Review

Bacillus subtilis: A plant-growth promoting rhizobacterium that also impacts biotic stress

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ARTICLE INFO

ABSTRACT

Plants encounter many biotic agents, such as viruses, bacteria, nematodes, weeds, and arachnids. These entities induce biotic stress in their hosts by disrupting normal metabolism, and as a result, limit plant growth and/or are the cause of plant mortality. Some biotic agents, however, interact symbiotically or synergistically with their host plants. Some microbes can be beneficial to plants and perform the same role as chemical fertilizers and pesticides, acting as a biofertilizer and/or biopesticide. Plant growth promoting rhizobacteria (PGPR) can significantly enhance plant growth and represent a mutually helpful plant-microbe interaction. *Bacillus* species are a major type of rhizobacteria that can form spores that can survive in the soil for long period of time under harsh environmental conditions. Plant growth is enhanced by PGPR through the induction of systemic resistance, antibiosis, and competitive omission. Thus, the application of microbes can be used to induce systemic resistance in plants against biotic agents and enhance environmental stress tolerance. *Bacillus subtilis* exhibits both a direct and indirect biocontrol mechanism to suppress disease caused by pathogens. The direct mechanism includes the synthesis of many secondary metabolites, hormones, cell-wall-degrading enzymes, and antioxidants that assist the plant in its defense against pathogen attack. The indirect mechanism includes the stimulation of plant growth and the induction of acquired systemic resistance. *Bacillus subtilis* can also solubilize soil P, enhance nitrogen fixation, and produce siderophores that promote its growth and suppresses the growth of pathogens. *Bacillus subtilis* enhances stress tolerance in their plant hosts by inducing the expression of stress-response genes, phytohormones, and stress-related metabolites. The present review discusses the activity of *B. subtilis* in the rhizosphere, its role as a root colonizer, its biocontrol potential, the associated mechanisms of biocontrol and the ability of *B. subtilis* to increase crop productivity under conditions of biotic and abiotic stress.

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Contents

1. Introduction

Many microbes have the capacity to promote plant growth and microbial products that enhance plant health and growth have been commercialized. The beneficial effects of bacteria derived from the plant rhizosphere on roots and overall plant growth have been demonstrated. These types of bacteria have been designated as plant-growth-promoting rhizobacteria (PGPR). The significant beneficial effect of these rhizobacteria on plant growth are achieved by both direct and indirect mechanisms. The direct methods include the production of compounds that stimulate plant growth and ameliorate stress (Goswami et al., 2016). PGPR exhibit a significant interaction with plant roots and have both direct and indirect positive effects on plant growth and the reduction of both biotic and abiotic stresses. Plant growth is enhanced by the induction of systemic resistance, antibiosis, and competitive omission and other mechanisms (Tripathi et al., 2012).

Viruses, bacteria, nematodes, weeds, and arachnids, all represent sources of biotic stress on plants. These agents injure their plant hosts, reduce plant vigor and can induce plant mortality. In addition, they also cause pre- and post-harvest losses in crop plants (Singla and Krattinger, 2016). Biotic and abiotic stresses negatively affect plant growth, development, yield, and biomass production (Chaudhary et al., 2012). The predominant genera of PGPR are *Pseudomonas* and *Bacillus*. The application of PGPR in the rhizosphere could be used to alleviate plants stresses due to their unique characteristics, diversity and relationship to plants. PGPR could be deployed in agricultural production systems to alleviate biotic and abiotic stresses and to produce sustainable, environmentally-friendly management tools (Grover et al., 2011; Vejan et al., 2016).

Plant roots are surrounded by a thin film of soil called the rhizosphere which represents the primary location of nutrient uptake, and is also where important physiological, chemical, and biological activities are occurring. Bacteria are the most abundant microbes present in the rhizosphere. *Bacillus* species are capable of forming long-lived, stress tolerant spores and secreting metabolites that stimulate plant growth and prevent pathogen infection (Radhakrishan et al., 2017). Thus, the application of microbes to the rhizosphere represents an approach to improving abiotic stress tolerance, especially the environmental stresses brought about by climate change. *Bacillus subtilis* also plays a significant role in improving tolerance to biotic stresses. This induction of disease resistance involves the expression of specific genes and hormones, such as 1-aminocyclopropane-1-carboxylate deaminase (ACC). Ethylene limits root and shoot growth and helps to maintain plant homeostasis. The degradation of the ethylene precursor (ACC) by bacterial ACC helps to relieve plant stress and maintain normal growth under stressful conditions (Glick et al., 2007). Some of the volatile organic compounds (VOCs) produced by *Bacillus subtilis* strain (GB03) also help plants to resist pathogen attack) (Ryu et al., 2005). *Bacillus* spp. also secrete exopolysaccharides and siderophores that inhibit the movement of toxic ions and help to maintain the ionic balance, promote the movement of water in plant

tissues, and inhibit the growth of pathogenic microbes (Radhakrishna et al., 2017). The present review mainly discusses the interaction of *B. subtilis* with host plants in the rhizosphere through root colonization, their biocontrol potential and mechanism of biocontrol, and the utilization of *B. subtilis* to maintain and/or increase crop productivity in the field under conditions of biotic and abiotic stress.

2. Root colonization

Colonization of roots by *Bacillus subtilis* is beneficial to both the bacterium and the host plant. Approximately 30% of the fixed carbon produced by plants is secreted through root exudates. Colonization of the roots by bacteria provides a nutrient source, and in exchange, plants are the recipient of bacterial compounds and activities that stimulate plant growth and provide stress protection to their hosts. *Bacillus subtilis* forms a thin bio-film on the roots for long-term colonization of the rhizosphere. Chemotaxis is required for *B. subtilis* to locate and colonize young roots (Allard et al., 2016). The chemotaxis machinery encoded in the bacterial genome is specific to individual species and is not associated with genome size. The bacterial genome possesses several chemoreceptor genes along with genes that regulate cell differentiation and their mutual relationship with living organisms (Krell et al., 2011). The primary function of a bacterial chemoreceptor is to help in the establishment of strong beneficial interrelationship between the plant and the bacterium. *Pseudomonas, Azotobacter chroococcum, Rhizobium, and Sinorhizobium meliloti* are attracted to root exudates (Webb et al., 2014). The first chemotaxis study was conducted on the interaction between *Escherichia coli* and a *Salmonella enterica* serovar and was later expanded to the study of gram positive bacteria, such as *B. subtilis*. The *B. subtilis* genome encodes 10 chemoreceptors known as ligands, which are composed of amino acids, carbon, and oxygen (Glekas et al., 2012). The chemoreceptors in *B. subtilis* enable it to find a specific environment, namely plant roots (Yang et al., 2015). *B. subtilis* is an important component of the plant rhizosphere (Hanlon and Ordal, 1994; Garrity et al., 1998). Colonization of plant roots by *Bacillus* spp. requires 24 h to form a biofilm that is induced by the presence of plant molecules, such as cell wall polysaccharides (Beauregard et al., 2013) and malic acid (Chen et al., 2012; Rudrappa et al., 2008). Biofilms consist of a multicellular bacterial community covered in a self-secreted matrix. The timing of the formation of a *B. subtilis* biofilm on host roots is also dependent on the promoter of the genes responsible for the production of the matrix when the bacterium initially contacts a root (Beauregard et al., 2013). One study reported that chemotaxis signals required for colonization by *B. subtilis* are activated 4 to 8 h post-inoculation, which is also the time frame for the activation of plant defense mechanisms against *P. syringae* pv. tomato DC infection (Rudrappa et al., 2008). Another previous study revealed that exudates from rice plants attract *Bacillus* spp., while soybean root exudates attract *Bacillus amyloliquefaciens* (Bacilio et al., 2003). Allard et al. (2016) root exudates from *Arabidopsis* play a

significant role in attracting *B. subtilis* and enhancing root colonization.

3. Biocontrol activity

The commercial production of agricultural crops requires the use of method that protect the crops from microbial pathogens that would otherwise reduce the yield and quality of the harvested crops. Alternatives to the use of synthetic chemicals has been an active area of research with the advent of organic and sustainable agriculture. Instead, more environmentally-friendly, safer methods of plant protection have been pursued; especially biocontrol approaches that utilize beneficial microbes (Warrior, 2000). Biological control, utilizing beneficial microbes, is an excellent approach to limiting the adverse effect of disease-causing microbes on plant health and productivity. Considerable effort has been placed on identifying microbial biocontrol agents that can repress phytopathogens, especially those that are responsible for soilborne diseases, and that can enhance agricultural productivity (Cazorla et al., 2007). *Bacillus* species are recognized as safe bacteria that produce substances that are beneficial for crops and the production of industrial compounds (Stein, 2005). In addition, *Bacillus* spp. also produce endospores, which helps the bacteria to survive harsh environmental conditions, can allow for germination by different environmental cues, can allow for long-term storage of the biocontrol agent, and reduce the complexity of the formulation process (Collins and Jacobsen, 2003). Notably, *Bacillus* species that are used for rhizosphere applications can also function as plant endophytes (McSpadden and Gardener, 2004) that also protect plants from pathogens (Romero et al., 2004). *Bacillus* spp. produce antimicrobial metabolites that can be used as a substitute to the use of synthetic chemicals or as a supplement to the use of bio-pesticides, and biofertilizers, for controlling plant diseases (Ongena et al., 2005). The success of biocontrol approaches depends on the proper selection of effective biocontrol agents and their ability to provide protection against specific target pathogens in specific crops.

3.1. Mechanism of action of microbial biocontrol agents

B. subtilis is a gram-positive bacterium that forms biofilms on inert surfaces and possesses many transcriptional factors (Stanley et al., 2003). Different strains of *B. subtilis* synthesize a variety of hydrolytic enzymes, including i.e. cellulases, proteases, and β-glucanases. Cazorla et al. (2007) suggested that since *B. subtilis* has the ability to secrete antibiotics and hydrolytic enzymes, it can modify its' environment in a self-beneficial manner and also produce resistant endospores to sustain itself under adverse conditions. The ability of *B. subtilis* to exhibit biocontrol activity is dependent upon three factors: (1). host vulnerability; (2). pathogen virulence; and (3). the environment. Potential biocontrol mechanisms of *B. subtilis* are presented in Fig. 1. Importantly, any molecular changes (changes in gene expression) can directly or indirectly influence the mechanisms illustrated in Fig. 1. Additionally, genetically engineered enhancement of *B. subtilis* with known biocontrol traits may interact with existing mechanisms in a synergistic manner (Dotaniya et al., 2016).

Bacteria also produce the cell-wall-degrading enzymes and various metabolites that can limit the growth or activity of other microorganisms (Shoda, 2000). Notably, *B. subtilis* strains are known to synthesize antibiotic lipopeptides, including fengycin, surfactin, and iturin. Lipopeptides are low molecular weight compounds with amphiphilic features. Surfactants and antimicrobial compounds produced by *B. subtilis* are receiving more attention. Lipopeptide genes occur in many species and strains of biocontrol agents and some with enhanced capacity to produce antibiotics and limit fungal root pathogens have been commercialized (Joshi and McSpadden Gardener, 2006). Romero et al. (2007) reported that lipopeptides provide protection to plants under both pre- and post-harvest conditions by directly suppressing pathogenic fungi or by inducing systemic resistance in host plants. *B. subtilis* strains PCL1608 and PCL1612 produce a high level of antibiotics, especially iturin A which serves as the principal mechanism underlying the control of *Fusarium oxysporum* and *Rosellinia necatrix* (Cazorla et al., 2007). These results are supported by previous reports indicating that iturin A exhibits antifungal activity against a variety of target fungi (Chitarra et al., 2003). A recent study reported that *B. amyloliquefaciens* L-1 was a good biocontrol agent against pear ring rot (Pingping et al., 2017). *Bacillus* strain 6051 exhibits strong, very stable biofilm formation and also produces surfactin, indicating that it would a good biocontrol agent against pathogenic bacteria (Bais et al., 2004). As previously mentioned, the lipopeptides produced by *B. subtilis* represent diverse antifun-
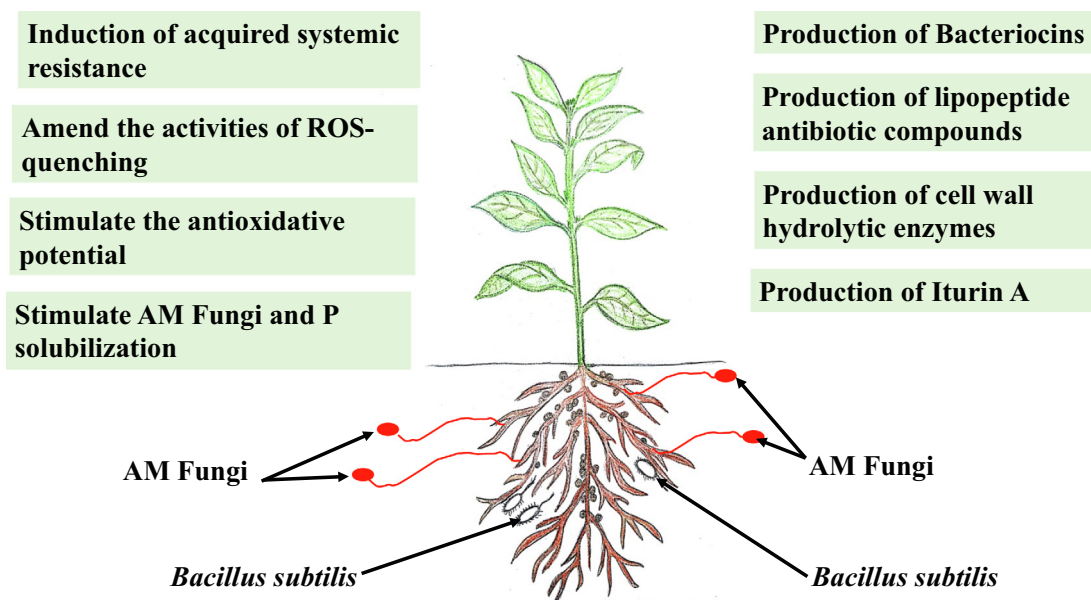

Fig. 1. Mechanisms of *Bacillus subtilis* in biological control of biotic stress.

gal and anti-bacterial antibiotics including fengycins, iturins and, surfactins (Mnif and Ghribi, 2015). Meena and Kanwar (2015) reported that while surfactants have strong antibacterial activity, they do not have an impact on fungi.

Iturins are categorized into A, C, D, and E iturins; mycosubtilin; D, F, and L bacillomycins; and bacillopeptin (Mnif and Ghribi, 2015). Iturins exhibit antimicrobial activity against fungi and yeast and are considered as an excellent biopesticide (Wang et al., 2015). Fengycins, a type of plipastatin, and A, B, or C fengycin (Wang et al., 2015) are less hemolytic than surfactins and iturins but have strong antifungal activity and limit the growth of bacteria and fungi (Ongena and Jacques, 2008). B. subtilis also produces peptide antibiotics called bacteriocins that play an important role in innate host immunity. Bacteriocins are grouped into four classes based on their genetic and biochemical properties. Class 1 bacteriocins, called lantibiotics, are commonly used as an antibiotic (Joseph et al., 2013). Lantibiotics synthesized by B. subtilis are categorized into A and B types based on their antimicrobial activity and chemical structure (Kumar et al., 2012).

The biocontrol activity exhibited by B. subtilis can also be attributed to indirect mechanisms. B. subtilis is a common soil microbe but is present freely except in soils where it has been applied in high doses. Evidence also indicates that B. subtilis occurs as an endophyte of plant roots (Fall et al., 2004). Indirect mechanisms associated with the biocontrol activity of B. subtilis against plant pathogens include, biofilm formation, plant growth promotion (PGP), competition for nutrients and colonization sites, ability to induce cell lysis, and induced systemic resistance (ISR) (Wang et al., 2018). Antibiotic substances play an important role in disease control by microbes, including B. subtilis. More than 24 antibiotic substances have been reported to be produced by B. subtilis. The produced substances include peptides, proteins, and non-peptides based substances. Non-peptide antibiotics can be categorized as ribosomal and non-ribosomal peptide antibiotics (Wang et al., 2015). B. subtilis also forms biofilms on plant roots which help to produced lipopeptides and augment their antimicrobial activity in the soil (Davey et al., 2003).

In summary, many strains of Bacillus subtilis exhibit the ability to act as biocontrol agents against pathogenic fungi and thus can be used to suppress disease. Several mechanisms, both direct and indirect, are responsible for their ability to control pathogenic fungi. These include the production of a wide array of antibiotic compounds (lipopeptides), the ability to form endospores, the ability to form biofilms on root surfaces, and the ability to induce host systemic host resistance, and stimulate plant growth. In this regard, biofilm development is more vigorous in wild strains of B. subtilis than in laboratory or commercial strains (Kinsinger et al., 2003).

3.2. Induction of host resistance and plant growth

B. subtilis is a species of PGPR that are known to activate plant host defense response (host resistance) against pathogens. Host cells undergo ultrastructural and cytochemical changes in response to a pathogen attack. B. subtilis is known to activate induced systemic resistance (ISR) in the hosts that they occupy, which increases host resistance to plant pathogens. The activation of ISR by B. subtilis is known to induce the synthesis of jasmonic acid (JA), ethylene, and the NPR1-regulatory gene in plants (Garcia-Gutierrez et al., 2013).

These defense responses are systemically activated at distances far-removed from the original site of disease and confer a level of disease resistance against viruses, fungi and bacteria throughout the plant. The activation of ISR is associated with cell wall degradation, de novo protein production of glucanases and chitinases, and the production of phytoalexins linked to disease resistance. The

application of B. subtilis strain (AUBS1) increases host production of phenylalanine ammonialyase (PAL), peroxidase (POD), and de novo protein synthesis in rice leaves (Jayaraj et al., 2004). Another study reported that B. subtilis strain (UMAF6614) induced the secretion of SA and JA defense-related responses in melons; making the plants more resistant to powdery mildew (Garcia-Gutierrez et al., 2013). Bacillus subtilis also enhances the synthesis of enzymes and PR proteins in host tissues in tobacco, resulting in increased resistance to mosaic virus, as evidenced by the reduced level of mosaic symptoms observed in plants treated with B. subtilis than in non-treated plants (Lian et al., 2011). Host enzymes that are induced by B. subtilis include peroxidase, (POD), polyphenol oxidase (PPO), and superoxide dismutase (SOD), as well as various hormones, whose increased synthesis results in ISR against early and late blight in tomato seedlings (Chowdappa et al., 2013). Bacillus subtilis strain (Sb4-23) mediates ISR in plant hosts through indirect, rather than direct mechanisms (Wang et al., 2018). The use of another strain of Bacillus subtilis strain reduced root-knot nematodes activity in tomato plants by activating ISR (Adam et al., 2014). The enhancement of plant growth is often linked with ISR. Bacillus subtilis (BS21-1) has been demonstrated to be an excellent biocontrol agent and has been reported to decrease disease incidence in four vegetable crops through ISR (Lee et al., 2014). In summary, B. subtilis has been shown to activate ISR in many plant crops, leading to increased disease resistance as evidenced by a lower number of pathogenic infections. It is an abundant and genetically diverse organism that has been used to produce numerous commercial biocontrol products. The application of a Bacillus strain activates ISR and promotes plant growth. Further studies should be conducted on Bacillus to identify new strains that can be used address many different plant diseases, while at the same time, acting as a PGPR and making host plants more stress tolerant.

3.3. Synergistic interactions between B. subtilis and root nodule bacteria

Inoculation of plant roots with rhizobia may result in a smaller number of nodules produced when a new strain is used. New strains may not be able to compete with indigenous strains. The root nodulation process is based on an exchange of signals between the host and bacterium which leads to the establishment of the rhizobia in host tissues, nodulation, and the promotion of plant growth through enhanced uptake of nutrients from the surrounding soil (Tilak et al., 2006). A positive effect on plant disease control and growth has been observed when plants have been exposed to both root nodule bacteria and B. subtilis. Microbes that are associated with roots, including free living, endophytic, rhizospheric, and symbiotic, can induce the synthesis of phytohormones in their plant hosts or in some cases produce the hormones directly (Sgroy et al., 2009). Zaidi et al. (2009) reported that B. subtilis is directly involved in P solubilization and exhibits a synergism with arbuscular mycorrhizal fungi (Kohler et al., 2007).

Various genera of bacteria have been isolated from the soil and rhizosphere, including Bacillus, Acinetobacter, Enterobacter, Pseudomonas, and Sinorhizobium (Sorty et al., 2016). Another study revealed that Bacillus, Enterobacter, Arthrobacter, Mycobacterium, Cellulosimicrobium, and Pseudomonas were all associated with soybean roots (Egamberdieva et al., 2016). While the application of a PGPR did not adversely affect the rhizobacterial strain that was present, inoculation with P. putida and Pseudomonas fluorescens or a Bacillus strain had a positive effect on root nodulation, enzyme production, and plant growth relative to non-inoculated plants (Tilak et al., 2006). Endophytic diazotrophic bacteria have been reported to synthesize plant growth hormones (JA, GA3, IAA, and ABA) in roots of the halophyte shrub, Prosopis strombulifera (Piccoli et al., 2011). In another study, the production of IAA by

Pseudomonas and *Ochrobactrum,* was confirmed in bacteria when subjected to adverse environmental conditions (Mishra et al., 2017). Großkinsky et al. (2016) reported that the *Bacillus* species, *B. megaterium, B. cereus,* and *B. subtilis,* produced cytokinins. Arbuscular mycorrhizal (AM) fungi together with *Bacillus subtilis* were applied to geranium with results indicating that AM fungi alone increased yield by 49.4%; and when AM fungi were combined with *B. subtilis,* yield increased by 59.5%. Although oil content did not increase on a dry weight basis, total oil yield was increased significantly due to greater biomass production (Alam et al., 2011). In summary, *B. subtilis* exhibit a synergistic effect on plant growth when they are applied in combination with AM fungi. The combined application results in greater promotion of plant growth, increased production of enzymes, antioxidants, P solubilization, biocontrol activity, root nodulation, and nitrogen fixation. The evidence indicates that a greater effort should be made to develop a commercial formulation of PGPR strains of *Bacillus* spp.; especially those that readily form endospores.

3.4. Induction of a systemic agent in plant roots

As previously discussed, soil contains many diverse microorganisms with the potential of beneficial antagonistic properties. Utilization of select microbes, such as *B. subtilis,* can result in increased plant growth and the suppression of plant pathogens. This is accomplished through the production of many defense-related compounds in plant host tissues that lead to ISR, by direct antibiosis through the synthesis of diverse antimicrobial substances by the beneficial microbes; as well the direct synthesis of plant hormones and other beneficial compounds by the beneficial microbes. Roots strongly bind soil particles and are readily colonized by microorganism (Barea et al., 2005). Bacteria compete for nutrients with other resident microbes and with plant roots. As a result, the interactions between rhizosphere microbes and plants are critical. Mutual beneficial interactions have evolved, such as the provision of carbon compounds to resident microbes by their plant hosts, and increased nutrient and water uptake for the plant host due to the activity of the beneficial microbes. Induction of ISR and enhanced plant growth are other benefits derived by plants through their interactions with microbes (Gouda et al., 2018). Among microbes, *B. subtilis* plays a significant role in PGPR activity and biocontrol. Activation of ISR is one of the benefits obtained from the use of *B. subtilis.* The ISR stimulus could be salicylic acid (De Meyer and Hofte, 1997) and/or the presence of rhizobacteria (Hallmann et al., 1999). *Bacillus subtilis* can be used to induce resistance (Aliye et al., 2008) by inducing the synthesis of defense enzymes in the host, such as POD, PPO, and PAL. Plants activate defense mechanisms when a pathogen attack is perceived. This defense response often leads to systemic acquired resistance (SAR) process and the induction of a hypersensitive reaction; resulting in the formation of brown, desiccated tissue (Ryals et al., 1996). Disease severity is limited when the defense signal transduction pathway is activated (Van Wees et al., 2000). Inoculation of plants with *B. subtilis* strain (pf4) resulted in a high level of SAR. In relative comparison to non-inoculated plants, much higher levels of germination (96.5%), shoot length (9.0 cm), root length (8.03 cm), and vigor index (1703) were for inoculated plants (Anand et al., 2010). Seed treatment with *Pseudomonas fluorescens* I and II enhanced root biomass production in sunflower (Bhatia et al., 2005). Similar results were obtained in Castor seeds inoculated with *P. fluorescence* and *B. subtilis,* with greater increases in growth obtained with *P. fluorescence* than with *B. subtilis* (Khanuchiya et al., 2012). When tomato seeds were treated with *Bacillus subtilis* (EPC016), a significant increase in seedling growth was observed relative to non-inoculated plants (Ramyabharathi et al., 2013).

3.5. Alleviation of biotic stress in plants by Bacillus subtilis

Members of genus *Bacillus* can survive as endospores for long periods of time under harsh environmental conditions. They can also secrete a variety of secondary metabolites that stimulate plants to grow and increase disease resistance. A few studies have been conducted to examine the physiological processes that increase stress tolerance in plants in response to the presence of *Bacillus* species (Radhakrishnan et al., 2017). Organic farming practices consider the application of bacterial agents as an eco-friendly and safe way to increase productivity and disease resistance in crops (Dihazi et al., 2012). Myresiostis et al. (2015) have stated that the utilization of *B. subtilis* can reduce use of synthetic pesticides and insecticides in modern agriculture. Chemical fungicides and insecticides have a negative impact on beneficial soil microbes present that help to increase plant growth. Thus, the use of beneficial bacteria, such as. *B. subtilis,* could augment the application of other microbial pesticides as the use of chemical pesticides are terminated (Girolami et al., 2009). *Bacillus thuringiensis* (Bt), and the use of Bt toxin, provide a broad range of insecticide control (Navon, 2002), Bt also inhibits the growth of insect larvae and increases plant growth (Arrizubieta et al., 2016). *B. cereus*, *B. amyloliquefaciens,* and *B. subtilis* are also used to control pests (Gadhave et al., 2016). PGPR, such as *B. subtilis*, *P. fluorescens*, *P. putida,* and *Paenibacillus* administered through the use of coated, aluminum, gold, or silver nanoparticles, not only increased plant growth but also limited fungal growth in the rhizosphere. Therefore, the concept of nano-biofertilizers should be considered. Encapsulated nano-biofertilizers have been reported to deliver fertilizer to target cells, thus dramatically reducing the amount of fertilizer needed and preventing pollution through runoff (Mishra and Kumar, 2009). Herbicides such as pendimethalin and metalochlor, used in conjunction with polymers, such as polystyrene sulphonate and polyallylamine hydrochloride, have also been used in an encapsulated form for the sustained release of active ingredient to a specific place; thereby greatly improving the efficiency and safety of weed control (Kanimozhi and Chinnamuthu, 2012).

4. Conclusion

Many microbes have the capacity to enhance plant growth, and microbial products that enhance plant growth have been commercialized. Bacteria derived from the plant rhizosphere have been demonstrated to have beneficial effects on roots. The presence of plant growth promoting rhizobacteria (PGPR) is significantly correlated with plant roots and positive direct and indirect effects on plant growth; including a reduction in biotic stress, have been documented. The beneficial microbes can enhance plant growth through the induction of systemic resistance (ISR), antibiosis, and competitive omission. These rhizospheric microorganisms, with their unique characteristics, diversity, and relationship with plants, should be further exploited to address the needs of organic and sustainable production systems; as well as the increased level of stress resulting from climate change. *Bacillus* species can form endospores that are extremely resilient to harsh environmental conditions and can also secrete metabolites that stimulate plant growth and health. Thus, the successful application of beneficial microbes provides a model for enhancing stress tolerance and adaptation to climate change. Some types of volatile organic compounds (VOCs) emitted by *Bacillus subtilis* strain (GB03) have been shown to assist plants to recover from stress. *Bacillus* species also secrete exopolysaccharides and siderophores that inhibit or stop the movement of toxic ions and help maintain an ionic balance, as well as the uptake of water by roots. These compounds also inhibit pathogenic microbial populations. A comprehensive study of

Bacillus species and strains would lead to the identification of new isolates that could be used for better and more efficient biocontrol strategies. There is potential to improve the beneficial interactions between plants and select microbes by further evaluation and identification of new isolates of microbes that have a significant effect in the rhizosphere, alter microbial biology, and positively impact biogeochemical cycles. Technology could be used to identify PGPR that will have a beneficial impact on stress tolerance, soil fertility, nutrient acquisition, and ultimately crop productivity. Further research is needed to screen and identify beneficial *Bacillus* isolates that form plant-associated microbial communities and enhance overall plant health and vigor. The use of a multidisciplinary approach that includes physiology, molecular biology, and biotechnology could provide new prospects and formulations with massive potential to manage biotic and abiotic stress.

Acknowledgements

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