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Review

Control of postharvest diseases in berries through edible coatings and bacterial probiotics

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ABSTRACT

The world's population is growing, which requires more resources, including food. Some necessary foods, such as berries, are very perishable fresh products that suffer contamination by pathogens, generating great economic losses. Various physical and chemical strategies have been used to mitigate these losses over the years, including the use of pesticides. However, the negative impact on the environment and human health of these chemical products has aroused interest in the development of other control methods. Biocontrol is one of these innovative strategies, in which various biological control agents can be used, including bacteria probiotics. Probiotics act as antagonists of fungal pathogens by competition for space and nutrients, production of secondary metabolites, such as volatile organic compounds (VOCs), lytic enzymes, and activation of plant defenses. On the other hand, there are materials in which protection against pathogens has been seen, such as edible coatings, since they have components, such as chitosan, with antimicrobial properties. In addition, probiotics can be used in conjunction with other elements such as edible coatings, resulting from a new control strategy against post-harvest diseases. This review compiles studies that use probiotics and/or edible coatings as a method of reducing post-harvest diseases, specifically, in berries.

1. Introduction

Currently, the world's population amounts to almost 8 billion people, having a growth projection to 8.3 billion in 2030 and 9.8 billion in 2050 (Lindgren et al., 2018; Tripathi et al., 2019). The population will generate an increment in food demand between 56-98% in 2050, needing a growth in agricultural production (Lindgren et al., 2018). The rise in global demand for food is not only due to population growth, but also to increase in *per capita* consumption, as a result of a greater accessibility to energy-rich meals (Godfray et al., 2010). Energy-rich foods require the use of more resources for their manufacture and consumption. Therefore, they have an impact on the environment such as deforestation or soil and water pollution that must be reduced (Fisher et al., 2018). The current degradation of soils by intensification of production is a major constraint on agriculture production (Kopittke et al., 2019). In addition, because of the pandemic caused by COVID-19 the population suffering from hunger has been increasing since 2020, resulting in a 9.2-10.4 % of the world population. Food security had slowly increased from 2014 to 2019, however, in 2020 there was a rapid increase coming (FAO et al., 2021), assuming increased pressure on the agricultural sector and food security.

Access to these energy-rich foods has been on the rise, causing changes in the diet of the population and increasing the demand for sustainably grown products (Pavagadhi and Swarup, 2020). Therefore, there is an increase in demand for fresh produce as fresh fruits and vegetables (Pavagadhi and Swarup, 2020). Fresh produce is defined as "*fresh fruits and vegetables that are likely to be sold to consumers in an unprocessed or minimally processed (i.e., raw) form*" (FDA, 2018). Fresh products are a good source of essential vitamins and minerals, however, they are very perishable products with a short self-life, generating large postharvest losses (Duarte-Sierra et al., 2020). Furthermore, this product suffers quality losses in the supply chain if the correct preservation methods are not used (Pace and Cefola, 2021). The evaluation of quality in postharvest focuses on food safety (chemical contamination, presence of heavy metals or microbiological contamination) and the maintenance of different established quality criteria (Pavagadhi and Swarup, 2020)

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such as aroma, texture, appearance, taste, and nutritional value (Mahajan et al., 2014). Some of the treatments used to maintain the quality and safety of fresh products are: (i) ozone treatment, (ii) irradiation, (iii) sulfur dioxide and (iii) use of edible coatings (Mahajan et al., 2014; Murray et al., 2017; Sheng and Zhu, 2021). However, there are other factors that affect the maintenance of quality, such as the state of maturity of the product at harvest time (Ansah et al., 2018).

Berries are defined as fleshy fruits that have a cartilaginous endocarp full of seeds (Tromp, 1996) that can be formed by simple fruits, such as blueberries, or composite fruits, such as blackberry or raspberry (Kumar et al., 2018). Currently, the consumption of berries has increased due to its characteristic organoleptic and antioxidant properties, among others, which represent great health benefits (Sobekova et al., 2013; Okatan, 2020). Berries are highly perishable fresh products as they have a high amount of water and water activity, which makes them susceptible to mechanical damage and contamination. Some of the factors that affect the quality in postharvest berries are: (i) respiration rate, (ii) ethylene production, (iii) composition changes, (iv) temperature and CO_2, and (v) attacks of pathogens (Kumar et al., 2018).

Pathogen attacks are one of the main causes of deterioration in fruits and vegetables in the postharvest process, reducing their shelf life. Global losses are estimated at 33% of total fruit and vegetable production (Dukare et al., 2019). The deterioration of fruits and vegetables is usually due to fungal pathogens, owing to the high content of water, nutrients and low pH (Dukare et al., 2019). Traditionally, synthetic fungicides have been used to control these pathogens (Jiménez-Reyes et al., 2019). However, its use has been declining in recent years due to the impact it generates on food security and the environment, contaminating waters and soils (Gupta and Dikshit, 2010). The use of synthetic fungicides has been reduced due to their toxicological problems, their impact on the environment and other reasons such as: (i) resistance of pathogens to some fungicides, (ii) new pathogen biotypes, (iii) shortage of different effective fungicides, (iv) increase of fungicide residues in products (Dukare et al., 2019). For this reason, it is important to develop new methods to combat these diseases, due to the toxicological problems presented by chemical fungicides. The main objective of this review is to analyze those strategies in which edible coatings and bacterial probiotics are used in combination and/or independently to effectively control the various post-harvest diseases in berries. For this purpose, the peer-reviewed publications databases Web of Science and Google Scholar were used, compiling all publications prior to November 2021. Our search terms were mainly "edible coatings", "probiotic bacteria", "berry", "postharvest" and "biocontrol". The criterion followed in the analysis of the publications was to use all those that focused on postharvest berries, and, more specifically, on the control of fruit diseases with edible coatings, probiotic bacteria, or both in combination.

2. Main pathogen-diseases of postharvest in berries

Fresh products, including fruits and vegetables, require long storage periods in their marketing. These products are rich in nutrients and moisture, being during this long process very susceptible to contamination by microorganisms, degrading and losing. Diseases produced during storage or postharvest diseases are a limiting factor in the process of extending the shelf life of fresh products. In addition, postharvest diseases generate greater economic losses than during cultivation, even in areas with more advanced postharvest conservation methods, such as packaging technologies or storage in controlled atmospheres (Barkai-Golan, 2001). This review focuses on postharvest diseases generated in berries.

Among the berries we can find strawberry (*Fragaria ananassa*), raspberry (*Rubus idaeus*), blackberries (*Rubus* spp.) and blueberries (*Vaccinium corymbosum*), among others. These fruits stand out for their acid taste, striking colors and other resources, such as antioxidant, antimicrobial or anti-inflammatory properties thanks to the presence of bioactive compounds (Piljac-Žegara and Šamec, 2011). However, berries are very delicate fruits due to lack of a protective layer, being therefore, very susceptible to water loss, mechanical damage and contamination by fungi (Sánchez et al., 2012; Horvitz, 2017). Postharvest losses of berries are due to various causes. There are mechanical damages generated during the handling or transport process that can result in juice losses, which increases susceptibility to rot (Zhao, 2007). Damage can also occur due to insects, which deposit their eggs in the fruit. Once the damage has occurred, the fruit is more susceptible to saprophyte contamination, being ill caused by fungi one of the most common causes and with higher economic losses in berries (Almenar et al., 2007; Zhao, 2007).

In the case of blueberries, the main postharvest diseases are gray mold (*Botrytis cinerea*), rot (*Alternaria* spp.) and anthracnose (*Colletotrichum* spp.) (Bell et al., 2021). *B. cinerea* is a necrotrophic fungus that attacks blueberry fruits in a temperature range of 15 to 25°C and with a humidity greater than 95%. Fungal infection occurs in the early stages of growth and development, developing various symptoms such as softening, dehydration or development of a portion of gray mycelium, among other things (Bell et al., 2021). On the other hand, *Alternaria* spp. is a fungus that can penetrate the blueberry taking advantage of the existence of previous wounds or openings that exist naturally in the fruit (Bell et al., 2021). In this case the fruit presents dark wounds along with white or greenish gray mycelium indicating spoilage (Zhu and Xiao, 2015). *Alternaria* spp. can grow at temperatures of 20 to 30°C and generates toxic secondary metabolites, such as alternariol (Munitz et al., 2013). In addition, in blueberries there is anthracnose, a disease caused by *Colletotrichum* spp., which appears when the fruit matures and produces its decay, observing wounds that have a pink color (Bell et al., 2021).

The most common fungal pathogens in raspberries and blackberries are *B. cinerea, Cladosporium* spp., *Fusarium* spp., *Penicillium* spp. and *Rhizopus* spp. (Huynh et al., 2019). In the case of raspberries, *B. cinerea* infects stems, petals, buds, and fruits, generating a berry-brown color and a soft texture once collected, while the fruit remains on the plant looks dry and covered with a powder-gray-produced by conidia (Carisse et al., 2018). Moreover, *B. cinerea* is considered the major fungal pathogen present in strawberries, affecting both fruits and vegetative tissues in humidity conditions greater than 80% (Petrasch et al., 2019). Both primary (open flowers) and secondary (receptacle tissue) infections can occur in strawberries (Petrasch et al., 2019). Strawberries can also be infected with *Rhizopus* spp., which presents pectic enzymes generating an aqueous decomposition of the fruit by rupture of pectin along with the appearance of a white mycelium (Tournas and Katsoudas, 2005).

Grapes are also part of berries, being a very important fruit both in the wine sector and in its fresh consumption, being highly appreciated for its bioactive components, its sensory properties and its vitamins (De Simone et al., 2020). More than 27 million tons of table grapes are produced annually in the world and more than 4 million tons are exported between countries, so the interest to extend the shelf-life during export has been increasing (De Simone et al., 2020). One of the most important pathogens in grapes is *B. cinerea* whose spores are usually found on the fruit surface and it provides an optimal environment for germination (De Simone et al., 2020). However, other genera such as *Penicillium* sp. and *Aspergillus* sp. are also pathogenic in grapes (Di canito et al., 2021).

Furthermore, there are bacterial pathogens that infect fruits and can affect food security, by generating diseases in humans (Zhao, 2007). In berries the main pathogenic bacteria are *Listeria monocytogenes, Salmonella typhimurium* and *Escherichia coli* that can be transmitted by soil, water or air and penetrate the plant through lesions or openings (Bell et al., 2021).

3. Postharvest disease management in berries

It is estimated that between 25% and 50% of economic losses occur in total fruit production (Nunes, 2012). Various physical and chemical methods are used to prevent or delay degradation of products (Kumar et al., 2018). Traditionally, the following physical and chemical methods have been used for preventing and delaying degradation of berries.

Physical methods include controlled atmosphere packaging, refrigeration, hot water treatment or the use of edible coatings (Kumar et al., 2018). Controlled atmosphere packaging is based on maintaining certain O_2 and CO_2 levels (Kumar et al., 2018). A good proportion of these gases has an inhibitory effect on many microorganisms since they intervene in their cellular metabolism (Bower, 2007). Ozone is an oxidizing agent used in the postharvest treatment of blackberries, blueberries, and raspberries. This compound is not considered toxic and is usually applied in the form of gas (Huynh et al., 2019). In addition, this compound can oxidize ethylene, thus favoring the delay of fruit ripening (Huynh et al., 2019). Furthermore, the use of gamma radiation is effective in inhibiting contamination by *Rhizopus* spp. and *B. cinerea* without affecting the qualities of the fruit can be used as an alternative to sulfur dioxide (Zhao, 2007).

On the other hand, among the chemical treatments, sulfur dioxide is used as a disinfectant gas in berries to reduce contamination by *B. cinerea* (Kumar et al., 2018). This component is mainly used in blueberries, being effective in reducing decomposition in a concentration of 8 to 15% (Paniagua et al., 2014; Saito et al., 2020). Sulfur dioxide is usually applied using small packages inside the packaging delaying the degradation of the fruit (Saito et al., 2020). Sulfur dioxide has antimicrobial activity because it inhibits enzyme catalyzed reactions (Lück and Jager, 1997). Fungicides are chemicals used to fight fungal diseases (Bell et al., 2021). Some of the fungicides most used in blueberries are azoxystrobin (against *Alternaria tenuissima*) or pyrimethanil (against *B. cinerea, A. tenuissima, Colletotrichum* spp.) (Bell et al., 2021). Azoxystrobin binds to cytochrome b by blocking electron transfer between cytrocromes b and c, resulting in inhibition of mitochondrial respiration (Zhang et al., 2019). Despite the good results in the protection and quality of the fruit, chemical treatments have great impacts on human health and the environment (Bell et al., 2021). That is why research into biological methods for disease control is on the rise.

3.1. Biological control

The biological control used to reduce the diseases caused by phytopathogens resulting in an important strategy for the control of fungal diseases. Biocontrol is based on the use of live microorganisms or products derived from them to stabilize or maintain plant pathogens at reduced levels, thus avoiding economic losses (Carmona-Hernandez et al., 2019). This system is effective in the short, medium, and long term and has no negative impact on the environment or on human and animal health (Cuthbert et al., 2018). As a short- to medium-term strategy, the use of natural plant-derived products, such as defense-related phytohormones, stands out (Wan et al., 2021). Generally, bacteria are used as antagonists for fungal control. The bacteria acts in front of fungi due to various causes such as: (i) competing with them for nutrients and space; (ii) produce hydrolytic enzymes so that parasites fungus and feed off of their cell walls; (iii) formed biofilms on the fruit, avoiding the entrance of the phytopathogen in case of injuries; (iv) production of antibiotics, such as iturin, which is a powerful anti-fungal produced by *Bacillus subtilis*; (v) bacteria can induce a host defense response through biochemical reactions (Carmona-Hernandez et al., 2019). Competition for space and nutrients is one of the main methods of action in bacterial BCAs, as they assimilate the carbon sources necessary for their survival and multiplication, limiting their available to the phytopathogenic fungi (Carmona-Hernandez et al., 2019). Competition for space and nutrients such as carbohydrates or amino acids is a method of action of BCAs described in numerous studies of antagonist such as *Metschnikowia pulcherrima* (Saravanakumar et al., 2008), *Pseudomonas syringae, Pantoea agglomerans* (Kim et al., 2016), *Pseudomonas fluorescens* (Tockhom et al., 2017) and *Cryptococcus laurentii* (Carmona-Hernandez et al., 2019; Dukare et al. 2019). The production of antifungal is the second most important mechanism. The literature reports that the main synthesized antibiotics are: (i) iturine, produced by *Bacillus subtilis and Pseudomonas cepacia* Burkh; and (ii) pyrrolnitrine, produced by *Pseudomonas cepacian* (Torres et al., 2014; Carmona-Hernández et al., 2019; Dukare et al., 2019; Jiang et al., 2019a). Antibiosis can also develop through the production of volatile organic compounds (VOCs) that are effective at low concentrations and can travel long distances. Among them are alcohols, ketones, lactones, and terpenes. Both antibiotics and VOCs inhibit the growth of phytopathogens (Carmona-Hernandez et al., 2019). Due to the production of lytic enzymes, bacteria parasitize the pathogenic fungus by feeding on the components of its cell wall, mainly chitin, glucans, and proteins (Spadaro and Droby, 2016). Chitin is a homopolymer formed by N-Acetyl glucosamine (β-1,4 bonds) (Carmona-Hernandez et al., 2019) and is hydrolyzed by chitinase that can act through two mechanisms: (i) exo-chitinase that segments extreme residues of N-Acetyl glucosamine; and (2) endo-chitinase, which activates bonds at random sites along the chain (Stoykov et al., 2015). On the other hand, the enzymes glucanases degrade glucans by exo-β-1,3-glucanase, which hydrolyzes the glucans slicing sequentially glucose residues from the non-reducing end; or the endo-β-1,3-glucanase active links in aleatory areas along the chain, in the release of oligosaccharides and glucose (Spadaro and Droby, 2016). In the induction of resistance to the bacterium elicits a defense response in the host by means of the over-production of various metabolites, and enzymes such as: (i) proteins related to pathogenicity (PR proteins); (ii) metabolites with antifungal capacity, such as the phytoalexins; (iii) accumulation of callose and lignin in the cell wall; (iv) produce reactive oxygen species (ROS); and (vi) closure of stomata (Carmona-Hernandez et al., 2019).

For postharvest control, these microbial agents are applied to products by immersion in a biochemical solution or by spraying (Carmona-Hernandez et al., 2019). In addition, it has been shown that this procedure is more effective in postharvest application than in pre-harvest (Dukare et al., 2019). Some of the bacteria used as biocontrol agents in berries are *Bacillus pumilus* and *Pseudomonas fluorescens* that inhibit *B. cinerea* in strawberries and blueberries and *A. alternata* in blueberries (Bower, 2007; Bell et al., 2021). The realization of a pre-harvest biocontrol could increase the effectiveness in disease control. Some studies showed a decrease in the diseases caused by *Penicillium digitatum* and *Penicillium italicum* in the orange (Cañamás et al., 2008; Hacquard et al., 2017). However, pre-harvest biocontrol is less effective since the BCAs used must be resistant to various factors such as the direct incidence of UVA light, extreme temperatures, water stress, nutrient limitation, and climatic changes (Dukare et al., 2019).

On the other hand, there are endophytic fungi capable of acting as antagonists against *B. cinerea* as *Trichoderma asperellum, A. pullulans* or *Fusarium proliferatum*, through production secondary metabolites and extracellular enzymes with an essential role in the biological control of pathogens (Bolívar-Anillo et al., 2020).

In the case of yeasts, they can also act as antagonists since they compete for space and nutrients with fungal pathogens, secrete lytic enzymes, produce toxins, release VOCs, induce defense mechanisms in plants and present mycoparasitism (Freimoser et al., 2019). Some of the yeasts registered as biological control agents in berries are *A. pullulans, Metschnikowia fructicola* or *Cryptococcus albidus* (Freimoser et al., 2019).

There are numerous studies that incorporate edible films and bacteria for post-harvest disease control. Salgado-Cruz et al., 2021 conducted a bibliometric study where they found that there are 875 documents that report the effectiveness of chitosan films as a biological control strategy in fruits and vegetables. Oregel-Zamudio et al., 2017 developed edible wax-based coatings in communication with *B. subtilis* as a biocontrol agent. These coatings managed to extend the useful life of strawberries maintaining the quality and pH parameters, decreasing putrefaction, and providing an important resistance against *R. stolonifer*, an important phytopathogen by producing biofilms, antibiotics or siderophores (Oregel-Zamudio et al., 2017). *Salmonella sp.* is also a phytopathogen present in strawberries, which obtained a significant reduction in the presence of an edible coating based on whey protein and a phage cocktail, by space competition (Sezer et al., 2022). Marín et al., 2019 developed edible films with lactic acid bacteria (*Lactobacillus plantarum*) that significantly reduced fungal rot of grapes by production of antifungal substances such as hydrogen peroxide, organic acids, fatty acids or cyclic dipeptics (Lappa et al., 2018).

4. Edible coatings

Edible coatings are formed directly on the food surface itself. These coatings would also reduce the microbial load of the surface and prevent the loss of quality of the product. They prevent exchange of moisture, oxygen, carbon dioxide, flavor and aroma transfer between the food components and the surrounding atmosphere (Krochta and De Mulder-Johnston, 1997). In addition, coatings can be able to transfer some beneficial compounds (antioxidants, antimicrobial and flavorings) into the food system.

Coatings are made of natural polymers: lipids, proteins, and/or polysaccharides. Other components can also be added into the materials matrix to enhance functionality, for instance plasticizers (glycerol, sorbitol, propylene glycol, etc.) The materials used for coatings should be edible (Albertos et al., 2019). The use of edible coatings has a great advantage due to the non-polluting nature. Moreover, benefits include the reduction of food waste, extending the shelf-life of perishable products and potential improvements in the nutritional and healthy properties of the food.

In the case of edible films and coatings, microbial control is achieved by using antimicrobial biopolymers and/or adding active ingredients. Chitosan has been widely studied for its antimicrobial properties. The antimicrobial mechanism of chitosan consists of that its positive charges may compete with Ca^{2+} for the negatively charged bacterial membrane (Coma et al., 2002). The more commonly antimicrobial ingredients used are organic acids, bacteriocins, lactoperoxidase and essential oils (Campos et al., 2011).

Numerous researchers have evaluated the effect of edible coatings on berry fruits. Berries are small in size and contain high antioxidant capacity. Coatings on berries attempted to reduce excessive softening and nutritional compounds loss. Fan et al. (2009) demonstrated as alginate coatings decreased weight loss and maintained the firmness of the strawberries over storage. Edible coatings acted as barriers, preventing water and firmness loss, which occurres during ripening. Coatings created an adequate internal micro-atmosphere in coated strawberries, which delayed senescence.

Chitosan coating incorporating different concentrations of blueberry leaf extracts maintain the quality and prevent blueberries decay (Yang et al., 2014). Chitosan coatings also maintained better the antioxidant compounds in strawberries (Rico et al., 2019), blueberries (Chiabrando and Giacalone, 2015) and table grapes (Shiri et al., 2013). Peretto et al. (2014) used strawberry puree with essential oils (carvacrol and methyl cinnamate) to prevent weight loss, visible decay, loss of firmness and delayed the loss of antioxidant capacity in strawberry fruit. Essential oils had antifungal activity and prevented weight loss due to a minor metabolic activity of coated-strawberries, as consequence of less microbial growth. Firmness of strawberries is related to the action of pectolytic enzymes. Essential oils decreased the amount of pectinase produced by post-harvest pathogenic fungi. Furthermore, the addition of essentials oils in coatings increased the antioxidant capacity of strawberries.

Recent advances in edible coatings included new technologies in the application of coatings as electrostatic spraying (ES). Strawberries covered on alginate coating using ES demonstrated better firmness, color retention and weight loss reduction than traditional coatings techniques (Peretto et al., 2017). Another promising innovation is the application of nano-technology in coatings. The application of essential oils and natural antioxidants in food preservation is limited by its high cost, particular flavor and volatile nature. This limitation can be avoided or lessened by encapsulation in nano-coatings. Dhital et al. (2017) developed nanocoatings of curcumin and limonene liposomes in methylcellulose for strawberry preservation. Limonene liposomes were found to be effective in maintaining total phenolic contents compared to other coatings. Different systems of emulsion to obtain coating were compared by Oh et al. (2017). They studied the effect of lemongrass oil droplet size in the chitosan emulsion for grape preservation. Coating with smaller lemongrass oil incorporated with chitosan revealed better retention of color and antioxidant activity during storage. Different edible coatings, such as chitosan, alginate or carboxymethylcellulose (CMC), have also been used to preserve the postharvest quality of blackberry, exhibiting a significant delay in weight loss and positive effects on the percentage of decomposition, total soluble solids, pH, titratable acidity, and sugar accumulation, compared to uncoated control fruit (Gol et al., 2015).

5. Bacterial probiotics

It is well known that gut microbiota plays a vital role in human health due to improved nutrient absorption of food, host resistance to infection, and enhanced intestine's immune system by different mechanisms (Nicholson et al., 2012). A recent report showed that about 100 trillion microorganisms are associated with the human digestive system, essential for gastrointestinal homeostasis (Eslami et al., 2019).

Probiotic bacteria improve microflora intestine types, maintaining eubiosis in equilibrium. Thus, their consumption has boomed. The most common probiotic species used by human belong to the genera *Bifidobacterium, Lactobacillus, Propionibacterium* and *Saccharomyces.* Various species have been studied so far, catalogued as safe probiotics. Some examples are *Lactobacillus acidophilus, L. casei, L. plantarum, L. paracasei, L. johnsonii, L. rhamnosus, L. reuteri, Bifidobacterium bifidum, B. infantis, B. lactis, Saccharomyces bourlardii* and *Propionibacterium freudenreichii* (Ghasemian et al., 2018). Consumption of probiotics bacterial trigger a variety of beneficial properties, such as to be highlighted masking pathogens' binding sites and inhibiting their colonization, stimulation and strengthening of the immune system, reducing blood cholesterol, remedy of vaginal yeast infection, improving the symptoms of irritable bowel syndrome and colitis, reducing oral lesions as dental caries, prevent various cancer as colorectal, and helping against obesity (Eslami et al., 2019; Mazloom et al., 2019; Portune et al., 2016). Therefore, the inclusion of these microorganisms in the diet, being present in berries, has great health benefits.

According to the literature, several studies use probiotic microorganisms with antimicrobial activity. Remarkably, the most significant number of species belong to the genera *Lactobacillus* and *Bifidobacterium* (Silva et al., 2020). Probiotics bacterial antimicrobial activities are described by diverse mechanisms, such as biofilms disruption, inhibition of quorum sensing, or mediated by the production of secondary metabolites. A study performance by Piewgan et al. (2018), showed that the consumption of *Bacillus* sp. probiotics abolished colonization by the dangerous pathogen *Staphylococcus aureus* responsible for triggering skin and soft tissue infections, endocarditis, osteomyelitis, bacteremia, and lethal pneumonia (Guo et al., 2020). In addition, the production of antimicrobial peptides has described another mechanism against *S. aureus* using *Lactobacillus johnsonii* (Rosignoli et al., 2018). In this sense, the presence of probiotic bacteria in berries could have a biocontrolling effect on human and plant pathogens.

These antimicrobial properties established their role as biocontrol agents. Currently, the protective capacity of the epiphytic microbiota of fruits and vegetables is fully known. Different species from the genera *Lactobacillus* has been isolated by Naeem et al. (2012) in strawberry and grapes; specifically, different strains of *Lactobacillus planatarum* were identified in both fruits. Similar observations were reported by Sagdic et al. (2014) in fermented gilaburu (*European cranberrybush*) fruit juices. Their studies found that *L. plantarum* was dominant, but other species were also identified as *L. casei, L. brevis, L.hordei, L. paraplantarum, L.*

coryniformis, L.buchneri, L.pantheris and *L. harbinensis.* In addition, two different species from the genus *Leuconostoc* were found, *L. mesenteroides* and *L. pseudomesenteroides*.

Another study performed by (Bae et al. (2006)), showed that isolation of lactic acid bacteria (LAB) from grapes was great from undamaged berries. Among them, *Lactobacillus lindneri* and *L. kunkeei*, isolated LAB from Japon′s vineyards, were essential to wine production (Yanagida et al., 2008). Their results showed *Lactococcus lactis* ssp. *lacti* was the most abundant type of LAB distributed in three koshu vineyards, followed by *L. pseudomesenteroides.*

These data suggested that these species are common in different berries, which may relate to their role as natural defence mechanisms. However, research is still incipient and needs further discussion.

6. Simultaneous use of edible coatings and bacterial probiotics in berries

The literature review shows that there have been few reports on probiotic edible coating on berries quality. *L. plantarum* was added to CMC edible coatings. Strawberry quality parameters such as weight loss and concentration of ascorbic acid and phenolic compounds improved in coated strawberries compared to control (Khodaei and Hamidi-Esfahani, 2019). Temiz and Özdemir (2021) studied the effect of *Lactobacillus rhamnosus* and inulin in gelatin coatings on the quality of refrigerated strawberries. These coatings reduced the weight loss over storage. In both works, coatings did not affect other quality parameters (pH, titratable acidity, and total soluble solids).

Bambace et al. (2019) incorporated of *Lacticaseibacillus casei* and *Bifidobacterium animalis* subsp. *lactis* into alginate-based prebiotic coatings in fresh blueberries. These coatings maintained quality (color and firmness) and sensory characteristics during the shelf-life. Initially, the coatings were not detected by sensory panel. However, negative sensory attributes were less affected for coated than uncoated blueberries at the end of storage.

7. Edible coatings and/or bacterial probiotics as biocontrol strategies in berries

This section aims to compile all the studies so far on the use of edible coatings and probiotic bacteria, in isolation and simultaneously, for the control of postharvest pathogens in berries.

7.1. Edible coatings

Microbial decay causes large losses in postharvest fruits and vegetables (Huang et al., 2021). In recent years, the use of edible coatings in postharvest is having great development, reducing microbial decay in numerous fresh produce (Sharma et al., 2019). As far as berries are concerned, Table 1 compiles all the studies to date where edible coatings have been used in the control of postharvest pathogens. Fig. 1 shows a summary infographic with the different mechanisms of action identified for edible coatings in postharvest.

Chitosan is a biopolymer derived from chitin (mainly present in fungi and arthropods) that is being widely used in different industries, due to its biocompatibility, biodegradability, and bioactivity. In agriculture, chitosan is used as a plant protector due to its antimicrobial capacity, to

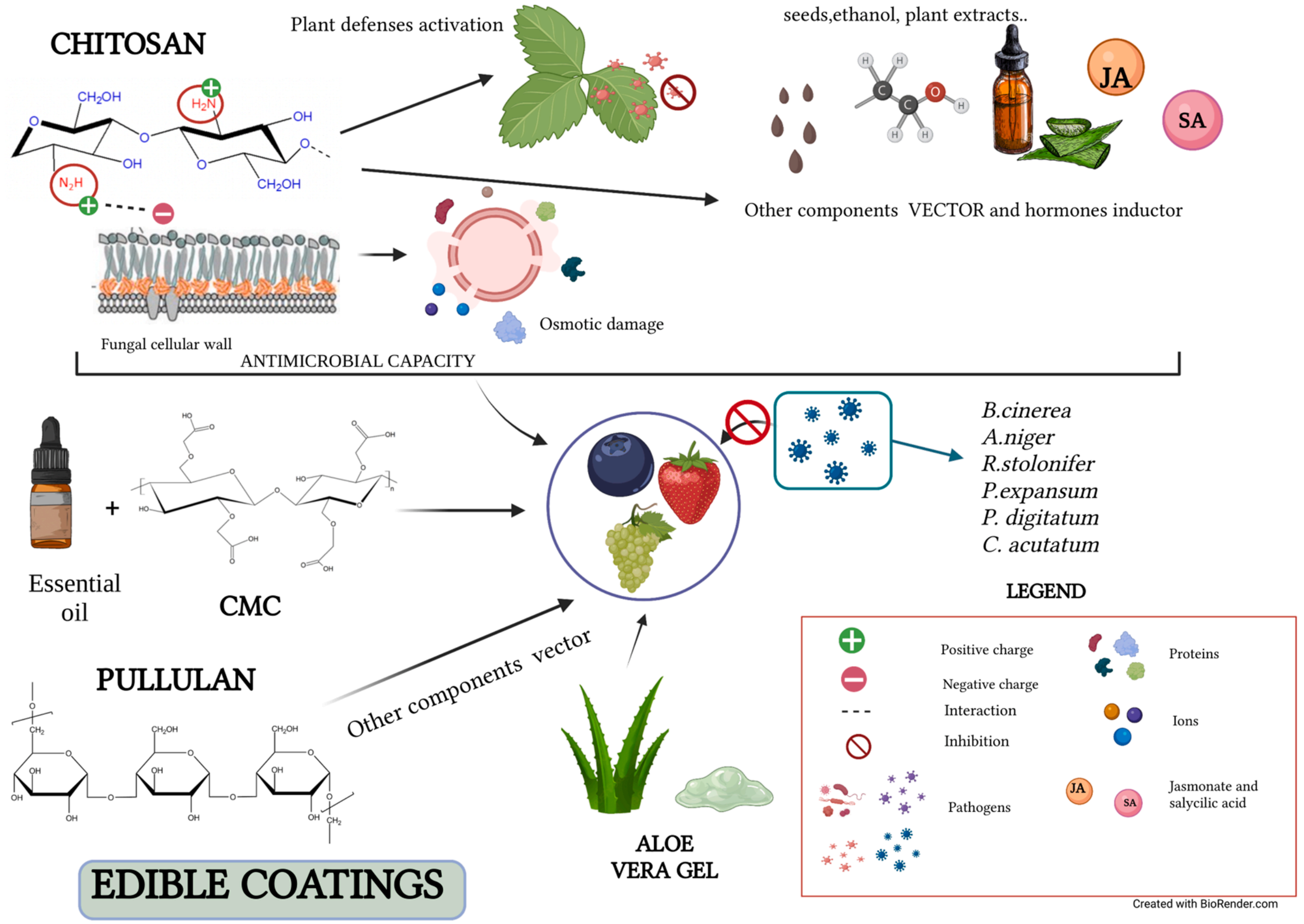

Fig. 1. Summary infographic on the use of edible coatings for the control of postharvest pathogens in berries.

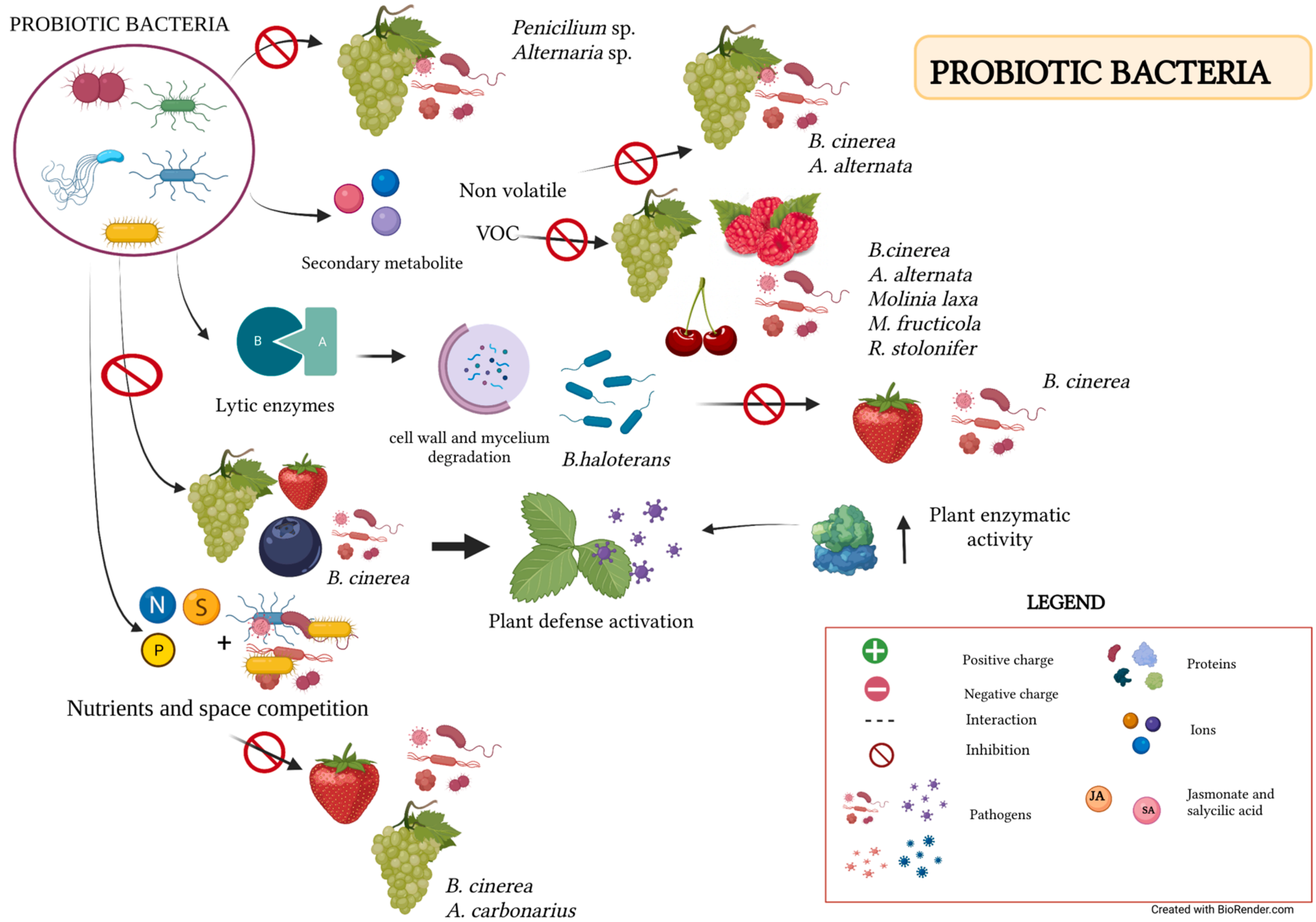

Fig. 2. Summary infographic on the use of probiotic bacteria for the control of postharvest pathogens in berries.

activate plant defenses, and to form films on treated surfaces (Romanazzi et al., 2019). The antimicrobial capacity of chitosan is based on the presence in its molecule of positively charged amine groups, which bind to the negatively charge surface of microorganisms-walls and plasma membranes. This entails a modification of the cellular permeability and a serious osmotic damage, causing the cellular expulsion of ions and proteins. In addition, chitosan can bind to nucleic acids and prevent the correct functioning of the cellular molecular machinery (Perinelli et al., 2018). Regarding the activation of plant defenses, this mechanism derives from the presence of chitin in pathogenic fungi and pest insects. When a plant is attacked, it produces chitinase enzymes that release chitin fragments from the attacking organism. Plant receptors recognize these chitin fragments and activate their defensive responses. Therefore, the application of chitosan in the plant implies the activation of defense responses (Li et al., 2020). The film-forming property of chitosan has been proven by applying to a plant surface by dipping or spraying. These edible coatings are characterized by forming a barrier for gas exchanges, reducing respiration and slowing down fruit ripening, doing fruit less sensitive to postharvest decay (Romanazzi et al., 2019). Due to all these mechanisms of action, chitosan is one of the main edible coatings used in the management of postharvest diseases in fruits and vegetables (Romanazzi et al., 2019).

The antimicrobial activity of chitosan has reported different results when used in berries for the control of postharvest pathogens. For example, in strawberries and grapes, chitosan has been reported to inhibit spore germination, germ tube elongation and radial growth, causing morphological changes in spores and hyphae of pathogenic fungi such as *B. cinerea, R. stolonifer, P. expansum* or *A. niger* (El Ghaouth et al., 1992; De Oliveira et al., 2014a, b). Thanks to these antifungal effects, chitosan has been very effective in reducing fungal decay caused by *B. cinerea, A. niger* and *R. stolonifer* in grapes (Romanazzi et al., 2002, 2009; Zhang et al., 2020a) and strawberries (Melo et al., 2020), as some examples. Furthermore, along with its antifungal capacity, the use of chitosan-based edible coatings helps to maintain the qualities of the berries, thanks to its film-forming capacity. In strawberries, chitosan protects against *B. cinerea, R. stolonifer* and *Colletotrichum fragariae*, and causes berries to be firmer and ripened at a slower rate as indicated by acidity, anthocyanin, phenolics and flavonoids content (Reddy et al., 2000; Khalifa et al., 2016; Ventura-Aguilar et al., 2018). Similar effects have been reported in blueberries protected against *Botryotinia fuckeliana* (Jiang et al., 2016).

Chitosan-based edible coatings can be used as vehicles for other compounds of interest. In this way, it has been possible to increase the antioxidant capacity of edible coatings, with synergistic effects against *B. cinerea, A. niger* and *R. stolonifer*, in grapes and strawberries by adding grapefruit seed extracts (Xu et al., 2007) or cinnamon leaf essential oil (Hafsa et al., 2016). However, the most widespread use is as a vehicle for antimicrobial compounds. Different extracts and essential oils have been used, from peony (Pagliarulo et al., 2016), *Aloe vera* (Vieira et al., 2016), lemon (Perdones et al., 2012) or *Salvia fruticosa* (Kanetis et al., 2017), increasing the antifungal effect against *B. cinerea*. Although the direct use of antimicrobial chemical compounds has also been proposed, such as ethanol (Romanazzi et al., 2007), tymol (Medina et al., 2019), monomethyl fumaric acid (Khan et al., 2019), or benzothiadiazole (Romanazzi et al., 2013), causing a great reduction of fungal decay by *B. cinerea, R. stolonifer* or *P. expansum* in grapes, strawberries and

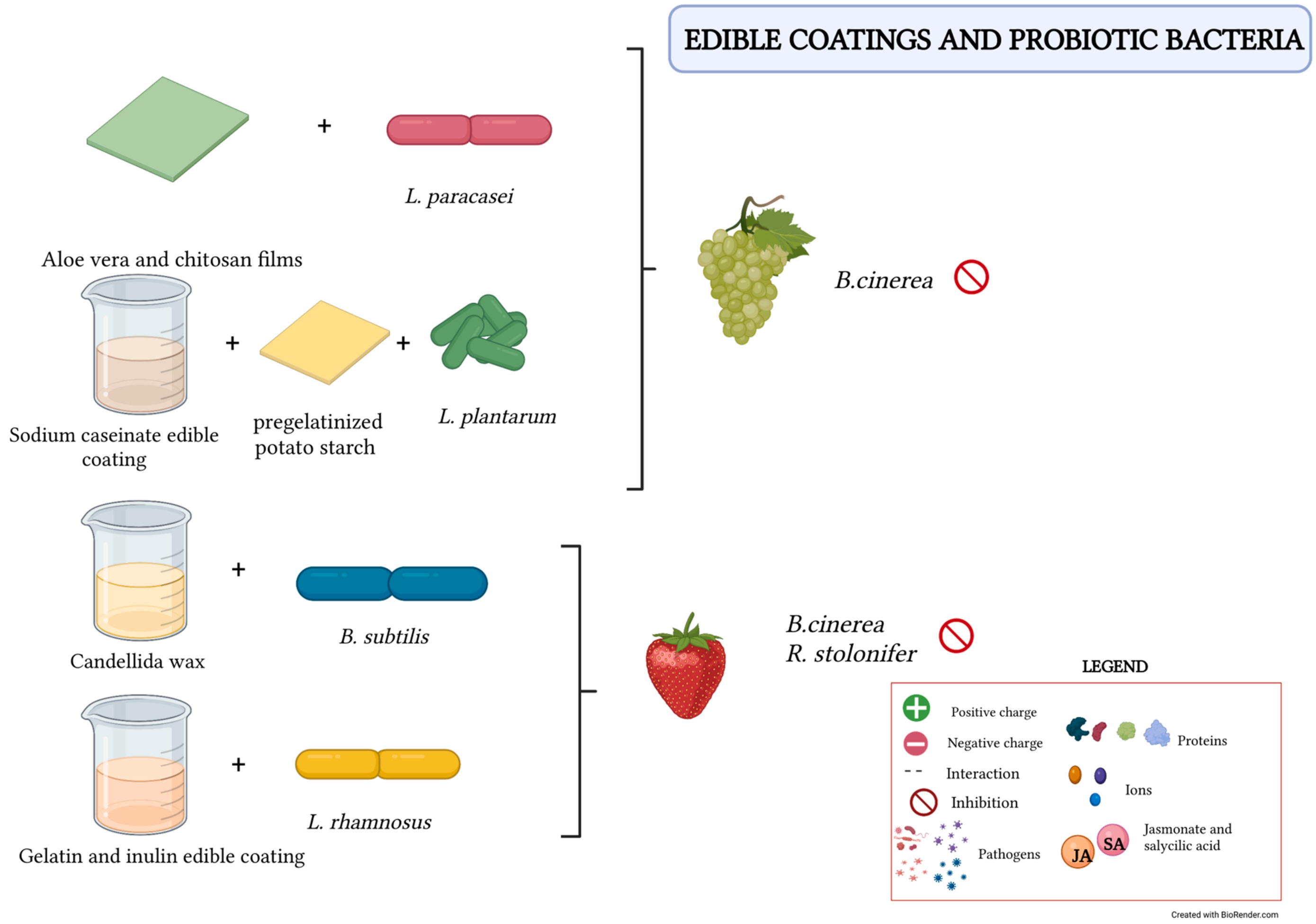

Fig. 3. Summary infographic on the use of edible coatings and probiotic bacteria, in isolation and simultaneously, for the control of postharvest pathogens in berries.

blueberries. In blackberries, the use of a chitosan edible coating as a vehicle for the antimicrobial compound lactic acid, significantly reduced the incidence and severity of the fungus *Mucor racemosus* (Vilaplana et al., 2020).

Regarding chitosan capacity to activate plant defense responses, there are several studies so far. An increase in the activity of enzymes-related to defense responses (phenylalanine ammonia-lyase and polyphenol oxidase) has been reported after the application of chitosan in grapes, reducing the fungal decay caused by *B. cinerea* (Romanazzi et al., 2002; Meng et al., 2010). Another reported defense responses have been the synthesis of antimicrobial metabolites, such as quercetin, myricetin, epigallocatechin gallate, catechin or resveratrol, also in grapes against *B. cinerea* (Feliziani et al., 2013; Zhang et al., 2020a). Furthermore, edible coatings based on chitosan can be used as vehicles for plant defense chemical inducers, such as the hormones jasmonic acid (JA) and salicylic acid (SA), and their derivatives (Poveda, 2020). In this sense, the addition of SA increases the isolated capacity of chitosan to induce phenylalanine ammonia lyase (PAL), chitinase (CHI), and β-1,3-glucanase (GLU) activities in grapes, and the accumulation of phenolic compounds against *B. cinerea* (Shen and Yang, 2017). In the case of the JA-derivative methyl jasmonate, its application together with chitosan caused a greater accumulation of lignin in the surface layers of Chilean strawberries (Saavedra et al., 2016).

A. vera gel has been used in the manufacture of edible coatings for 3000 years. Although noted for its antimicrobial activity, *A. vera* gels contain approximately 110 potentially active constituents with numerous functions and form an edible barrier for atmospheric gases and moisture in fruits and vegetables, helping to preserve their postharvest quality (Kahramanoğlu et al., 2019). In berries, it has been determined how the use of *A. vera* gels as edible coatings is capable of significantly reducing the fungal decay of grapes caused by *B. cinerea* and *P. digitatum*, thanks to the action of different antifungal secondary metabolites (Castillo et al., 2010). Furthermore, the use of these edible coatings can induce plant defense responses in postharvest berries, as has been reported in rasperries, through an increase in the enzymatic-defensive activity of glutathione peroxidase (GSHPOD), glutathione reductase (GR), superoxide dismutase (SOD), ascorbate peroxidase (AsA-POD) and guaiacol peroxidase (G-POD) enzymes (Hassanpour, 2015).

Natural plant-based gums are formed by polymeric polysaccharides exuded by different plant organs, being a material widely used in recent years as edible coatings in different food industries (Saha et al., 2017). When used in postharvest berries, these gums are able to activate plant defense responses and reduce disease caused by pathogens such as *B. cinerea*. Specifically, gum arabic edible coatings increase the polyphenol oxidase (PPO) enzymatic activity in strawberries (Tahir et al., 2018), and peach gum the activity of CHI, GLU, PAL, POD and PPO in blueberries (Shi et al., 2019). Complex mixtures of many different edible coatings have also been used, including cassava starch, whey protein, beeswax, chitosan, glycerol, stearic acid and glacial acetic acid. With this complex edible coating it was possible to reduce fungal decay in blackberry, increasing its shelf life by 100% (Rodriguez et al., 2020).

The rest of edible coatings used in the control of postharvest diseases in berries are based on being vehicles for different antimicrobial chemical compounds or biological control agents. Pullulan is a microbial exopolysaccharide produced from *Aureobasidium pullulans*, using as

Table 1
Edible coatings used in the control of postharvest pathogens in berries, indicating the mechanism of action involved.

EDIBLE COATING MATERIAL	IN COMBINATION WITH	USE IN BERRIES	PATHOGEN	EFFECT	MECHANISM OF ACTION	REFERENCE
Alginate	*Cryptococcus laurentii*	Strawberries	Unidentified	Reduction of fungal decay	Biological control agent maintenance	Fan et al., 2009
	Carvacrol and methyl cinnamate	Strawberries	Unidentified	Reduction of fungal decay	Antimicrobial compounds vehicle	Peretto et al., 2017
Aloe vera gel	-	Grapes	*Botrytis cinerea* *Penicillium digitatum*	Reduction of fungal decay	Antifungal activity by secondary metabolites	Castillo et al., 2010
	-	Raspberries	Unidentified	Reduction of fungal decay	Plant defenses activation	Hassanpour, 2015
Calcium caseinate	*Quillaja saponaria* shoots extracts and ionizing energy treatment	Strawberries	*B. cinerea*	Disease reduction	Antifungal compounds vehicle (phenolic compounds)	Zúñiga et al., 2012
Carboxymethylcellulose	Essential oils of *Lippia sidoides*	Strawberries	*Rhizopus stolonifer*	Disease reduction	Antifungal compounds vehicle (phenolic compounds)	Oliveira et al., 2019a
	Essential oils of *L. sidoides*	Strawberries	*Colletotrichum acutatum*	Disease reduction	Antifungal compounds vehicle (phenolic compounds)	Oliveira et al., 2019b
Cassava starch, whey protein, beeswax, chitosan, glycerol, stearic acid and glacial acetic acid	-	Blackberries	Unidentified	Reduction of fungal decay	Unidentified	Rodríguez et al., 2020
Chitosan	-	Strawberries	*B. cinerea* *R. stolonifer*	Inhibition of microbial growth	Antifungal activity	El Ghaouth et al., 1992
	-	Strawberries	*B. cinerea*	Reduction of fungal decay	Antifungal activity	Reddy et al., 2000
	-	Grapes	*B. cinerea*	Reduction of fungal decay	Antifungal activity Plant defenses activation	Romanazzi et al., 2002
	Hydroxypropyl methylcellulose	Strawberries	*Cladosporium* sp. *Rhizopus* sp.	Reduction of fungal decay	Antifungal activity	Park et al., 2005
	Ethanol	Grapes	*B. cinerea*	Disease reduction	Antifungal activity	Romanazzi et al., 2007
	Grapefruit seed extracts	Grapes	*B. cinerea*	Disease reduction	Antifungal activity Antioxidant activity	Xu et al., 2007
	-	Grapes	*Colletotrichum* sp.	Disease reduction	Antifungal activity	Muñoz et al., 2009
	-	Grapes	*B. cinerea*	Disease reduction	Antifungal activity	Romanazzi et al., 2009
	C. laurentii	Grapes	Unidentified	Reduction of microbial decay	Plant defenses activation	Meng et al., 2010
	-	Grapes Strawberries Sweet cherries	Unidentified	Reduction of fungal decay	Antifungal activity Plant defenses activation	Romanazzi, 2010
	Limonene	Strawberries	*B. cinerea* *R. stolonifer*	Reduction of fungal decay	Antifungal activity	Vu et al., 2011
	Lemon essential oil	Strawberries	*B. cinerea*	Reduction of fungal decay	Antifungal activity	Perdones et al., 2012
	-	Grapes	*B. cinerea*	Reduction of fungal decay	Plant defenses activation	Feliziani et al., 2013
	Benzothiadiazole	Strawberries	*B. cinerea* *R. stolonifer* *P. expansum*	Reduction of fungal decay	Antifungal activity Plant defenses activation	Romanazzi et al., 2013
	-	Grapes	*B. cinerea* *P. expansum*	Reduction of fungal decay	Antifungal activity	De Oliveira et al., 2014a
	-	Grapes	*Aspergillus niger* *R. stolonifer*	Reduction of fungal decay	Antifungal activity	De Oliveira et al., 2014b
	Potassium silicate	Strawberries	*B. cinerea*	Reduction of fungal decay	Unidentified	Lopes et al., 2014
	Refrigeration (0°C)	Blackberries	Unidentified	Reduction of fungal decay	Unidentified	Oliveira et al., 2014
	-	Strawberries	*B. cinerea R. stolonifer*	Reduction of fungal decay	Unidentified	Feliziani et al., 2015
	Cinnamon leaf essential oil	Strawberries	*A. niger B. cinerea* *R. stolonifer*	Reduction of fungal decay	Antifungal activity Antioxidant activity	Hafsa et al., 2016
	-	Blueberries	*Botryotinia fuckeliana*	Reduction of fungal decay	Antifungal activity	Jiang et al., 2016
	Olive oil	Strawberries	*R. stolonifer*	Reduction of fungal decay	Antifungal activity	Khalifa et al., 2016
	Peony extracts	Strawberries	Saprophytic yeasts	Inhibition of microbial growth	Antifungal activity	Pagliarulo et al., 2016

(*continued on next page*)

Table 1 (*continued*)

EDIBLE COATING MATERIAL	IN COMBINATION WITH	USE IN BERRIES	PATHOGEN	EFFECT	MECHANISM OF ACTION	REFERENCE
	Methyl jasmonate	Chilean strawberries	Unidentified	Reduction of decay	Plant defenses activation	Saavedra et al., 2016
	A. vera extract	Blueberries	*B. cinerea*	Reduction of fungal decay	Antifungal activity	Vieira et al., 2016
	Salvia fruticosa extract	Grapes	*B. cinerea*	Reduction of fungal decay	Antifungal activity	Kanetis et al., 2017
	Salicylic acid	Grapes	*B. cinerea*	Reduction of fungal decay	Plant defenses activation	Shen and Yang, 2017
	Carotenoproteins	Strawberries	Unidentified	Fruits postharvest life extension Reduction of fungal decay	Antifungal activity	Hajji et al., 2018
	Cinnamon essential oil	Strawberries	*Colletotrichum fragariae*	Reduction of fungal decay	Antifungal activity	Ventura-Aguilar et al., 2018
	Monomethyl fumaric acid	Strawberries	Unidentified	Inhibition of pathogen growth	Antimicrobial activity	Khan et al., 2019
	Tymol	Blueberries	*B. cinerea*	Reduction of fungal decay	Antifungal activity	Medina et al., 2019
	-	Strawberries	Unidentified	Reduction of fungal decay	Antifungal activity	Hassan et al., 2020
	-	Strawberries	*B. cinerea R. stolonifer A. niger*	Inhibition of pathogen growth	Antifungal activity	Melo et al., 2020
	Lactic acid	Blackberries	*Mucor racemosus*	Reduction of fungal decay	Antifungal activity	Vilaplana et al., 2020
	-	Grapes	*B. cinerea*	Reduction of fungal decay	Antifungal activity Plant defenses activation	Zhang et al., 2020a
Guar gum	Ginseng extract	Sweet cherries	Unidentified	Reduction of decay	Unidentified	Dong and Wang, 2018
Gum arabic	-	Strawberries	Unidentified	Reduction of fungal decay	Plant defenses activation	Tahir et al., 2018
Liposome	D-limonene	Blueberries	*B. cinerea Penicillium chrysogenum*	Inhibition of pathogen growth	Antifungal compounds vehicle	Umagiliyage et al., 2017
Peach gum	Bamboo vinegar	Blueberries	*B. cinerea*	Disease reduction	Plant defenses activation	Shi et al., 2019
Pullulan	Cinnamaldehyde	Strawberries	Unidentified	Inhibition of pathogen growth	Antifungal compounds vehicle	Trinetta et al., 2020
	Propolis extract	Blueberries	Unidentified	Inhibition of pathogen growth	Antimicrobial compounds vehicle	Pobiega et al., 2021
Whey protein	*Q. saponaria* shoots extracts and ionizing energy treatment	Strawberries	*B. cinerea*	Disease reduction	Antifungal compounds vehicle (phenolic compounds)	Zúñiga et al., 2012

nutrient resources different agro-industrial wastes (Singh et al., 2019). In berries, pullulan has been used as an edible coating vehicle for different antimicrobial compounds, such as cinnamaldehyde in strawberries (Trinetta et al., 2020) or propolis extracts in blueberries (Pobiega et al., 2021), significantly reducing microbial decay in postharvest. Carboxymethylcellulose (CMC) is a polysaccharide formed after the carboxymethylation of cellulose, which use as an edible coating is increasing in recent years, due to its biodegradability, absence of toxicity, solubility in water and good ability to form transparent films (Salama et al., 2019). CMC has been used in strawberries as an edible coating, along with essential oils of *Lippia sierides*. In these fruits, the presence of antifungal phenolic compounds in essential oils significantly reduced the diseases caused by the pathogens *R. stolonifer* and *C. acutatum* (Oliveira et al., 2019a, b).

Other examples of edible coatings used as vehicles for antimicrobial compounds in postharvest berries are found in calcium caseinate/whey protein and *Quillaja saponaria* shoots extracts in strawberries against *B. cinerea* (Umagiliyage et al., 2017), or liposome and D-limonene in blueberries against *B. cinerea* and *Penicillium chrysogenum* (Umagiliyage et al., 2017). In addition, apart from being a vehicle for antimicrobial compounds, some edible coatings can be used as carriers for biological control agents. Alginate, an anionic polysaccharide found in the outer cell wall of brown algae, is used in combination with carvacrol and methyl cinnamate in strawberries, significantly reducing fungal decay (Peretto et al., 2017). However, it is also used in combined application with the antagonist yeast *Cryptococcus laurentii*, maintaining its populations for a longer time (Fan et al., 2009).

7.2. Probiotic bacteria

The use of probiotics for the control of postharvest diseases has opened a new path in the management of postharvest plant pathogens in fruits and vegetables (Srilatha and Borkar, 2017a). Regarding berries, Table 2 shows all the studies to date where bacterial probiotics have been used in the control of postharvest pathogens. Fig. 2 shows a summary infographic with the different mechanisms of action identified for probiotic bacteria in postharvest berries.

In 2017, different commercial probiotics from human food were used to identify the possible capacity of their microorganisms to act as biological control agents against *Penicillium* sp. and *Alternaria* sp. in grapes. Those products, that presented the bacteria *Lactobacillus acidophilus, L. rhamnosus* and *Bifidobacterium longum* (Darolac), and *Streptomyces faecalis, Clostridium butyricum, Bacillus mesentaricus* and *Lactobacillus sporogenes*, were able to reduce fungal decay, being also beneficial to the human health for their presence on the consumable fruits (Srilatha and Borkar, 2017b).

Bacteria can antagonize the growth of different pathogens thanks to their better ability to use the ecological niche and nutrients

Table 2
Probiotic bacteria used in the control of postharvest pathogens in berries, indicating the mechanism of action involved.

PROBIOTICS	USE IN BERRIES	PATHOGEN	EFFECT	MECHANISM OF ACTION	REFERENCE
Bacillus amyloliquefaciens	Cherries	*Monilinia laxa M. fructicola B. cinerea*	Inhibition of fungal growth	Production of antifungal volatiles	Gotor-Vila et al., 2017
	Grapes	*B. cinerea*	Reduction fungal decay	Plant defenses activation	Zhou et al., 2020
B. halotolerans	Strawberries	*B. cinerea*	Reduction fungal decay	Plant defenses activation Lytic enzyme production	Wang et al., 2021a
B. ginsengihumi	Grapes	*B. cinerea*	Reduction fungal decay	Unidentified	Calvo-Garrido et al., 2019
B. licheniformis	Blackberries	*R. stolonifer*	Inhibition of fungal growth Reduction fungal decay	Siderophores production	Chávez-Díaz et al., 2014, 2019
	Indian gooseberries	*P. digitatum*	Reduction fungal decay	Plant defenses activation	Sen et al., 2018
B. mesentaricus	Grapes	*Penicillium* sp. *Alternaria* sp.	Reduction fungal decay	Unidentified	Srilatha and Borkar, 2017b
B. siamensis	Raspberries	*B. cinerea R. stolonifer*	Reduction fungal decay	Production of antifungal volatiles	Zhang et al., 2020b
B. sonorensis	Grapes	*P. digitatum*	Reduction fungal decay	Plant defenses activation	Deng et al., 2020
B. subtilis	Blackberries	*R. stolonifer*	Inhibition of fungal growth Reduction fungal decay	Siderophores production	Chávez-Díaz et al., 2014, 2019
	Blueberries	*B. cinerea Al alternata*	Reduction fungal decay	Production of non-volatiles antifungal compounds	Kurniawan et al., 2018
	Blueberries	*B. cinerea*	Reduction fungal decay	Plant defenses activation	Lu et al., 2021
Bifidobacterium longum	Grapes	*Penicillium* sp. *Alternaria* sp.	Reduction fungal decay	Unidentified	Srilatha and Borkar, 2017b
Clostridium butyricum	Grapes	*Penicillium* sp. *Alternaria* sp.	Reduction fungal decay	Unidentified	Srilatha and Borkar, 2017b
Lactobacillus acidophilus	Grapes	*Penicillium* sp. *Alternaria* sp.	Reduction fungal decay	Unidentified	Srilatha and Borkar, 2017b
L. delbrueckii	Grapes	Unidentified	Reduction microbial decay	Production of non-volatiles antifungal compounds	Fang et al., 2020
L. plantarum	Grapes	*Aspergillus carbonarius*	Inhibition of fungal growth and toxin production	Competition for space and nutrients	Lappa et al., 2018
	Strawberries	*B. cinerea*	Reduction fungal decay	Competition for space	Chen et al., 2020
L. rhamnosus	Grapes	*Penicillium* sp. *Alternaria* sp.	Reduction fungal decay	Unidentified	Srilatha and Borkar, 2017b
L. sporogenes	Grapes	*Penicillium* sp. *Alternaria* sp.	Reduction fungal decay	Unidentified	Srilatha and Borkar, 2017b
Leifsonia acuatica	Blackberries	*R. stolonifer*	Inhibition of fungal growth Reduction fungal decay	Siderophores production	Chávez-Díaz et al., 2014, 2019
Leuconostoc lactis	Grapes	Unidentified	Reduction microbial decay	Production of non-volatiles antifungal compounds	Fang et al., 2020
Pseudomonas brenneri	Blueberries	*B. cinerea A. alternata*	Reduction fungal decay	Production of non-volatiles antifungal compounds	Kurniawan et al., 2018
P. chlororaphis	Chinese cherries	*B. cinerea*	Reduction fungal decay	Production of antifungal volatiles	Wang et al., 2021b
P. fluorescens	Blackberries	Unidentified	Reduction fungal decay	Plant defenses activation	Ramos-Solano et al., 2015
	Grapes	*B. cinerea*	Reduction fungal decay	Plant defenses activation	Jiang et al., 2019b
	Grapes	*B. cinerea*	Reduction fungal decay	Production of antifungal volatiles	Zhong et al., 2021
P. koreensis	Blueberries	*B. cinerea Al alternata*	Reduction fungal decay	Production of non-volatiles antifungal compounds	Kurniawan et al., 2018
Streptomyces faecalis	Grapes	*Penicillium* sp. *Alternaria* sp.	Reduction fungal decay	Unidentified	Srilatha and Borkar, 2017b

(carbohydrates, nitrogen-sources, iron, oxygen). For example, bacteria are able to colonize the wounds on the surface of fruit and vegetables faster than pathogens, preventing the pathogenic invasion and pathogenic achieving the control of postharvest diseases (Huang et al., 2021). Regarding berries, the probiotic bacterium *Lactobacillus plantorum* has been described as a biological control agent in postharvest through competition for space and nutrients with pathogens (Lappa et al., 2018; Chen et al., 2020). *Aspergillus carbonarius* is a pathogen that causes black rot in table grapes and synthesizes a toxin very harmful to human health, ochratoxin A. In this sense, it has been described as *L. plantarum* is capable of inhibiting fungal growth up to 88%, in addition to reducing toxin production up to 100%, thanks to the rapid colonization of the grape surface (Lappa et al., 2018). Similarly, the rapid colonization of wounds in strawberries is able to reduce the incidence of *B. cinerea* by 75% (Chen et al., 2020).

The secondary metabolism of probiotic bacteria allows them to synthesize and release to the environment a very wide variety of secondary metabolites with very diverse biological activities (Jiang et al., 2019a). These secondary metabolites include diffusible non-volatile compounds and VOCs, with a great antimicrobial capacity (Jiang et al., 2019a; Poveda, 2021).

Regarding non-volatile secondary metabolites, their role in the control of postharvest pathogens has been studied by obtaining extracts from liquid cultures. Extracts obtained from *Bacillus subtilis, Pseudomonas brenneri* and *P. koreensis* can reduce the incidence of *B. cinerea* and *A. alternata* in blueberries by 50% and 64%, respectively. Specifically, the inhibition of spore germination and reduction of mycelia growth is due to metabolites such as arthrofactins (Kurniawan et al., 2018). On the other hand, the secondary metabolites present in these extracts can have other effects on the treated fruits. In grapes treated with supernatants from liquid cultures of *Lactobacillus delbrueckii* and *Leuconostoc lactis*, in addition to a reduction of microbial decay, a significant reduction in weight, titratable acidity and total phenols losses, and a delay in maturity and senescence could be reported (Fang et al., 2020). Other compounds of interest in biocontrol are siderophores, molecules that sequester the iron present and prevent its use by pathogenic organisms. In blackberries, several bacteria have been described with the ability to reduce the growth of *R. stolonifer* and its incidence by producing siderophores, including *B. subtilis, B. licheniformis* and *Leifsonia acuatica* species (Chávez-Díaz et al., 2014, 2019).

Regarding the production of VOCs, several probiotic bacteria used in berries are able to produce alkanes, aldehydes and ketones, alcohols, alkenes, acids, esters, aromatic and sulfur compounds (Wang et al., 2021b). In grapes, *Pseudomonas fluorescens* inhibits the incidence of *B. cinerea* by producing the VOCs dimethyl trisulfide, dimethyl disulfide, geranyl formate, acetic acid, butyric acid, 2-methylbutyric acid, isobutyric acid and isovaleric acid (Zhong et al., 2021). *Bacillus amyloliquefaciens* and *B. siamensis* are able to inhibit the growth and incidence of *Monilinia laxa, M. fructicola, B. cinerea* and R. *stolonifer* in cherries and raspberries through the production of VOCs as thiophene, 2,6-di-tert-butyl-4-methylphenol and 2,4-di-tert-butylphenol (Gotor-Vila et al., 2017; Zhang et al., 2020b).

On the other hand, bacteria have the ability to produce different cell wall lytic enzymes. By secreting these hydrolases, such as chitinases and glucanases, bacteria are capable of degrading the cell wall and mycelium of postharvest pathogens (Huang et al., 2021). For example, *Bacillus halotorelans* reduces fungal decay in strawberries by producing chitinases that act against the *B. cinerea* mycelium (Wang et al., 2021a).

As is the case of other plant organs, bacteria are capable of indirectly acting as biological control agents, activating plant defense responses locally and systemically, when they come into contact or colonize the tissues of fruits and vegetables (Huang et al., 2021). In grapes, the probiotic bacteria *P. fluorescens* and *B. amyloliquefaciens* are capable of reducing the incidence of *B. cinerea* by increasing the plant enzymatic activity of PPO, POD, catalase (CAT), PAL, CHI and GLU (Jiang et al., 2019b; Zhou et al., 2020). Also against *B. cinerea*, in strawberries and blueberries it has been reported that *B. halotolerans* and *B. subtilis*, respectively, induce a higher activity of the enzymes CHI, GLU, PAL, POD, and PPO in plant tissues (Lu et al., 2021; Wang et al., 2021a). Plant defense responses similar to those induced by *B. licheniformis* and *B. sonorensis* in Indian gooseberries and grapes, respectively, against the pathogen *P. digitatum* (Sen et al., 2018; Deng et al., 2020). In blackberries, it has been described how *P. florescens* produces various elicitors of plant defensive responses that reduce fungal decay due to an accumulation of phytoalexins (Ramos-Solano et al., 2015).

7.3. Edible coatings and probiotic bacteria

The combined use of edible coatings and probiotics for the control of postharvest pathogens has been highly studied in the last 5 years. This strategy is used to maintain probiotic populations and their antifungal activity for a longer time, as has been reported with chitosan and *A. vera* films together with *Lactobacillus paracasei* bacteria probiotic (Barragán-Menéndez et al., 2020). Table 3 compiles all the studies where both combined strategies are used in the control of postharvest pathogens in berries. Fig. 3 shows a summary infographic with the different mechanisms of action identified for edible coatings and probiotic bacteria in postharvest berries.

The probiotic bacterium *L. plantarum* has been used in combination with pregelatinized potato starch and sodium caseinate edible coatings on grapes. These results demonstrated the ability of *L. plantarum* to colonize the grape surface and have antifungal capacity by bacteriocins. The use of these films increases bacterial survival and their ability to control fungal decay caused by *B. cinerea*. In addition, the use of these edible coatings in grapes supposes a greater maintenance over time of the acidity and maturity index during storage (Marín et al., 2019). In strawberries, the combined use of candellida wax, as edible coating, and *B. subtilis*, as probiotic bacteria, reported a 100% reduction in fungal decay by *R. stolonifer*. Although the exact mechanism of action has not been elucidated, it has been shown that *B. subtilis* colonizes the plant surface faster than the pathogenic fungus, and produces antifungal compounds, such as iturine. In addition, the film was able to maintain the weight of the strawberries, their pH and total soluble solids for 6 days (Oregel-Zamudio et al., 2017).

The use of edible coatings based on alginate/gelatin and inulin, in combination with the bacterium *L. rhamnosus*, is able to reduce in a significantly the bacterial and fungal decay in blueberries and strawberries (Bambace et al., 2019; Temiz and Özdemir, 2021). In the case of gelatin and inulin edible coating, an increase in the shelf-life of strawberries was also reported, maintaining weight, pH, titratable acidity and total soluble solids (Temiz and Özdemir, 2021).

8. Future challenges and perspectives

Traditionally, farmers have dealt with postharvest diseases using chemicals. However, there is a worldwide trend to reduce the use of these compounds due to their negative impact on both the environment and human health (Morales-Cedeno et al., 2021). For this reason, alternatives to these products should be sought, such as the use of biological control agents (Carmona-Hernandez et al., 2019). The use of biological control agents as substitutes for chemical pesticides is complicated, as it is necessary to verify that these agents have the same effectiveness as chemicals (Zhang et al., 2020c). However, advances in DNA technologies along with bioinformatics have allowed for a greater understanding of host, antagonist, and pathogen interactions. In addition, the evolution of omics, such as genomics and proteomics, allows a better study of the disease control mechanisms of biological control agents (Dukare et al., 2019). In biocontrol, proteomics is of greater importance, since it allows to know the proteins that are expressed during the infection process and that generate physiological, structural, and biochemical changes during the pathogen-host interaction; allowing the determination of virulence factors (Kannojia et al., 2019). There are studies in which edible coatings have been developed together with active components for the biological control of strawberries, blueberries, grapes with an antifungal effect, however in future research other aspects such as interference with the sensory properties of the fruit should be considered (Maringgal et al., 2020).

Despite the promising results obtained with the use of edible coatings and probiotic bacteria in the control of postharvest diseases in berries, the actual establishment of this strategy within the industry must solve several problems. The use of BCAs in agriculture is always linked to important constraints, such as bureaucratic barriers, risk aversion, and insufficient communication between scientists and society (Barratt et al., 2018). The use of chemical fungicides allows for more efficient

Table 3
Combination of edible coatings and probiotic bacteria used in the control of postharvest pathogens in berries.

EDIBLE COATINGS & PROBIOTICS	USE IN BERRIES	PATHOGEN	EFFECT	MECHANISM OF ACTION	REFERENCE
Alginate and inulin & *L. rhamnosus*	Blueberries	*Escherichia coli Listeria innocua*	Reduction bacterial decay	Unidentified	Bambace et al., 2019
Candelilla wax & *B. subtilis*	Strawberries	*R. stolonifer*	Reduction fungal decay	Unidentified	Oregel-Zamudio et al., 2017
Gelatin and inulin & *L. rhamnosus*	Strawberries	Unidentified	Reduction fungal decay	Unidentified	Temiz and Özdemir, 2021
Pregelatinized potato starch & *L. plantarum*	Grapes	*B. cinerea*	Reduction fungal decay	Unidentified	Marín et al., 2019
Sodium caseinate & *L. plantarum*	Grapes	*B. cinerea*	Reduction fungal decay	Unidentified	Marín et al., 2019

and consistent postharvest disease management in berries. However, the use of live organisms as BCAs in berries depends on many factors for efficiency, posing a major instability factor for the industry. Furthermore, the commercial development of these biological strategies requires more bureaucracy than in the case of chemicals. Currently, registration of a microbial BCA in the European Union takes an average of 1369 days (down from 1845 days before 2009), while in the United States the average time is 781 days (Frederiks and Wesseler, 2019). Therefore, much research and public awareness of the benefits of using these strategies in postharvest berries is still needed to establish their widespread use in the industry. However, the growing demand for chemical pesticide-free foods may greatly accelerate this transition in industrial uses.

9. Conclusions

Berries are very perishable and easily contaminable products, especially in post-harvest, generating great economic losses. Traditionally, chemical fungicides have been employed to reduce these losses. However, due to the negative impact of these chemical compounds on human health and the environment, the use of other disease control strategies, such as biocontrol, is a necessity. The use of biological control agents, such as microorganisms that are antagonists to fungal pathogens, is an effective method in the protection and conservation of berries. In addition, there are other effective biological control methods such as the use of edible films or coatings with certain compounds such as chitosan, which have antimicrobial capacity, protecting against fungal pathogens. Likewise, both strategies can be combined, observing studies in which coatings have been used together with antagonists obtaining positive results in the protection of the different fruits. Some studies show the effectiveness of the combination of edible coatings and probiotics in the protection of berries against post-harvest diseases, as well as improved maintenance of fruit quality such as firmness. However, there is little research in this area. Therefore, the use of antagonists together with edible coatings can be a beneficial method for the establishment of new biocontrol strategies.

Contributions

J.P. conceptualized and designed the manuscript. J.R., I.A., A.D. and J.P. performed the bibliographic search, analyzed the information, wrote different manuscript-sections, contributed to the manuscript correction and critical reading. All authors have read and agreed to the published version of the manuscript.

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Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

No data was used for the research described in the article.

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