Chapter 8
Mechanisms Involved with Bacilli-Mediated Biotic and Abiotic Stress Tolerance in Plants

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Abstract Due to increased demand for food and feed, plants are being grown in marginal lands dominated by abiotic stresses. These abiotic stresses predispose plants to biotic stresses compromising the yield and quality. Mitigation efforts of these stresses with synthetic chemicals further complicated the situation. However, use of beneficial microbes opened a new horizon for managing these stresses in the agricultural ecosystem. To date, an appreciable amount of research elucidated the underlying mechanisms how these microbes, especially numerous species belonging to the genus *Bacillus*, play a positive role in mitigating these stresses. Colonization of plant rhizosphere or phyllosphere by these microbes contributes to alleviating these stresses through up- or downregulation of major metabolic pathways in plants. Regulation of metabolic pathway helps in reducing/neutralizing the level of stressors or inducing plants to overproduce stress-mitigating biochemicals. This chapter compiles all the major mechanisms pertaining to biotic and abiotic stress alleviation in plants by *Bacilli* to aid in elucidating more complex mechanisms by future research endeavors.

Keywords Stress alleviation · Metabolic pathway · Molecular mechanisms · Gene expression · Peptides · Climate change · Biotic factors · Agro-ecosystem · Plant health · Toxic effluent · Innate immune system · *Bacillus* sp.

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8.1 Introduction

Crop productivity is influenced by a combination of environmental and genetic factors (Kleinwechter et al. 2016). Genetic potential of many crop varieties is not achieved since crops in most cases are grown in stressful or less-than ideal growing conditions, which include unfavorable edaphic and climatic environments. It is universally proven that various stress factors adversely influence the physiology of a plant starting from germination through growth and yield. These stresses are primarily classified into two major groups: abiotic and biotic. Our agro-ecosystem is subjected to continuous exposure from a series of ever-changing abiotic and biotic factors, many of which eventually create an unfavorable environment for soil health, fertility, crop growth, and productivity. It is now well documented that these abiotic and biotic stresses can affect all aspects of plant growth including biomass production and intended yield (Pandey et al. 2017). While all biotic stresses are of biological origin like diseases, insects, and weeds; abiotic stresses are generally physical or chemical, and imposed on plants by their environment. Disease-causing organisms include fungi, bacteria, viruses, nematodes, and phytoplasmas. Abiotic stresses on plants are on the rise due to human activities that drive global warming and climate change, releasing toxic effluent to arable land. Despite the consequences, people attempt to grow crops in saline or nutrient-deficient, unsuitable land, due to the increased demand for food and feed worldwide. Exposure of plants to abiotic stresses predispose them to biotic stresses such as pathogens, insects, and may also reduce their ability to compete with weeds. Combined abiotic and biotic stresses can severely affect crop productivity. Even if these stresses occur separately, 50% and 30% of worldwide agricultural productivity could be lost to abiotic and biotic stresses, respectively. However, plants have evolved a sophisticated defense network, also called innate immune system, in response to fluctuating environmental conditions that provide protection to some extent against these stress factors. There are no simple solutions to fully counteract these stresses with modern agricultural technologies discovered over the last few centuries. However, many plant-beneficial microbes living in the soil and microbes existing on or inside plants as endophytes or epiphytes have been found in several studies to trigger a plant's innate defense system, thereby promoting growth and protecting plants from biotic and abiotic stress factors (Glick 1995; Radhakrishnan et al. 2014, 2017; Tonelli et al. 2010). These beneficial microbes contributed to boosting crop yield by minimizing either abiotic or biotic or both types of stresses. Among the microbes, *Bacillus* and *Pseudomonas* species are the major plant stress mitigators and growth-promoting bacteria (Kang et al. 2015a). However, the ability of *Bacilli* to form spores distinguishes them from that of *Pseudomonas*. The survival capacity of the members of this genus for a long time under unfavorable environmental conditions make them suitable to be used for prevention of both biotic and abiotic stresses encountered by plants. That is why *Bacillus* spp. is ranked at the top as a microbial agent for mitigating both abiotic and biotic plant stresses due to their unparalleled genetic fitness. Dihazi et al. (2012) noted that organic and sustainable farming practices prefer application of *Bacillus* or other bacterial biocontrol agents as an eco-friendly option to enhance disease resistance in crops, which is also considered as a safer method of increasing crop productivity. Use of synthetic pesticides can be reduced in modern agriculture by utilization of *Bacillus*-derived formulations or products due to their proven efficacy (Myresiotis et al. 2015). In addition, an appreciable number of studies have been directed towards understanding *Bacillus*-mediated protection of crop against adverse biotic and environmental stresses at the physiological, biochemical, and molecular levels. Similar advancements through numerous studies have also taken place in the area of *Bacillus*-based remediation or detoxification of metals and other pollutants from the edaphic environments. As a result, remarkable development has occurred in elucidating the underlying mechanisms pertaining to biotic stress tolerance in plants by the use of *Bacillus* (Choudhary and Johri 2009; Ongena and Jacques 2008). However, information on *Bacillus*-mediated abiotic stress tolerance mechanisms are still very inadequate (Arkhipova et al. 2007; Wolter and Schroeder 2012) as most of the studies on *Bacillus*-based abiotic stress tolerance focused on evaluating plant growth promoting effects rather than unraveling specific mechanisms (Dimkpa et al. 2009). *Bacillus*-mediated stress mitigation mechanisms have been explored by many researchers to improve efficacy by using a consortium of beneficial microbes and combining them for diverse multiple modes of action. Many potential stress mitigation mechanisms that have been observed indicated that *Bacillus* spp.-induced actions on the adverse environmental factors and host plants are diverse, numerous, and may be indirect or direct (Berg 2009; Numan et al. 2018; Perez-Garcia et al. 2011; Turan et al. 2012). It is not uncommon for some species of *Bacillus* to mitigate multiple stresses if present at the right time in ample populations. This chapter highlights the major *Bacillus*-mediated plant abiotic and biotic stress tolerance mechanisms by comparing with plants' innate responses to stresses.

8.2 Major Abiotic Stresses and Their Impacts on Crop Growth and Yield

Abiotic stressors are a major cause that puts obstacle against enhancement of worldwide crop production (Bray et al. 2000; Wang et al. 2003). Crop plants have to cope with adverse environmental and edaphic factors with biological mechanisms that are intrinsic to them like hormonal signaling (Nguyen et al. 2016) and interaction with beneficial microbes (Numan et al. 2018). Plant growth, development, and productivity can suffer immensely if they fail to counteract those stresses (Pereira 2016). As more arable land is lost to urbanization and non-agricultural use, crops are being grown in less-suitable areas where abiotic stresses are common. As a result, 50–82% of major crops encounter losses that pose a serious threat to agriculture and food security due to adverse environmental conditions like drought, salinity, extreme temperature, UV radiation, heavy metals, or various oxidative stresses

(Benedetto et al. 2017; FAO 2016). By impairing biochemical/physiological and molecular processes, these stress factors (individually or combined) may induce numerous hostile effects in plants, eventually reducing plant growth, development, and productivity. Stresses from abiotic factors are now considered as one of the biggest potential threats all over the world to agricultural productivity that may affect yields up to 70% for staple food crops as projected by many studies (Kaur et al. 2008; Mantri et al. 2012). Among many different types of abiotic stresses, accumulation of various heavy metals in agricultural soil has created a major concern to the agriculture system and health of many millions of people in countries such as Zambia, Ukraine, Russia, Peru, China, and India (ENS 2006). Wang et al. (2003) estimated that 30% arable land may be lost by the end of 2028, and at this rate it may reach 50% by mid-twenty-first century due to high salinity. Other environmental factors such as the projected increase of mean temperature by 3 °C due to the rise in CO_2 concentration by the end of twenty-first century by about 500–1000 ppm, which will cause heat stress to crops (Khan et al. 2013). Thus, salinity of arable land, nutrient deficiency, drought, metal toxicity, and unforeseen impact of climate change are likely to significantly worsen the problem (Anjum et al. 2014). The combined effect of these stresses may result in losses of soil microbial diversity, soil fertility, and availability of nutrients (Chodak et al. 2015). Plants require a favorable growing site for their physiological and developmental processes. Less than favorable growing condition induced abiotic stress factors can also predispose plants to biotic stresses that interfere with normal growth and development thereby reducing productivity. Plants use their intrinsic recognition mechanism to detect and respond to stresses to some extent by activating the defense pathways to support their nourishment (Jiang et al. 2016; Ahmad et al. 2015; Crane et al. 2011). However, this response may not be enough to overcome stresses if stress levels exceed a certain threshold. When beneficial microbes such as *Bacilli* are present in or on plants within a stressful environment, they modulate the environment and provide enhanced stress tolerance capacity to plants through several procedures described below.

8.2.1 Mechanisms of Abiotic Stress Alleviation

Plants have developed an efficient innate defense network that is turned on by external stimuli representing abiotic (environmental) and biotic stresses. Depending on the genetic makeup of plants, they can employ various self-defense mechanisms to prevent these stresses through up- or downregulation of major metabolic pathways, such as TCA cycle, photosynthesis, accumulation of secondary metabolites, and specific sugars or amino acids (Lotfi et al. 2010; Rai 2002; Lewis et al. 2001). This wide array of different metabolites may play a significant role in plant stress tolerance. For example, phytohormones profoundly influence control of specific molecular mechanisms in plants, and thus optimizing plant responses against stresses of abiotic nature (Nguyen et al. 2016). However, presence of plant beneficial microbes such as *Bacillus* alleviate these stress factors by either reducing/neutralizing the level of stressors or inducing plants to overproduce stress-mitigating biochemicals. During low water availability, salt and heavy metals can accumulate on top soil layers. Heavy metal accumulation in agricultural soil has also been increasing due to the release of industrial effluent and spread with water. *Bacillus* spp. if present in an environment can produce ample amount of exopolysaccharides and siderophores to bind Fe, which usually prevent the movement of toxic ions and adjust the ionic balance and water transport in plant tissues. Plants can also rapidly sense changing environmental conditions and defend themselves with their innate defense mechanism. Plant responses to abiotic stress involve an induced metabolic cross talk within various biosynthetic pathways. Root system can also sense abiotic stress signals and respond accordingly to the stresses originating from soils (khan et al. 2016). These responses are results of an intricate mechanism that involves changes at genetic, cellular, metabolic, and physiological levels (Atkinson and Urwin 2012). Major impact of abiotic stress is water-deficient conditions created within cells, which is followed by a series of biochemical, molecular, and phenotypic defense action (Xu and Zhou 2006; Almoguera et al. 1995). As the number of stressors experienced by a plant increases, so does the complexity of their responses when compared to plants with a single stress. The complex nature of such responses is due to the activation of a specific gene along with metabolic programming in cells against individual stresses in a specific growing condition. Stress tolerance is a vital phenomenon that may vary with different stages of plant development. Abiotic stress responses may reduce or increase the susceptibility of plants toward biotic stress caused by pests or pathogens (Rizhsky et al. 2004). This becomes more important in agricultural crops because, in various agricultural systems, most crops grow in unfavorable environmental conditions that restrict genetic growth and development potential of plants (Bray et al. 2000). Metabolic regulations including wide changes in the composition, concentration, and distribution of secondary and primary metabolites are among the common responses of plants to abiotic stresses. While secondary metabolites such as alkaloids and flavonoids produced by plants in response to stresses are utilized mostly for their defense, primary metabolites such as carbohydrates and amino acids play a crucial role in the plant's growth and development. Major *Bacillus*-mediated abiotic stress mitigation mechanisms are presented below:

8.2.1.1 Mechanisms to Mitigate Drought Stress on Plants

Global climate change is arguably one of the most pressing ecological concerns of our lifetime. Future changes in water availability and increasing drought stress will likely alter the crop production system, ultimately leading to exploring sustainable mitigation measures and necessary modifications to the system. Drought was identified as a key factor that limits crop productivity among various abiotic stresses plants encounter in noncontrolled environments or vast crop growing environments that lack irrigation facilities. Incidence and effect of drought is predicted to get worse in the coming years as a result of global warming and adverse climate change.

Crop breeders continue their efforts to overcome drought problems with resistant varieties (Araus et al. 2002). However, it is true that many of these varieties can only tolerate and survive under drought stress for a short period of time. As such, any other natural agent such as *Bacillus* spp. capable of alleviating drought stress is considered one of the significant agricultural inputs as it relates to sustainable agriculture. Lack of water availability primarily restricts nutrient uptake and photosynthesis as plants curtail water loss by increased diffusive resistance and make morpho-physiological adaptations, such as closing their stomates. As a result, plants lose turgidity, and leaf size expansion, stem extension, and root proliferation are halted. Overall, innate plant adaptation strategies against drought stress include either or all of physiological, biochemical (increased production of multiple phytohormones, accumulation of compatible osmolytes, antioxidant and other secondary metabolites or signaling molecules), and molecular (upregulation of multiple drought stress related genes) mechanisms (Chaves et al. 2003; Krasensky and Jonak 2012). These changes help plants maintaining turgor pressure of cells, protect cell membranes, macromolecules and enzymes from oxidative injury (Krasensky and Jonak 2012; Gill and Tuteja 2010). Unfavorable environmental stimuli such as drought can affect normal plant metabolism leading to suppression of crop growth and yield. Association of *Bacillus* with plant rhizosphere or phyllosphere stimulates plant immunity against drought stress by altering stress-responsive genes that optimize production of proteins, phytohormones, and other related metabolites.

8.2.1.2 *Bacillus*-Mediated Mechanisms of Mitigating Drought Stress

As most of the studies conducted to evaluate efficacy of *Bacillus* in providing abiotic stress tolerance and unraveling the associated mechanisms had to exert drought stress on plants, effect of *Bacillus* could be confounded with innate drought response of plants. However, additive effects from *Bacillus* application and quantitative expression of responses were indicative of the role of beneficial microbes. For example, exposure of *Bacillus* inoculated timothy (*Phleum pratense* L.) plants to drought stress for 8 weeks provided enhanced shoot (26.6%) and root (63.8%) biomass, stomatal conductance (214.9%), and photosynthetic activity (55.2%) compared to plants grown under similar drought stress conditions without inoculation (Gagne-Bourque et al. 2016). Underlying mechanisms that supported increased stress tolerance in this study by *Bacillus* included enhanced accumulation of osmolytes, such as many different types of amino acids and sugars in roots and shoots. Another documented mechanism of drought stress avoidance in wheat by *Bacillus* is production of growth-promoting phytohormones such as indole-3-acetic acid (IAA) and 1-aminocyclopropane-1-carboxylate deaminase (ACCD) to counteract the stress-induced increase of abscisic acid (Barnawal et al. 2017). *Bacillus* spp. treatment of plants exposed to drought were found to increase the uptake of water and macronutrients like N, P, and K (Barnawal et al. 2013), which is the direct influence of increased root growth by enhanced IAA production. A higher production of scavenging enzymes of reactive oxygen species (ROS) was observed by Saikia et al.

(2018) when mung bean was inoculated with a group of plant growth enhancing bacteria including *Bacillus subtilis* RJ46 followed by exposure to drought stress. Quantity of ROS scavenging enzymes (ascorbate peroxidase, SOD, PO, CAT, glutathione reductase) and relevant compounds (glutathione, ascorbic acid, and cysteine) that prevent buildup of ROS is usually found to be higher in *Bacillus*-inoculated plants, and they lessen the oxidative damage that occurs at the time of drought stress (Kaushal and Wani 2015). Thus, production of antioxidants is the most important known mechanism of *Bacillus*-mediated drought stress management.

8.2.1.3 Extent and Impact of salinity Stress on Plants

Climate change and global warming has been affecting regular rainfall and distribution over recent decades. More specifically, productivity of agricultural land has been worsening worldwide due to accumulation of salt that resulted from low rainfall, improper irrigation practices and high water evaporation rates due to dry weather condition (Al-Karaki 2006). The high concentration of salts in saline soils cause oxidative, osmotic, ionic, and water stress in plants. Accumulation of salt in upper soil layers eventually affects nutrient and water uptake by plant roots due to reduced soil water potential (Porcel et al. 2012). This mimics a drought stress situation that induces plant response to accumulate compounds with osmo-protective properties such as special types of sugars, amino acids, and other secondary metabolites that were previously absent or present in lower quantity. Under conditions of salinity, plants are subjected to nutrient imbalance like K^+ deficiency and Na^+ toxicity and may also suffer from oxidative stress. Plants may eventually face metabolic pathway disorders related to respiration, photosynthesis, homeostasis in redox system, and phytohormone regulation. As a result, carbohydrate and amino acid syntheses are affected leading to reduced seed germination, plant vigor, growth, and yield (Radhakrishnan and Lee 2013, 2014; Rady 2011; Munns and Tester 2008). However, induction of osmoregulators may counteract the above disorders as well as protect structures of different cellular organelles including membranes (Hare et al. 1998). These osmoregulators also work as scavengers of free radicals to prevent their damaging effects to DNA (Ashraf and Foolad 2007).

8.2.1.4 *Bacillus*-Based Mechanism of Salinity Stress Tolerance

Inoculation of plants with beneficial microbes including *Bacillus* spp. enhances plant growth and development during salt stress compared with non-inoculated. This is considered an eco-friendly approach to counteract abiotic stresses and make agriculture more sustainable (Hashem et al. 2015, 2016a, b; Radhakrishnan et al. 2014). Production of growth hormones such as IAA has been found by Bochow et al. (2001) as one of the mechanisms to compensate salt stress-induced growth and yield loss. Authors found significant yield increase in pepper and eggplant due to inoculation with *B. subtilis* FZB24 compared to the nontreated, despite irrigating the plots with saline groundwater. For further investigation to unravel the mode of action, pepper seedlings were pretreated with millimolar amounts of auxin precursors (indole-3-acetic aldehyde or indole-3-pyruvic acid, tryptophan) followed by exposure to saline water. Results revealed that auxin precursors treatment had compensated 75% growth loss of seedlings after 1 week that would occur due to salt stress. This finding further supports that one of the *Bacillus*-based modes of action of alleviating salinity-induced stress in plants is production of IAA. However, other investigators found that growth hormones like gibberellins were also produced by *Bacillus* and played a role in addition with enhanced uptake of N, P, K^+, $Mg2^+$, and $Ca2^+$(Mohamed and Gomaa 2012). They also reported decreased abscisic acid and Na^+ and Cl^- content compared to the non-inoculated, which may have occurred due to the relatively high uptake of required nutrients as facilitated by *Bacillus* to alleviate stress induced by salinity. Egamberdieva et al. (2017) also reported improved uptake of N, P, K, and Mg by chickpea, grown under saline soil conditions that were inoculated with a consortium of *B. subtilis* and *Mesorhizobium ciceri* compared with non-inoculated plants. Salinity stress significantly increases reactive oxygen species level and H_2O_2 in plants resulting in peroxidation of membrane lipid (Yazici et al. 2007; Koca et al. 2007). Thus, reduction of membrane lipid peroxidation or oxidation of other cellular organelles due to *Bacillus* inoculation under salinity is a proof of *Bacillus*-based stress mitigation. Lastochkina et al. (2017) reported reduction of stress-induced lipid peroxidation (MDA) in wheat due to inoculation of plants by *B. subtilis* 10–4 followed by exposure to water containing 2% NaCl salt compared with non-inoculated plants. If *Bacilli* colonize plants under salt stress, they trigger general antioxidant defense process resulting in synthesis of various anti-oxidant enzymes namely peroxidase, catalase (CAT), nitrate reductase (NR), superoxide dismutase (SOD), polyphenol oxidase (PO), glutathione reductase (GR), and guaiacol peroxidase (GP) that may vary with plant species (Chawla et al. 2013). However, halotolerant (HT) PGPR *Bacillus licheniformis* A2 recovered from saline soil showed higher growth promoting effect when plants were inoculated with the organism and grown in saline soil. Although several plant growth-promoting features such as production of IAA, phosphate solubilization, and siderophore production were considered as potential *Bacillus*-based mechanisms in alleviating the salt stress-induced detrimental effects and increasing plant growth of stressed peanuts (Goswami et al. 2014), study conducted by Zhang et al. (2008) with Arabidopsis in salt-affected soil revealed that HT *Bacillus subtilis* reduced the uptake of Na^+ by roots that involved downregulation of high-affinity potassium transporter (HKT1). However, IAA synthesis being transcriptionally related to ethylene production in plants via the expression of ACC synthase gene can halt their growth and development despite ethylene's capacity of providing salt tolerance to plants. Thus, after the initial ethylene production step, HT Bacilli start synthesizing ACC deaminase (ACCD) enzyme to stop ACC and ethylene production, supporting resumption of growth of stressed plants (Nabti et al. 2015). In addition, *Bacillus* can excrete exopolysaccharides (EPS) that facilitate binding of Na^+ in root cells thereby preventing their translocation to foliage. Similar binding of Na^+ by EPS may take place in the rhizosphere by *Bacillus* excreted EPS to prevent its absorption like a physical barrier around the roots (Arora et al. 2020). Thus, association of *Bacillus* spp. with salt-stressed plants has the potential to alter their metabolism to sustain or promote plant growth. Halotolerant *Bacillus*-mediated expression of genes to alleviate salinity stress is presented in Table 8.1.

Table 8.1 Bacillus-mediated gene expression in plants that were identified to be responsible for salinity stress amelioration

Plant species	*Bacillus* species included in the study	Genes responding to stresses	Role/Results
Triticum aestivum	*Bacillus safensis* W10	Upregulation of multiple genes including sulfur-rich thionin, S adenosylmethionine decarboxylase precursor, expansins, endotransglucosylase/ hydrolase and metallothionines Downregulation of protein phosphatases, flavonones hydroxylases, oxalates, and oxidases	Mitigation of salt stress
Solanum lycopersicum	*Bacillus megaterium*	Expression of MT2 receptor and gamma response (GR1)	Synthesis of metallothionin and glutathione reductase enzyme
Glycine max	*Bacillus firmus* SW5	Upregulation of salt tolerance genes GmVSP, CHS, GmPHD2, GmbZIP62, GmOLPb, and GmWRKY54 Expression of antioxidant enzyme-encoding APX, Fe-SOD, CAT and POD	Production of antioxidant enzyme, salinity tolerance, flavonoid biosynthesis
Zea mays	*Bacillus amyloliquefaciens* SQR9	Upregulation of several genes including NHX1, NHX2, RBCS, RBCL, H + -PPase, and NHX3	Enhanced photosynthesis, Na^+ sequestration, and export
Puccinellia tenuiflora	*Bacillus subtilis (GB3)*	Upregulation of *PtSOS1* and *PtHKT1;5* Downregulation of NCED	Modulation of Na^+ homeostasis
Oryza sativa	*B. Amyloliquefaciens* SN13	Upregulation of EREBP, *NADP-Me2, SOSI, SERK1*, and *BADH* Suppression of *GIG* and *SAPK4*	Na^+/H^+ reverse porter system, ion homeostasis; abiotic stress response and oxidative decarboxylation of L-malate
Arabidopsis thaliana	*Bacillus subtilis* (GB03)	Expression of HKT1	Na^+ transport in roots

Adapted from Arora et al. (2020)

8.2.1.5 Impact of Heavy Metal Stress on Plants

Due to unplanned industrialization all over the world, arable lands are inadvertently getting contaminated with metal toxicants that are part of industrial effluents released. These contaminants are affecting ecology of food chain by altering microbial communities and crop cultivation (Hu et al. 2009; Ashraf et al. 2017). Accumulation of Cu, Mn, Zn, Pb, Cr, and other heavy metals are listed as major pollutants in soil and water that are not degraded into harmless substances easily (Ma et al. 2009; Arthur et al. 2012). These metal-contaminated soil and water are not only toxic to the flora and fauna in a certain area but also create a huge risk to human health if contaminated soils are used for crop production and metal is taken up and transferred into food chain at higher-than-acceptable concentrations (Oves et al. 2016). Heavy metal content can affect activities of microorganisms, such as respiration and metabolism (metabolic entropy response), thereby affecting soil respiration (Blagodatskaya et al. 2006). Thus, microbes such as *Bacillus* that can survive these harsh conditions are more suitable for heavy metal remediation. Traditionally, chelators have been used to reduce metal toxicity from soil; however, chelators can be harmful to organisms in the edaphic environment (Tandy et al. 2006). In contrast, beneficial microorganisms like *Bacillus* spp. solubilize and change toxic metals to nontoxic forms. This method can be utilized in management of heavy metal phytoremediation when used in the integrated approach with hyperaccumulator plants (Kang et al. 2015c, Bosecker 1997). However, this remediation method of heavy metals is also known as bioremediation when microbes are used solely, which is considered the most sustainable, environmentally friendly, and cost-effective without any adverse effect to any component of the environment (Dixit et al. 2015). The release of *Bacillus* spp. into soil contaminated with heavy metals can enhance reduction of toxic effects of these metals on plant growth when combined in a phytoremediation effort. Brunetti et al. (2012) found that *B. licheniformis* enhanced Cu, Zn, Cd, Pb, especially Cr accumulation in *Brassica* plants that were grown to test their capacity as hyperaccumulators of metals for phytoremediation of heavy metal-contaminated soil. This eventually led to reduced levels of toxic metals in soil compared to nontreated plants. However, due to the low bioconcentration factors (>1), investigators could not conclude the suitability of the species for the phytoextraction of toxic metals from polluted soils. However, these species can be utilized successfully for low metal polluted soil. Besides accumulation and uptake of heavy metals or supporting enhanced uptake by plants, *Bacillus* and similar microbes mitigate plant stress from heavy metal through other mechanisms described below.

8.2.1.6 *Bacillus*-Based Heavy Metal Stress Alleviation in Plants

Rhizospheric and endophytic bacteria including *Bacillus* enhance growth and development of plants in metal polluted soils by two major methods: i) These microbes can remove heavy metals from soil or modify capacity of metal accumulation through efflux of ions outside the cells, transformation of metal ions to lower forms of toxicity, sequestration of metal ions on the cell surface or in polymers inside cells, and biomethylation, precipitation, adsorption or desorption; ii) these microbes can also alleviate heavy metal-induced plant stress through production of beneficial plant growth enhancing substances that may include solubilization/transformation of mineral nutrients, such as phosphate, nitrogen, and potassium, and production of plant beneficial enzymes, siderophores, and phytohormones (Ma et al. 2011).

8.2.1.6.1 Adsorption and Absorption of Heavy Metal by *Bacillus*

Bacillus can remove large amount of soil heavy metals by both adsorption and absorption, although Wang et al. (2013, 2001) reported that the principal mechanism of heavy metal ion accumulation is adsorption, which normally is independent of energy metabolism. However, absorption, a closely related mechanism depends largely on energy metabolism and occurs mostly in living cells. Active export of heavy metals via an ATPase efflux P-type pump was found by Shin et al. (2012) in an endophytic bacterial strain *Bacillus* sp. MN3–4. *Bacillus* has evolved a well-defined metal-resistance mechanism, which is capable of transporting metal ions against the concentration gradient across cell membranes to enhance hyperaccumulator plants' capacity of removing heavy metals from soil. This process uses ATP hydrolysis-released energy. In this regard, Wang et al. (2001) found that *Bacillus* could saturate 60% of its Cu^{2+} adsorption capacity within the first minute and reach an equilibrium as early as within 10 min. However, Wierzba (2015) found that addition of ethylenediaminetetraacetic acid (EDTA) and lemon oil in the media could improve removal rates by 31.5 and 26.3%, respectively.

8.2.1.6.2 Bioleaching

The process of extracting metals from waste or ores by using microorganisms is defined as bioleaching as microbes oxidize the metals and produce soluble compounds in the form of organic acids. Thus, production of organic acids and chelating or complexing compounds that are excreted into the environment are used for metal extraction. Bacteria belonging to the genus *Thiobacilli* are considered the most active group in bioleaching of metal ions; they generally grow under aerobic conditions. It was shown that bacteria leach a higher amount of heavy metals from sludge deposited when elementary sulfur was added as a stimulant for the activity of thionic acidophilic *Bacilli*. It took place by way of bacterial oxidation of elementary sulfur releasing sulfuric acid (Marchenko et al. 2015). As a result, the pH of sludge deposits goes down, which is an important factor for effective leaching of heavy metal.

8.2.1.6.3 Other Mechanisms of *Bacillus*-Based Heavy Metal Remediation

Microbial cells are capable of converting metals from one oxidation state to another, which can reduce their toxicity. Microbial enzymes and other secretions from their metabolic activities can dissolve heavy metals that are stuck in soil particles. Thus, precipitation, biosorption, and enzymatic transformation are the processes used by *Bacillus* and similar microbes to degrade, detoxify, or transform heavy metals to more stable, less mobile, or inert forms (Kumar and Bharadvaja 2020). *B. subtilis* inoculation of rice under Cd stress showed that roots and shoots at 45 days after inoculation (DAI) and grains at 120 DAI had lower Cd accumulation compared with non-inoculated (Treesubsuntorn et al. 2017). Authors hypothesized that the mechanism by which *B. subtilis* reduced Cd accumulation was its capacity to effectively absorb Cd from the medium. Their findings also suggested that *B. subtilis* was more effective in absorbing Cd compared to *B. cereus*. Ahmad et al. (2014) showed that *Bacillus* and a few other bacterial genera such as *Klebsiella*, *Stenotrophomonas*, and *Serratia* had supported plant growth under Cd stress by increasing water uptake and reducing electrolyte leakage in maize and wheat. As *Bacillus* increases availability and uptake of essential nutrients, heavy metal uptake by plants is reduced due to competitive exclusion. For example, Naseem et al. (2016) found that *Bacillus* sp. AMP2-inoculated wheat seedlings took up less Cr of different chromium salts (CrCl3, K2CrO4, K2Cr2O7) both at 10 and 20 ppm concentrations than control. Similar to other *Bacillus*-based abiotic stress mitigation mechanisms, when *Bacillus*-inoculated plants were grown in high concentration of heavy metal containing medium, it was found that tissues increased antioxidant enzyme activity including CAT, PA, APX, and SOD and concurrent decrease of metal concentration in the roots compared to non-inoculated plants (Hao et al. 2015). Inoculation of *B. subtilis* could also increase dry weight of rice plant as well as protect them from Cd stress. Mechanisms included ability of *B. subtilis* producing IAA, solubilizing phosphate, and controlling ethylene levels by the activity of ACC deaminase (Treesubsuntorn et al. 2017).

8.2.1.7 Mechanism of Nutrient Stress Alleviation by *Bacillus*

Multiple species of *Bacillus* were found to improve plant uptake of P and K by solubilizing fixed soil nutrients (Chen et al. 2006). For example, use of insoluble K sources together with *Bacillus edaphicus* NBT strain to treat soil for growing cotton and rape could increase K content in plants by 30% and improve growth compared with no *Bacillus* inoculation (Sheng and He 2006). Plant growth promotion in this study was attributed to K solubilization by *B. edaphicus* strain. In a similar study, Wu et al. (2005) found improved N, P, and K assimilation in maize due to *B. megaterium* and *B. mucilaginous* inoculation. Several other investigators also reported similar mechanism of nutrient stress alleviation such as solubilization of tricalcium phosphate (Calvo et al. 2010; Almoneafy et al. 2012) and zinc (Ajilogba and Babalola 2013) by *B. amyloliquefaciens* isolated from potato. Phosphate solubilization abilities of multiple *Bacillus* species, *B. thuringiensis*, *B. sphaericus*, and *B. megaterium*, were found by Akgul and Mirik (2008).

8.3 Biotic Stress Mitigation in Plants by *Bacillus* spp.

8.3.1 Extent and Impact of Biotic Stress on Crop Growth and Productivity

Like abiotic stresses, plants encounter many different types of biotic agents such as fungi, viruses, bacteria, nematodes, and insects during their life cycle. These entities may exert biotic stresses when they invade plants to use them as their host resulting in disruption of plant's normal metabolism. This interrupts plant growth, and in some cases, biotic stresses become the cause of plant mortality (Hashem et al. 2019). Many of these biotic agents can also cause post-harvest losses of crop yield (Singla and Krattinger 2016). However, in most cases plants do well even under these stressful situations because some beneficial microbes, if present in the micro-environment, interact with their host plants symbiotically or synergistically to counteract harmful effects from pathogenic microbes. These beneficial microbes can play similar role as synthetic fertilizers or pesticides to minimize adverse effect from biotic stresses and promote plant growth. Due to their significant role in plant growth enhancement they are often termed as plant growth promoting rhizobacteria (PGPR), where *Bacillus* is considered a prominent member. PGPR, including *Bacillus,* have been used in agricultural, especially crop production, systems to alleviate biotic stresses and develop environmentally friendly, sustainable management options (Grover et al. 2011, Vejan et al. 2016) for a long time, which is now gaining momentum. Application of beneficial microbes to the rhizosphere in an augmentative approach can be utilized for improving biotic stress tolerance. A few *Bacillus* species including *B. megaterium*, *B. subtilis*, and *B. cereus* were found by GroBkinsky et al. (2016) to produce cytokinins and other growth hormones. Synergism is another known mechanism of effect of Bacilli when used with other beneficial organisms for plant growth and development. Alam et al. (2011) applied *B. subtilis* together with arbuscular mycorrhizal (AM) fungi to rose-scented geranium. Results indicated a synergistic effect of *B. subtilis* that increased >10% yield (59.5%) compared to AM fungi alone (49.4%). Total oil yield from the harvested biomass was increased significantly as biomass production went up, although oil content percentage did not increase on a dry weight basis. Underlying mechanisms of *B. subtilis* providing synergistic effect to greater promotion of plant growth included increased growth supporting enzyme production, higher antioxidants and P solubilization, root nodulation, nitrogen fixation, and biocontrol activity.

8.3.2 *Mechanism of Biotic stress Mitigation in Plants by* Bacilli

Members of the genus *Bacillus* alleviate biotic stress of plants through a variety of mechanisms that include depriving biotic agents by outcompeting them for nutrients and space on plant rhizosphere or phyllosphere; inhibition of biotic agents by producing a variety of inhibitory biochemicals; induction of plant resistance; and facilitating plant growth by producing hormones, so that plant pathogens fail to infect plants. These can further be divided into two groups: direct and indirect mechanisms. The direct mechanism refers to production of biochemicals by cells of *Bacillus* spp. such as synthesis of several secondary metabolites (antibiotics, cell wall-degrading enzymes, hormones, antioxidants) that stimulate plant growth and assist plants to defend against pathogenic attack (Goswami et al. 2016). Stimulation of plant growth and induction of acquired systemic resistance are among the major indirect mechanisms involved with *Bacillus*-based biotic stress mitigation in plants.

8.3.2.1 Depriving Biotic Agents by Outcompeting them for Nutrients and Space

Early colonization of plant roots by *Bacillus* can provide a barrier against pathogenic microorganism invasion (Bais et al. 2004). Root exudates provide required nutrients to rhizosphere microbes to thrive. That is why microbial density in proximity of roots is higher compared to areas away from them, and there is always a competition for space on the root surface. Due to the competitive advantage of *Bacilli* for nutrients and space in plant rhizosphere, they can suppress pathogen proliferation, which is an important feature of the mode of action of *Bacillus*-based biotic stress alleviation in plants (Cawoy et al. 2011). It was found that many members of *Bacilli* can form biofilms, a densely packed surface or multicellular interface of associated aggregates under unfavorable environmental factors (Morikawa 2006) occupying most of the root surface. Formation of a biofilm by *Bacillus* on plant root can be very quick, requiring only a few hours (Allard-Massicotte et al. 2016), thus preventing attachment of pathogenic microbes on roots (Morikawa 2006). In general, bacteria utilize chemotaxis for finding root to colonize at early stages of plant growth (Allard-Massicotte et al. 2016). Due to the presence of many chemoreceptors involved in root colonization, *Bacilli* can efficiently colonize root system in soil (Allard-Massicotte et al. 2016). In the case of lack of availability of nutrients to *Bacilli*, major competition occurs for carbon, and is considered an important factor in biological control. *Bacillus* also competes for several micronutrients with other biotic disease-causing biotic agents that include copper, manganese, iron, and zinc. Among these elements, iron is highly important because of its limited presence in available form in soil (Loper and Henkels 1997). Due to their ability of producing siderophores that have a strong affinity for iron, *Bacillus* can solubilize and acquire ferric ions efficiently. Thus, depriving other soil microbes, including pathogens, from acquiring iron (Cawoy et al. 2011; Haas and Defago 2005; Loper and Henkels 1997).

8.3.2.2 Production of Inhibitory Biochemicals by *Bacillus*

Production of compounds of low-molecular-weight including antibiotics is common to many *Bacillus* species (B. subtilis, *B. megaterium*, *B. amyloliquefaciens*, *B. cereus*, *B. licheniformis*, *B. mycoides*, and *B. pumilus*) that directly affect other microorganisms through a process known as antibiosis (Weller and Thomashow 1993; Handelsman and Stabb 1996; Weller 1988). Some of these species can produce multiple antibiotics. For example, *B. subtilis* can produce more than two dozens of antimicrobial compounds with diverse structures (Stein 2005). These include polymyxin, subtilin, difficidin, and mycobacillin usually possessing broad-spectrum antimicrobial activity. *Bacilli* can produce antibiotic molecules during most of their life cycle, but production reaches very high levels during sporulation. Most of these compounds belong to the peptide class despite very high diversity in their sizes and structures. These antibiotics mostly contain amino acids and, in some cases, other residues that help them forming linear, cyclic or basic aminoglycoside type antibiotics (Stein 2005). Almost all the antimicrobial cyclic peptides can directly affect the integrity of fungal cell membranes through lysis and change their structure, thereby inhibiting their growth and development. *Bacillus*-produced antimicrobial peptides can reliably be used as fungicides due to their direct interaction with fungal cell membrane or interference in biosynthesis of chitin, glucan, and sphingolipid that are essential components of fungal cell wall and membrane. In this regard, positive results have been obtained by investigators from numerous studies. For example, two *B. brevis*- and *B. polymyxa*-produced peptide antibiotics gramicidin S and polymyxin B, respectively, inhibited gray mold-causing fungus *Botrytis cinerea* both in vitro and in vivo (Haggag 2008). The three main *Bacillus* spp.-produced families of cyclic lipopeptides (CLPs) are surfactins, iturins, and fengycins. It was reported that all three may although be present in bacterial secretion/culture filtrate but may not be needed for antimicrobial activity. In a study by Waewthongrak et al. (2015) on the inhibitory effect of all three CLPs, they found that growth of *Penicillium digitatum* was inhibited by iturin A and fengycin to control green mold on mandarin, but surfactins had no direct effect. However, Surfactin likely supports bacterial colonization of root tissues and establishment in the rhizosphere of plants through biofilm layer formation (Mihalache et al. 2017; Cawoy et al. 2014), and is considered essential component of the mechanisms by which *Bacilli* become successful in alleviating biotic stresses in plants. Investigators from different studies with different strains of *Bacilli* found diverse peptide antibiotics such as bacillomycin D, subtilisin, and xanthobaccin. However, due to the consistency and frequency of its occurrence, bacilysin is regarded taxonomically the most related and significant for the genus *Bacillus* (Loeffler et al. 1990). In addition, chitinase, amylase, protease, cellulase, pectinase, glucanase, and similar cell wall-degrading enzymes or substances like HCN can damage pathogens and pests to lower their population on plants.

8.3.2.2.1 Specific Mechanism Associated with Activity of Cyclic Peptides

Some cyclic peptide molecules disrupt membrane structure by binding only to the surface without passing through. However, other cyclic peptides can bind with specific membrane-associated structures such as ion channels, transporters and different types of receptors by traversing membranes. After successful binding, cyclic peptide molecules aggregate in a specific site on membrane to form variable size aqueous pores. Ions and other solutes pass through the channels of these pores in an uncontrolled way that ultimately leads to cell death. Debono and Gordee (1994) found that impairment of biosynthesis microbial cell wall macromolecular components such as glucan, chitin, and mannoproteins was the underlying mechanism of antifungal activity of several cyclic peptides. These cyclic peptides have the capacity to form a complex with the precursor molecule of microbial cell wall macromolecules that eventually promote pore formation and cell wall disruption. While pore formation on membrane or degradation of cell walls is the major mode of action, alternation of ribosome function is also considered a potential mechanism to suppress growth of pathogenic microbes. For example, Katz and Demain (1977) found that bacitracin A produced by *B. licheniformis* inhibited cell wall synthesis but the butirosin complex belonging to amino glycosides produced by *B. circulans* altered ribosome function of diverse microbial groups (Defuria and Claridge 1976).

8.3.2.3 Induction of Host Defense against Biotic Stress

In addition, with above-mentioned mechanisms, some strains of *Bacilli* activate defense systems in host plants that results in an enhanced level of resistance against pathogen attack (Conrath et al. 2006). This can be explained as supporting plant's immune defense arsenal through sensitization and priming to defeat invading pathogens. This process initiated by biotic stimuli helps in scaling up expression of a plant's defense-related genes to accumulate antifungal biochemicals. Strains of *Bacilli* or their metabolites can turn on plant's defense system when pathogens attack host plants or can be triggered by pre-inoculation (Schonbeck et al. 1993) that results in an enhanced resistance level (Conrath et al. 2006). Higher level of induced resistance in plants is superior over other modes of action of *Bacilli* such as antibiosis or competition, as it provides protection to plants usually for a long period of time even when bacterial population subsides. This happens as the response has already transduced to the distal organ of the plant from the point of instigation. Induction of systemic resistance occurs through a well-orchestrated sequence of biological events. Beneficial rhizobacteria such as *Bacilli* can trigger a defense response by stimulating the plant through activation of a variety of cellular defense responses in a well-coordinated manner. These responses result in oxidative burst, defense-related enzymes buildup (Rahman et al. 2015), cell-wall strengthening (Heil and Bostock 2002), and production of secondary metabolites (Yedidia et al. 2003). The presence of the microbe is detected by pattern recognition receptors (PRRs) of a plant cell membrane through microbe-associated molecular patterns (MAMPs), which may include lipopolysaccharides, flagellin, glycoproteins, and chitin (Jones and Dangl 2006). These are also known as elicitors. *Bacillus* spp. are also known to produce lipopeptides and volatile compounds, which can play similar role as elicitors for inducing systemic resistance in plants. Surfactin produced by *B. subtilis* strain S499 was found to induce systemic resistance (Ongena et al. 2007). Complex interaction between PRRs and MAMPs (elicitors) subsequently results in immunity (PTI) through defense-related gene expression, oxidative burst, and callose deposition (Schwessinger and Ronald 2012; Altenbach and Robatzek 2007) from ISR-type defense signaling. Different *Bacillus* spp. may induce different but relevant signaling pathways. For example, ISR mediated by *Bacillus cereus* AR156 required both SA and JA/ET signaling pathways together with NPR1 (Niu et al. 2011). Defense response against pathogens involve several molecules such as phytoalexins, pathogenesis-related proteins (proteinase inhibitors, chitinases, β-1,3-glucanases), and lignin (Van Loon 2007). Fungal hyphal growth during infection process is prevented by thickened cell wall in combination with PR proteins (Lugtenberg et al. 2001).

8.3.3 Mechanism of Bacterial Disease Prevention by **Bacillus** *Spp.*

Together with fungi, viruses, and nematodes, plant disease-causing pathogenic bacteria pose major challenges to plant health and yield in agricultural production systems (Hussey and McGuire 1987; Guo et al. 2013; Narasimhan and Shivakumar 2015). Major pathogenic bacteria that are known to infect plant with detrimental effect on plant growth and development include but not limited to *Pseudomonas, Xanthomonas, Erwinia,* and *Ralstonia*. Although *Bacillus* spp. belong to microbial group bacteria, upon inoculation of plant or plant growing media they not only counteract and suppress pathogen growth but also promote plant growth (Krid et al. 2012; Yi et al. 2013). Mechanisms of *Bacillus*-based protection of plant from bacterial infections include biofilm formation around the root surface and their secretion of several toxins such as surfactin, iturin, macrolactin, bacillomycin, and fengycin that destroy pathogenic populations of bacteria resulting in plant disease control (Hinarejos et al. 2016; Chen et al. 2013; Huang et al. 2014; Elshakh et al. 2016). Pathogenic bacterial cell walls can be degraded quickly by the secretions of *Bacillus* spp., eventually killing the pathogen (Elshakh et al. 2016).

8.3.4 Mechanism of Fungal Disease Control

Mycelial growth of many different fungi is inhibited by the antagonistic activity of *Bacillus* spp. to control fungal diseases (Handelsmann and Stabb 1996; Aydi-Ben-Abdallah et al. 2016; Abdalla 2015; Chowdhury et al. 2015a; Akram et al. 2016;), thereby enhancing plant growth and yield (Narasimhan and Shivakumar 2015).

Underlying mechanism of *Bacillus* spp.-mediated fungal disease control include either or all of the events and interactions occur when *Bacillus* come in contact with fungal pathogens. Immediately after attachment of *Bacillus* to the mycelial cell walls, production of fungal cell wall-degrading enzymes (chitosanase, protease, glucanase, cellulase siderophores) and HCN takes place from the bacteria, which crack and deform the hyphae leading to altered cell functions and structures such as protoplast leakage and vacuolation (Ben-Khedher et al. 2015; Han et al. 2015). Mitigation of pathogen-induced biotic stress may also occur via *Bacillus* spp.-mediated physiological changes in plants. These include alteration of respiratory and photosynthetic pathways in diseased plants together with regulation of phenyl-propanoid, carbohydrates, defense-related proteins, and nitrogen metabolism (Jain et al. 2015). Plant beneficial *Bacillus* spp. increase antioxidant enzymes (APX, CAT, GR, GPX, POD, PPO) and reduce lipid peroxidation in plants. They also enhance production of other defense enzymes such as PAL, β-1,3-glucanase, chitinase, and phenolic acids that lessen the hostile effects of plant infection by pathogens (Chowdappa et al. 2013; Jain et al. 2013; Solanki et al. 2012).

8.3.5 Mechanism of Nematode and Virus Disease Control by Bacillus

Viruses, the second largest group of plant pathogens cause most plant diseases after fungi. Many *Bacillus* spp., produce antiviral compounds that minimize the adverse effects of these pathogens on plants (Esawy et al. 2011). Prevention of viral diseases by *Bacillus* spp. has been reported in a few cases. However, in most cases it was due to reduction of disease rate as a consequence of *Bacillus* spp. induced systemic resistance (ISR) in plants. Zhang et al. (2004) reported enhanced plant growth of cucumber during cucumber mosaic virus infection when plants were inoculated with *Bacillus* compared to non-*Bacillus* treated. Formation of biofilm and surfactin production by *B. amyloliquefaciens plantarum* was found to subvert the viral disease in plants by Chowdhury et al. (2015b). Underlying mechanism in this case was due to triggering of ISR machinery. Similarly, viral disease caused by tobacco mosaic virus was suppressed by *Bacillus* spp. because of inhibition of viral coat protein synthesis from induced systemic resistance. Additional mechanisms involved were increased expression of plant defense genes (PR-1a and PR-1b), disease-resistant signaling genes (*Coil* and *NPR1*), and cell wall expansion (*NtEXP2* and *NtEXP6*) genes (Wang 2009).

Nematodes, which are known as microscopic worms, can also damage plants by being parasitic and feeding on roots. Among many plant parasitic nematodes, root-knot causing ones are most damaging worldwide. Nearly 5500 plant species are within the host range of this nematode (Trudgill and Blok 2001). Prevention of root-knot nematode infection in crops by *Bacillus* spp. includes resistance development and reduction of gall and egg masses (Adam et al. 2014). Chowdhury et al. (2015b) reported that *Bacillus* spp. synthesized antimicrobial peptides such as bacteriocins that inhibit pathogenic nematode growth. Genes encoding nematicidal activity were identified by Liu et al. (2013) as PZN gene cluster in *B. amyloliquefaciens*. *Bacillus* spp. secreted crystal proteins (Cry5B and Cry6A) were found to control the growth of plant-parasitic and free-living nematodes *Meloidogyne hapla* and *Caenorhabditis elegans*, respectively (Yu et al. 2015).

8.4 Mechanism of Insect Stress Alleviation in Plants by *Bacillus*

A broad range of insect control in plants is provided by *Bacillus thuringiensis* (Bt)-produced Bt toxin (Navon 2000). In addition, Bt was also found to inhibit the growth of insect larvae, thereby decreasing plant damage and increasing growth (Boukedi et al. 2016; Arrizubieta et al. 2014). Upon sporulation, *B. thuringiensis* forms crystals of proteinaceous insecticidal δ-endotoxins also known as crystal proteins or Cry proteins (Roh et al. 2007). In most strains of *Bacillus*, genes located on a plasmid instead of a chromosome that are known as cry genes encode these toxins. Cry toxins show precise activities against insect species belonging to several orders such as Coleoptera (beetles), Diptera (flies and mosquitoes), Lepidoptera (moths and butterflies), and Hymenoptera (wasps, bees, ants and sawflies) (Schnepf et al. 1998). Upon ingestion of toxin crystals by insects, insoluble crystals get denatured in their alkaline digestive tracts. Proteases from the insect gut then cut these soluble crystals to liberate the toxin. Inside the insect gut, the Cry toxin at this stage is injected into the cell membranes, which paralyzes the digestive tract including formation of pores. The insect starves to death as it stops eating. Live Bt bacteria from the environment may also colonize the insect causing death. Additional findings on the mechanism suggested that bacteria in the midgut of susceptible larvae stimulate insecticidal activity of *B. thuringiensis* (Broderick et al. 2006). Some relevant studies suggested that due to its insecticidal and plant growth promotion properties, *B. thuringiensis* could be used as a biological control agent (Compant et al. 2005).

8.5 Conclusion and Future Perspectives

Field grown plants are constantly exposed, either sequentially or simultaneously, to many abiotic or biotic stresses. These biotic and abiotic stresses significantly affect crop yield, food quality and ultimately global food security. Plants must cope with these stressful conditions to thrive and complete their life cycle. Among many beneficial microbes, *Bacillus* species are exceptional, as members of this group can form endospores that are extremely robust under harsh environmental conditions, suppress harmful microbes, and can also secrete secondary metabolites that stimulate plant growth. Thus, beneficial microbes such as *Bacillus* provide a model for enhancing stress tolerance upon successful application in plant growing environment. *Bacillus* spp. were found in numerous studies to alleviate biotic and abiotic stresses and improve plant growth either directly or indirectly. Both biotic and abiotic stresses can cause physiological, biochemical, and molecular changes in plants affecting normal growth and development. *Bacillus* spp. either prevent or counteract these negative changes through a series of biological and biochemical mechanisms that have been interpreted from an appreciable number of studies. *Bacilli*-mediated abiotic and biotic stress tolerance in plants includes biological, physiological, biochemical, metabolic, and molecular mechanisms triggered in response to stresses. Promotion of plant growth by these underlying mechanisms usually involve regulation of plant hormones, improved nutrition acquisition, siderophore production, and enhanced antioxidant activity. Secretion of exopolysaccharides and siderophores by *Bacillus* spp. inhibit or stop movement of toxic ions and assist in uptaking water by roots as well as maintaining ionic balance. These compounds were also found to inhibit pathogenic microbial populations through multiple mechanisms that have been unraveled by numerous studies. However, many of the possible mechanisms either remain unclear or not compiled in a systematic method to make them available to researchers of *Bacillus* spp. This review compiled most of the processes unraveled by various studies to date and provides a reliable source of information for designing relevant research plan to further explore the mechanisms that have not been fully elucidated to the molecular level. As new and more effective strains of *Bacilli* to counteract plant abiotic and biotic stresses are discovered on a regular basis, future studies should focus on discerning mechanisms associated with enhanced efficacy.

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