Review Article

A REVIEW ON BIO-BASED CONTROL OF POST-HARVEST DISEASES

Abstract: Postharvest diseases significantly reduce the shelf life of harvested fruits/vegetables worldwide. *Bacillus* spp. is considered to be an eco-friendly and bio-safe alternative to traditional chemical fungicides/bactericides due to their intrinsic ability to induce native anti-stress pathways in plants. A numerous examples of successful *Bacillus* spp. application in controlling various post-harvest-emerged pathogens of different fruits/vegetables during handling, transportation, and storage have been described in the literature. The mechanisms of such action are still largely unknown; however, it is suggested that they include: i) competition for space/nutrients with pathogens; ii) production of various bioactive substances with antibiotic activity and cell wall-degrading compounds; and iii) induction of systemic resistance. With that, *Bacillus* efficiency may depend on various factors including strain characteristics (epiphytes or endophytes), application methods (before or after harvest/storage), type of pathogens/hosts, etc. Endophytic *B. subtilis*-based products can be more effective because they colonize internal plant tissues and are less dependent on external environmental factors while protecting cells inside. Nevertheless, the mechanisms of *Bacillus* action on harvested fruits/vegetables are largely unknown and requires further detailed investigations to fully realize their potential in agricultural/food industries.

Keywords: Post-harvest, Bioactive substances, *Bacillus* spp., Fungicides, Bactericides, Endophytes,

1. Introduction

The Food and Agriculture Organization [25] estimates that about 45% of fruits, vegetables, roots, and tubers harvested are lost because of disease incidence between harvest and consumption. In addition to pest infestations and pathogens (bacteria, fungi, and insects), unfavourable storage conditions (rain, humidity, frost, and heat), water loss, scarification and sprouting, most of this loss occurs during storage. Despite their effectiveness in preventing postharvest decay, chemical fungicides and/or food preservatives can be hazardous to humans, animals, and the environment [21]. Due to the toxicological risk of residual chemicals in food products, their use in the post-harvest period has been restricted to a few registered chemicals, and some European countries have prohibited their use completely [79]. As food and environmental problems become more relevant, along with the growing need for energy conservation through green technologies and organic products, an approach to reducing post-harvest food losses that is novel, efficient, environmentally friendly and bio-safe would be highly desirable. A research-led alternative to synthetic fungicides and/or food preservatives for controlling post-harvest diseases could be biologically based products derived from beneficial strains, such as plant growth-promoting bacteria (PGPB). Plant metabolism is altered by these products, leading to systemic resistance and a prolonged shelf life without adverse effects on plants, humans or the environment [18,4,64].

In addition to promoting plant growth, disease resistance and tolerance to abiotic stresses, PGPBs are non-pathogenic beneficial bacteria. They may live autonomously in the soil or colonize the rhizosphere, phyllosphere and plant interior tissues (endophytes) [18,76,6,41,66]. An interesting PGPB is *Bacillus subtilis*, a member of the genus *Bacillus* spp. one of the most attractive natural plant protection agents. The FDA recommends this *Bacillus* spp. are generally recognized as safe microorganisms for food applications. They have a similar niche to many pathogens and produce an array of bioactive substances that have antibiotic properties. Furthermore, *Bacillus* spp. induced various physiological features in plant metabolism without adverse effects on the environment or human health [64,45]. The endospores of it survive dynamic physical and chemical treatments, such as heat, desiccation, organic solvents, and UV radiation, so they can trigger defense responses in host plants even when conditions are unfavourable [53,27]. By doing so, *Bacillus*-based biological products can be easily formulated and stored, and they serve as powerful bioactive components against pathogens. It is well documented in the literature that *Bacillus* strains protect plants from biotic (pathogens, pests) and abiotic stressors (drought, salinity, extreme temperatures, toxic metals, *etc*.) threats. A wide range of biologically active compounds are synthesized by *Bacillus* spp., including antibiotics, siderophores, lipopeptides, enzymes, and 1-aminocyclopropane-1-carboxylate deaminase are known to affect the regulation of phytohormone biosynthesis pathways, modulate ethylene levels in plants and influence the emission of volatile organic compounds (VOCs) and the launch of host plants systemic resistance/tolerance [4,76,41,53,28,67,10,58].

B. subtilis have been used to treat numerous postharvest diseases during handling, transportation, and storage of a wide variety of fresh fruit and vegetables [4,78,37]. Among strawberries, pear, apple, and tomato *B. subtilis* suppresses Gray mold pathogens (*Botrytis cinerea* and *B. mali*) during postharvest time. The study of microbial antagonists from the *Bacillus* genus suggests that they possess substantial potential to increase vegetables/fruit sets, quality, resistance to postharvest diseases and tolerance to temperature fluctuations. Additionally, they reduce mechanical injuries caused during transportation, unloading, packaging, and storage of products [35,51]. Their role in controlling postharvest disease and the underlying mechanisms regulating fruits and vegetables storage quality remains largely unknown, but they play an important role in plant growth, development, and health under normal and stressful conditions.

2.Post-harvest loss reduction

The first microorganism patented as a postharvest biocontrol agent for brown rot of stone fruits was Bacillus *subtilis* [60]. The use of antagonistic microorganisms, such as *Bacillus* spp., to improve the post-harvest physiology of various fruit/vegetables began to emerge as time passed, establishing them as enhancers of fresh fruit/vegetable resistance to post-harvest diseases and unfavourable storage conditions associated with extending shelf life and maintaining nutritional qualities [35]. In melon fruits (*Cucumis melo* L.), *B. subtilis* EXWB1 has been shown to suppress post-harvest diseases caused by *Alternaria alternata* by 77.2%. Also thought to have a positive effect on melon fruit surfaces and wounded tissues, as EXWB1 inhibited the growth of *A. alternata* hyphae. *B. subtilis* EXWB1 suppresses ethylene production by 72.3% and decreases respiration rates by 26.1% and 71.9% of infected and non-infected melons, respectively after harvest of melon [78]. A possible scenario for delayed senescence and rot development in melon fruit was suppressed ethylene biosynthesis caused by *B. subtilis* EXWB1. In the same way, it was shown that EXWB1 treated fruit which maintained turgor pressure, increased titratable acidity in close proximity to fresh fruit, increased sugar content by 36.7%, and reduced weight loss during storage. According to another study of different bacterial isolates (*B. subtilis, B. pumilus, B. cereus, B. megaterium*, and *Agrobacterium radiobacter*), treatment with *B. subtilis* and *A. radiobacter* was most effective in controlling post-harvest citrus fruit disease caused by *Penicillium digitatum* [52]. There has been consistent evidence that *B. pumilus* and *B. amyloliquefaciens* suppress the development of Gray mold on Pears and tomatoes caused by *Botrytis cinerea* [50]. It was found that *Bacillus* strains (*B. pumilus* B19, *B. subtilis* 1J, *B. crerus* B16, *B. subtilis* B11, and *B. cereus* B17) controlled Gray mold in apple caused by *Botrytis mali* [41], which had an inhibitory effect ranging from 13.6 to 74% in dual culture samples; 12.3 to 87% in cell-free metabolite tests; and 11 to 53% in volatile experiments [33].

The effectiveness of *B. subtilis* AG1 against Vine wood fungal pathogens such as *Phaeoacremonium aleophilum*, *Phaeomoniella chlamydospora*, *Verticillium dahliae,* and *Botryosphaeria rhodina* has also been demonstrated [3]. A study has shown that *B. subtilis* produces antibiotics and VOCs that suppress post-harvest pathogens such as *Rhizopus stolonifer* (soft rot), *Botrytis cinerea* (Gray mold), and *Colletotrichum* spp.) Berries (Fragaria x ananassa). A strain of *B. subtilis* SK1-2, which has high antagonistic activity against *Botryosphaeria dothidea*, *Diaporthe actinidiae*, and *Botrytis cinerea* in in vitro culture, has been identified as an effective antagonist to control post-harvest rot in Kiwifruit [37]. In addition to its strong antifungal activity against *Botryosphaeria dothidea*, *B. subtilis* 9407 significantly reduces Apple fruit ring rot [56]. In Dioscorea fruit, fungi such as *Aspergillus niger*, *Botryodiploidia theobromae*, and *Penicillium oxalicum* have caused post-harvest fungal rot. When *B. subtilis* strain GA1 was applied to Apple trees after pathogen inoculation, postharvest infection caused by *Botrytis cinerea* was reduced by 80% over the next 10 days [74]. The inhibitory effect of *B.subtilis* in Litchi fruits have been treated to prevent fading (30 days at 5 °C) and to maintain their proper quality (total dissolved solids, ascorbic acid contents, and titratable acidity). It has been reported that no change in fruit taste has been observed in all treatments by *B. subtilis* bacterial cells [35]. When stored at 10 °C for 36 days, the *B.subtilis* CF-3 strain retained 65% fruit quality, which was more than 30% higher than that of non-treated controls [27]. The antagonist *B. subtilis* alleviated Citrus fruit bacterial decay caused by *Penicillium digitatum* and *P. italicum* [70].

Several studies suggested that the mechanism of *B. subtilis* H110's inhibition of pathogens is influenced by its ability to produce antagonistic proteins and natural competition for nutrients and space [61]. It has been shown that *B. subtilis* can control fungal rot in Citrus [70] as well as *Monilinia fructicola* infection in Peaches and Cherries [60,75]. A processing method using *B. subtilis* strains APEC170 and *Paenibacillus* (*Bacillus*) *polymyxa* APEC136 reduced symptoms of Anthracnose in fruit caused by the fungal pathogens *Colletotrichum gloeosporioides* and *C. acutatum* and White rot caused by *Botryosphaeria dothidea* [38]. *Rhizopus stolonifer* and other pathogens, such as *Monilinia fructicola, Cephalothecium, Rhizoctonia,* and *Alternaria,* were effectively controlled by *B. subtilis* SM21 in Peach fruit [77]. During storage, the development of Anthracnose, the Avocado fruit rot complex (*Dothiorella/Colletotrichum*) was significantly reduced by co-application of *B. subtilis* and commercial wax Tag, enriched with different concentrations [39]. Incubation of fruit in water containing bacterial cells yielded a similar result. *B. subtilis* Ch-13 has been shown to reduce the colonization of bacterial antagonists on Potato tuber surfaces during cold storage and during the growing season [12]. In cold storage, microbial preparations can be used to intensify the adaptive immune response of Potato tubers, resulting in more than double the amount of defense response. A *B. subtilis*-based microbial preparation increased potato tuber peroxidase activity, phytoalexin production, and ascorbic acid concentration by 2.4, 3.1, and 1.3 times, respectively, compared with a control preparation. A mixture of *Pseudomonas fluorescens* Pf1, *Bacillus* sp. EPB10, and *Bacillus* sp. EPB56 was applied to Banana fruit (*Musa* sp.) to reduce *Fusarium oxysporum* development [36].

3. *Bacillus* as an endophyte

A key part of bio-control has been the development of endophytic *Bacillus* strains that are able to colonize plant tissues and live in the same ecological niches as pathogens, thus preventing post-harvest diseases. In this way, they are able to survive without external environmental influences while conferring economically useful properties on host plants [58,46]. Plants were protected from certain defects by the introduction of endophytic bacteria (*B. subtilis* 26D) before planting or during the vegetative phase. Those effects were sustained for a prolonged period, which led to improved preservation during storage [59]. A combination of *B. subtilis* 10-4 and salicylic acid (SA), combined with anti-stress activity, improved plant growth [1]. Compared to non-treated tubers, tubers treated with *B. subtilis* 10-4 and SA was less infected by pathogenic micromycetes *Aspergillus*, *Pennicillium*, and *Alternaria* and had fully faded *Cladosporium*, *Fusarium*, and *Mucor*. The tubers treated with both *B. subtilis* 10-4 and SA maintained antifungal activity for up to 30 days after storage, indicating the prolonged protective effect of *B. subtilis*. Interestingly, co-application of endophytic *B. subtilis* together with SA is more effective in bio-controlling potato diseases during storage than *B. subtilis* alone [47,42]. In addition to improving nutritional quality and extending fruit/vegetable shelf life, SA can also be used as a pre-harvest and post-harvest control strategy. SA reduces chilling injury and decay, delays ripening, and improves fruit and vegetable health benefits by improving disease resistance and antioxidant capacity. Thus, the application of bacterial antagonists, particularly endophytic strains, either alone or in combination with other natural regulators, enhances the defense response in plant tissues of harvested fruits/vegetables during storage. This offers insight into developing bioactive components that can extend crop longevity while maintaining quality and nutrition. Commercial development of preparations based on antagonistic bacteria is hindered by a lack of knowledge about mechanisms of the interactions between *Bacillus* spp.–host plant–pathogen.

4. *Bacillus* sp. Inducing Systemic Resistance in hosts

In harvested fruits and vegetables, *Bacillus* spp. suppress disease development through the synthesis of fungicidal compounds as well as indirectly by launching multiple defense response mechanisms. Phytohormones such as SA, ABA, JA, ethylene, as well as CLPs regulate these indirect mechanisms as they form ISR and SAR (in whole host plant organisms) [47]. Several bacteria have been shown to induce auxins, cytokinins, gibberellins, ABA, JA, and SA [20,19,71,40]. Many strains of bacteria were found to synthesize ABA, especially when under stressful conditions, and to influence its level in plants. The genera *Bacillus*, *Azospirillum*, *Pseudomonas*, *Brevibacterium*, and *Lysinibacillus* were among these strains [20,9]. Inoculating Maize plants with ABA-producing *Azospirillum lipoferum* (strain USA59b) stimulated their growth under drought stress and induced ABA accumulation [15]. A “binary” system developed by ABA-deficient mutants of Tomatoes, flacca and sitiens. *Bacillus megaterium* synthesizing ABA has demonstrated that the host's growth depends heavily on maintaining ABA levels in both normal and stress conditions in Tomato plants [79]. Hormones and their precursors are synthesized and catabolized by phytopathogenic bacteria in plants. A strain of bacteria isolated from Rice's rhizosphere can dispose of ABA for Tomato plant growth promotion via an ABA-dependent mechanism. Under the influence of PGPB, plants can undergo an endogenous hormonal balance shift. Phytohormones are found in both beneficial bacteria and pathogens. Pathogen phytohormones suppress the host's defense systems, whereas PGPB optimizes the hormonal balance of plants. Along with other compounds, phytohormones produced by PGPB can also initiate some mechanisms involved in protecting hosts from pathogens.

In some *Bacillus* strains, low molecular weight VOCs are produced (usually with a molecular weight of less than 300 grams). These VOCs can easily spread over long distances by diffusion in the air and soil pores. VOCs have been shown to redistribute endogenous auxins tissue-specifically [80] and cause *Arabidopsis* ABA content to decrease [81]. Furthermore, these compounds can activate ISR against pathogens and abiotic stressors. *B. subtilis* UMAF6639 stimulates JA- and SA-dependent protective reactions in melon to enhance Powdery mildew resistance. SA is also used as a signaling molecule in other bacteria to induce defense responses [72]. The majority of post-harvest technologies manipulate the metabolism of the harvested product by inhibiting respiration. In addition, ethylene functions as a key regulator of the ripening and senescence of fresh fruit and vegetables. After harvest, overproduction of ethylene accelerates senescence and reduces shelf life [63,44]. Numerous studies have suggested that PGPBs capable of producing ACC-deaminase play a major role in modulating the levels of ethylene in plants, thereby preventing harmful stress responses and promoting disease tolerance [45,8,26]. ACC-deaminase-producing bacteria were demonstrated to significantly reduce ethylene production in plants, which prevented plant growth inhibition caused by a variety of stress factors (eg. flooding/anoxia, drought, salinity, heavy metals, organic contaminants, fungal and bacterial pathogens, nematodes). Since ethylene causes quick ripening, applying ACC-deaminase-producing bacteria during storage reduced ethylene levels in stored fruits/vegetables, extending their shelf life and aging process.

According to several studies, microbial antagonists also contribute to the induction of defense mechanisms in host cells by producing antifungal compounds. In this way, fruit and vegetable diseases can be prevented biologically. In plants, *B. subtilis* triggers ISR mechanisms by producing iturin and fungicin, which cause plant genes to express phenylpropanoid metabolism genes. Induction mechanisms of the protective system that are mediated by LPs may also involve the pathway of SAR related to ROS generation and triggered by SA. A strain of *B. subtilis* 168 producing surfactin and fengycin enhanced Tomato and Bean plant resistance by activating lipoxygenase enzymes [57], which produce JA, which is essential for regulating ISR. Surfactin induced ISR in Beans, Melon, Tomato, Tobacco, and Grapes, while fengycin induced protective responses in Potatoes, Tomatoes, and Tobacco. As a result of the JA/ethylene-dependent signaling protective pathway, *B. amyloliquefaciens* strains producing surfactin induced ISR in *Brassica napus* against *Botrytis cinerea* [65], and *B. amyloliquefaciens* FZB42 induced ISR in lettuce against *Rhizoctonia solani* [13]. In Grape plants, mycosubtilin triggers protective reactions [64]. In contrast, recombinant strains of *B. amyloliquefaciens* FZB42 which are deficient in the synthesis of surfactin (CH1), as well as in the synthesis of surfactin, fengycin, and bacillomycin D (CH5), were unable to enhance lettuce resistance to *Rhizoctonia* [13]. Strain BBG111 of *B. subtilis* induces ISR. Rice rhizospheres are infected by *R. solani* due to the secretion of fengycin and surfactin, which results in hypersensitivity and cell death. As a result of immune responses, the pathogen's growth and development are prevented in the early stages of pathogenesis through the JA/ethylene, ABA, and auxin-dependent defense signaling pathways [11]. Zhang and co-workers [82] used genomic shuffling to create a *B. amyloliquefaciens* strain (FMB72) capable of synthesizing 8.3 times more fengycin than *B. amyloliquefaciens* ES-2-4 isolated from *Scutellaria baicalensis* Georgi. This strain exhibited high biocidal activity against pathogens. Numerous studies have demonstrated that *Bacillus* spp. by accumulating phytoalexins (scoparone and scopoletin), elicit defense mechanisms in harvested fruits and vegetables and prevent postharvest decay. It has been demonstrated that microbial products derived from *B. subtilis* (Ch-13 strain) increased the activity of peroxidase, ascorbic acid concentration, and phytoalexin production in potato tubers during storage at 18 °C and doubled the protective response.

In plants, ISR induced by endophytic bacteria can be preserved for a long time and was effective against pathogens when stored properly [47]. Immediately following infection onset, ROS accumulate rapidly, including H_2O_2, and redox-sensitive transcription factors and PR genes are unregulated as a result. It was found that *Pseudomonas putida* LSW17S induced the rapid accumulation of transcription PR genes and the production of H_2O_2 in Tomato plants infected with *P. syringae* pv. tomato DC3000 inhibited pathogen growth [2]. *Rhizopus stolonifer* growth was reduced on Peach fruit treated with *B. cereus* AR156 and B. *subtilis* SM21 was associated with producing H_2O, overexpression of chitinase genes, 1,3-glucanase, and phenylalanine–ammonium-lyase, and the activity of their protein products [77]. In pepper seedlings infected with *Pythium aphanidermatum* [54], *B. subtilis* BSCBE4 and *P. chlororaphis* PA23 activate peroxidases and polyphenol oxidases that catalyze the final lignin biosynthesis reactions. It is known that *Pseudomonas fluorescens* (Pf1 and Py15 strains), *Trichoderma viride* (Tv1 and Tv13 strains), and Bs16 strains produce peroxidase, polyphenol oxidase, and phenylalanine-ammonia-lyase to protect plant tissues against pathogens [73]. ROS can play a critical role in the priming effect of ISR induced by endophytic bacteria in plants. By priming the host genome under the influence of bacteria, hypersensitivity to foreign substances occurs. An increase in plant resistance can be achieved by activating the cellular mechanisms of plant protection faster and stronger under pathogens or insect invasion, and it can last for quite some time. It is suggested that such priming in response to bacterial infection is associated with a change in DNA methylation status in the plant genome [16]. There is still a lack of understanding of the undelaying protective mechanisms that *Bacillus* induces in fruit and vegetables against pathogens.

5. *Bacillus* strains application

The effectiveness of potential microbial antagonists in suppressing pathogens in harvested fruits and vegetables depends on both strain characteristics and the method of their application. In general, microbial agents can be used either pre- or post-harvest [55].

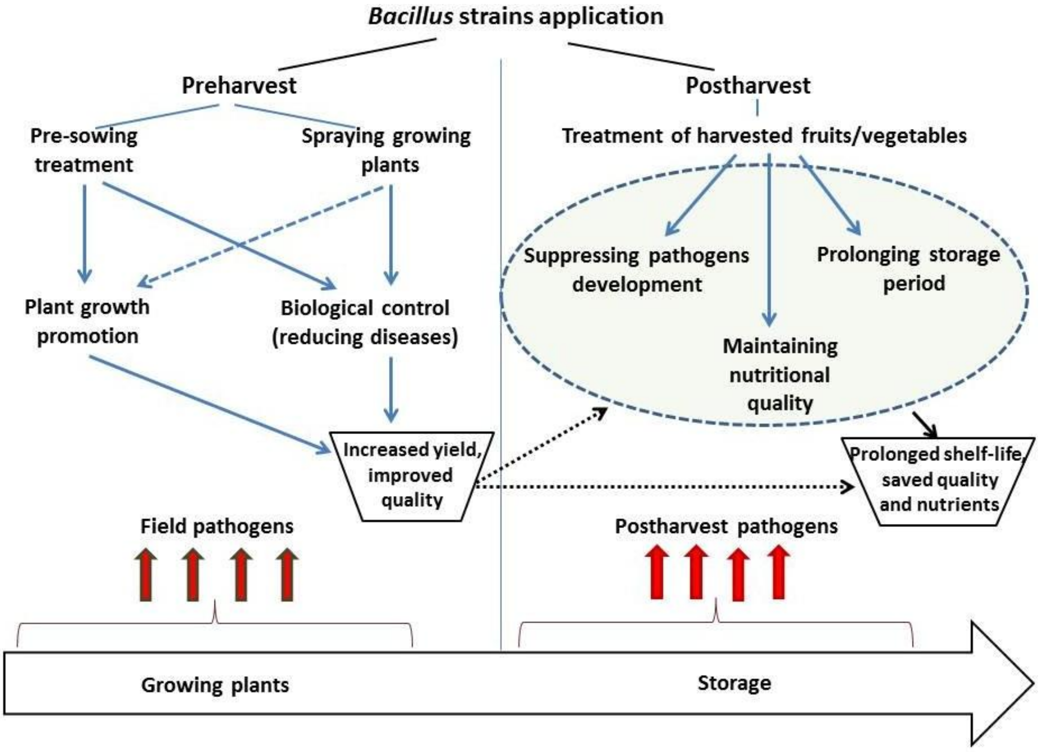

Figure 1. Scheme of *Bacillus* strains application strategies for diseases management of harvestedfruits/vegetables during storage.

5.1. Pre-harvest

In the field, pathogens usually infect fruit and vegetables and live in plant tissues without causing any symptoms; however, these "hidden" infections can lead to significant food losses when they develop during storage. Researchers have found that microbial inoculants, particularly *B. subtilis*, reduce stress-induced defects and improve crop yield during storage [27,48]. Potato tubers (*Solanum tuberosum* L.) tubers were treated with endophytic *B. subtilis* strains 10-4 and 26D in the field positively influenced plant growth, development, and yield. The inoculated tubers are less likely to be infested with pathogenic micromycetes such as *Aspergillus*, *Pennicillium*, and *Alternaria*, and they are less likely to develop *Cladosporium*, *Fusarium*, and *Mucor* [42] compared to non-inoculated control tubers. In other words, preharvest application(s) of microbial agents are often effective in controlling post-harvest diseases of fruits and vegetables [29,30]. By using *B. subtilis* under field conditions, the microbial antagonist colonizes the Apple fruit surface before harvest. Consequently, the post-harvest pathogens *Penicillium expansum* and *Botrytis cinerea* are effectively controlled in Apples [43]. Infection usually occurs shortly before harvest. Symptoms of these infections may not appear during harvest, but may become apparent post-harvest, especially when the congenial conditions are present for pathogens to develop. Infections that develop late tend to be caused by pathogens like *B. cinerea*, *Monilinia fructicola*, *Sclerotium rolfsii*, and *Geotrichum candidum* [14]. It has been shown that the application of antagonistic microorganisms immediately before harvest helps fruit surfaces colonize and protects them from pathogens in storage, according to Ippolito and Nigro [29]. In spite of its success in some cases, this approach is generally not commercially viable due to the poor survival rate of microbial antagonists in the field.

5.2. Post-harvest

The application of microbial antagonists after harvest has been proposed as a practical method of controlling fruit and vegetable diseases. Preparations containing microbial antagonists may be sprayed on harvested fruit and vegetables or applied as solutions [31,7]. In spite of this, a single microbial antagonist cannot prevent all fruits/vegetables from decaying during storage after harvest. Selecting a single microbial strain with a broad spectrum of activity against a wide range of pathogens is difficult [23,69,7]. Manufacturers to enhance the protection of biological preparations can use a variety of bacterial strains. As an example, 'Companion' (Growth Products Ltd., USA) contains *Bacillus* spp. (*B. subtilis* GB03, *B. lichenoformis*, and *B. megaterium*) and 'Bactril' (Biopharmatec, Russia) contain *B.*

subtilis GB03, *B. subtilis* MBI600, and *Bradyrhizobium japonicum* [46]. As part of an integrated vision of disease management, *Bacillus* spp. can also be considered one element, applied alongside other biological and physical methods. Two or more post-harvest diseases can be controlled with polymicrobial mixtures by combining diverse antagonistic microorganisms with diverse microbial activity and combining various bio-controlling characteristics [68]. By adding enhancer effectors, microbial antagonists can be enhanced in their effectiveness in preventing post-harvest decay on fruits/vegetables. It is possible to combine microbial antagonists with wax agents during pre-and post-harvest periods. Examples include calcium chloride, calcium propionate, sodium bicarbonate, ammonium molybdate, sodium carbonate, potassium metabisulphite, SA, *etc*. A combination of microbial antagonists and physical methods, such as curing or heat treatment, could enhance the bioefficacy of microbial agents [23,68]. In light of the extensive knowledge available about microbial antagonists (*Bacillus* spp.), biologically active compounds, and induced resistance, it is not unlikely that more effective formulations, application methods, and combinations with additional approaches will be developed [21]to enhance additive and/or synergistic effects.

6.Conclusion

It is believed that *Bacillus* spp. have a positive effect on fruits and vegetables' post-harvest physiology by enhancing their resistance to different postharvest pathogens, resulting in a longer storage period and a longer "marketing" life, as well as preserving freshness and nutritional value. A bio-control agent can decrease postharvest decay of fruits and vegetables by utilizing *Bacillus* strains (especially endophytic). Despite *Bacillus* species, commercial development of these microbial antagonists for postharvest biological control is a promising prospect. As an eco-friendly method of preventing food losses during storage, it has a clear advantage, but little is known about its effects on postharvest physiology or preservation under pathogenic infection and requires further study.

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