

Review

Biocontrol of Postharvest Fruit Fungal Diseases by Bacterial Antagonists: A Review

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Abstract: This review deals with the main mechanisms of action exerted by antagonistic bacteria, such as competition for space and nutrients, suppression via siderophores, hydrolytic enzymes, antibiosis, biofilm formation, and induction of plant resistance. These mechanisms inhibit phytopathogen growth that affects postharvest fruit since quality and safety parameters are influenced by the action of these microorganisms, which cause production losses in more than 50% of fruit tree species. The use of synthetic fungicide products has been the dominant control strategy for diseases caused by fungi. However, their excessive and inappropriate use in intensive agriculture has brought about problems that have led to environmental contamination, considerable residues in agricultural products, and phytopathogen resistance. Thus, there is a need to generate alternatives that are safe, ecological, and economically viable to face this problem. Phytopathogen inhibition in fruit utilizing antagonist microorganisms has been recognized as a type of biological control (BC), which could represent a viable and environmentally safe alternative to synthetic fungicides. Despite the ecological benefit that derives from the use of controllers and biological control agents (BCA) at a commercial level, their application and efficient use has been minimal at a global level.

Keywords: postharvest; biocontrol; fruit; antagonistic bacteria; biological control agents

1. Introduction

Nowadays, postharvest fruit loss caused by phytopathogen fungi is estimated to account for more than 50% of total agricultural fruit production [1]. In general, control of fungal phytopathogens is performed by applying synthetic fungicides. However, their use has led to problems for the environment and human and animal health [2]. Furthermore, the global trend of consumers in acquiring agricultural products that come from systems without synthetic product application keeps growing every day. Thus, a worldwide priority has been the search for alternatives to control postharvest phytopathogen fungi. In recent years, several strategies have been developed to biologically control phytopathogens, mainly based on the use of microbial antagonists, such as bacteria [3]. Biological control (BC) is an important management strategy for fungal diseases. Its principle is based on utilizing live microorganisms to reduce and/or maintain the population of a phytopathogen below the levels which cause economic loss. This BC method is efficient in the short,

medium, and long term, and does not represent a risk to the environment or cause harm to humans and animals [4]. Bacteria show diverse antagonistic mechanisms toward phytopathogen fungi, notably space and nutrient competition, hydrolytic enzymes, induction of resistance, volatile compound synthesis, and biofilms [5,6]. The use of bacteria as biocontrol agents (BCA) has been very important in the integrated management of cultivations and organic production, where their value as a postharvest control of fungal diseases stands out [7].

2. Biocontrol as a Method for Decreasing Phytopathogen Abundance

BC methods provide plant protection against fungal diseases, and currently represent a viable alternative for fruit protection against phytopathogens at the postharvest stage [8]. Implementing BC in cultivation management offers diverse benefits, such as a decrease of causal agents; cultivation protection; low cost; lack of contamination of soil, water, and plant; and lack of waste management problems [9,10]. The scope of BC shows some important limitations, such as temperature, humidity, its narrow range of activity, and so on. For these reasons, BC strategies in the field are subject to significant variability, which constitutes an important limitation to their practical implementation [11]. After more than three decades of BC research, it has been scaled up to allow greater integration in agricultural production systems [12].

2.1. Selection and Identification of a Biological Control Agent

Among the different types of microorganisms utilized in BC, bacterial communities show antagonistic effects toward phytopathogens, so they can be exploited as a form of BC (Table 1). A continuous interaction exists in the biological world between phytopathogens and their antagonists, in such a way that the latter inhibit disease presence and development. For the adequate use of this type of microorganism, it is important to understand the mechanisms of action involved in BC activity for the safe development of the application processes and as a basis for selecting the most efficient bacterial strains [13,14]. The selection of bacteria with potential for use as BCA starts from their isolation from soil samples or from any part of the plant. After that, they are identified by chemical and molecular biology methods; their antagonistic mechanisms against phytopathogens are characterized, and several tests are performed to determine whether they are non-toxic for the environment, plants, and human and animal health [15]. Bacteria should have particular characteristics to be considered as BCA, notably genetic stability, efficacy at low concentrations, and colonization capacity in diverse hosts (Table 2).

Table 1. Examples of biological control of postharvest disease by bacterial species.

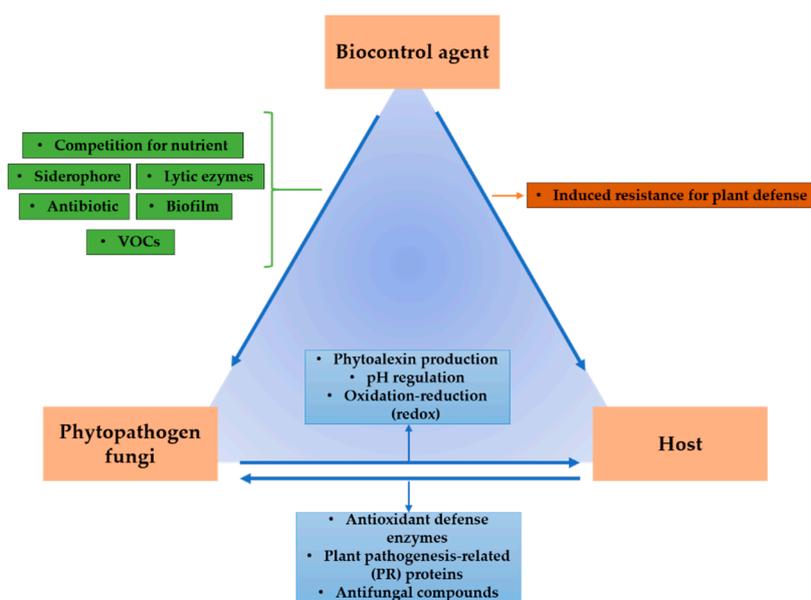
Bacterial	Diseases	Phytopathogens	Hosts	Inhibition (%)	References
<i>Bacillus amyloliquefaciens</i>	Brown rot	<i>Monilinia</i> sp.	Apple	75	[16]
<i>Pseudomonas synxantha</i>	Brown rot	<i>Monilinia fructicola</i>	Peach	70	[17]
<i>Pseudomonas fluorescens</i>	Blue mold	<i>Penicillium expansum</i>	Apple	88	[18]
<i>Bacillus megaterium</i>	Damping-off	<i>Aspergillus flavus</i>	Peanut	41	[19]
<i>Stenotrophomonas rhizophila</i>	Anthraxnose	<i>Colletotrichum gloeosporioides</i>	Mango	89	[20]
<i>Bacillus subtilis</i>	Anthraxnose	<i>Colletotrichum musae</i>	Banana	72	[21]
<i>Pantoea agglomerans</i>	Anthraxnose	<i>Colletotrichum musae</i>	Banana	94	[22]
<i>Bacillus amyloliquefaciens</i>	Blue mold	<i>Penicillium expansum</i>	Apple	80	[23]
<i>Paenibacillus polymyxa</i>	Anthraxnose	<i>Colletotrichum gloeosporioides</i>	Apple	83	[24]
<i>Pseudomonas syringae</i>	Green mold	<i>Penicillium digitatum</i>	Citrus	28	[25]
<i>Bacillus</i> sp.	Gray mold	<i>Botrytis cinerea</i>	Grape	50	[26]
<i>Pseudomonas syringae</i>	Blue and green mold	<i>Pseudomonas digitatum</i> and <i>Pseudomonas italicum</i>	Citrus	31	[27]
<i>Bacillus subtilis</i>	Rot	<i>Alternaria alternata</i>	Melon	77	[28]

Table 2. Ideal characteristics of a biological control agent [29].

Genetically stable
Effective at low concentrations
Non-demanding in terms of required nutrients
Survival capability under adverse environmental conditions (including low/high temperature, storage with controlled atmospheres)
Capability of adhering to and colonizing the host surface
Showing more than one antagonistic mechanism against phytopathogens that need to be controlled
Effective against a range of phytopathogens
Production in a low-cost growth medium
Preparation in a simple formulation that can be stored for long time periods
Environmentally friendly
No production of secondary metabolites or harmful toxins

2.2. Antagonistic Mechanisms of Bacteria Utilized as Biocontrol Agents

Phytopathogen inhibition by bacteria is generally performed with at least two antagonistic mechanisms, which make it more efficient to control diseases in postharvest fruit [5]. Several modes of anti-phytopathogen action of bacteria have been described [29,30], notably space and nutrient competition, parasitism, volatile compounds, and biofilms, among others (Figure 1). The main antagonistic mechanisms exerted by bacteria against phytopathogens are described below.

**Figure 1.** Mechanisms of action of biocontrol agents.

2.2.1. Competition for Space and Nutrients

Competition for space and carbon sources is one of the main antagonistic mechanisms exerted by bacteria against phytopathogens [31]. The capacity of bacteria to colonize damaged fruit depends on the adaptation to assimilate the necessary carbon sources for survival and multiplication, limiting carbohydrate disposition for the phytopathogen fungus, reducing its spore germination percentage and thus its capacity to invade the host [32]. Different *in vitro* studies have demonstrated that antagonistic microorganisms limit phytopathogen fungi by different carbon sources, mainly saccharose, fructose, and glucose, among others [33]. Phytopathogen inhibition can be greater if the cellular dose of the antagonist increases; thus, there is a need to perform studies on the application of different bacterial doses on the host to determine the minimum concentration required to inhibit the phytopathogen [34]. Yu and Lee [35] demonstrated that the bacteria *Pseudomonas putida* inhibited spore germination of *Penicillium digitatum* due to nutrient availability of the host. Other bacteria have inhibited different

phytopathogen fungi by carbon sources, such as *Pseudomonas syringae*, *Pantoea agglomerans* [24], *Pseudomonas fluorescens* [30] and *Bacillus megaterium* [16].

2.2.2. Siderophores

Iron is an essential element for microorganism growth [36]; Fe^{2+} oxidizes Fe^{3+} to form stable iron oxide complexes in the presence of oxygen and water. These molecules are sequestered by siderophores; they are produced by bacteria and are defined as small peptide molecules that contain lateral chains and functional groups that can provide a set of high-affinity to coordinate iron ions [37]. Siderophores are classified into four types: carboxylates, hydroxamates, catolate phenate, and pyridoxines [38]. When bacteria produce siderophores in a medium, they displace and inhibit phytopathogens in the host, limiting their spore germination and mycelial growth [39]. Diverse types of siderophores produced by antagonistic bacteria have been identified and reported; some of them are recognized and utilized by different microorganisms, while others are specific for each bacterial species (Table 3). Their production confers competitive advantages to the bacteria used as BCA by excluding other microorganisms (including phytopathogens) of the host [40,41]. Under competition conditions to acquire iron, siderophore production by antagonistic bacteria can determine a greater phytopathogen inhibition in the host [42].

Table 3. Siderophore production by antagonistic bacteria.

Bacteria	Disease	Siderophore Type	Phytopathogen	Host	Reference
<i>Pseudomonas</i> sp.	Damping-off	Pyoverdine	<i>Pythium ultimum</i>	Cucumber	[43]
<i>Burkholderia cepacia</i>	Anthracnose	Pyoverdine	<i>Colletotrichum gloeosporioides</i>	Mango	[44]
<i>Bacillus</i> sp.	Bacterial wilt	Bacillobactin	<i>Ralstonia solanacearum</i>	Banana	[45]
<i>Pseudomonas aeruginosa</i>	Damping-off	Pyoverdine	<i>Rhizoctonia solani</i>	Pepper	[46]
<i>Bacillus subtilis</i>	Anthracnose	Bacillobactin	<i>Colletotrichum</i> sp.	Pepper	[47]
<i>Pseudomonas fluorescens</i>	Anthracnose	Pyoverdine	<i>Colletotrichum gloeosporioides</i>	Avocado	[48]
<i>Rahnella aquatilis</i>	Molds	Enterochelin	<i>Penicillium expansum</i>	Fruit	[49]
<i>Pseudomonas</i> sp.	Piriculariosis	Pyoverdine	<i>Pyricularia grisea</i>	Rice	[50]

2.2.3. Parasitism (Lithic Enzyme Production)

In BC, parasitism takes place when the antagonist feeds on the phytopathogen, producing partial or total lysis of its structures. Specifically, bacteria feed on the cell walls of fungi, mainly on chitin, glucans, and proteins, which constitute 20%, 50–60%, and 20–30% of the cell wall, respectively [51]. Chitin is a lineal and insoluble homopolymer formed by sub-units of N-Acetyl glucosamine linked by β -1,4, and acts as the medullar support of the cell wall [52]. β -1,3-glucan is considered as the main structural constituent of the cell wall, to which other components of the cell wall are covalently linked, providing mechanical strength and integrity. The majority of the cell wall proteins are glycoproteins with diverse modification with oligosaccharides. The proteins of the cell wall play an important role in maintenance of the cell form, synthesis and remodeling of the cell wall components, molecule absorption, and cell protection against external molecules. The decomposition of the fungal cell wall requires the participation of different enzymes, mainly β -1,3-glucanase, chitinase, and protease [5]. Glucan enzymes produced by bacteria can hydrolyze glucans by two possible mechanisms: (1) exo- β -1,3-glucanase, which hydrolyzes glucans by sequential segmentation of glucose residuals from the non-reducer extreme; and (2) endo- β -1,3-glucanase, which activates the links to aleatory sites along the polysaccharide chain, in which oligosaccharides and glucose are released in small amounts [51]. Chitinases hydrolyze chitin, the non-branched homopolymeric N-Acetyl glucosamine in a 1,4 link by two possible mechanisms: (1) exo-chitinase or N-Acetyl-b-glucosaminidase, which sequentially segments the NAG extreme residues; and (2) endo-chitinase, which activates links in aleatory sites along the polymer chain [53]. Proteases can be divided into four main groups according to their site of action, namely, serine proteinases, cysteine proteinases, aspartic proteinases, and metalloproteinases [54]. During the last decade, different research studies have been performed on

hydrolytic enzymes that produce bacteria and yeasts [29]. The genera *Bacillus* and *Pseudomonas* are considered as some of the most efficient antagonists in phytopathogen control due to the direct action of chitinase [55]. Shivakumar et al. [56] performed partial purification, characterization, and kinetic studies of the chitinase enzyme of the bacteria *Bacillus subtilis* JN032305, in which the partially purified enzyme not only showed antifungal activity against *Rhizoctonia solani* and *Colletotrichum gloeosporioides* but also increased pepper seed germination when infected by the mentioned fungi. Mohammadi et al. [57] performed a study on potential bacterial isolation (*Bacillus subtilis*, *Bacillus pumilus*, *Bacillus megaterium*, and *Agrobacterium radiobacter*) for BC in citrus fruit against blue mold caused by *Penicillium digitatum*, in which bacterial extracellular enzymatic activities were determined, showing that all chitinase and glucanase enzymes were positive and protease enzyme activity was positive except for the bacteria *Agrobacterium radiobacter*.

2.2.4. Formation of Biofilms and Quorum Sensing

To colonize fruit surfaces successfully, antagonistic bacteria should have specific characteristics that facilitate their adherence, colonization, and multiplication. In the majority of cases, these characteristics are associated with the formation of biofilms, in which the microcolonies are within a protein-hydrated matrix produced by bacteria and nucleic and polysaccharide acids. The formation of this structure is measured by quorum sensing with regulators, such as tyrosol, farnesol, and phenethyl alcohol. The microcolonies maintain a form of communication through quorum sensing, employing diverse chemical signals to supervise their environment, altering the genetic expression and obtaining advantage over their competitors [58]. In BC, the formed biofilms act as barriers that stand between the host lesion surface and the phytopathogen. However, little is known about the main functions and mechanisms involved in the formation of biofilms. It has been suggested that the environmental signals that regulate the morphogenetic transformations help to select the bacteria more efficiently as BCA. In agricultural environments, there is a growing number of studies on the formation of biofilms [59,60]. The basis that links these models is that *Bacillus subtilis* functions as a cooperative community by population differentiation of specialized isogenic progenitors, as well as the production of macromolecules that form the biofilm matrix [61,62]. The matrix of this bacterium consists of proteins called TasA and TapA [63,64] besides a secreted polysaccharide of high molecular weight [65]. The assemblage of the mature biofilm also requires the presence of a coating protein called biofilm BsIA, previously known as YuaB [65–67]. Haggag and Timmusk [68] demonstrated that the bacteria *Paenibacillus polymyxa* colonizes plant roots, forming structures that look like biofilms and thus protecting the roots against diseases caused by phytopathogens. Another example is the highly mutant mucoid (forming an improved biofilm) of *Pseudomonas fluorescens* strain CHA0, which showed an improved capacity to colonize carrot roots [69]. Another study showed that a strain of *B. subtilis* (ATCC6051) can form biofilm-type structures in the roots of *Arabidopsis* plants and thereby protect them from infection by the bacteria *Pseudomonas syringae* [70].

2.2.5. Antibiosis

Antibiotic production is one of the mechanisms that has been classified as important after space and nutrient competition. The main antibiotics produced by antagonistic bacteria are iturin, a potent antifungal peptide produced by the bacteria *Bacillus subtilis*; pyrrolnitrin, produced by *Pseudomonas cepacia*; and trichothecene, produced by *Myrothecium roridum* [71]. Antibiosis can also be performed through the production of low-molecular-weight compounds by microorganisms, called volatile organic compounds (VOCs), which have a direct effect on phytopathogen growth. They are active in low concentrations and belong to several chemical groups, such as alcohols, aldehydes, ketones, esters, lactones, terpenes, and sulfur compounds. Due to their volatility, these compounds can travel great distances in structurally heterogeneous environments, as well as in solid, liquid, or gas compounds, which is a great advantage for BCA. VOCs have received limited attention compared to other antagonistic mechanisms. However, recent research studies have focused on these volatile

metabolism products [72]. Fruit bio-fumigation using microorganisms that produce VOCs in closed chambers can be a viable alternative to control phytopathogens [73]. However, it is worth mentioning that VOCs emitted by BCA can only provide a limited contribution to phytopathogen control since they show fungistatic activity. Nevertheless, some phytopathogens can also introduce a wide array of VOCs. Thus, this approach should be assessed in-depth in future research studies [51]. Layton et al. [74] mentioned that the bio-controlling action of the genus *Bacillus* was measured by its biochemical profile since they are producers of multiple secondary metabolites that are biologically active. For example, iturin A and fengycin are produced by *Bacillus subtilis*, and *Brevibacillus brevis* produces gramicidin S (1–5) metabolites, which are capable of inhibiting the growth and development of diverse phytopathogens; therefore, both *Bacillus subtilis* and *Brevibacillus brevis* are recommended for BC. Velázquez-Becerra et al. [75] found that *Arthrobacter agilis* UMCV2 produced VOCs. This was confirmed by using gas chromatography–mass spectrometry analysis, which identified dimethyl hexadecylamine as the compound that inhibited *Botrytis cinerea* and *Phytophthora cinnamomi*, demonstrating an inhibitory activity 12 times higher than that caused by the fungicide Captan. Furthermore, Raza et al. [76] demonstrated that the bacteria *Bacillus amyloliquefaciens* SQR-9 produced VOCs capable of inhibiting the growth of *Ralstonia solanacearum*. The strain SQR-9 produced 22 organic volatile compounds; however, only nine showed 1–11% antibacterial activity against the disease.

2.2.6. Induction of Resistance

Induction of resistance is the capacity of an antagonistic bacterium to provoke defense response in the host through several chemical or biochemical reactions, including changes in tissue structure and protein production related to pathogenesis, expressed either locally or systemically [29]. Induction of resistance in fruit by bacteria, as BCA, has been considered a mode of action to control postharvest diseases [32,77]. Induction of defense response is given by the overproduction of different enzymes and metabolites, notably (1) proteins linked to pathogenicity (PR proteins), which include glucanases, chitinases, peroxidases, superoxide dismutase, catalase (which protects tissue against oxidative damage), protein inhibitors, or lipid-transport proteins; (2) compounds with antimicrobial activity as phytoalexins; and (3) papillae formed by callose and lignin deposited in the cell wall assuring their strengthening. Other patterns that trigger immunity are (1) the production of reactive oxygen species (ROS) with a signaling role and direct antimicrobial effect; and (2) stomatal closing. In the case of plants, the immune response is mediated by and dependent on phytohormones, as well as salicylic acid, jasmonic acid, ethylene, and abscisic acid and their interaction, allowing the activation of immune responses against specific organisms [78,79]. Although induction of resistance in the host tissue by the antagonistic bacterial treatment is correlated, direct evidence of the capacity of the substances induced to inhibit phytopathogen infection has not been established [51].

2.3. Commercializing Biological Products

Numerous microbial antagonists of postharvest phytopathogens have been identified in laboratory and field studies and exploited commercially [12]. To date, the development of products based on beneficial microorganisms is relevant to reducing chemical contaminants in the food supply [80]. Microorganisms can be isolated from environments such as soil and sea, including some parts of plants [81]. Developing a BCA is a complex, long, costly, and interactive process. Despite the great amount of research invested in studying BCAs, it is paradoxical that their commercial use has been very limited. One of the greatest constraints to products based on BC reaching a high level of commercial consumption is efficiency under field conditions. These conditions depend on environmental factors which are not possible to control, such as temperature, humidity, precipitation, and so on, abiotic aspects which synthetic fungicides have overcome and remained as an essential medium to control phytopathogens [2]. Before starting to develop a product based on antimicrobial agents, it is necessary to have a detailed knowledge of several factors of the fungal disease to be defended against, namely, the phytopathogen species, type of hosts it attacks, epidemiology of the disease, phytopathogen resistance,

and environmental conditions under which the BCA will be used. Therefore, the antagonist should be selected successfully to avoid future difficulties. For a BCA product to be released into the market, it should pass different studies, and the production process should be scaled up to an experimental level to obtain sufficient quantities of the product to carry out its assessment in greenhouse, field, warehouse, or packing plant. If the product shows sufficient attributes, and its production, both technical and economic, is viable, its registration and commercialization follows [82]. The general objective of the majority of the research groups related to BC is to develop a product with a commercial purpose. However, despite all the efforts, only some BCs are commercially available for postharvest application, as has been described recently by Droby et al. [83].

There are currently several commercial products for BC of phytopathogens, which are considered first-generation biocontrol products for postharvest and whose active ingredients are antagonist yeast and bacteria that are available at commercial level in pre- and postharvest operations. Some of these products are *Candida oleophila* (Aspire, Ecogen, Langhorne, PA, USA) [84], *Cryptococcus albidus* (YieldPlus, Lallemand, Montreal, QC, Canada), *Candida sake* (Candifruit, Sipcam Ibérica, Valencia, Spain) [85], and *Pseudomonas syringae* (BioSave, JET Harvest, Longwood, FL, USA) [86]. Biosave Aspire and Candifruit were commercialized a few years ago; however, they were suspended due to commercial deficiencies related to marketing. Biosave still has a limited use in the USA market for application in fruit cultivation [87]. *Bacillus subtilis* (Avogreen, Pretoria University, Pretoria, South Africa) was introduced in South Africa to fight the spot caused by *Cercospora* sp., a disease in postharvest avocado; however, it did not reach commercial success due to inconsistent results [88]. *Candida oleophila* (Nexy, Leasafre, Lille, France) was developed in Belgium and was presented for statutory approval in 2005 for application in postharvest phytopathogen control in citrus and banana fruit [89]. Nexy received regulatory approval in all of the European Union in 2013 [90]. *Aureobasidium pullulans* (Boni-Protect, Bio-Ferm, Tulln, Austria) should be applied before preharvest to control phytopathogens in lesions developed in fruit during storage [91]. Pantovital (*Pantoea agglomerans* CPA-2) has been used to control pre- and postharvest diseases in fruit, such as citrus; it was formulated but never commercialized [9]. Amylo-X, made by Biogard CBC in Grassobbio, Italy, was based on *Bacillus amyloliquefaciens* and used to control fungal and bacterial diseases of several vegetables [92]. *Metschnikowia fructicola* (Shemer, Bayer, Leverkusen, Germany) was recorded in Israel to be applied pre- and postharvest in citrus fruit, grapes, peach, and strawberry, representing the most successful example of a postharvest biocontrol product. Shemer was acquired by Bayer CropScience (Monheim, Germany) and then sub-licensed to Koppert (Berkel en Rodenrijs, the Netherlands) [51]. Serenade was made by Bayer in Leverkusen, Germany; its active ingredient was the bacteria *Bacillus subtilis*, and it was used to control diseases in peach, strawberry and tomato cultivations [92]. However, none of these are used as an alternative to synthetic products [93].

2.4. Search for New Antagonists

In general, the majority of the antagonistic microorganisms are isolated from the surface of the fruit, plant (roots, leaves, flowers, and seeds), sea, or soil [81]. A study performed by Maida et al. [93] dealt with antagonistic interactions between isolated bacteria from three ecological niches (rhizospheric soil, roots, and stem-leaves) of *Echinacea purpurea*, whose antagonistic potential has also been exploited as medicine. Furthermore, Goudjal et al. [94] mentioned that wild plants adapt better to difficult soil conditions, especially to the attack of phytopathogens transmitted by themselves, which is why they are considered a potential source for isolating antagonistic endophyte microorganisms. Recent studies on antagonistic microorganisms have made evident their potential use in controlling phytopathogens, which affect important crops [95,96]. Endophyte microorganisms with bacteria that are antagonistic against phytopathogens are promising candidates for BC strategies [97]. Diverse studies have mentioned that the role of endophyte communities in seeds of different cultivations is poorly characterized [98–100]. Santos et al. [101] isolated endophyte bacteria in guarana seeds; the isolations showed growth inhibiting capacity of diverse phytopathogens. Antagonists have also

been isolated from fruit, and these have shown potential for exploitation as BCA of postharvest diseases [14]. The marine environment is also a deposit of new bioactive compounds; thousands of unique compounds have been isolated from this environment [102,103]. In recent years, any bioactive compound and different samples from marine environments have been searched for. Many studies have shown that antagonistic bacterial communities associated with marine environments may have a beneficial role for plant protection [104]. However, little information has been found with respect to the study of microorganisms isolated from marine environments with the potential to control phytopathogens in postharvest, which could have agronomic potential compared to synthetic fungicides [105]. In China, bacteria isolated from marine environments have great potential for BC in peanut cultivation [16]. Thus, marine bacteria have gained attention as possible BCA against fungal postharvest diseases, mainly due to their high inhibiting capacity, fast colonization in fruit lesions, and simple nutritional requirements [106]. Bibi et al. [107] mentioned that compost could be considered as a source of microorganisms capable of producing secondary metabolites of agricultural interest for phytopathogen control. Other antagonists could be actinomycetes, which are characterized by the production of metabolites with antimicrobial activity. Marine actinomycetes are considered major producers of secondary metabolites that inhibit mycelial growth of phytopathogen fungi, a quality that allows them to be considered as candidates to be used in BD against phytopathogen bacteria [108,109].

2.5. Application of Biocontrol Agents in Preharvest Stages

Several antagonistic microorganisms have been recommended to be used in fields before harvest with the purpose of protecting postharvest cultivation [7,29]. Lopes et al. [110] assessed the efficacy of different antagonistic microorganisms in controlling *Colletotrichum acutatum* with applications on preharvest citrus fruit and found promising results. Silva and De Costa [111] assessed the potential of *Burkholderia spinosa* with preharvest applications for the BC of phytopathogens in banana (*Musa* spp.). Camañas et al. [112] assessed the efficiency of different formulations of the antagonistic bacteria *Pantoea agglomerans* with preharvest application to control postharvest diseases in citrus fruit; the results showed an efficient protection of orange against *Penicillium digitatum* during storage. Luo et al. [78] showed that the preharvest application of antagonistic microorganisms decreased the presence of diseases caused by *Penicillium digitatum* and *Penicillium italicum* significantly in orange cultivation. The combination of antagonists with other antimicrobial compounds could be an efficient method to improve the yield of BC. Combination with salts, such as bicarbonates, and natural compounds, such as chitosan, have improved the yield of BCA [113].

2.6. Application of Biocontrol Agents Postharvest

Microbial antagonists are applied directly to fruit by pulverization or immersion in solution. Suppressing phytopathogen agents during storage was shown to be more successful in several studies of BC compared with previous application at harvest [6]. Antagonistic bacteria isolated from natural habitats produce several metabolites with antifungal and antibacterial capabilities [114]. In recent years, several strains of the genera *Bacillus*, *Burkholderia*, *Enterobacter*, and *Pseudomonas* have been studied and used effectively to treat diseases caused by phytopathogens. Suppressing fungal growth has been achieved by using antagonistic bacterial species such as *Bacillus subtilis*, *Bacillus thuringiensis*, *Burkholderia* sp., *Enterobacter cloacae*, *Pantoea agglomerans* and *Serratia plymuthica* [21]. Nevertheless, due to the high cost and complex process of the sanitary registry, as well as the limited market and strong demand for phytosanitary products, the number of BCAs registered is lower than the large number of research studies that have been performed on BC [93].

3. Conclusions

The residue of synthetic products on fruit has been and will continue to be one of the main worries of regulatory agencies and consumers. The growing concern about the hazards involved relating to human health and environmental contamination has led to a demand for the development of

alternatives to control postharvest diseases. The use of BCA as an alternative to synthetic products has been a focus of research in the last 30 years by many researchers and several commercial enterprises worldwide. This review has provided a general description on modes of action that antagonistic bacteria exert, which are considered viable alternatives to synthetic fungicides, as well as the success of some of them under laboratory conditions, leading to the production of biological products based on antagonistic bacteria for postharvest application. More research should be developed with respect to the mode of action of antagonists to better understand the phytopathogen–antagonist–host interactions. In recent years, there has been an advance in the use of molecular techniques that contribute to improving the knowledge of antagonistic mechanisms of BCA. Nonetheless, the search for new antagonists should be ongoing to widen the use of BCA postharvest.

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