Chapter 4
Bacillus subtilis and Its Effect on the Postharvest of Fruit and Flowers

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4.1 Introduction

We live in an era of science and technological advances in all the fields of knowledge, including those associated with agriculture. These advances in the past 60 years have created disease-resistant, high-yielding, and profitable crops and have developed more effective agricultural inputs. However, famines still arise, and the indiscriminate use of synthetic inputs has had a negative impact on the environment (Unfao 2010; Bhardwaj et al. 2014).

Famine has fostered the development of technologies that take a holistic advantage of nature. Studying the ecological side of agriculture has allowed us to use its resources more effectively, such as rhizospheric microorganisms, including plant growth-promoting rhizobacteria (PGPRs), like *Bacillus subtilis* that has the capacity to form thermoresistant spores and biofilms (Rivera Pérez 2009). Originally, these bacteria were only associated with the production of root growth, but there is

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new evidence that these rhizospheric bacteria can function as biofertilizers or biocontrol agents that promote the growth of more vigorous plants, increase their yield, and improve their response to biotic stress (Tejera Hernández et al. 2013). Recent findings have revealed that the inoculation of agricultural crops with *B. subtilis* can improve the final quality of their products, having a positive impact on attributes, like size and firmness (Olalde-Portugal and Mena-Violante 2008). This impact may involve the activity of hormone-like substances that affect plant growth, flowering, and fruit ripening as well as involve nutritional mechanisms and protection against pathogens. This paper addresses the potential of applying *B. subtilis* as a biofertilizer, a biocontrol agent, and a biostimulant to improve the quality and shelf life of agricultural products in the context of sustainable agricultural production.

4.1.1 The Challenge of Sustainable Agricultural Production

The world is currently experiencing a food crisis in which approximately 30% of the population suffers some form of malnourishment. More than half of the diseases in the world are associated with nutrient deficiency (Unfao 2010). The nutritional requirements of humanity initiated the development of a massive farm production model based mainly on the use of great expanses of land, the intensive application of fertilizers, the improvement of crops, and the application of pest-control substances with the objective of assuring a bountiful harvest which eventually gave way to the well-known green revolution (Bhardwaj et al. 2014; Glick 2012).

Data from the FAO (2000) suggest that by 2030, the agricultural production in developing countries will be 70% higher than it was in 1995–1997. Around 80% of this production will come from intensive farming systems that will require an increase in the amount of arable land. Around 120 million of hectares will be turned into agricultural soil (Unfao 2010). Innovations in fertilization, plant nutrition, and irrigating systems, as well as the control of diseases and pathogens, have allowed high yields in crops over the last 50 years. However, these technologies have had a highly negative impact on the environment (Pingali 2012).

The ecological study of agriculture is crucial for discovering the best production methods with the least negative impact on the environment. A deeper understanding of the ecological nature of the agricultural systems will make it possible to improve their capacity to benefit mankind. One of the biotechnological alternatives for sustainable agricultural production is the use of beneficial soil microorganisms functioning as biofertilizers, particularly from the rhizosphere, because these microorganisms produce metabolites during their life cycle that produce positive effects on the crops and improve the soil quality (Bhardwaj et al. 2014). The rhizosphere is the region of the soil surrounding and affected by the root, wherein the root can give shelter to more than 1×10^{11} cells of microorganisms per gram of soil and can contain more than 30,000 prokaryotic species (Egamberdieva et al. 2008). The group of microbial communities that inhabit the rhizosphere is called the microbiome, and its interactions may determine the health and efficacy of a crop that grows in an agroecosystem (Mendes et al. 2013).

Hiltner (1904) suggested that the volume of the rhizosphere or soil adherent to the plant root is richer in free-living microorganisms than the rest of the surrounding soil where the root has less influence (reviewed by Lugtenberg and Kamilova 2009). This phenomenon could be due to the fact that an important percentage of carbon fixed by the plants (5–21% depending on the plant) is secreted into the environment through radicular exudates. The plant root secretes a complex mix of metabolites into the soil, including sugars, peptides, phenols, and hormones that are used by the different microorganisms in the rhizosphere. This concentration of metabolites may explain why the concentration of microorganisms in the rhizosphere is 10 to 100 times denser than in the rest of the soil (Lugtenberg and Kamilova 2009). These microbial associations result in a wide range of benefits involving biochemical and physiological changes that occur in the host plants (Gunes et al. 2015). The use of microorganisms in different crops promotes a significant increase in the production of fruits, vegetables, and grains (Glick 2012; Bergottini et al. 2015).

Field and greenhouse experiments have shown yield increase when the beneficial microorganisms are inoculated into the soil, such as plant growth-promoting rhizobacteria (PGPRs). However, improvements occur not only in biomass production but also in terms of crop protection and the quality of agricultural products (Olalde-Portugal and Mena-Violante 2008; Ordookhani et al. 2010).

4.1.2 Plant Growth-Promoting Rhizobacteria (PGPRs)

Plant growth-promoting rhizobacteria (PGPRs) are organisms associated with plant roots, and they stimulate plant growth, facilitate nutrient assimilation, and provide protection against infectious agents (Bais et al. 2004). These microorganisms live in a mutualistic relationship with their host. Initially it was observed that their presence promoted plant tissue growth, hence the name (Kloepper et al. 1989). Several studies have suggested that there are multiple mechanisms through which PGPRs can promote plant growth. Some of these microorganisms have the ability to produce molecules comparable to auxins (Ahmed and Hasnain 2014), cytokinins (Liu et al. 2013), gibberellins (Kang et al. 2012), and abscisic acid (Cohen et al. 2015) that act as plant growth hormones.

It has been established that the presence of PGPRs enhances the efficacy of nutrient absorption into plants. This can be done by modifying kinetic transport, modifying root structure, or promoting the bioavailability of nutrients (Bashan et al. 1989; Bais et al. 2004; Glick 2012). It has been shown that some PGPRs have the ability to process molecules containing nitrogen, phosphorus, and iron into forms that can be assimilated by plants (Antoun 2013).

Nitrogen fertilizers are among the most indispensable and costly of agricultural inputs. Only 45% or less of applied nitrogen is used by the plants, while the remainder is lost through gaseous emissions or through filtrations causing a serious contamination issue. An alternative would be to utilize a group of bacteria having the ability to fix nitrogen, capturing the atmospheric nitrogen in its nonreactive state N_2 and changing it into ammonia NH_3. This conversion is carried out by the enzyme nitrogenase and is known as biological nitrogen fixation (Bhattacharjee et al. 2008). Also, soluble phosphate availability can be a limiting factor on plant growth. Some PGPRs solubilize phosphorus from organic and inorganic sources to facilitate phosphorus absorption and bioavailability through the release of low-molecular weight organic acids functioning as chelating agents (Antoun 2013; Baldan et al. 2015).

Additionally, some PGPRs produce siderophores, low-molecular weight compounds with chelating potential containing a high affinity for metal ions, particularly Fe^+, which bind to form a Fe-siderophore that can be assimilated by the plant or bacteria. This assimilation leads to an increase in the amount of iron available in the internal tissues constituting a nutritional benefit and an indirect defense tool against pathogens (Aguado-Santacruz et al. 2012; Kloepper et al. 1989).

4.2 *Bacillus subtilis*

B. subtilis—one of the 65 species of the genus *Bacillus*—is a soil microorganism widely distributed in several habitats. The successful colonization of *B. subtilis* is due to its capacity to form thermoresistant endospores as a response to several environmental stress factors, such as nutritional deprivation and the lack of moisture (Rivera Pérez 2009), and it is dispersed by wind. *B. subtilis* has a high reproduction rate and produces extracellular hydrolytic enzymes and antibiotic substances (Earl et al. 2008). The use of fluorescent antibodies to distinguish the vegetative state of the spore in different soil samples revealed that *B. subtilis* is found predominantly in this state when it is associated with organic materials found in decomposition (Norris and Wolf 1961). Experiments proved *B. subtilis* to be a saprophytic organism. Soil samples saturated with twice as much volume of sterile organic matter were inoculated with *B. subtilis* spores, wherein spore germination and the proliferation of the vegetative form of the inoculum were observed for several days, until final sporulation occurred due to nutrient deficiency (Vilain et al. 2006).

For a long time, it was taken for granted that *B. subtilis* was an obligate aerobe. Sequencing of its genome in 1968 showed genes possibly associated with the synthesis of nitrate reductase enzymes (Kunst et al. 1997), suggesting that it can grow in anaerobic conditions using nitrate instead of oxygen as an electron acceptor (Folmsbee et al. 2004; Kunst et al. 1997). Additionally, *B. subtilis* has been found to complete its vegetative cycle under anaerobic conditions like those present in the gastrointestinal tract of animals (Hong et al. 2005; Tam et al. 2006).

4.2.1 Biofilms Formed by **Bacillus subtilis**

A biofilm is a bacterial population in which bacteria adhere to each other and to a surface through the excretion of various polymers, generating an array of several attached layers (Costerton and Lewandowski 1995). Initially during biofilm formation, bacteria change their phenotype according to their proximity to the surface. As the process continues, fastened cells interact as microcolonies with similar cells and those of other species (Fletcher 1991). Different bacterial biofilms respond to specific microenvironmental conditions with different growth patterns (Costerton et al. 1987) that may be pure or mixed cultures of cellular aggregates on different surfaces under controlled or natural conditions (Andrews and Harris 2000). Biofilms have aroused interest in the study of plant-microorganism interaction. It is well known that most of naturally free-living bacteria are associated with different surfaces in the form of multicellular clusters known as biofilms (Branda et al. 2005). Biofilms growth offers some benefits to its constituents, including improved resistance to severe weather, access to nutrients, and protection (Davey and O'Toole 2000).

B. subtilis also has the ability to form biofilms, since it can develop into a functional cooperative community with specialized cells differentiated from an isogenic progenitor population and produce the necessary molecules to form the biofilm matrix (Vlamakis et al. 2008). This biofilm matrix is generally made of exopolysaccharides and the TasA protein that polymerizes into amyloid fibrils-like structures (Beauregard et al. 2013).

One of *B. subtilis*' characteristics that holds great significance is the capacity to colonize on the roots of a large number of plants and to grow in a mutualistic relationship with them. There is evidence correlating the capacity of *B. subtilis* to form biofilms with root colonization, promotion of growth and protection against pathogens (Beauregard et al. 2013; Cairns et al. 2014).

4.2.2 **Bacillus subtilis** *as a Biofertilizer*

Crop yield and the quality of agricultural products depend directly on the quality of the soil that provides the plant with nutrients and support. In many cases, low crop productivity has been associated with a poor handling of the soil. Loss of arable land is mainly caused by excessive exploitation of arable lands without the addition of organic material and the increase in salinity due to the use of fertilizers and the occurrence of droughts (Yuan et al. 2007). For more than 60 years, the application of soil endemic microorganisms, particularly those associated with the rhizosphere, has been proposed as an alternative to chemical fertilizer use. The supporters of sustainable agriculture and biosecurity programs are becoming very interested in this method to resolve infertile soil limitations (Bhardwaj et al. 2014).

Biofertilizers contain live microorganisms which have the ability to enrich native soil flora. Moreover, several studies have shown that biofertilizers enhance the texture and other features of soil where the crops grow (Bhardwaj et al. 2014). Thus, biofertilizers are defined as substances that contain live microorganisms that colonize in the rhizosphere or internal part of the plant when they are applied to a seed, a root surface, or soil. Additionally, some microorganisms have the capacity to release chemical compounds that may regulate the plant as well as antibiotics (Vessey 2003).

Phosphorus is the most indispensable nutrient for the optimal growth of a plant after nitrogen (Rajankar et al. 2007; Tejera Hernández et al. 2013). Most of the phosphorus present in soil cannot be assimilated by plants with only 0.1–0.4% of phosphorus being present in organic form (Corrales Ramírez, et al. 2014). Phosphorus forms metal compounds with iron and aluminum in very acidic soils, and it forms compounds with calcium carbonate in very alkaline soils. Some microorganisms are known to have the capacity to solubilize phosphorus from various sources through several methods (Toro et al. 1997). These methods mainly include reducing the pH of the soil by means of organic acid excretion which dissolves phosphorus-rich minerals or chelate cations joined to phosphorus, thereby releasing it (He et al. 2007). The genus *Bacillus* is one of the most studied bacteria regarding its capacity to solubilize phosphorus (Rajankar et al. 2007). Several species that belong to this genus have the ability to solubilize phosphates that are associated with promoting growth of the bacteria in different economically important crops, such as corn and wheat (Egamberdiyeva et al. 2004). Various studies have proven that several *B. subtilis* strains have the capacity to solubilize phosphorus in vitro (Qureshi et al. 2012). Likewise, field studies suggest that *B. subtilis* can enhance phosphorus mobilization in the soil by functioning independently or along with other microorganisms like *Pseudomonas aeruginosa* or arbuscular mycorrhizal fungi. In these cases, excretion of organic acids is the main mechanism of solubilization that occurs with cation exchange allowing insoluble phosphate to become soluble and available to the plant. Citric acid, lactic acid, succinic acid, and propionic acid are among the most common excreted organic acids (Adesemoye et al. 2008; Tejera Hernández et al. 2013; Toro et al. 1997).

Most plants absorb iron, an essential nutrient, as a ferrous ion (Fe^{2+}), but the ferric ion (Fe^{3+}) is the most abundant in the soil that can be precipitated as ion-oxide forms easily. Most plants exude compounds that can interact with Fe^{3+} so they can assimilate it. The "chelating" compounds deposit the Fe^{3+} on a root surface where it is reduced to Fe^{2+} and then absorbed. The siderophores link to Fe^{3+} and allow it to be absorbed through the plasmalemma (Vessey 2003). The production of siderophores is considered a secondary mechanism through which PGPRs stimulate plant growth, since they facilitate iron ions bioavailability in the rhizosphere. Additionally, siderophores are believed to inhibit the growth of certain pathogens (Kloepper et al. 1980). In a study conducted by Díaz Peralta et al. (2012), *B. subtilis* strains were found to produce hydroxamate siderophores also identified in other bacterial species classified as promoting plant growth.

Consequently, *B. subtilis* strains can be supplementary components to the conventional handling of soil fertilization along with crop rotation, residue reincorporation, and pathogen biocontrol (Sahoo et al. 2013). Several studies documented the positive effects of PGPRs on crops caused by an increase in the content of certain plant nutrients. Karlidag et al. (2007) reported that the inoculation of apple trees (*Malus domestica* L. cv. Granny Smith) with *B. subtilis* had a significant impact on the nutrient content (i.e., P, K, Ca, Fe, Mn, Cu, and Zn) in addition to increasing growth and yield. Karakurt et al. (2011) tested strains of *Bacillus* OSU-142 (N_2-fixing) and M3 (N2-fixing and phosphate solubilizing) in isolation and in combination with organically grown primocane raspberry (cv. Heritage) and found an increase in the crop growth and yield. Additionally, the contents of nitrogen, phosphorus, and calcium in raspberry leaves inoculated with both strains, and the contents of iron and manganese on raspberry leaves treated with M3 increased.

Published information about nutrient content of agricultural products coming from plants inoculated with PGPR is scarce. In this regard, Dursun et al. (2010) sprayed PGPR on tomato (*Lycopersicon esculentum* L.) and cucumber (*Cucumis sativus* L.) and found that the application of *B. subtilis* BA-142 increased the mineral content (i.e., N, P, Mg, Ca, Na, K, Cu, Mn, Fe, and Zn) in fruits of both crops. The results showed that there are positive nutritional effects on plants fertilized with *B. subtilis* causing an increase of fruit nutritional quality.

4.2.3 **Bacillus subtilis** ***as a Biostimulator***

Over the past few years, an important group of secondary metabolites synthesized by several microorganisms have aroused interest among biotechnologists. They are molecules classified as plant growth hormones due to their similarity to those compounds produced by plants during their growth. Even though the early reports about these metabolites date back to the 1960s, they have drawn attention recently because of their results when applied to sustainable agricultural models. Several species of microorganisms have been reported to synthesize indole-3-acetic acid, gibberellin, zeatin, and abscisic acid (Karadeniz et al. 2006).

About three decades ago, *B. subtilis* strains were reported to produce chemical compounds promoting plant growth with most of the studies documenting the presence of indoleacetic acid and abscisic acid (Araújo et al. 2005). Abscisic acid inhibits root elongation setting up a negative correlation between tissue growth and the endogenous content of abscisic acid. On the other hand, indoleacetic acid has been associated with secondary roots and root hair proliferation. Consequently, it has been hypothesized that the production of these substances from *B. subtilis* contributes to plant growth, especially when observing root length, increase of woody tissue density, greater vigor, and flower and fruit production (Díaz Peralta et al. 2012).

The angiosperms, also known as “flowering plants,” are defined in botany as plants with seed(s) and flowers having whorls or arrangement of sepals, petals, stamens, and carpels. While the carpels contain the ovules, the pollen makes contact with the carpels stigmatic surface instead of directly with the ovule, as in gymnosperms. The main role of the floral organ is the production of seeds through sexual reproduction in order to perpetuate and propagate the species. This has led to the growth of attractive crowns and modified edible ovaries, known as fruits (Ferrara Sarmiento et al. 2013).

The use of flowers has gained great interest in the scientific and commercial fields to such an extent that strategies have been searched to control the development of these organs through techniques ranging from the application of chemical compounds similar to plant hormones to genetic engineering (Klee and Giovannoni 2011). The economic interest has led to the overexploitation and indiscriminate use of uncontrolled nutritional systems.

In recent works, the application of *B. subtilis* strains has altered flower growth as well as plant life span. These alterations have been associated with better nutrition and plant stimuli that are typical of the interaction with these microorganisms. Ornamental flowers of the genus *Lilium* are produced under intensive systems due to their high demand. It was observed that when these plants were inoculated with *B. subtilis* along with mycorrhizal fungi *Glomus fasciculatum* and a minimum dose of phosphorus, plants were more vigorous, taller, heavier with greater stem diameter, and had a more intense color. In addition, flowers from the treated plants bloomed faster and lived significantly longer (Rubí Arriaga et al. 2012).

B. subtilis application has also been reported to influence the quality of some agricultural products. Mena-Violante and Olalde-Portugal (2007) showed that fruit and pericarp firmness increased in the latest ripening stages when tomato plant roots were inoculated with *B. subtilis*. The changes in firmness involved alterations in the components of the primary cell wall, such as cellulose, pectin, and glucans, that normally occurred during ripening (Brownleader et al. 1999) and are associated with ethylene production. Ethylene is the hormone that controls the expression of ripening genes (Alexander and Grierson 2002), and it is engaged in the promotion of plant growth (Glick et al. 1998). Although these changes occur in the roots, they could be associated with signaling pathways that affect the fruit growth and ripening (Mena-Violante and Olalde-Portugal 2007). Changes associated with tomato texture (*Solanum lycopersicum* Mill.) in plants inoculated with *Bacillus subtilis* BEB-13bs were also studied. The results showed that the fruit pericarp firmness at the light red ripening stage was significantly higher in fruits from inoculated plants. In addition, the treatment with *B. subtilis* significantly reduced the activity of the polygalacturonase enzyme (PG) in the fruit at the light red ripening stage. Finally, it was reported that the expression pattern of Aco, the gene that encodes for the aminocyclopropane carboxylic acid oxidase—enzyme regulating ethylene synthesis during ripening—showed a significant decrease in the transcript accumulation in red fruit from inoculated plants. The expression pattern changes of this gene associated with ripening, along with the PG enzymatic activity, show the influence of *B. subtilis* on the ripening process. The fact that only the bacteria on the roots produced these effects on the fruit suggested that the participation of signals somehow influenced the ethylene biosynthetic pathway. However, further research is needed to study this possibility.

Another biostimulating effect associated with the fruit quality was documented by Karakurt et al. (2011), who reported that the foliar application of *B. subtilis* promoted the biomass growth in cherry trees and significant changes on the fruit chemical composition, suggesting that the fruit quality could be indirectly affected by bacteria through the production of substances comparable to phytohormones.

4.2.4 **Bacillus subtilis** *as a Postharvest Biocontrol Agent*

Fruits and vegetables are considered living beings even after harvest since they continue breathing and release energy in the form of heat and water. This makes them perishable products that are susceptible to the loss of desirable features that can lead to the loss of commercial value (Giovannoni 2004).

Various technologies have been developed to preserve the organoleptic features (i.e., color, flavor, texture) of fruits and vegetables, such as controlled atmosphere refrigeration systems and radiation at different wavelengths (Ayala Gil 2011). The use of synthetic chemicals to inhibit pathogen growth has contributed to a significant decrease in sprouting and reduced the loss of product (Kim et al. 2015). However, over the long term, it has been negatively observed that the excessive use of these technologies can raise product prices, eventually lose their efficacy, may be toxic for people, and may contribute to environmental deterioration. These drawbacks have promoted the search of less dangerous and more effective alternatives. In this regard, biocontrol of postharvest decay in agricultural products could provide an effective alternative technology to chemical control.

B. subtilis is one of the most commonly used bacteria for disease biocontrol (Ongena and Jacques 2008) and, along with other *Bacillus* species, represents half of the commercially available biopesticides for postharvest disease control worldwide (Fravel 2005). The capacity of *B. subtilis* to form spores makes it one of the best candidates for the development of effective biopesticides (Ongena et al. 2007) in addition to being able to produce metabolites with strong antifungal properties, high degradability, and being environmentally friendly (Chen et al. 2008).

B. subtilis sequencing revealed that a large portion of its genome (4%) produces secondary metabolites. These secondary metabolites include antibiotic peptides that inhibit fungi and bacteria growth (Emmert et al. 2004), volatile compounds (Yuan et al. 2012), and several types of lipopeptides (Bais et al. 2004; Hossain et al. 2015) associated with *B. subtilis* biocontrol activity. In addition, it has been documented that *B. subtilis* produces catabolic enzymes (proteases, kinases, and glucanases) and other components that are toxic to phytopathogens (Ashwini and Srividya 2013).

Since the 1980s, beneficial effects have been observed regarding the application of organisms to different fruits, such as peaches, nectarines, apricots, and plums. For example, spraying with *Pseudomonas* and *Bacillus* bacterial cultures demonstrated antagonist activity against the fungal pathogen *Monilinia fructicola* (Pusey and Wilson 1984). In this work, the treatment with the strain B-3 of *B. subtilis* affected the development of brown rot caused by fungi in all the treated cases. Jiang et al. (2001) reported that *B. subtilis* and its cell-free extracts inhibited the occurrence of *Peronophithora litchi*. The use of *B. subtilis* to control pathogens in several crops has been reported recently (Bais et al. 2004; Choudhary and Johri 2009), and some strains have been proposed as biocontrol agents for the development of bioproducts to control postharvest fruit decay caused by fungi (Arrebola et al. 2010; Casals et al. 2010; Obagwu and Korsten 2003). However, they are not currently commercially available. For instance, Obagwu and Korsten (2003) isolated *B. subtilis* strains from a citrus surface and assayed their capacity to inhibit the occurrence of *Penicillium digitatum* and *Penicillium atalicum.* They found that a treatment of *B. subtilis* combined with sodium bicarbonate was as effective as the mixture of commercial fungicides use to control these pathogens. In a study where *B. subtilis* was applied to avocado plantations to control fungus-causing stalk rot that infected plants from flowering, Demoz and Korsten (2006) demonstrated the capacity of *B. subtilis* to colonize different surfaces of the plant, such as the flower and stomata, and to reduce the incidence of infections associated with fruit rot.

There is a considerable interest in using *B. subtilis* strains that produce antibiotic lipopeptides (e.g., iturine and surfactin) (Bais et al. 2004). Meticulous studies have shown that *B. subtilis* CPA-8 in culture (i.e., cells, spores, and antifungal metabolites), cells, and cell-free supernatant are effective to control brown rot on stone fruit mainly through the production of fengycin lipopeptides (Yánez-Mendizábal et al. 2012).

An orange fruit study associated with *B. subtilis* showed that these bacteria were capable of reducing the postharvest incidence of *Penicillium crustosum* by 25% (Arrebola et al. 2010). Raw extracts of the same *B. subtilis* strain were used to reduce the incidence and decay of *Penicillium digitatum* in mandarin oranges (Leelasuphakul et al. 2008). The biocontrol observed in *B. subtilis* may be due to the production of volatile compounds that can affect the production of mycelium, such as ketones, organic acids, alcohols, sulfur-nitrogen compounds, and esters, including more than 21 different types of compounds (Arrebola et al. 2010).

A postharvest study on the *Malus domestica* “Golden Delicious” apple reported that strains from different *Bacillus* species, including *B. subtilis*, showed antagonist activity against gray mold caused by *Botrytis mali*, preventing its growth and reducing the lesion diameter (Jamalizadeh et al. 2009). Dimkić et al. (2013) showed that the ethyl acetate extracts from the cell-free supernatants of two *B. subtilis* strains were active against several apple fungal pathogens after the harvest, in vitro and in vivo. The mass spectrometry analysis of the extracts confirmed the presence of surfactin. Kim et al. (2015) demonstrated the capacity of the *B. subtilis* strain HM1 as a control agent for apple anthracnose caused by C*olletotrichum acutatum* fungi, one of the phytopathogens that most affects postharvest fruits. *B. subtilis* HM1 exhibited a wide spectrum of antagonistic properties to several phytopathogenic fungi, and the production of lipopeptides was identified to attribute to the inhibitory properties of this strain. The authors reported that the application of *B. subtilis* could prevent up to 80.7% of infection caused by *Colletotrichum acutatum*, while the cell-free supernatant only showed 69.4% efficacy on anthracnose control. Interestingly, three compounds associated with the phytopathogenic fungi inhibition were identified in the supernatant: iturine A, fengycin, and surfactin.

Despite much research, the mechanisms of *B. subtilis* to function as a biocontrol agent are still not completely clear, and it is suggested that this antimicrobial activity may be due to the production of mycolytic enzymes. Srivastava et al. (2012) reported that the *B. subtilis* JN032305 strain isolated from the chili rhizosphere produced three mycolytic enzymes: chitinase, glucanase, and cellulase, showing a wide spectrum antagonistic property against bacteria and phytopathogenic fungi.

Interestingly, the application of bacteria to influence the quality of agricultural products regarding pre- and postharvest disease is just beginning to be documented. Feliziani et al. (2015) carried out research in which several alternative treatments were applied and demonstrated that the routine pre- and postharvest application of the treatments reduced the loss of desirable features by 33%, such as color and turgor in strawberry (*Fragaria* × *ananassa*).

4.2.5 **Bacillus subtilis** *as an Agricultural Product Quality Promoter*

The quality of fruits and vegetables is defined as their degree of excellence (Abbott 1999) and centers around organoleptic properties (i.e., texture, color, flavor), bioactive substances content (i.e., carotenoids and dietary fiber), and essential nutritional compounds (i.e., proteins and vitamins), in addition to the absence of unwanted attributes (i.e., pesticides and heavy metals) (Schreiner 2007).

The quality of agricultural products is affected by several pre- and postharvest factors. The preharvest factors that affect the quality of products already harvested include biological factors (i.e., pathologic and entomological), physiological (i.e., nutritional imbalance and ripeness), and cultural (i.e., fertilization and growth regulators) (Mattheis and Fellman 1999). In this regard, the PGPR can be considered as preharvest agent that influences the yield and quality of fruits, vegetables, and other agricultural products (Mena-Violante and Olalde-Portugal 2007; Mena-Violante et al. 2009).

The quality of fruits and vegetables is highly dependent on their ripening stage. Fruit ripening consists of a number of biochemical and structural changes that make the fruit more attractive to seed dispersal vectors (Brummell 2006). It is a highly complex and coordinated process that involves different metabolic pathways, involving pigment biosynthesis *(*Andersen et al. 2004), sugars, acids, and volatile compounds that alter the flavor (Darbellay et al. 2004), degradation of the cell wall and the middle lamella (Osorio et al. 2013), as well as the synthesis and action of regulation hormones (Given et al. 1988). Color is the main indicator of fruit ripeness, and it depends on pigment accumulation, such as carotenoids and flavonoids, that have been attributed to nutraceutical properties (Andersen et al. 2004; Wang et al. 2014).

Reports on organoleptic fruit properties caused by the inoculation of crops with PGPR are scarce, but one of these studies was carried out by Mena-Violante and Olalde-Portugal (2007). They demonstrated that the *B. subtilis* BEB-13bs strain had positive effects on tomato quality (*Solanum lycopersicum*), particularly on the size and texture. Interestingly, firmer fruits from plants inoculated with *B. subtilis* were obtained. It was suggested that the effects on the texture (i.e., firmness) of fruits could be associated with the changes in ethylene production. In this regard, it is known that the plant hormone regulates ripeness (Alexander and Grierson 2002) and is also involved in the promotion of plant growth by the PGPR (Glick et al. 1998). Although these changes occur in the roots, they could be associated with signal pathways that affect the growth and ripeness of fruit.

Mena-Violante et al. (2009) reported that during the latest ripening stages, pericarp, and whole fruit firmness increased when the tomato roots were inoculated with *B. subtilis*. Texture changes include alterations in the primary wall components, such as cellulose, pectin, and glucan, that normally occur during ripening (Brownleader et al. 1999). Texture is a very important quality parameter, because it generally determines the shelf life of fruit (Brandy 1987; Manning 1996; Paniagua et al. 2014). Low quality in fruit is mainly caused by excessive softening (Giovannoni 2004). The firmest fruits are expected to be more resistant to decay caused by microorganisms and consequently have a longer shelf life. In this regard, the authors found that the decay percentage of fruit after 10 days in storage was significantly reduced in fruits from plants treated with *B. subtilis*.

Some research showed that applying *B. subtilis* as a biofertilizer or as a biocontrol agent had a positive impact on the shelf life of agricultural products. Pusey and Wilson (1984) reported that the treatment of coffee with the *B. subtilis* B-1849 strain reduced fruit decay. Jiang et al. (2001) reported that *B. subtilis* as well as its cell-free extracts inhibited the growth of *Peronophithora litchi*. In addition to controlling infection, fruits were stored up to 30 days at 5 °C without acquiring unwanted alterations when the microorganisms or its extracts were applied after harvest.

Similarly, in research carried out at the Ecological Biochemistry Laboratory of CINVESTAV-IPN Irapuato, we obtained results similar to those reported by Jiang et al. (2001). After spraying with *B. subtilis* strains and storing at commercial refrigeration temperatures, strawberries exhibited better preservation of physical features for a longer period of time compared to the controls.

It is important to note that other positive effects of plant roots inoculated with *B. subtilis* have been observed on fruit quality. Datta et al. (2011) found through a field study that C2 and C25 bacterial strains identified as *Bacillus* species isolated from the rhizosphere of the chili cultivar “Suryamukhi” promoted a significant increase in fruit weight, thus demonstrating that fruit quality benefited in terms of size. On the other hand, Erturk et al. (2012) showed that *Bacillus* species not only increased the yield and growth of the strawberry “Fern” but also positively influenced fruit quality features, such as average weight, diameter, soluble solids content, and vitamin C content. Pırlak and Köse (2009) studied the effects of several PGPR strains containing biofertilizing and biocontrolling features on the strawberry cultivar “Selva,” and they reported that the inoculation of strawberry roots with the *Bacillus* OSU-142 strain resulted in increased yields and soluble solids content as well as affected sugar content.

4.3 Conclusions

Bacillus subtilis is a rhizospheric bacterium with potential for applications in sustainable agricultural production due to its capacity to form endospores and biofilms and to its properties as a biofertilizer, a biostimulant, and a biocontrol agent. This potential of *B. subtilis* lies within mechanisms involving plant growth regulators' synthesis, secondary metabolites, and mycolytic enzymes.

B. subtilis is known to promote plant growth and to increase yield as well as to prevent and control disease. In addition, these bacteria can improve the quality of agricultural products, like flowers and fruits. Several quality features in these products, such as size, color, firmness, and shelf life, can be positively affected by the application of *B. subtilis*.

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