Chapter 17
Role of *Bacillus* Species in Alleviating Biotic Stress in Crops

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Abstract Feeding the growing world population has become a crucial issue with each passing year. At present, the prime focus of farmers and scientists is on maximizing yield and minimizing the damages to food crops by diseases and harsh environmental conditions. Synthetic pesticides and fertilizers are being used abundantly in agricultural fields to increase productivity but the indiscriminate use of synthetic chemicals has resulted in severe pollution of soil and water. Consequently, practices as the use of biopesticides and biofertilizers have become an eco-friendly alternative for harmful agrochemicals, thus encouraging sustainable agriculture. A group of bacteria characterized as plant growth-promoting rhizobacteria (PGPR) has been known to reinforce plant growth and development and also mitigating abiotic and biotic stresses. Many weeds and phytopathogens such as bacteria, fungi, viruses, and nematodes may induce biotic stress in their plant hosts resulting in reduced biomass, crop quality, and yield. Various species of *Bacillus* are well-known PGPR and are also considered as potential biocontrol agents for many plant diseases. These are used to combat biotic stresses by inducing physiological changes in plants and secreting several metabolites in response. The present chapter focuses on the biotic stress management by *Bacillus* spp. and the various mechanisms involved in it.

Keywords Biopesticides · Biofertilizer · Plant growth-promoting bacteria · Phytopathogens · Biocontrol · Biotic stress

17.1 Introduction

Human beings depend on agriculture to a large extent for their food necessities. India is an agriculture-based economy with 18% of its GDP contributed by the agriculture sector. Also, 70% of its rural households and 58% of the total population

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depend predominantly on agriculture for their livelihood (FAO 2020; Tripathi et al. 2020). The world population at present is about 7.7 billion (https://www.worldometers.info/worldpopulation) and is projected to increase by 10 billion in the next 50 years (Etesami and Maheshwari 2018; Glick 2014), hence, requiring 70% more food production (FAO 2009). To achieve this, the expansion of agricultural land and a significant increase in production will be the major target. Inadequate food supply may create an alarming situation worldwide in the future. So the agriculture sector requires much more attention from the research community and the government.

For many years, various synthetic chemicals have been used to enhance food production which has caused serious threats to the environment and human health. Moreover, the environmental stresses including abiotic and biotic stresses have also been a big hurdle and limiting factor for agricultural production (Etesami et al. 2020). Therefore, the use of biological environment-friendly alternatives to agrochemicals came into a trend to overcome problems associated with chemical-based products. Microorganisms play a significant role in enhancing plant growth and mitigating biotic and abiotic stresses posed by harsh environmental conditions and phytopathogens. PGPR is a well-known group of bacteria used extensively in plant growth and health promotion of various crops. Several microorganisms belonging to genera *Acetobacter*, *Azospirillum*, *Azotobacter*, *Bacillus*, *Burkholderia*, *Klebsiella*, *Pseudomonas*, and *Serratia* are the most studied plant growth promoting bacteria and also reported for abiotic and biotic stress mitigation (Jha et al. 2013; Mishra et al. 2017; Verma et al. 2019). *Bacillus* and *Pseudomonas* are dominantly used PGPR for agricultural applications due to their beneficial role in plant growth and development, however *Bacillus* based biofertilizers are more effective than *Pseudomonas* due to their spore-forming nature and more efficient metabolite production capability which increases their commercial applicability (Haas and Défago 2005; Ongena and Jacques 2008). *Bacillus* species possess some unique characteristics that make it a potential candidate for biological control as it replicates rapidly and has large genetic biodiversity. Also, due to spore-forming ability, it can survive in extreme environmental conditions like high or low temperatures, unsuitable pH, and insufficiency of nutrients or water (Albayrak 2019). *Bacillus* is a ubiquitously found genera in nature, some species are free-living, while others are endophytic and can colonize the rhizospheric zone of plant root and internal tissues. It is a gram-positive spore-forming bacterium having immense applications in industry, agriculture, and medicinal fields (Lyngwi and Joshi 2014). Further, *Bacillus* spp. have been identified for their presence in stressed environments and also reported for alleviating biotic and abiotic stress (Yadav et al. 2016; Mishra et al. 2017; Ahmad et al. 2018). It has shown a good response in tolerating abiotic stresses like salinity, water deficit, heavy metal toxicity, flooding, extreme temperatures, and nutrient deficiency (Etesami et al. 2020). On the other hand, biotic stresses like weeds, nematodes, and phytopathogens (bacteria, fungi, and viruses) affect crop quality, biomass, and yield negatively and the species of *Bacillus* have been found very effective against them. Therefore, various species of *Bacillus* have been reported to act as a biocontrol agent for various phytopathogens and pests (García-Fraile et al. 2015; Kang et al. 2015). The phytopathogens can be controlled by the action of several cell wall degrading enzymes produced by

Bacillus such as cellulase, chitosanase, glucanase, protease, and other compounds viz. hydrogen cyanide and lipopeptides (Radhakrishnan et al. 2017). Also, a range of metabolites produced by *Bacillus* spp. including antibiotics, lipopolysaccharides (LPS), salicylic acid (SA), siderophores, and hydrolytic enzymes (Hassan et al. 2010, 2015; Qin et al. 2011) were found to be responsible for suppressing the growth of pathogens and boosting up the plant defense mechanisms (Rais et al. 2017).

As shown in Fig. 17.1, *Bacillus* can control plant diseases through various mechanisms such as competition for nutrients and ecological niche in the rhizosphere, production of inhibitory chemicals and metabolites, and induced systemic resistance (ISR) in plants (Cawoy et al. 2011; Rais et al. 2017). *Bacillus* spp. are also responsible for enhancing plant immunity by altering stress-responsive genes, phytohormones, proteins, and allied metabolites and also induce physiological changes including nutrient uptake, regulation of water transport, etc. (Radhakrishnan et al. 2017). In addition, *Bacillus* species significantly stimulate the production of antioxidant defense enzymes like superoxide dismutase, peroxidase, and other enzymes, which are known to suppress diseases in plants by diminishing the reactive oxygen species (ROS) causing oxidative stress (Liu et al. 2011; Shi et al. 2006; Yasmin et al. 2016). The association of *Bacillus* spp. with plant roots promoted plant growth by the formation of biofilm (Beauregard et al. 2013) and enhanced the availability of nutrients such as phosphate (by P solubilization) for plant uptake (Jha et al. 2012; Minaxi et al. 2012). Various species of *Bacillus* genera can produce an enzyme 1-aminocyclopropane-1-carboxylate (ACC) deaminase, which in turn can alleviate environmental stresses by reducing the ethylene level in the host plant (Minaxi et al. 2012; Misra and Chauhan 2020). This enzyme cleaves ACC (a precondition of ethylene production) to α-ketobutyrate and ammonia and thus reduces ethylene levels in plants (Etesami et al. 2020). In addition to ACC deaminase, the genera also produced indole-3-acetic acid and gibberellic acid that regulated intracellular

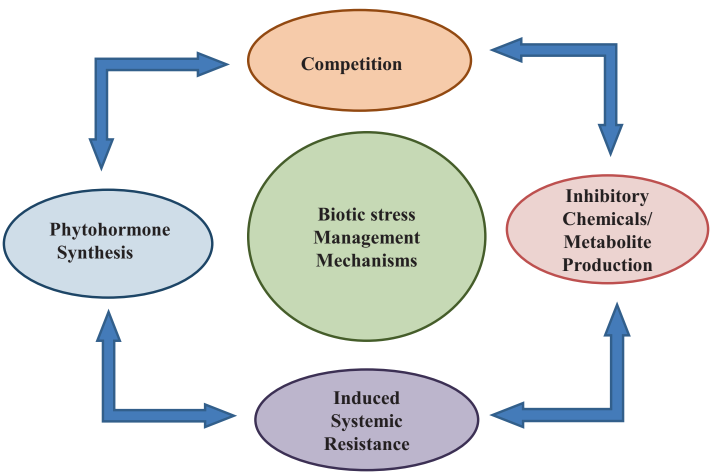

Fig. 17.1 Various mechanisms involved in the mitigation of biotic stresses

phytohormone metabolism, which consequently increased plant stress tolerance considerably (Minaxi et al. 2012; Radhakrishnan et al. 2017).

The global biopesticide market was estimated to grow about 3.0 billion USD in 2018 and is expected to grow about 6.4 billion USD by 2023, at a CAGR of 15.99%. Furthermore, the major driving force for the growth of the biopesticide market is the rise in the organic industry, increase in the cost of synthetic pesticides, growing insect resistance to these chemicals, and awareness towards hazards caused by chemical pesticides to the environment (https://www.marketsandmarkets.com). Among all bacterial biocontrol agents, approximately 70% of the total sale is contributed by *Bacillus thuringiensis* (Cawoy et al. 2011). This bacterium is the source of the Bt gene used in “Bt GMO crops” and about half of the commercial bacterial biocontrol agents belong to this species (Cawoy et al. 2011). There are numerous advantages of using biopesticides over chemical products. Microbial pesticides do not cause pollution as they decompose quickly and are not toxic for nontarget species (Cawoy et al. 2011). Also, they do not have any bad impact on health and the environment.

A limited number of studies are available on physiological changes induced by *Bacillus* species that occur in plants in stressed conditions. The present chapter deals with different biological stresses in crops and the beneficial effects of *Bacillus* species in alleviating biotic stresses through different mechanisms.

17.2 Alleviation of Biotic Stress in Plants by the *Bacillus* Species

Plants may encounter biotic stress due to the presence of weeds, phytopathogens, nematodes, etc. in agricultural fields which affect crop productivity inversely. *Bacillus* species and other PGPR have the capacity to promote the growth of plants as well as mitigate biotic and abiotic stresses. The effect of these PGPR on plant growth and their role in plant disease control has been well demonstrated (Etesami and Maheshwari 2018; Compant et al. 2005).

As illustrated in Fig. 17.2, plants under biotic stress generally employ two defense mechanisms. First, constitutive defense includes performed barriers like walls, waxy epidermal cuticles, bark, and metabolites, whereas the second is inducible defense, that is triggered by signal compounds, invaders, or herbivore attack and responds with the production of toxic chemicals, pathogen-degrading enzymes, and deliberate cell suicide (Freeman and Beattie 2008). Again, inducible mechanism has two categories, one is systemic acquired resistance (SAR), which relies on salicylic acid (SA) pathway, and another is induced systemic resistance (ISR), induced by some microorganisms such as mycorrhizal fungi and PGPR relying on ethylene (ET) and jasmonic acid (JA) signaling pathway (Boubakri 2020).

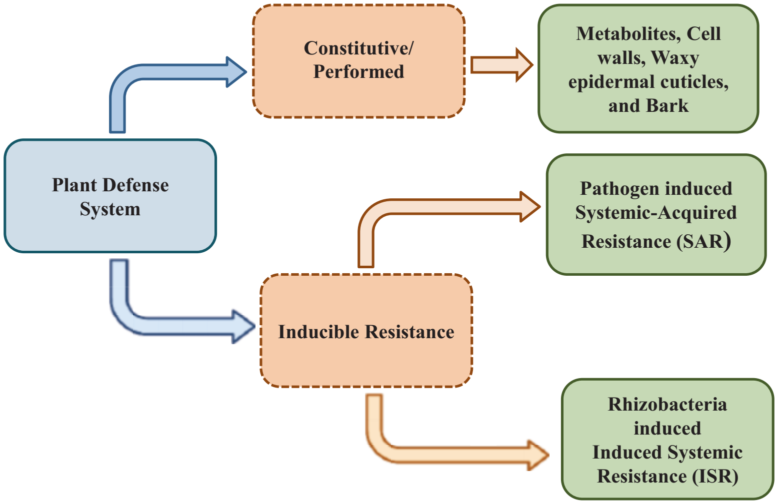

Fig. 17.2 Plant defense mechanism under biotic stress

Furthermore, Fig. 17.3 describes the direct and indirect mechanisms employed by *Bacillus* species to ameliorate biotic stress or plant diseases. Several PGPR including *Bacillus* species adopts one of these two basic mechanisms to combat biotic stress. The compound released in response to stress that stimulated plant growth and ameliorates stress comes under a direct mechanism (Goswami et al. 2016). This encompassed a number of compounds like secondary metabolites including antioxidants (superoxide dismutase and peroxidase) and antibiotics. Various hydrolytic enzymes (cellulose, chitosanase, glucanase, hydrogen cyanide, lipopeptides, and protease), siderophores, hormones (IAA, gibberellic acid, etc.), and other metabolites such as LPS and SA were found to be produced in response to biotic stresses directly by species of *Bacillus* (Hashem et al. 2019). Also, nitrogen fixation, mineralization of organic phosphates, and solubilization of insoluble inorganic phosphates are also part of this mechanism, through which plants get nutrition for their growth and are able to survive in stressed conditions (Etesami and Beattie 2017; Etesami and Maheshwari 2018; Glick 2012; Hayat et al. 2012). Further, induction of systemic resistance and competitive omission support plant growth through an indirect mechanism in stressed conditions (Tripathi et al. 2012).

17.2.1 Molecular Mechanisms Behind Inducible Resistance (SAR and ISR)

The ISR is a systemic resistance developed by some non-pathogenic rhizobacteria that are able to suppress disease in plants (Van Loon et al. 1998). In contrast, SAR is a type of induced resistance that is developed in plants by prior exposure to a

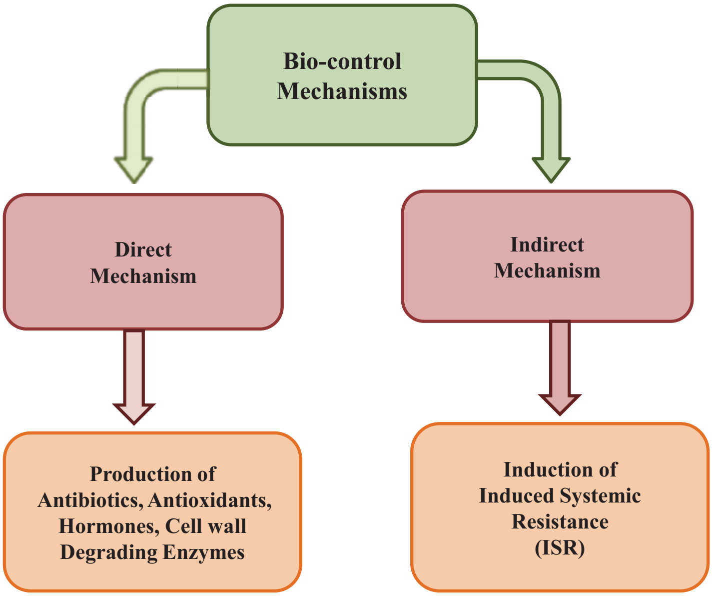

Fig. 17.3 Biocontrol mechanisms of *Bacillus* species

pathogen (Nie et al. 2017). A redox-sensitive transcription factor NIM1/NPR1 (nonexpressor of PR1) that regulates the expression of pathogenesis-related (PR) genes is a key player in both SAR and ISR mechanisms, as illustrated in Fig. 17.4 (Pieterse et al. 1998, 2014; Conrath et al. 2015). NPR1 induces the expression of pathogenesis-related (PR) genes in response to SAR signal molecule, salicylic acid (Hermann et al. 2013). The NPR1 translocates to the nucleus after getting activated by SA and functioning as a coactivator of PR genes providing SAR, whereas during the development of ISR, NPR1 was found to act in the cytosol, though its exact role is unidentified (Asari et al. 2017). Elicitation of ISR by plant-associated bacteria was first demonstrated in *Pseudomonas* spp. and other gram-negative bacteria. Besides *Pseudomonas*, various *Bacillus* spp. specifically *B. amyloliquifaciens*, *B. cereus*, *B. mycoides*, *B. pasteurii*, *B. pumilus*, *B. sphaericus*, and *B. subtilis* are also reported as elicitors of ISR (Kloepper et al. 2004). In most cases, these ISR eliciting species of *Bacillus* genera have also been found to elicit plant growth promotion (Kloepper et al. 2004). Several species of *Bacillus* were found independent of the salicylic acid pathway but dependent on jasmonic acid, ethylene, and the regulatory gene NPR1 in elicitation of ISR. However, some ISR eliciting species of *Bacillus* are independent of jasmonic acid and NPR1 and dependent on salicylic acid (Choudhary et al. 2007; Kloepper et al. 2004). Moreover, in some cases, ISR mediated by the rhizobacterium *Bacillus* species such as *B. cereus* strain AR156 employed both the JA/ET and SA signaling pathways, and NPR1 (Niu et al. 2011). Numerous *Arabidopsis* mutants and reporter lines revealed that the activation of JA-dependent genes VSP2 and PDF1.2 signifying the participation of MYC/ABA

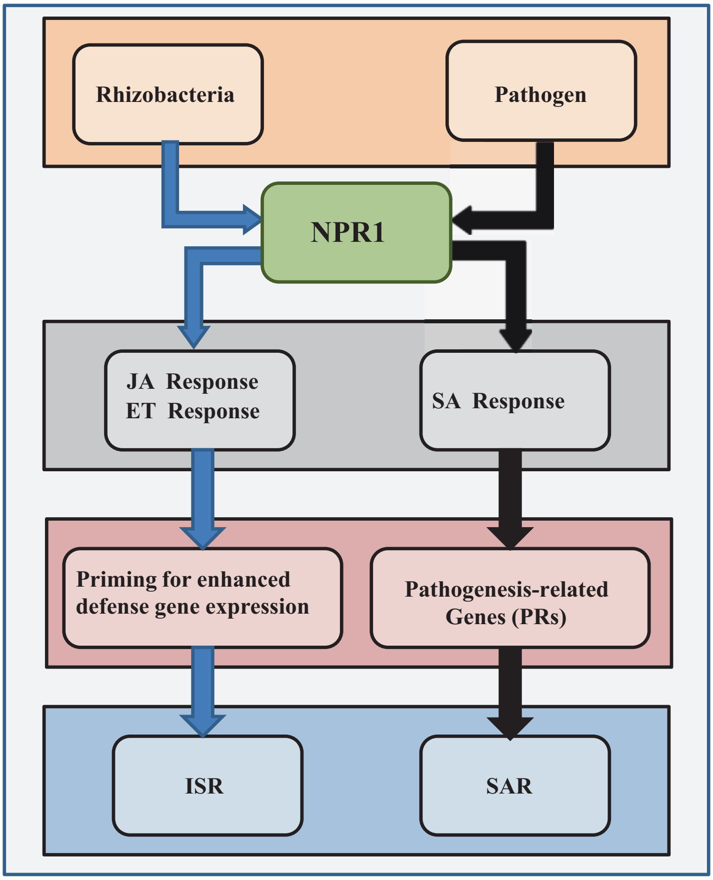

Fig. 17.4 Molecular mechanism of inducible resistance in plants

and ERF/ethylene, respectively (Pieterse et al. 2012). Further, SAR and ISR are well-characterized on the basis of key regulators such as NPR3 and NPR4 or COI1 (SAR) and MYB72 and MYC2 (ISR) with activation of defense genes, such as pathogenesis-related (PR) genes (SAR) or gene encoding plant defensin 1.2 (PDF1.2) and VSP2 (ISR) (Pieterse et al. 2014). However, the molecular mechanism for priming of ISR is not well acknowledged (Asari et al. 2017).

ISR is a sequential process involving three steps: (i) plant cells encounter elicitors produced by the inducing agents, (ii) initiation of signal transduction that propagates the induced state, and (iii) expression of defense mechanisms to inhibit the entry of the pathogen into the host tissues (Van Loon 2007). Salicylic acid and jasmonic acid pathways produce characteristic molecules like pathogenesis-related (PR) proteins (chitinases, β-1, 3-glucanases, proteinase inhibitors, etc.), phytoalexins (antimicrobial compounds), oxidative enzymes (peroxidases, polyphenol oxidases, and lipoxygenases) to diminish ROS and lignin for reinforcement of cell walls (Boubakri 2018; Van Loon 2007). ISR-based biocontrol strategies have been investigated and some trials were successfully performed under field conditions. *Bacillus* spp. have been found to produce volatile compounds (VOCs) such as 2, 3-butanediol (Ryu et al. 2005), and lipopeptides that were recognized as elicitors of ISR (Cawoy et al. 2011).

17.2.2 Crop Protection from Pathogenic Fungi by the Application of **Bacillus** *spp.*

Crops are susceptible to various fungal diseases. They can adversely affect crop productivity and their growth leading to major losses in food production and storage worldwide (Savary et al. 2012). Various trends of *Bacillus* have been reported for controlling a wide range of plant diseases. Different *Bacillus*-based biocontrol agents and their target fungal diseases/fungi are listed in Table 17.1.

Members of the *Bacillus* genus are distinguished as the good source of biologically active molecules, which have antagonistic activities towards a wide variety of phytopathogens (Meena and Kanwar 2015). Direct and indirect mechanisms as discussed before are used to biologically control the growth of pathogenic fungi in the host plant. Under direct mechanism, *Bacillus* spp. produce a number of metabolites and enzymes which directly inhibit the growth of pathogenic microorganisms and are effective against a broad spectrum of fungal species (Stein 2005). Lipopeptides such as surfactin (bacillomycin D), iturin, fengycin, and kurstakin, which are commonly found in *Bacillus* genera, have been well-known for their antimicrobial properties. These lipopeptides are composed of a lipophilic fatty acid chain and a hydrophilic peptide ring (Toure et al. 2004). Surfactins and iturins are amphiphilic cyclic peptides composed of 7 α-amino acids and fengycins by 10 α-amino acids. Moreover, iturins are linked to a single β-amino fatty acid, while surfactins and fengycins linked to a β-hydroxy fatty acid (Dimkić et al. 2017).

On the other hand, lytic enzymes like β-1, 3-glucanase, protease, and chitinase play a key role in controlling the growth of fungi through their cell wall degrading activity. Other than that, the volatile organic compounds (VOC) recognized by their antifungal activity are 2, 3-butanediol, benzene acetic acid, benzaldehyde, 1-decene, phenylethyl alcohol, and tetradecane and have also been studied for their role in biocontrol activity against a variety of fungal pathogens by Ryu et al. (2005) and Dhouib et al. (2019). Studies on the indirect mechanism of biocontrol found in several *Bacilli* reveal that it has a significant role in enhancing and boosting up the plant defense system through inducible resistance, namely SAR and ISR. Characteristic molecules of inducible resistant such as pathogenesis-related (PR) proteins (chitinases, β-1, 3-glucanases, proteinase inhibitors, etc.), phytoalexins (antimicrobial compound), oxidative enzymes (peroxidases, polyphenol oxidases, and lipoxygenases), and VOCs have been studied and well-demonstrated in the findings of García-Gutiérrez et al. (2013), Jangir et al. (2018), Pingping et al. (2017), Myo et al. (2019), Rais et al. (2017), and Waewthongrak et al. (2014).

Table 17.1 *Bacillus* based biocontrol of fungal diseases

Biocontrol agent	Crops	Mechanism of control	Fungal diseases/fungi	References
B. subtilis	Tomato	Direct inhibition (lytic enzymes)	*Fusarium oxysporum*	Chebotar et al. (2009)
		Indirect inhibition (ISR)	*Fusarium semitectum*	Nihorimbere et al. (2010)
		Direct inhibition (antibiosis)	*F. oxysporum f.* sp. *lycopersici*	Abd-Allah et al. (2007) and Baysal et al. (2008)
	Banana	Direct inhibition (antibiosis)	*Pseudocercospora musae*, *Colletotrichum musae*	Fu et al. (2010)
	Cotton	Direct inhibition (hydrolytic enzymes)	*F. oxysporum*	Gajbhiye et al. (2010)
	Lettuce	Competition/direct inhibition (antibiosis)	*Pythium aphanidermatum*	Correa et al. (2010)
	Peach, nectarine	Direct inhibition (antibiosis/enzymes)	*Monilinialaxa*(Brown rot)	Casals et al. (2010)
			Moniliniafructicola	Fan et al. (2000)
	Pea	Direct inhibition (antibiosis/enzymes) and indirect inhibition (ISR)	*Fusarium* spp. (Fusarium wilt)	Khan et al. (2011)
	Chilli	Direct inhibition (mycolyticenzymes)	*Colletotrichum gloeosporioides*OGC1	Ashwini and Srividya (2014)
	Cucumber	Competition, direct inhibition (inhibitory metabolites), and indirect inhibition (ISR)	*Podosphaer axanthii* (powdery mildew), *Didymella bryoniae* (gummy stem blight) *F. oxysporum* f. sp. *radicis-cucumerinum* (Fusarium root), *Pythium* spp. (Pythium crown and root rot)	Ni and Punja (2019)
	Tomato	Direct inhibition (antibiosis and inhibitorymetabolites)	*P. aphanidermatum*	Kipngeno et al. (2015) and Shankar (2016)
		Direct inhibition (antifungal compounds) and indirect inhibition (ISR)	*F. oxysporum* f. sp. *lycopersici* (*Fusarium wilt*)	Abd-Allah et al. (2007), Akram and Anjum (2011) and Shafi et al. (2017)
		Direct inhibition (antibiosis)	*Penicillium* spp. (Blue mold rot)	Punja et al. (2016) and Soleyman et al. (2014)
*B. subtilis*BCB3-19	Tomato	Indirect inhibition (ISR)	*Botrytis cinerea* (Grey mold)	Siripornvisal (2010)

(continued)

Table 17.1 (continued)

Biocontrol agent	Crops	Mechanism of control	Fungal diseases/fungi	References
*B. subtilis*WXCDD105	Tomato	Direct inhibition (antibiosis)	*B. cinerea* (Grey mold)	Wang et al. (2018)
B. subtilis UMAF6639	Melon	Indirect inhibition (inducible resistance)	*P. xanthii* (Powdery mildew)	García-Gutiérrez et al. (2013)
B. subtilis CCTCC M207209	Table grape	Direct inhibition (inhibitory metabolites/ antibiosis)	*Aspergillus carbonarius* CCTCC AF2011004	Jiang et al. (2014)
B. subtilis 30VD-1	Pea	Direct inhibition (lytic enzymes/VOCs/ inhibitory metabolites)	*Fusarium* spp.	Khan et al. (2018)
B. subtilis CICC 10034	Apples	Direct inhibition (cell wall degrading enzymes/antibiosis)	*Penicillium expansum*	Wang et al. (2016b)
B. subtilis ABS-S14	Citrus fruit	Indirect inhibition (ISR)	*Penicillium digitatum*	Waewthongrak et al. (2014)
B. subtilis HZ-72	Flax	Direct inhibition (cell wall degrading enzymes/antibiosis)	*Rhizoctonia solani* (Flax seedling blight)	Tan et al. (2019)
B. subtilis, *B. megaterium*	Peanut	Direct inhibition (enzymatic lysis)	*Aspergillus niger* (Root rot disease)	Yuttavanichakul et al. (2012)
B. amyloliquefaciens 9001	Apple	Direct inhibition (lytic enzymes) and indirect inhibition (ISR)	*Botryosphaeria dothidea* (Apple ring rot)	Li et al. (2013)
B. amyloliquefaciens	Wheat	Direct inhibition (metabolites/ antifungal compounds)	*Fusarium graminearum* (Fusarium head blight)	Crane and Bergstrom (2014)
B. amyloliquefaciens Q-426	Spinach	Direct inhibition (antibiosis)	*F. oxysporum* f. sp. *Spinaciae*	Zhao et al. (2014)
B. Amyloliquefaciens subsp. *Plantarum*	Ginseng	Direct inhibition (antifungal activity/lytic enzymes) or antagonistic	*F.* cf. *incarnatum* (Ginseng root rot)	Song et al. (2014)
B. amyloliquefaciens W19	Banana	Direct inhibition (antibiosis, iturin and bacillomycin D)	*F. oxysporum* f. sp. *Cubense* (FOC)	Wang et al. (2016a)

B. amyloliquefaciens strain BLB369, *B. subtilis*BLB277, *Paenibacilluspolymyxa* BLB267	Durum wheat	Direct inhibition (antibiosis)	*F. graminearum*	Zalila-Kolsi et al. (2016)
B. amyloliquefaciens L-1	Pear	Direct inhibition (antioxidant enzymes)	*Botryosphaeria berengeriana* (Pear ring rot)	Pingping et al. (2017)
B. amyloliquefaciens, *B. megaterium* (B5)	Wheat plants	Direct inhibition (antagonistic)	*Cochliobolus sativus*, *Alternaria alternata*, and *F. graminearum*	El-Gremi et al. (2017)
B. amyloliquefaciens, *B. subtilis*	Pistachio	Direct inhibition (antibiosis)	*Aspergillus parasiticus*	Siahmoshteh et al. (2017)
B. pumilus	Tomato, melon	Direct inhibition (antibiosis/enzymatic lysis)	*Xanthomonas campestris* and *F. oxysporum* f. sp. *melonis*	Suárez-Estrella et al. (2013)
	Tomato	Direct inhibition (antibiosis/enzymatic digestion) and indirect inhibition (ISR)	*F. oxysporum* f. sp. *lycopersici* (Fusarium wilt)	Heidarzadeh and Baghaee-Ravari (2015)
B. cereus AR156	Sweet cherry fruit blue rot	Direct inhibition (cell wall degrading enzymes)	*P. expansum*	Wang et al. (2015)
B. toyonensis, *B. cereus*, *B. aryabhattai*, *B. megaterium*, *B. aerius*, *B. stratosphericus*, *Paenibacillus*, *Barcinonensis*	Tomato	Direct inhibition (antagonistic/enzymatic digestion)	*F. oxysporum*f. sp. *lycopersici* (Fusarium wilt)	Rocha et al. (2017)
B. stratosphericus (FW3)	Ginseng	Direct inhibition (antagonistic metabolites)	*Ilyonectria* sp., *Neurospora* sp., *Cladosporium* sp., *Eutypella* sp., *Aschersonia* sp. and *Fusarium* sp. (Ginseng root rot disease)	Durairaj et al. (2018)

(continued)

Table 17.1 (continued)

Biocontrol agent	Crops	Mechanism of control	Fungal diseases/fungi	References
B. atrophaeus B5	Anthracnose soursop and avocado	Direct inhibition (antibiosis)	*Colletotrichum*, *Gloeosporioides*	Guardado-Valdivia et al. (2018)
B. velezensis C2	Tomato	Direct inhibition (antibiosis, enzymatic lysis) and ISR (VOCs)	*Verticillium dahlia* (Verticillium wilt disease)	Dhouib et al. (2019)
B. velezensis NKG-2	Tomato	Direct inhibition (enzymatic lysis) and ISR (VOCs)	*F. oxysporum* (Wilt disease)	Myo et al. (2019)
Bacillus spp.	Rice	Indirect inhibition(ISR)	*Pyriculariaoryzae*	Rais et al. (2017)
	Tomato	Direct inhibition (enzymatic lysis, metabolite production) and indirect inhibition by ISR (VOCs)	*F. oxysporum* f. sp. *Lycopersici*	Jangir et al. (2018)
Bacillus sp. P12	Bean	Direct inhibition (metabolite production/lipopeptides)	*Macrophomina phaseolina*	Sabaté et al. (2019)

Pathogenic fungi cause diseases in plants and some of them also produce mycotoxins, which contaminate the food and feed. Mycotoxins are toxic secondary metabolites produced by toxigenic fungi (Albayrak 2019). In the literature survey, *Bacillus* spp. were also found active against a number of mycotoxin producing fungi and destroyed them by antibiosis. *B. subtilis* SQR9 synthesized fengycin and bacillomycin antibiotics which inhibit mycelial growth and conidial germination of *F. oxysporum* f. sp. *couperin* (Cao et al. 2012). Also, *B. subtilis* fmbJ produced bacillomycin D which was active against *Aspergillus flavus* and was liable for injury to cell wall and membrane (Gong et al. 2014). Ayed et al. (2014) reported that antibiotic fengycin, surfactin, and pumilacidin produced by *B. mojavensis* acted against gram (+ve), gram (−ve), and many fungal pathogens. Further, antibiotic bacillomycin D from *B. subtilis* fmbJ caused the distortion of mycelia and disruption of spores, induction of more ROS, and apoptosis of *Aspergillus ochraceus* through cell and DNA damage (Qian et al. 2016). Ochratoxin A (OTA), a mycotoxin mainly produced by species of *Aspergillus* and *Penicillium* was very efficiently removed by *Bacillus megaterium* through adsorption as reported by Shang et al. (2019).

17.2.3 **Bacillus** *spp. in Prevention of Bacterial Diseases*

A number of bacterial diseases that are biologically controlled by the various species of *Bacillus* are listed below in Table 17.2.

As it can be clearly seen from Table 17.2, the *B. subtilis* and *B. amyloliquefaciens* have emerged as the most potential biocontrol agent for bacterial diseases. Different strains of *B. subtilis* produced a good range of hydrolytic enzymes, including i.e., cellulases, beta-glucanases, and proteases. This bacterial species also produced several metabolites and antibiotics that could limit the growth of invading pathogens and microorganisms. It has been reported in the literature that the indirect mechanism like ISR played a significant role in suppressing bacterial diseases in plants. Remarkably, *B. subtilis* strains are well-recognized for synthesizing antibiotic lipopeptides, including fengycin, surfactin, and iturin (Hashem et al. 2019). Surfactants are antimicrobial compounds and can also have an important role behind inhibiting phytopathogens.

17.2.4 **Bacillus** *in Pest/Insect/Nematode Control and* **Bacillus**-*Based Commercial Products*

Some important species of *Bacillus* efficient in controlling pest/insects and nematodes are listed in Table 17.3.

*Bacillus thuringiensis*is, a well-known species of *Bacillus*, used as biopesticide worldwide since biopesticides came into existence. Approximately 95% of

Table 17.2 *Bacillus* species as a biocontrol agent for bacterial diseases

Biocontrol agent	Plant/crop	Mode of action	Target disease/bacteria	References
B. subtilis	Arabidopsis	Antibiosis (lipopeptide surfactin) and biofilm formation	*Pseudomonas syringae* pv. *tomato* DC3000 (root infection)	Bais et al. (2004)
	Mulberry	Biofilm formation and indirect inhibition (ISR)	*Ralstonia solanacearum* (bacterial wilt)	Ji et al. (2008)
	Tomato	Indirect inhibition (ISR and SAR)	*Xanthomonas euvesicatoria* *Xanthomonas perforans* (bacterial spot)	Roberts et al. (2008)
B. subtilis, *B. amyloliquefaciens*	Potato	Competition, fertilization, induction of antagonist (microbial) population	*R. solanacearum* (bacterial wilt)	Chen et al. (2013)
B. subtilis AP-01 (Larminar™), *Trichoderma harzianum* AP-001 (Trisan™)	Tobacco	Direct inhibition (antibiosis, metabolite secretion)	*R. solanacearum* (bacterial wilt)	Maketon et al. (2008)
B. subtilis 9407	Melon	Direct inhibition (antibiosis by surfactin)	*Acidovoraxcitrulli* (bacterial fruit blotch)	Fan et al. (2017)
Endophytic *B. subtilis* SR63	Grapes	Direct inhibition (antibiosis, metabolite secretion)	*Agrobacterium tumefaciens* (crown gall)	Ferrigo et al. (2017)
Endophytic *B. amyloliquefaciens*	Rice	Direct inhibition (metabolite secretion-siderophores, IAA etc. and root colonization)	*Xanthomonas oryzaepv. oryzae* (bacterial leaf blight)	El-shakh et al. (2017)
B. amyloliquefaciens BL10	Tomato	Direct inhibition (antibiosis)	*R. solanacearum* (bacterial wilt)	Nawangsih et al. (2011)
B. subtilis	Chili	Direct inhibition (growth promotion, metabolite secretion)	*R. solanacearum* (bacterial wilt)	Istifadah et al. (2017)
B. pseudomycoides NBRC 101232 *B. thuringiensis* ATCC 10792 *B. mycoides strain* 273		Direct inhibition (antibiosis etc.) and indirect inhibition (ISR)		Yanti et al. (2018)

Bacillus sp.	Eggplant	Direct inhibition (inhibitory compound production) and indirect inhibition (ISR)	*R. solanacearum* (bacterial wilt)	Achari and Ramesh (2014)
B. amyloliquefaciens strain S1	Tomato	Direct inhibition (antibacterial metabolite, siderophores and lytic enzymes production)	*Clavibactermichiganensis* ssp. *michiganensis* (bacterial canker)	Gautam et al. (2019)
B. subtilis, *B. amyloliquefaciens* (FZB 24), EPB 9, EPB10, EPCO 29 and EPCO 78	Rice	Indirect inhibition (ISR)	Bacterial leaf blight, sheath blight	Krishnan et al. (2013)
Endophyte B. velezensis	Citrus species	Direct inhibition (bioactive secondary metabolites production)	*Xanthomonas citri* subsp. *citri* (citrus bacterial canker)	Rabbee et al. (2019)
B. amyloliquefaciens and *Trichoderma asperellum*	Tomato	ISR and growth promotion by enhanced nutrients (P, K, Mg) availability	*Xanthomonas perforans* (bacterial spot)	Chien and Huang (2020)
B. velezensis	Potato	Bacteriostatic activity and antibacterial mechanisms	*Streptomyces* (potatp scab)	Cui et al. (2020)

Table 17.3 *Bacillus* species in controlling pests/nematodes/insects/weeds

Biocontrol agent	Crops	Pest	Mode of action	References
B. subtilis	Soybean	*Heterodera glycines*	Direct inhibition (antibiosis/metabolite production)	Araújo et al. (2002)
	Tomato	*Meloidogyne incognita* (root-knot nematode)	Direct inhibition (inhibitory metabolites)	Araújo and Marchesi (2009) and Siddiqui and Futai (2009)
	Pulses	*M. incognita* (root-krot nematode)	Direct inhibition (antibiosis) and indirect inhibition (ISR)	Khan et al. (2011)
Bacillus strains (EPCO 102 and EPCO 16)	Cotton	Cotton bollworm	Indirect inhibition (ISR)	Rajendran et al. (2007)
B. Thuringiensis	Potato	Coleopteran insects, boll weevil, Colorado potato beetle	Bt toxin	Herrnstadt et al. (1986)
	Soybean	Caterpillars, stink bugs	Membrane pore formation and cell lysis	Schünemann et al. (2014)
B. thuringiensis var. tenebrionis Xd3 (Btt-Xd3)	Alder	*Agelasticaalni* (Alder leaf beetle)	Bt toxin	Eski et al. (2017)
B. flexus JIM24	–	*Lathyrus aphaca* weed	Aminolevulinic acid production	Phour and Sindhu (2019)

biological control products for agricultural pests belong to this species (Lambert et al. 1992). It produces the toxic proteins Cry, Cyt, and vegetative (secretable) insecticidal proteins (Vip) known as Bt toxins, which are highly lethal against a wide range of insects but nontoxic for mammals (Schnep et al. 1998). Bt toxins present in spore get activated on cleaving with proteases in the alkaline environment of the insect gut. That is why they act in a very specific manner and do not have any toxic effect on nontarget species (Bravo et al. 2007). Coleoptera, Lepidoptera, and Diptera are the major insect families against which Bt toxins (Cry/Cyt) are very effective.

Due to the promising results in controlling a range of pathogenic diseases, the commercial applicability of *Bacillus*-based biocontrol agents has increased. Hence, a good range of *Bacillus*-based biocontrol agents is available in the market. Some commercial *Bacillus*-based biocontrol agents are given in Table 17.4.

Table 17.4 Commercial *Bacillus* based biocontrol agents

Biocontrol agent	Product	Manufacturer	Target disease/organism	Crops
B. subtilis	Avogreen®	Ocean Agriculture South Africa	*Colletotrichum gloeosporioides* and *Cercospora* spot	Avocado
	Biosubtilin	Biotech International Ltd. India	*Fusarium*, *Verticillium*, *Pythium*, *Cercospora*, *Colletotrichum*, *Alternaria*, *Ascochyta*, *Macrophomina*, *Myrothecium*, *Ramularia*, *Xanthomonas*, and *Erysiphe polygoni*	Cotton, cereals, ornamental plants, and vegetable crops
	Stanes Sting®	Stanes Company, India	*M. incognita*	Tomato
B. subtilis strain GB34	GB 34	Gustafon, USA	*Rhizoctonia*, *Fusarium*	Soyabean
B. subtilis strain GB03	Kodiac companion	Growth Products, USA	*Rhizoctonia*, *Aspergillus*	Wheat, barley, pea
B. megaterium	Bioarc®	Sphere Bio-Arc Pvt Ltd.	*Tylenchulus semipenetrans* (nematode)	Cooton, beans, orange
B. firmus	BioNem®	Agro-green Minrav group of Israel	*M. incognita*	Tomato
B. amyloliquefaciens	RhizoVital® 42 liand RhizoVital 42 TB	ABiTEP GmbH, Germany	Soilborne pathogens	Potato, corn, strawberry, tomato, cucumber, ornamental plants
B. thuringiensis aizawai	Agree-WP	Certis USA L.L.C., USA	Armyworms, diamondback moth	Fruits, nuts, vegetables
	Florbac	Valent Biosciences Libertyville, USA		
	XenTari WG	Nufarm, Canada		
	Xantari®	Valent Biosciences Libertyville, USA		

(continued)

Table 17.4 (continued)

Biocontrol agent	Product	Manufacturer	Target disease/organism	Crops
B. thuringiensis kurstaki	Biobit®	GroChem, New Zealand	Lepidoptera	Apple, avocado, citrus, flowers, grapes etc.
	Cordalen®	Agrichem Bio, Madrid, Spain		
	Costar-WG	SKL Biosynthesis, Italy		
B. thuringiensis israelensis	Teknar® SC, VectoBac®	Valent Biosciences, Libertyville, USA	Mosquitoes and black flies	–
	Vectobar™	AgriLife, AP, India		
B. thuringiensis tenebrionis	Novodor®	Valent Biosciences, Libertyville, Illinois, USA	Colorado potato beetle	Potato
	Trident®	Certis USA L.L.C., USA		
B. thuringiensis sphaericus	VectoLex®, VectoMax®	Valent Biosciences, Libertyville, USA	Mosquitoes	–
B. pumilus	Yield Shield®	Bayer Crop Science, USA	*R. solani* and *Fusarium* (root rot)	Soybean
B. thuringiensis var. kurstaki	DiPel 2x®	Nufarm, Canada	*M. incognita* , Lepidoptera pests	Several vegetables

17.3 A Comparison of Biopesticides and Synthetic Pesticides

There are several advantages of using biopesticides. *Bacillus* species are recognized as safe bacteria that produce substances that are beneficial for crops and the production of industrial compounds (Stein 2005). As a biocontrol agent, *Bacillus* has the advantage of long-term storage and reduced complexity of formulation process due to its ability to form spores that help it to survive in adverse environmental conditions (Collins and Jacobsen 2003). In addition, biopesticides are nontoxic and easily degradable, which makes them more beneficial than any chemical pesticide. Although biopesticides offer a lot of advantages but have not replaced conventional pesticides completely as they are not so popular and common in use, and have specific requirements. Since they are highly specific, farmers will need different biopesticides for different pathogens or insects. Furthermore, maintaining the viability of these biocontrol agents is extremely important (inside.battelle.org).

17.4 Future Perspective

Developing new biopesticides itself is a very tedious process due to several challenges like cost, efficacy, and commercialization process. Delay in the authorization process is common due to the lack of enough expertise and regulatory model for biopesticides in India (Tripathi et al. 2020). Besides the investigation of new biomolecules, recombinant DNA technology is also being used for improving the efficiency of biopesticides. Novel fusion proteins, made up of toxins combined with a carrier protein, have been developed as next-generation biopesticides, and this technology makes this fusion protein toxic to target insects or pests after it is consumed orally (Fitches et al. 2004). More research is required in order to have an effective pest management in production systems. Funding agencies and government policies are influencing factors in biopesticide research and promotion. Government can control the use of hazardous pesticides by enforcing laws and encouraging the biopesticide industry for organic agriculture (Moosavi and Zare 2016).

Also, a strict regulatory mechanism is equally important for the desired quality and reasonable cost of biopesticides (Kumar and Singh 2015). Other than that, biological control agents (BCAs) may behave differently in different environmental and climatic conditions, hence, every country needs to develop indigenous BCAs (Keswani 2020). Moreover, limitations like slow in killing pests, cost, production, and formulation problems are the major drawbacks associated with biological pesticides. Therefore, working on these limitations to improve the performance may help in the global acceptance of biopesticides. Nanoformulations may play a significant role in improving the residual action and stability of biopesticides (Damalas and Koutroubas 2018; Tripathi et al. 2020). Recombinant DNA technology, molecular biology, and biotechnology can help to enhance the performance of biopesticides in their field use.

17.5 Conclusion

Biological stress is considered as one of the major restrictions to crop production in agricultural fields, which also exacerbates with climate change (Etesami et al. 2020). The use of biological agents to control plant diseases has become a very good alternative to conventional pesticides as they are nonhazardous for living beings and the environment. Several species of *Bacillus* are able to suppress plant diseases through various mechanisms, categorized into direct and indirect mechanisms. These mechanisms are responsible for the production of a broad range of antibiotic compounds (lipopeptides), lytic enzymes, antioxidants, siderophores, formation of biofilms, and various other metabolites which inhibit the growth of pathogens by their action. Moreover, through indirect mechanisms such as ISR, *Bacillus*-based biocontrol agents induce the plant immune/defense system and help them to grow in harsh conditions of stress. Also, *Bacillus* has a prominent role in alleviating induced ethylene levels under biological and nonbiological stresses, which suppress plant growth. Biopesticides and *Bacillus*-based products are gaining much attention that is why huge numbers of commercial products are available in the market belonging to *Bacillus* species. It has been well demonstrated that *Bacillus* species have immense potential to mitigate biotic stresses and encourage the growth and development of plants. However, these agents are not able to provide full protection against diseases but biopesticides combination with synthetic pesticides, fertilizers, and different types of tillage, incorporated into integrated pest management systems can fulfill the purpose to some extent. Apart from this, extensive research in new active ingredients, biopesticide formulation, and efficacy will give a new insight into biopesticide application in agriculture.

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