. terrigena* DSM 21567 is available in NCBI and IMG database. 16S rRNA phylogenetic analysis of *Paenibacillus* sp. revealed that *P. terrigena* DSM 21567 exhibited very low levels of similarity (not more than 94 %) which is sufficient to indicate that strain DSM21567 represents a novel member of the genus (Stackebrandt and Goebel 1994; Xie and Yokota 2007).

11.3 Ecology of *Paenibacillus* Species

Endospore-forming *Paenibacillus* bacteria are essentially ubiquitous. They have been isolated from a wide range of extremely diverse habitats (McSpadden Gardener 2004; Lal and Tabacchioni 2009). Cold and warm springs, glaciers, sea sediments, desert soil, animal feces, plant nodules, industrial wastewater, etc. are some of the habitats where different *Paenibacillus* species can thrive. *Paenibacillus* bacteria have been also isolated from human specimen, namely blood, urine, cerebrospinal fluid, and sputum and have been associated with some human health disorders, such as bacteremia, endocarditis, meningitis, prosthetic osteoarticular infection, and chronic prostatitis (Reboli et al. 1989; Noskin et al. 2001; Roux and Raoult 2004; Ko et al. 2008; Ouyang et al. 2008; Rieg et al. 2010).

The spread of *Paenibacillus* sp. over so different habitats reflects a tremendous degree of ecologically relevant diversity at the species level in this genus, as revealed by the phenotypic characterization of culture isolates. For example, although most species are mesophile, several psychro- or thermo-tolerant species are able to colonize or to survive in extreme environments, such as hot springs and Antarctic soil (Mead et al. 2012; Van Houdt et al. 2013). Diversity can also be observed as far as nitrogen fixation is concerned. In fact, nitrogen fixation occurs in *P. azotofixans*, *P. macerans*, *P. polymyxa*, *Paenibacillus massiliensis*, *Paenibacillus stellifer*, *P. forsythiae*, *P. sophorae*, and in several other species, but not in the majority of *Paenibacillus* species (Xie et al. 2012a, b). Another example of ecological diversity at the species level concerns *Paenibacillus* invertebrate pathogens: *P. larvae*, known to cause American foulbrood in honeybees, and *P. popilliae* and *P. lentimorbus*, causative agents of type A and type B milky disease in Japanese beetle and related scarab larvae (Pettersson et al. 1999; Ashiralieva and Genersch 2006). On the other

hand, niche specificity and important ecological activities appear to span phylogenetic boundaries. Most species can survive as saprophytes in soils, which are considered the primary reservoirs of these bacteria; however, most viable cells probably occur as inactive spores at any given time. Furthermore, multiple species can be recovered as epiphytes and endophytes of plants and animals, as well as foodstuffs and composts derived from them. The rich variety of organic substrates and micro-niches present in those environments supports a complex milieu of microbial species, so it is perhaps not surprising that multiple species of *Paenibacillus* inhabit them. Moreover, it is well known that most *Paenibacillus* species produce a wide array of hydrolytic enzymes, such as chitinases, amylases, xylanases, cellobiohydrolases, proteases, etc., which can confer an advantage in the colonization of the abovementioned environments (Mavingui and Heulin 1994; Budi et al. 2000; Lee and Lim 2004). Thus, it is reasonable to infer that functionally distinct isolates occur within and among the phylogenetically distinct species of this genus. This is clearly the case for isolates functionally defined as "beneficial" to plant health because only a fraction of isolates of *P. polymyxa*, for example, can be shown to inhibit the activity of a pathogen under a given set of conditions (McSpadden Gardener 2004).

Spore formation and metabolic versatility associated with other characteristics as, for example, the ability to fix nitrogen, to solubilize phosphorus, to degrade polyaromatic hydrocarbons, and to produce antimicrobial substances and phytohormones may well explain the impressive display of colonization ability of the genus *Paenibacillus*.

Beside soil, the major isolation source of *Paenibacillus* spp. is represented by plants; indeed, around 40 % of *Paenibacillus* species have been isolated from different soil types, such as volcanic, desert, antarctic, and alkaline soil, but more than 20 % can be isolated from different plant species. As far as the latter are concerned, the rhizosphere is the major source of new *Paenibacillus* species; however, several species have also been isolated from the phyllosphere, plant tissues, and root nodules.

11.3.1 Paenibacillus *in the Rhizosphere*

Multiple *Paenibacillus* sp. can be readily cultured from both bulk and rhizosphere soils. Culturable counts of these bacteria range from log 3 to log 6 cells per gram fresh weight, with soil counts typically exceeding those obtained from the rhizosphere (McSpadden Gardener 2004). Single *Paenibacillus* species can colonize different plant species: *P. polymyxa*, for example, has been recovered from a large variety of plants (Lal and Tabacchioni 2009). While multiple species of *Paenibacillus* can be detected in the soils and rhizosphere, few studies have addressed the question of which are the most commonly isolated species or the relative dominance of single *Paenibacillus* species. Native rhizosphere-colonizing populations of *Paenibacillus* have been shown to vary with time, soil type, crop cultivar, and cropping pattern. da Mota et al. (2005), while studying the *Paenibacillus* community in two different

types of soil in Brazil, found that in one soil, *P. amylolyticus* and *P. graminis* were more abundant, whereas in the other, *Paenibacillus flavisporus* were most prevalent. Also, at the intraspecific level, natural factors can significantly influence the population structure. In fact, when four different cultivars of maize were planted in the same type of soil, the same authors found that the *P. polymyxa* strains isolated from the rhizospheres of the various maize cultivars were genotypically significantly different. Cheong et al. (2005) investigated the diversity of root-associated *Paenibacillus* spp. in winter crops. They found that 56 % of *Paenibacillus* isolates were classified as *P. polymyxa*, the type species for the genus, implying that *P. polymyxa* is the dominant species among root-associated *Paenibacillus* spp. in winter crops. Interestingly, as far as nitrogen fixation ability is concerned, 49 % of the *Paenibacillus* isolates did not contain the *nifH* gene. Moreover, the majority of the *Paenibacillus* isolates exhibited antagonistic activities toward various plant pathogens, suggesting that *Paenibacillus* spp. may be effective as biological control agents; however, no significant relationship between root colonization ability, the presence of the *nifH* gene, and plant growth-promoting effect could be observed. Furthermore, Cheong et al. (2005) tested the *Paenibacillus* strains for their ability to secrete extracellular enzymes, such as amylase, cellulose, and protease and found that the vast majority of isolates exhibited strong hydrolytic activity, indicating that the synthesis of extracellular hydrolytic enzymes would seem to be very common among *Paenibacillus* bacteria isolated from plant roots and that these enzymes are apparently necessary for adaptation to the rhizosphere soil environment.

11.3.2 **Paenibacillus** *in Root Nodules and Plant Tissues*

Prosopis farcta, a woody legume, is a widespread species in North Africa and the Middle East, whose root noodles harbor a variety of nodulating and non-nodulating bacteria. Among the latter, several nitrogen-fixing *Paenibacillus* sp. have been recovered, and a new species, *P. prosopidis*, has been described (Valverde et al. 2010). This is not the only endophytic *Paenibacillus* species found in root nodules. Recently, a new species, *Paenibacillus endophyticus*, has been found in nodules of *Cicer arietinum* and a strain of *P. polymyxa* has been observed to invade roots and root nodules of soybean upon inoculation (Annapurna et al. 2013; Carro et al. 2013). It has been assumed that the common trait of these endophytic bacteria is their inability to nodulate; therefore, the endophytic *Paenibacillus* sp. so far isolated can be considered as nonsymbiotic endophytic bacteria associated to root nodules. In fact, it has been observed that root nodules of legume species can be invaded and massively colonized by different bacterial taxa and that these replace the putative nitrogen-fixing rhizobia symbionts in the nodules. However, in contrast with the general assumption of *Paenibacillus* endophytic strains as nonsymbiotic bacteria, Latif et al. (2013) isolated a strain of *Paenibacillus* capable of nodulating roots of red clover (*Trifolium pratense*). The activity the various endophytic *Paenibacillus*

species exert in root nodules is not always clear. Annapurna et al. (2013) have reported a stimulatory effect on soybean growth by a strain of *P. polymyxa*. Upon colonization of root nodules by this strain alone or in combination with *Bradyrhizobium japonicum*, an increase in both shoot and root dry weight was observed.

Endophytic *Paenibacillus* bacteria are not limited only to root nodules legumes. *Paenibacillus* sp. has been recovered as an endophyte from different plants like pine, ginseng, coffee, and poplar. Recently a *P. polymyxa* strain has been isolated from the internal stem tissue of a lodgepole pine (*Pinus contorta* var. *latifolia* (Dougl.) Engelm.) seedling naturally regenerating in central British Columbia, Canada (Bal et al. 2012). This strain is unique as it is the only microorganism that has been reported to fix substantial amounts of N_2 in association with tree species (Anand et al. 2013). Reintroduction of the strain to lodgepole seed under controlled environment results in rhizospheric and endophytic colonization of resultant seedlings as well as provision of increasing amounts of foliar N_2 as seedlings develop. Another strain of *P. polymyxa* has been isolated from the internal tissues of ginseng leaves. Inoculation of the same strain by foliar application enhanced plant growth parameters (Gao et al. 2015). A recent study reveals the importance of the *Paenibacillus* strains as endophytic bacteria in micropropagated tissue cultures of woody plants (Ulrich et al. 2008). In fact, high densities of endophytic *Paenibacillus* bacteria were found in plant material from poplar, larch, and spruce that had been micropropagated for at least 5 years. The majority of the isolates showed a close relationship to *Paenibacillus humicus*. Faria et al. (2013) isolated several endophytic strains belonging to the species *P. lentimorbus* and *Paenibacillus macerans* from the meristem tissues of in vitro grown orchid *Cymbidium eburneum*. They were all able to synthesize indole-3- acetic acid (IAA), and when inoculated in *Cattleya* seedlings, they all enhanced biomass in both shoots and roots.

11.3.3 Paenibacillus *in the Phyllosphere*

Various *Paenibacillus* species have been found on the leaves of different plant species (Rivas et al. 2005a, 2007; Valverde et al. 2008), able to excrete a diverse range of extracellular polysaccharide-hydrolyzing enzymes, including cellulases and xylanases. The abundance and hydrolytic ability of these bacteria indicate that they could have a prominent role in the degradation of leaves after drying and detachment from the plant. In fact, it has been suggested that these and other polymer-degrading bacteria can be involved in the first stages of the degradation processes in leaves. For example, in the phyllosphere of palm tree bracts (*Phoenix dactilyfera*), several of these bacteria have been found, mostly belonging to the genus *Paenibacillus* (*Paenibacillus phyllospherae* and *Paenibacillus cellulolyticus*) (Rivas et al. 2007). *P. phyllosphaerae* is able to hydrolyze cellulose and xylan, the most abundant polysaccharides and the major components of the plant cell wall (Rivas

et al. 2005a). In the case of the sweet chestnut (*Castanea sativa*), degradation of leave tissues starts when the leaves are still attached to the tree after drying. Among polymer-degrading bacteria found on the leaves of this plant a new species, *P. castaneae* has been isolated (Valverde et al. 2008).

11.4 *Paenibacillus* spp. as Plant Growth-Promoting Rhizobacteria

Plant growth-promoting rhizobacteria (PGPR) can promote plant growth either through direct effects or by indirect effects – the former including the production of phytohormones, the solubilization of soil phosphorous and iron and providing the host plant with fixed nitrogen (N_2) and the latter involving the suppression of plant diseases caused by deleterious microorganisms and stimulation of plant host defense mechanisms (Kloepper and Metting 1992; Kuklinsky-Sobral et al. 2004). As shown in Table 11.3, several species of the *Paenibacillus* genus have been described as plant growth promoters (PGPs) exerting their activity by multiple mechanisms such as phytohormone production, N_2-fixation, phosphorous solubilization, and antagonistic activity against soilborne pathogens (Govindasamy et al. 2011).

11.5 Production of Plant Growth Regulators, Nutrient Supply, and N_2-Fixation

Bacteria belonging to different *Paenibacillus* species isolated from soils and the rhizosphere of crop plants and used as rhizosphere inoculum, effectively improve plant growth (von der Weid et al. 2003; Lapidot et al. 2015; Naing et al. 2015). Plant growth promotion by strains isolated from sources other than soil and rhizosphere of crop plants has been also described, providing the evidence for utilizing bacterial strains from unconventional sources for plant growth promotion (Das et al. 2010; Chaudhry et al. 2013).

Although most PGP strains belonging to the *Paenibacillus* genus have been described as N_2-fixing bacteria, their involvement in the soil phosphate solubilization and production of phytohormones has also been reported (Das et al. 2010; Turan et al. 2012; Khan et al. 2012a, b; Kadyan et al. 2013; Faria et al. 2013; Pandya et al. 2015). *P. elgii* isolate SMA-1-SDCH02, recovered from chitin-rich soil, displayed mineral phosphate solubilization apart from its chitinolytic and antifungal activities to promote the growth of groundnut and tobacco plants in greenhouse and under in vitro studies, respectively. This isolate significantly enhanced the growth of the groundnut and tobacco in terms of shoot height, root length, and fresh and dry weight besides increasing the total chlorophyll content in the leaves (Das et al. 2010).

The effect of inoculation of wheat with *P. polymyxa* RC05 on yield and phosphorus solubilization was investigated in field trials. Although this strain resulted to be

Table 11.3 Plant growth promoting activity of *Paenibacillus* sp. bacteria

Strain	Source	Activity	Tests	References
P. alvei K165	Tomato root tips	Biocontrol against *Fusarium oxysporum* f.sp. *melonis* and *Verticillium Dahliae*	Field	Antonopoulos et al. (2008), Charalambous et al. (2013)
P. elgii SMA-1-SDCH02	Soil (premises of a chitin/chitosan producing company)	PGP (groundnut, tobacco)	Gnotobiotic system	Das et al. (2010)
P. elgii HOA73	Tomato field	Biocontrol against root knot nematode *Meloydogine incognita* in tomato	Greenhouse	Nguyen et al. (2013)
P. ehimensis RS820	Vegetable garden	Biocontrol against root knot nematode *M. incognita* in tomato	Greenhouse	Hong et al. (2013)
P. kribbensis PS04	Soil from insecticidal botanical garden	Biocontrol of *Rhizoctonia solani* in rice	Greenhouse	Gao and Liao (2014)
P. lentimorbus B30488^{r}	Cow's milk	Biocontrol against *Alternaria solani* in tomato, PGP (chickpea) in the presence of Cr	Greenhouse	Khan et al. (2012a, b)
P. macerans	Meristems tissues of *Cymbidium eburneum* orchids	PGP (*Cattleya loddigesii*)	Greenhouse	Faria et al. (2013)
P. polymyxa P2b-2R	Internal stem tissues of naturally regenerating pine seedlings	PGP (pine)	Gnotobiotic system	Anand et al. (2013)
P. polymyxa GBR-1	Rotten ginseng roots	Biocontrol against root knot nematode *M. incognita* in tomato	Greenhouse	Khan et al. (2008)
P. polymyxa SQR-21	Watermelon rhizosphere	Biocontrol against *F. oxysporum* f.sp. *niveum*	Greenhouse	Raza et al. (2009)

(continued)

Table 11.3 (continued)

Strain	Source	Activity	Tests	References
P. polymyxa 12.4.1	Marine clay soil	Biocontrol of *F. oxysporum* f.sp. *radicis lycopersici* and *Phytium aphanidermatum* in tomato	Greenhouse	Postma et al. (2013)
P. polymyxa RC05	Wheat rhizosphere	PGP (wheat)	Field	Turan et al. (2012)
P. polymyxa E681	Winter barley rhizosphere	Biocontrol against soilborne pathogens complex of sesame *Pseudomonas syringae*, *Phytophthora capsici*	Field, greenhouse	Ryu et al. (2006), Lee et al. (2012b), (2013b)

effective in enhancing wheat yield and phosphorus (P)-solubilization processes in the soil in comparison to the control, it resulted to be less effective than *Bacillus subtilis* OSU-142 and *Azospirillum brasilense* Sp245 under the same experimental conditions demonstrating that plant growth promotion may vary depending not only on growth conditions and crop management but also on plant and bacterial species (Turan et al. 2012).

P. lentimorbus strain B-30488r (B-30488r) was reported both as plant growth-promoting and bioremediation agent useful in Cr-contaminated rhizosphere soil of chickpea. This strain, isolated from Sahiwal cow's milk, shows antagonism against phytopathogens, *Fusarium oxysporum* f. sp. *ciceri* and *Alternaria solani* (DasGupta et al. 2006; Chaudhry et al. 2013). In vitro studies showed that it can tolerate 200 µg ml-1 of Cr and produce the plant growth-promoting substance indole acetic acid (IAA) in the presence of inorganic Cr. Both in absence and presence of supplemented Cr(VI) the enhancement of biofilm formation by sodium alginate (SA) and calcium chloride ($CaCl_2$) as compared to unsupplemented control was also observed. The plant growth-promoting effects caused by *P. lentimorbus* B-30488^r were evaluated in greenhouse experiments on chickpea plants cultivated in the presence of Cr(VI). Based on the measure of shoot and root length and plant dry matter, the authors suggested a phytoprotective role of the biofilm produced acting as a shield in preventing the direct access of toxic Cr to plant tissues, thus reducing its uptake in plants (Khan et al. 2012a).

P. macerans NBRFT5, a strain isolated from the rhizosphere of *Typha latifolia* grown on fly ash dumps, was used in combination with *Bacillus endophyticus* NBRFT4 and *Bacillus pumilus* NBRFT9 isolated from the same source, in phytoremediation of metals from the fly ash of the wild-type plant *T. latifolia*. Results revealed the potential of this consortium to induce phytoremediation of metal from fly ash as it was able to enhance concentration of both essential and nonessential

metals like Pb, Fe, Cu, Zn, Cr, Ni, and Cd in different plant parts and also to promote the growth of *T. latifolia* plants (Tiwari et al. 2013).

IAA-producing bacteria belonging to the species *P. macerans*, previously isolated from the meristems of *Cymbidium eburneum* orchids, have been reported to promote plant growth during seedling acclimatization in the orchid species *Cattleya loddigesii* (Faria et al. 2013). Experiments were carried out in a greenhouse using bacteria-free micropropagated *C. loddigesii* seedlings. It is noteworthy that these bacteria were not able to solubilize phosphate, thus, the authors suggested IAA production as responsible of plant growth promotion.

Production of IAA was also observed in *Paenibacillus* sp. strain JP44SK7 isolated from the rhizospheric soil of *Phyllanthus amarus*, an important medicinal herb in Indian traditional system cultivated at a commercial level. However, its ability to promote the growth of *Phyllantus amarus* needs further investigation (Kadyan et al. 2013).

Several species of *Paenibacillus* genus have been described to be able to fix N_2 with the *P. polymyxa* species accounting for the majority of N_2-fixing strains isolated so far (Lal and Tabacchioni 2009; Xie et al. 2012a, b). Although the members of N_2-fixing *Paenibacillus* species have great potential uses as biofertilizers in agriculture, the role of N_2-fixation in promoting plant growth needs to be assessed for most isolates. *P. polymyxa* strain P2b-2R is a N_2-fixing bacterium that was isolated from the internal stem tissue of a lodgepole pine (*Pinus contorta* var. *latifolia* (Dougl.) Engelm.) seedling naturally regenerating in central British Columbia, Canada (Bal et al. 2012). This strain is unique as it is the only microorganism that has been reported to fix substantial amounts of N_2 in association with tree species. Reintroduction of this strain to lodgepole pine seeds under a controlled environment resulted in rhizospheric and endophytic colonization of seedlings as well as provision of increasing amounts of foliar N as seedlings develop (Bal and Chanway 2012a; Anand and Chanway 2013a, b). The foliar N content and biomass of pine seedlings had increased more than twofold during 13 months after seed inoculation (Anand et al. 2013). Similar effects but of lesser magnitude were observed when seedlings generated from western red cedar (*Thuja plicata* Donn.) seeds inoculated with P2b-2R were grown under controlled environmental conditions (Bal and Chanway 2012b; Anand and Chanway 2013b).

Bacteria belonging to *Paenibacillus* genus have also been proved to have a synergistic effect when inoculated with other N_2-fixing bacteria. Cerqueira Rodriguez et al. (2013) performed experiments of co-inoculation of cowpea with *Bradyrhizobium* sp. (BR 3267) and plant growth-promoting bacteria belonging to the genera *Bacillus*, *Brevibacillus*, and *Paenibacillus* in Leonard Jar. They observed synergism in plant growth promotion of cowpeas using the pairs *Bradyrhizobium* BR 3267 + *P. graminis* (MC 04.21) and *Bradyrhizobium* BR 3267 + *P. durus* (C 04.50).

A mixed inoculum containing a N_2-fixing *P. polymyxa* strain, and several other PGPR capable of solubilizing phosphate or producing auxins such as *Rahnella* sp., *Serratia* sp., and *Pseudomonas* sp. have been used to verify its ability to promote the growth of switchgrass (*Panicum virgatum* L.) plants under field conditions with low N_2 inputs (Ker et al. 2012). All these bacteria were isolated from switchgrass

rhizomes that had not received N_2 fertilizers for over 10 years and which increased plant growth in the absence of N_2 fertilizers under growth chamber conditions. Overall, inoculation with the mixed inoculum resulted in a seeding year yield increase of 43 %, compared with the N_2 fertilizer treatment alone with a yield increase of 83 %. A combination of N_2 fertilizer (100 kg N $ha^{-}1$) and the mixed inoculum increased yield by 123 %. More tillers per unit area within a stand, as well as a greater population of medium- and tall-sized tillers were produced within PGPR treated stands. As the inoculum used in this study was a mixture of PGPR, which have been shown to be capable of solubilizing P, producing IAA-like substances, and, in the case of *P. polymyxa*, to fix N_2 the authors hypothesized a combination of these mechanisms responsible for plant growth promotion.

11.6 Biocontrol

Bacteria of the genus *Paenibacillus* are among the most efficient microbial biocontrol agents for crop protection against diseases. Their mode of action is supposed to be related to their production of antibiotics, such as cyclic lipopeptides, lantibiotics, macrolides, and polyketides as well as the production of hydrolytic enzymes, the competition with pathogens for ecological niche and substrate in the rhizosphere, and the reinforcement of the host plant-defensive potential via stimulation of its immune machinery (McSpadden Gardener 2004; Debois et al. 2013).

To determine which compound and/or mechanisms are involved in the antagonism of *Paenibacillus* bacteria toward other microorganisms represents a significant challenge in view of developing more efficient biocontrol agents to be used for crop protection. In many reports, the role in antagonism for a given antibiotic is suggested simply by the fact that the strain (or its crude culture extract), known to produce these compounds, displays some pathogen inhibition potential. To relate the antagonistic activity with specific antibiotics, polymerase chain reaction (PCR) with specific primers for the detection of the corresponding genes in the genome of the specific strain or genome mining using published sequence data of close relatives have also been performed. However, none of these approaches allows to draw any conclusion about the link between antibiotic potential and biocontrol activity, nor does it clearly prove the involvement of a specific compound in the antagonism developed by the strain against phytopathogens. Testing single purified compounds from culture broth necessitates extensive fractionation of crude culture extracts involving the combination of various chromatographic steps. The use of impaired (or overproducing) mutants and correlation with the respective loss (or increase) in the antagonistic activity compared with the wild-type strain may also represent a valuable approach to identify compounds playing a crucial role.

Among the genus *Paenibacillus*, the species *P. polymyxa* accounts for the majority of *Paenibacillus* strains showing the ability to suppress several plant diseases (Ryu and Park 1997; Lal and Tabacchioni 2009). *P. polymyxa* strains, isolated from the rhizosphere of several crops, are capable of producing several hydrolytic

enzymes, including proteases, β-1,3-glucanases, cellulases, xylanase, lipase, amylase, and chitinases which play a significant role in the biocontrol of plant pathogens (Beatty and Jensen 2002; Raza et al. 2008; Choi et al. 2008a; Petersen et al. 1996). *P. polymyxa* is also known to produce mainly two types of peptide antibiotics: polymyxins and fusaricidins. Polymyxins are active against bacteria whereas fusaricidins are active against fungi and actinomycetes (Beatty and Jensen 2002). Bacteria belonging to the species *P. polymyxa* have been proven to be effective in the control of gray mold in strawberries caused by *Botrytis cinerea* (Helbig 2001), as well as of *F. oxysporum* and *Pythium* spp. – causal agents of seedling blight and wilt, root rot of cucumber and watermelon (Dijksterhuis et al. 1999; Yang et al. 2004), and sesame damping-off (Ryu et al. 2006). Furthermore, several strains of *Paenibacillus* sp. are able to control diseases caused by *Phytophthora palmivora*, *Pythium aphanidermatum*, *Erwinia amylovora*, and *Pseudomonas syringae* pv. maculicola ES4326 (Timmusk and Wagner 1999; Lee et al. 2012a; Niu et al. 2013). Recently, the matrix-assisted laser desorption/ionization-Fourier transform ion cyclotron resonance mass spectrometry (MALDIFTICR MS) method was applied to identify the compounds present in the fungus growth inhibition area during simultaneous growth of *P. polymyxa* strain Pp56 and *F. oxysporum* (Debois et al. 2013). Fusaricidins A, B, and C and numerous members of the LI-F antibiotics family were identified. MALDIFTICR mass spectrometry imaging was then used to follow the diffusion of lipopeptides involved in the inhibitory activity over time. The authors concluded that some lipopeptides such as fusaricidin B and a mixture of antibiotics of the LI-F family were mainly involved in the defense mechanism of *P. polymyxa* Pp56. Suppression of a fungal pathogen mediated by the production of fusaricidins was demonstrated for the *P. polymyxa* strain SQR-21 isolated from the rhizosphere of healthy watermelon plant roots in a heavily wilt-diseased field (Ling et al. 2010). MALDI-TOF MS analysis revealed that *P. polymyxa* SQR-21 produces four kinds of fusaricidins: A, B, C, and D. The whole gene cluster for the production of fusaricidin (*fus*A) was isolated and identified from this strain, and its role in fusaricidin biosynthesis was confirmed by gene disruption. Indeed, the lack of fusaricidin production and abolishment of the antifungal activity by the *fus* disruption mutant of SQR21 confirmed the crucial role of the *fus* gene cluster in fusaricidin synthesis, as well as the importance of fusaricidin in antifungal activity (Choi et al. 2008b; Li and Jensen 2008). These results provided useful knowledge about transcription and regulation of the *fus* gene cluster in *P. polymyxa*, as well as the direction of gene engineering for improving the production of fusaricidins.

A study on the influence of ferric ion (Fe^{3+}) on the growth and fusaricidins production by *P. polymyxa* strain SQR- 21 revealed that the production of fusaricidin type increases only up to 50 μM Fe^{3+} and higher levels of Fe^{3+} are inhibitory. As Fe^{3+} concentration increases in the culture medium, the content of intracellular protein, intracellular carbohydrate, extracellular protein, and polysaccharide rises while the intracellular lipid content increases only up to 50 μM Fe^{3+}. Moreover, the authors found that the regulatory effects of Fe^{3+} were reflected by the increase in total RNA content and relative expression of the fusaricidin synthetase gene (*fusA*) up to 50 μM Fe^{3+}, after which a continuous decrease was observed (Raza et al. 2010).

P. polymyxa M-1 is a good candidate for the biocontrol of fire blight, a serious disease of apple and pear caused by the pathogen *E. amylovora*, due to its wide variety of secondary metabolites with antimicrobial activity produced. In particular, this strain synthesizes two components of polymyxin P, polymyxin P1, and P2 that have been characterized by matrix-assisted laser desorption ionization-time of flight mass spectrometry (MALDI-TOF-MS) in combination with bioautography. Using agar diffusion tests, it was observed that culture supernatants of *P. polymyxa* M-1 suppressed the growth of the phytopathogenic strains *E. amylovora* Ea 273 and *E. carotovora*. The corresponding polymyxin synthetase gene cluster was also identified and further characterized by domain analysis as being different from the *pmx* gene clusters encoding polymyxin A and B, respectively (Niu et al. 2013).

P. polymyxa 12.4.1, known for its ability to mobilize phosphate and for its potential to control plant pathogens (Postma et al. 2010), was tested in greenhouse as biocontrol agent of *P. aphanidermatum* and *F. oxysporum* f. sp. *radicis-lycopersici* causing, respectively, damping-off and crown and root rot of tomato plants (Postma et al. 2013). Animal bone charcoal, a phosphorous-rich waste product, was used as a carrier to deliver the biocontrol agent into the soil, thus combining recycling of phosphorous from animal bones and biocontrol of plant pathogens. Results presented in this study reveal that *P. polymyxa* 12.4.1 controlled *P. aphanidermatum* significantly, whereas it was not effective against *F. oxysporum* f. sp. *radicis-lycopersici*.

The low-rate-sporulating *P. polymyxa* 18SRTS, isolated from the rhizosphere of the medicinal plant *Calendula officinalis*, showed in vitro antagonistic activity against the plant pathogenic fungi *F. oxysporum* and *B. cinerea*. However, the mode of action of this strain needs to be elucidated; indeed, it does not produce siderophores and produces high concentrations of IAA up to 53 μM ml^{-1} (Ait Kaki et al. 2013).

Some PGPR are known to suppress diseases by inducing systemic resistance (ISR) in the plant against both root and foliar pathogens (Wei et al. 1996; Choudhary et al. 2007). This mechanism has also been observed in some PGPR belonging to the genus *Paenibacillus*.

P. polymyxa E681 was isolated from roots of winter barley (*Hordeum vulgare L.*) in southern Korea and is a promising biological control agent that could promote growth and elicit biological control activity in diverse crop systems (Ryu et al. 2006). It is active against the foliar pathogen *P. syringae* pv. maculicola ES4326 (Lee et al. 2012a) and Phytophthora blight of red pepper (Lee et al. 2013b). Suppression of early seedling damping-off in cucumber (*Cucumis sativus L.*) and sesame (*Sesamum indicum L.*) was observed after seed treatments with this strain under greenhouse and field conditions, respectively (Ryu et al. 2005a, b, 2006). Moreover, another possible mechanism for plant growth promotion by *P. polymyxa* E681 is the synthesis of plant growth regulators auxin and cytokinin (Lebuhn et al. 1997; Timmusk et al. 1999). Whole genome sequencing of strain E681 revealed that it encodes an entire set of genes related to the production of indole acetic acid (IAA) (Kim et al. 2013). Recently, Lee et al. (2012b) found that it promotes the growth of *Arabidopsis* seedlings producing volatile organic compounds (VOCs) that prime

transcriptional expression of the salicylic acid, jasmonic acid, and ethylene signaling marker genes *PR1*, *ChiB*, and *VSP2*. They also found that *P. polymyxa* E681 produces a novel class of long-chain bacterial volatile organic compounds (VOCs), i.e., the C13 hydrocarbon tridecane that can also elicit ISR as can C4 alcohols such as 2,3-butanediol. The potential of the antibiotic fusaricidin, produced by this strain, as one of the ISR elicitors for protecting red pepper plants against *Phytophthora* blight under greenhouse conditions, was also reported (Lee et al. 2013b). Indeed, these authors observed that application of fusaricidin at the lowest concentration (0.1 ppm of fusaricidin) by foliar spray significantly reduced *Phytophthora* leaf blight infection when compared with water-treated control plants. Moreover, they proved that fusaricidin is responsible for the activation of the defense gene PR-1a involved in the ISR by means of mRNA accumulation in the leaves of *Arabidopsis thaliana* plants treated with fusaricidin.

P. kribbensis PS04, isolated from soil samples of an insecticidal botanical garden in China showed antagonistic activity against *Rhizoctonia solani* causing rice sheath blight in both in vitro and in vivo experiments (Gao and Liao 2014). Crude metabolites were tested against mycelia in plate assays whereas spray treatments using crude metabolites and fermentation broth were used 24 h before and after an infestation of rice seeds with *R. solani*. The inhibitory effect on *R. solani* observed in both in vitro and in vivo experiments was correlated to the defense-related enzyme activity, i.e., peroxidase and polyphenol oxidase of plants, suggesting that *P. kribbensis* could trigger induced resistance of rice plants to suppress the pathogen (Gao and Liao 2014).

The antagonistic activity of *P. alvei* K165 against the soilborne fungus *Verticillium dahliae* has been reported under greenhouse and field trials (Tjamos et al. 2004, 2005; Antonopoulos et al. 2008). Root dipping and soil drenching of eggplants with this strain resulted in reduced disease severity compared to the control treatment under high *V. dahliae* inoculum.

In heavily *Verticillium*-infested potato fields, experiments with potato seeds dusted with the bacterial talc formulation showed a significant reduction in symptom development and a 25 % increase in yield over the untreated controls (Tjamos et al. 2004). Furthermore, it was observed that *P. alvei* K165 triggers induced systemic resistance (ISR) in a salicylic acid-dependent pathway in *Arabidopsis thaliana* plants against *V. dahliae* (Tjamos et al. (2005). Moreover, this strain was able to reduce the microsclerotia germination of *V. dahliae* in the root tips and the zone of elongation of eggplants as well as in the soil without plants (Antonopoulos et al. 2008). Recently, an in vitro activity of *P. alvei* K165 against Fusarium wilt of melon caused by *F. oxysporum* f. sp. *melonis* was reported by Charalambous et al. (2013). They observed that incorporating *P. alvei* K165 into the transplant soil plug at a ratio of 10 % allowed an adequate biocontrol agent population size in the rhizosphere that reduced Fusarium wilt symptom development and triggered the expression of the plant defense-associated genes *Chi1* and Pal1. Fusarium wilt of melon is a major disease affecting melon production worldwide. Management of this disease is mainly through chemical soil fumigation and the use of resistant cultivars. However, the broad spectrum biocides used to fumigate soil before planting are environmen-

tally damaging, and, on the other hand, resistance appears to be genetically complex and thus a difficult trait to confer by breeding (Berrocal-Lobo and Molina 2008). Therefore, the development and use of biocontrol agents against Fusarium wilt of melon based on *P. alvei* K165 seems an appealing management strategy for both the conventional and organic farming industry.

A multifactorial mode of action of *P. lentimorbus* B-30488^{r} against the tomato plant pathogen *A. solani* including the activation of the plant defense mechanisms and the competition for substrate utilization has been proposed by Khan et al. (2012b). They observed that spray foliar treatments of infested tomato plants grown under greenhouse conditions resulted in the reduction of the incidence of the early blight disease caused by *A. solani* by 45.3 % as compared to the control. The evidence of the upregulating expression of genes encoding defense-related plant proteins and the similarity of the utilization profiles of *P. lentimorbus*B-30488^{r} and *A. solani* of carbon sources presumed to be available in the phyllosphere suggest the involvement of activation of the plant defense mechanisms and the competition for substrate utilization in the biocontrol activity of this strain.

A relationship between the antagonistic activity against the plant pathogenic bacterium *Ralstonia solanacearum*, responsible of tomato wilt, and the in vitro biofilm formation was observed for both *P. polymyxa*and *P. macerans* strains by Li et al. (2011). The ability of seven strains of *P. polymyxa* and nine strains of *P. macerans*, previously isolated from either mycorrhizal or non-mycorrhizal systems, to form biofilm in vitro and to protect tomato plants from *R. solanacearum* under growth chamber conditions was investigated. Results revealed that most *Paenibacillus* strains tested had the ability both to form biofilm in vitro and to protect tomato seedlings from bacterial wilt suggesting a possible role of biofilm in biocontrol activity. Moreover, the *Paenibacillus* strains were able to protect tomato plants independently from the incubation time needed to form biofilm under in vitro conditions.

A bioorganic fertilizer containing *P. polymyxa*SQR21 was used to control Fusarium wilt of watermelon by Ling et al. (2010). They prepared the biofertilizer fermenting aerobically a mixture of amino acid fertilizer and pig manure compost with *P. polymyxa* SQR21 for 6 days at 45 °C. Application of the bioorganic fertilizer both in the seedling nursery soil and in transplanted soil resulted in the lowest Fusarium wilt disease incidence of watermelon in both experiments. Moreover, it not only suppressed Fusarium wilt but also significantly promoted watermelon growth. Nursery applications resulted in the effective colonization by *P. polymyxa*SQR21 in both the rhizosphere and on the root surface, thus protecting plant roots from the invasion of *Fusarium* pathogens before seedlings are transplanted.

Another bioorganic fertilizer based on *P. polymyxa* SQR-21 and two other biocontrol agents (*Bacillus subtilis* SQR-9 and *Trichoderma harzianum* SQR-T037) was used to test its efficacy to control Fusarium wilt on cucumber plants in field experiments (Qiu et al. 2012). It was developed by fermenting mature composts with the three biocontrol agents. Application of the bioorganic fertilizer in combination with a commercial chemical fertilizer suppressed the disease incidence by 83 % and reduced yield losses threefold compared with the use of the commercial chemical fertilizer alone. Analysis of microbial communities in rhizosphere soils by

high-throughput pyrosequencing showed that more complex microbial community was present in the soil treated with the bioorganic fertilizer than in the soil treated with the organic fertilizer (amino acid fertilizer and pig manure composts, 1:1). The dominant taxonomic phyla found in both samples were *Proteobacteria*, *Firmicutes*, *Actinobacteria*, and *Acidobacteria* among bacteria and *Ascomycota* among fungi. The abundance of beneficial bacteria or fungi, such as *Trichoderma*, *Hypoxylon*, *Tritirachium*, *Paenibacillus*, *Bacillus*, *Haliangium*, and *Streptomyces*, increased compared to the treatment with the organic fertilizer, whereas the soilborne pathogen, *Fusarium*, was markedly decreased.

Research on biological control of root-knot nematodes using rhizosphere microorganisms has been well documented (Yoon et al. 2012). Bacteria belonging to the genus *Paenibacillus*are among those bacteria showing nematicidal activity against root-knot nematode, Meloidogyne incognita. It was demonstrated that both under in vitro and in greenhouse conditions *P. polymyxa* strain GBR-1 and *Paenibacillus ehimensis* strain RS820 can suppress root galling and final nematode population of *M. incognita*on tomato plants (Khan et al. 2008; Huang et al. 2013). Culture filtrate of *P. polymyxa* GBR-1 significantly reduced *M. incogni ta* egg hatch and caused substantial mortality of its juveniles. Moreover, it reduced the root galling of tomato and nematode populations in the potting soil in greenhouse experiments and increased tomato plant growth and root mass production compared with untreated control (Khan et al. 2008). A mixed compost containing increased amounts of chitin and inoculated with *P. ehimensis*RS820, a chitinolytic soil bacterium previously isolated from soil in Korea, was used to control the root-knot disease in tomato plants. Results showed reduction of the disease and plant growth promotion in relation to the amount of inoculation with the biocontrol agents (Huang et al. 2013).

Although several strains of the *Paenibacillus* genus are reported to act as PGPR, at this time no *Paenibacillus*-based products have been commercialized in Europe or the United States yet. To our knowledge 12 patents based on *P. polymyxa*, *P. alvei*, and *P. macerans* species related to formulations and methods for controlling and suppressing plant pathogens have been deposited (http://patentscope.wipo.int/). One of the factors limiting the commercialization of products based on *Paenibacillus* bacteria is the poor information available on field tests under production conditions. A more thorough understanding of their ecology can help to figure out which problems to work on, how to approach them, when and where to apply the PGPR and predict situations in which control would not be expected to work.

11.7 Conclusions

The *Paenibacillus* genus includes species that have been isolated from a wide range of sources, and new species colonizing amazingly different habitats are continuously discovered.

An increasing number of studies have recently been published to test the capability of bacteria belonging to the different species of the *Paenibacillus* genus to pro-

mote plant growth and control plant diseases. Most of these studies have been carried out under in vitro and greenhouse conditions, and only a few of them rely on field tests. Patents based on *P. polymyxa*, *P. alvei*, and *P. macerans* species are related to formulations, and methods for controlling and suppressing plant pathogens have been deposited, but no commercial products are available yet. The complete genome sequence of several *Paenibacillus* sp. bacteria isolated from the soil and rhizosphere was recently made available. These data together with those resulting from experiments performed under field conditions will help to clarify the potential of *Paenibacillus* bacteria for developing effective biofertilizers and biocontrol agents to be used in sustainable agriculture.

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