Advances in Postharvest Diseases Management of Fruits and Vegetables: A Review

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Abstract: Sustainable agriculture requires factors to directly stimulate plant growth and induce the plant's innate immune system to protect against stresses. Protection of plants is one of the main approaches to the supply of food resource. Furthermore, improved techniques for plant disease management must be environmentally sustainable, reliable, acceptable by society, and chemical-free to ensure sustainable food security. Although it is not possible to accurately determine postharvest losses due to diseases and physiological disorders, the use of proper harvesting and transportation methods that minimize damage to the product, along with optimal storage conditions that prevent the development of diseases, will be effective in reducing these postharvest losses. Since handling and storage conditions are potential threats for postharvest spoilage, it is necessary to identify environmentally friendly approaches and their precision mechanisms for postharvest disease management. Recently, biological control, non-chemical, and eco-friendly techniques have been investigated for this purpose.

Keywords: biological control; biosensors; combined treatments; edible coatings; nanotechnology

1. Introduction

Plant diseases are a major threat to various ecosystems and crops, so researchers develop new strategies to prevent pathogen growth and increase produce quality. The use of resistant species and cultivars produced by gene transfer [1] is eco-friendly and affordable in inhibiting losses caused by pathogens [2,3]. As well, the selection of somaclonal variation and mutation induction provides an essential strategy for disease management [4]. The importance of genes such as smutin and peroxidase that contain antifungal compounds for inducing resistance to pathogens has been proved [5]. Down-regulation of terpenes in transgenic oranges induces defense reactions against *Penicillium digitatum* [6,7]. In addition, it has been noted that myrcene stimulates the spore germination of *P. digitatum* through the upregulation of central carbon and energy metabolism [8], and terpene limonene causes citrus green mold through the regulation of reactive oxygen species (ROS) homeostasis in *P. digitatum* spores [9]. Additionally, appropriate agricultural practices [10], including lack of planting pathogen-host plants near fruit trees, removing sources of inoculation such as diseased branches or fruits, and using windbreaks to reduce spore dispersal will be effective [11].

The factors limiting the shelf life such as postharvest diseases are among the biological limitations that cause more economic losses than occur during cultivation [12,13]. Most postharvest pathogens are necrotrophic fungi that destroy cells using cell-wall-degrading enzymes (CWDEs) or mycotoxins (toxic secondary metabolites of fungi). Fungal species from the genera *Alternaria*, *Aspergillus*, *Botrytis*, *Colletotrichum*, *Fusarium*, *Geotrichum*, *Gloeosporium*, *Monilinia*, *Mucor*, *Penicillium*, and *Rhizopus* are known to produce mycotoxins and postharvest diseases [14,15]. Mycotoxins are low molecular weight compounds able

to elicit a toxic response in humans through exposure at very low levels [16]. Postharvest disease development is influenced by pathogen biology, growth stage, and handling. Infection of pathogens could be delayed by using resistant cultivars [17]. On the other hand, the production of mycotoxins depends on physical, biological, and environmental factors [18]. The most important environmental factors are temperature, relative humidity, carbon dioxide levels, nutrient availability, and physical damage [19]. Due to the increase in world population, prevention of postharvest losses has become more critical. Generally, good agricultural practices and controlled storage conditions are essential to minimize pathogen contamination. In recent years, physical methods such as thermal treatments (hot water, steam heat, and hot air) to control plant pathogens have been effective [20–22]. The thermal process disrupts normal metabolism (ripening or senescence) by creating moderate and reversible stress [23]. Proteomic analysis showed that up-regulated proteins by heat treatment were related to defense response and redox metabolism. Therefore, the loss reduction is due to the expression of proteins related to carbohydrate and energy metabolism [24]. Investigating the effect of thermal processing on the microbiome of apple fruit indicates a decrease in fungal–bacterial diversity [25]. However, heat treatment has undesirable effects on nutritional quality among vitamin reduction, protein denaturation, and sensory properties [26]. In order to reduce the adverse effects, non-thermal food processing techniques such as ionizing radiation, cold plasma, and high-pressure processing pulse electric field radiation were used [27].

Microwave heating is used as dielectric heating through the emission of electromagnetic waves for pasteurization and sterilization [20]. Electromagnetic energy leads to an increase in the internal temperature and a decrease in the pasteurization time, and it maintains the bioactive components, antioxidant activity, and appearance characteristics [28]. Other physical methods, such as radiation and ultrasound, have been investigated to control fungi and mycotoxins [29]. Resistance mechanisms induced by radiation, the expression of pathogenicity-related proteins (PR) [30], the activity of antioxidant enzymes [31], the synthesis of phenolic compounds, and cell-wall strengthening were mentioned [30]. Gamma radiation is a method for the disinfection of various fruits [32]. Gamma radiation inhibits fungal growth by disrupting the fungal cell membrane leading to the loss of intracellular contents and cell death [33]. Similarly, Yoon et al. (2020) stated X-ray irradiation is an effective method to inhibit strawberry decay and maintain sensory and physicochemical characteristics [34]. In the mentioned methods, there is a limitation in using an effective radiation dose to control the disease without damaging the DNA and cell membrane and destroying essential proteins.

Meanwhile, the new physical method of interest to researchers is the non-thermal technique of cold plasma to control fungus and mycotoxin. Cold plasma is an ionized gas containing partially ionized atoms and molecules with a roughly zero net electrical charge [35]. Cold plasma treatment destroys fungal DNA and cell walls and allows the leakage of intracellular contents [35,36]. Also, cold plasma causes rapid destruction of mycotoxins [35,37]. Despite the above mentioned, physical methods play a role as a surface disinfectant by suppressing pathogen activity and following it application of other techniques is necessary for sustainable resistance. Therefore, new and effective strategies for controlling postharvest diseases, which are also safe for the environment are necessary.

This review summarizes studies that use innovative techniques as management strategies to reduce postharvest diseases of fruits and vegetables.

2. Postharvest Diseases Management

2.1. Biological Control

Despite recent advances in genetic engineering, interest in biological control as a potential approach to plant pest and disease management has increased [38,39]. With regards to developing biological control products with promising economic benefits, we will be examining the use of microbial antagonists to control diseases and their commercialization potential. Basic approaches to using microorganisms in postharvest disease control include

managing beneficial microflora on fruit surfaces or artificially introducing antagonists against postharvest pathogens. Biological control using artificially introduced antagonists is a more effective technology [40].

The primary benefit of a fruit-based diet is the modification of nutrients, including enrichment with fiber, phenolic compounds, and complex sugars that maintain a healthy microbiota in the human gut [41,42]. One of the most effective methods to prevent disease is the application of biological control agents (BCAs) [43]; through competition for nutrients, the production of secondary metabolites such as volatile organic compounds (VOCs), lytic enzymes, and the activation of the plant defense system, they function as antagonists of fungal diseases [44–46] (Figure 1). Microbial antagonists significantly modulate the fruit microbiome and improve fruit health by inhibiting pathogenic aerobic microbial species and promoting beneficial microorganisms [47]. The role of endophytic microorganisms in increasing resistance to stresses, availability to nutrients, and promoting growth has been proven [48]. Endophytes *Debaryomyces hansenii*, *Galactomyces geotrichum*, *Pichia kudriavzevii*, *Rhodotorula glutinis*, and *Schwanniomyces vanrijae* isolated from apple fruit [49], *Proteobacteria*, *Actinobacteria*, and *Bacilli* isolated from banana, guava, mango, papaya fruits [50], *Metschnikowia*, *Hanseniaspora*, *Acinetobacter*, *Gluconobacter* isolated from grape berries [51] and *Lactobacillus plantarum* CM-3 in strawberries [52] as microbial antagonists through the synthesis of phytohormones and VOCs inhibit fruit pathogens [53]. VOCs are low molecular weight compounds that are composed of alcohols, aldehydes, esters, aromatic and aliphatic hydrocarbons, terpenes, nitrides, and sulfides with strong antimicrobial effect [54]. VOCs as bio-fumigants exert their antifungal effects by destroying cell membranes and the morphology of fungal hyphae such as alteration of cell vacuolation, membrane permeability, and swelling in the hyphae [55]. Aiello et al. (2019) observed that *Pseudomonas synxantha* isolated from kiwi fruit significantly inhibited pathogens that affect stone fruits such as *Monilinia fructigena* and *Monilinia fructicola* [56]. Similarly, the microbial antagonists of *Lactococcus lactis* and *Weissella cibaria* led to the inhibition of *Erwinia mallotivora* and the reduction of papaya fruit disease [57].
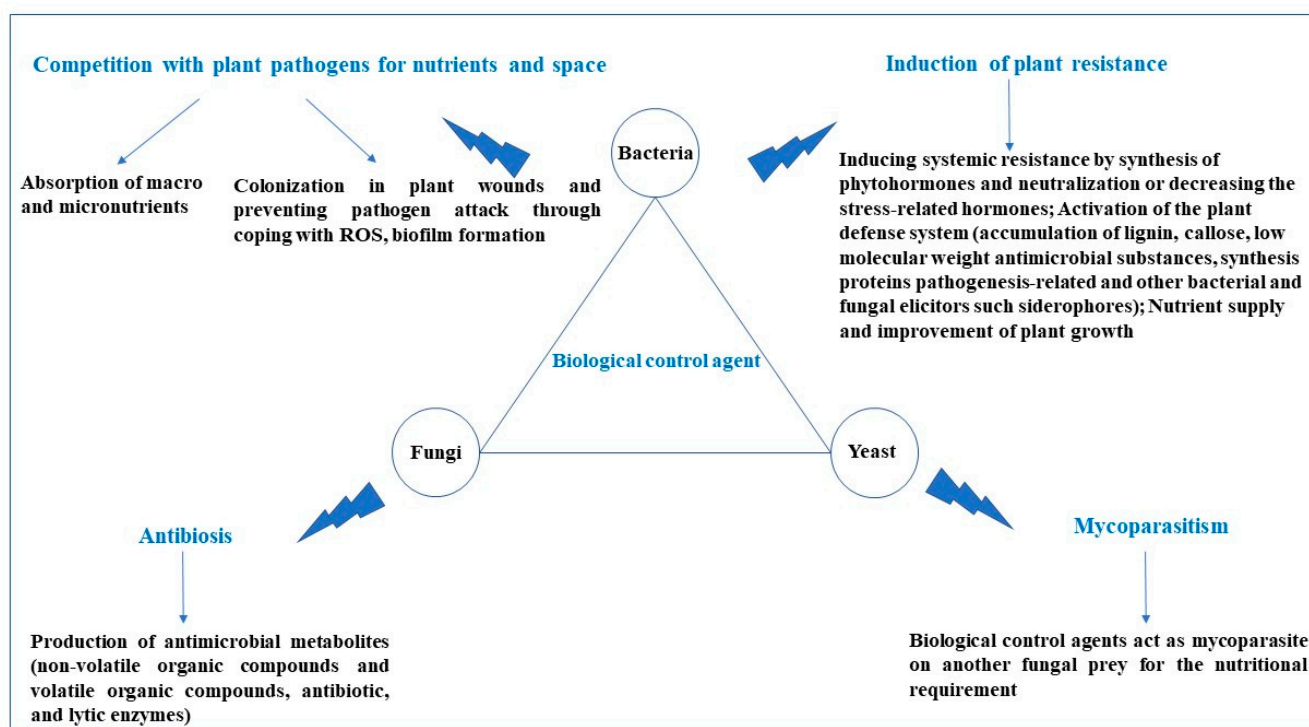
Figure 1. Proposed mechanisms of action biological control agents against plant pathogens.

Acceptance of bacteria as BCAs in the control of fungal diseases can be attributed to their strong inhibitory capacity, rapid colonization, and low nutritional requirements [39,44].

Probiotic bacteria's secondary metabolism enables them to synthesize and release secondary metabolites with antimicrobial capacity, such as non-volatile organic compounds and VOCs with a broad range of biological functions [58,59]. Bacterial antagonists belong to the group of plant growth-promoting bacteria (PGPB) [60]. PGPB are a group of non-pathogenic beneficial bacteria that live autonomously in the soil or rhizosphere, the phyllosphere (epiphytes), and plant tissues (endophytes) [61]. Plant growth-promoting rhizobacteria (PGPR) reduce the level of ethylene under stress and pathogen attack [62], suppress the activity of pathogens through competition for nutrients, production of lytic enzymes, inhibition of the synthesis of toxins [63], and stimulation of plant growth and survival [62]. PGPR both rhizospheric and endophytic bacterial strains inhibited Panama disease in field and greenhouse by inducing resistance to Fusarium wilt in banana [64], and compounds produced by PGPR such as antibiotics with pathogen control are related [65]. Antibiotics are a heterogeneous group of low molecular weight organic compounds [66] which inhibit the growth of phytopathogenic fungi such as *Aspergillus flavus*, *Alternaria solani*, *Fusarium oxysporum*, *Colletotrichum gloeosporioides* by disrupting the structure of the cell wall or the function of the membrane of microorganisms, disrupting the synthesis of proteins and the function of respiratory enzymes [67]. Iturin, pyrrolnitrin, and syringeomycin are the most important antibiotics for postharvest diseases [68]. PGPR known as NJN-6 of *Bacillus amyloliquefaciens* produces various secondary metabolites for inhibiting soil-borne pathogens. Therefore, the NJN-6 strain reduced the severity of Panama disease and improved the growth of banana seedlings [43]. Fan et al. (2017) showed the ability of *Bacillus subtilis* in producing antibiotics and VOCs to suppress postharvest pathogens such as *Botrytis cinerea*, *Rhizopus stolonifer*, and *Colletotrichum* spp. in strawberries [69]. Likewise, *B. subtilis* antagonist in inhibiting *Penicillium italicum* and *Penicillium digitatum* in orange was shown to be involved [70]. *B. cinerea* in strawberries and blueberries and *Alternaria alternata* in blueberries was inhibited by *Bacillus pumilus* and *Pseudomonas fluorescent* bacteria [71]. Biological control of mango anthracnose using bacterial antagonists has been successful [72–74]. *Bacillus siamensis* reduces the decay of *R. stolonifer* and *B. cinerea* in raspberries by producing volatile antifungal compounds [75]. *Pseudomonas chlororaphis* reduces *B. cinerea* rot in Chinese cherries through the production of volatile antifungal compounds such as alkanes, aldehydes and ketones, alcohols, alkenes, acids, esters, aromatic compounds, and sulfur [76]. In grapes, *Pseudomonas fluorescent* prevents *B. cinerea* rot by producing volatile antifungal compounds such as dimethyl disulfide, dimethyl trisulfide, geranyl formate, acetic acid, butyric acid, 2-methyl butyric acid, isobutyric acid, and isovaleric acid [77–79]. *Lactobacillus delbrueckii* reduces grape rot through the production of non-volatile antifungal compounds [80]. *Bacillus licheniformis*, *B. subtilis*, and *Leifsonia aquatica* inhibit the growth of *R. stolonifera* and decay by producing siderophores in blackberries [81]. The growth and colonization of iron-dependent microorganisms are limited by siderophores [82]. Bacillus strains significantly inhibit the growth of *B. cinerea* in strawberries and grapefruit [83], *Colletotrichum musae* in bananas [84], and *Alternaria brassicae*, *Botrytis cinerea*, *Fusarium graminearum*, *Pyricularia oryzae*, *Rhizoctonia solani* Kuhn in pear after harvest [85] due to lipopeptide production, cellulase, and protease activity [85]. Pang et al. (2021) reported that the endophytic strain of *B. amyloliquefaciens* isolated from kiwi showed antifungal activity against *Botryosphaeria dothidea* and the C12-surfactin A lipopeptide secreted by the bacteria was effective in its function [86]. On the other hand, bacteria can produce lytic enzymes [87]. Bacteria destroy the cell wall and mycelium of pathogens by secreting hydrolases such as chitinase and glucanase [13]. For example, *B. amyloliquefaciens* inhibits *Fusarium oxysporum* by the destruction of the cell wall [88]. *Bacillus halotolerans* reduces strawberry rot by producing chitinases against *B. cinerea* [89]. Antagonist fungi such as *Purpureocillium lilacinum* inhibit *P. digitatum* by damaging the main cell wall components [90]. *B. amyloliquefaciens* can change the structure of fungal hyphae (production of deformed and evacuated hyphae) due to the secretion of metabolites [91]. *Bacillus velezensis* inhibited hyphal growth and sporulation of *C. gloeosporioides* [84].

Bacteria indirectly activate local and systemic responses in plants [13]. Studies have shown that genes related to L-phenylalanine metabolism, amino acid biosynthesis, plant hormone signal transduction, and programmed cell death (PCD) regulation are induced by antagonistic microorganisms [92]. Bacterial antagonist *B. siamensis* decreased the expression

of catalase (CAT); however, the expression of superoxide dismutase (SOD) was increased. Increasing SOD activity can enhance defense against pathogens [93]. In grapes, *P. fluorescent* and *B. amyloliquefaciens* reduce the incidence of *B. cinerea* by increasing the enzyme activity of CAT, peroxidase (POD), polyphenol oxidase (PPO), phenylalanine ammonia-lyase (PAL), and chalcone isomerase (CHI) [94,95]. It has been reported that *Bacillus halotolerans* and *B. subtilis* induce activities of POD, PPO, PAL, and CHI enzymes in strawberries and blueberries for resistance to *B. cinerea* [89,96]. The responses induced by *Bacillus licheniformis* and *Bacillus sonorensis* against the pathogen *P. digitatum* in Indian gooseberries and grapes are considered a type of plant defense response [97,98]. The application of *Aureobasidium pullulans* cell suspension maintained chitinase and 1,3-glucanase levels of avocado fruit [99], and *Serratia* sp. bacterial extracts showed high potential to control postharvest rot caused by *C. gloeosporioides* in avocados [100]. Likewise, the extracts of *B. subtilis*, *Pseudomonas brenneri*, and *Pseudomona koreensis* significantly inhibited germination and hyphae growth of *B. cinerea* and *A. alternata* in blueberries by producing metabolites like arthrofactins [101].

According to several studies, when antagonists are combined with natural compounds such as growth regulators, chitosan, amino acids, antibiotics, and bicarbonates they more effectively controlled postharvest pathogens [39,102,103]. *B. amyloliquefaciens* combined with salicylic acid (SA) controlled the brown rot of nectarine [104]. Up-regulation of defense genes, such as PAL, and the expression of pathogenesis-related (PR) genes is associated with the SA signaling pathway [105,106]. Similarly, the antagonist bacteria *B. amyloliquefaciens* and SA inhibited *P. digitatum* citrus and reduced disease severity [107]. Calcium, iron, potassium, magnesium, and sodium levels of treated oranges were significantly affected [107]. These changes may be a defense response against the pathogen and were confirmed by measuring the activity of PAL, total polyphenols, and flavonoids. Changes in the content of phenolic and aromatic ring bands using Fourier-transform infrared spectroscopy (FTIR) of citrus peel indicated induced resistance against pathogenic fungi [107]. Therefore, polyphenols, flavonoids, and PAL, which have antifungal activity, were affected by biological treatments. In addition, the content of some bands, especially lignin and carbohydrates, decreased in the presence of biological treatments, which indicates degradation of the fungal cell wall [107]. The efficacy of *M. guilliermondii* Y-1 and melatonin against apple gray mold was due to a significant increase in PAL [108]. Yeasts act as antagonists due to their ability to secrete lytic enzymes, synthesize toxins, and release VOCs that lead to the induction of defense responses and mycoparasitism [109]. *Candida oleophila* yeast was effective in inhibiting *P. expansum* and *B. cinerea* kiwi [110], and *Meyerozyma guilliermondii* yeast was effective in inhibiting *P. italicum* and *P. digitatum* of orange after harvest [111]. *Pichia membranefaciens* yeast had a significant biological effect against Rhizopus rot of peaches by inducing the activity of defense enzymes, such as CAT, POD, PAL, and PPO [78]. *P. membranefaciens* induced mitogen-activated protein kinase (MAPK) cascade signaling pathway and ethylene (ET), jasmonate (JA), and SA signal transduction pathways to regulate transcription factors (TFs). TFs activate the downstream defense-related genes, glutathione S-transferase genes, and genes involved in secondary metabolite synthesis to increase disease resistance [78]. Pretreatment *Debaryomyces hansenii* yeast with mannitol and sorbitol [112] or mild stress [113] improved biocontrol efficiency by increasing the expression of antioxidant genes, such as CAT and copper-zinc superoxide dismutase (CuZnSOD). Palmieri et al. (2022) observed the antagonistic activity of *Papiliotrema terrestris* yeast against *Monilinia fructigen* of plum fruit [114]. It was stated that direct contact is essential for nutrient and space competition. *Yarrowia lipolytica* yeast grew on tangerine wounds more than *P. digitatum* and *P. italicum* pathogens at different temperatures [115]. Similarly, the rapid colonization of *Metschnikowia citriensis* in citrus wounds leads to competition for nutrients with *Geotrichum candidum* var. citri-aurantii [116]. Competition is the essential mechanism of BCAs to suppress postharvest decay. Colonization and nutrient reduction during the first 48 h after the application of yeasts are vital due to their direct effect on fungal spore germination [117]. On the other hand, endophytic fungi act as antagonists against *B. cinerea* or *Fusarium proliferatum* through the synthesis of secondary

metabolites and extracellular enzymes [118]. *A. pullulans* mold was considered as a microbial antagonist against *Penicillium expansum* of pears [119]. Di Francesco et al. (2018) reported that *A. pullulans* reduced kiwi gray mold by increasing glutamic and aspartic acids [120] (Table 1).

Table 1. Direct and indirect effects of microbial antagonists in the control of postharvest diseases of fruits and vegetables.

Biological Control Agents	Mode of Action Biological Control Agents	Main Function of Biological Control Agents	References
Antagonistic bacteria	Rapid colonization in host tissue; Synthesize and release secondary metabolites (non-volatile organic compounds and volatile organic compounds); Produce siderophores and inhibit the growth and colonization of iron-dependent microorganisms; Suppress the activity of pathogens through competition for nutrients, production of lytic enzymes, inhibition of the synthesis of toxins; Activation of the plant defense system; Neutralization or decrease the stress-related hormones and stimulation of plant growth; Nutrient supply and improvement of host plant growth	Inhibition of postharvest pathogens	[39,44–46,59,62,63,82,87]
Antagonistic fungi	Synthesis of phytohormones and volatile organic compounds; Destruction cell membrane and the morphology of fungal hyphae	Inhibition of postharvest pathogen	[90,91]
Antagonistic yeasts	Suppress the activity of pathogens through competition for nutrients, production of lytic enzymes, inhibition of the synthesis of toxins; Increasing the expression of antioxidant genes; Induction of defense system and mycoparasitism	Inhibition of postharvest pathogens	[78,109]

2.2. Biosensors

Disease development is closely related to physiological stages, host tissue characteristics, and environmental conditions. Biosensors transform biological responses into detectable electrical signals [121]. Biosensors such as antibodies, antimicrobial peptides, cells, organelles, microorganisms, enzymes, and nucleic acid [121] have the capacity to monitor the microbial flora of fruits and vegetables. Antibodies and antimicrobial peptide-based biosensor design to detect bacteria due to their superior properties such as stability, multiple site for bacteria capture and high specificity were considered [122]. Nucleic acids are molecules with high affinity and specificity to interact with a target [123] and enzymatic sensors measure target components by utilizing the catalytic reaction of enzymes with sugars, amino acids, proteins, and lipids as substrates [123]. The development of sensors based on phytochemicals or ripening genes is effective in controlling spoilage. Recently, a sensor composed of a metal catalyst and carbon nanotubes has been developed to monitor ethylene to determine the time of spoilage of fruits and vegetables [124]. Based on the luminescent responses of the bacteria to changes in VOCs following contamination, whole-cell bacterial biosensors can detect *P. digitatum* in oranges [125]. In this way, a colorimetric sensor containing AuNPs modified with the *Aspergillus niger* spore-binding peptide was developed to detect *A. niger* spores [126]. Addition of nanoparticles to electrochemical biosensors was used for rapid monitoring of Penicillium through immobilization of penicillinase enzyme using N-5-azido-2-nitrobenzoemideyl [127].

2.3. Nanotechnology

Nanotechnology use is efficient for antimicrobial agents in fresh products. Nanomaterials offer advantages such as bioavailability, controlled release, bio preservatives, and performance improvement. Nanoparticles are variable in size and amorphous or crystalline and are able to link with biological molecules like nucleic acids, peptides, and proteins [128,129]. A wide range of metals and their oxide-based single- and multi-walled carbon nanotubes and nanocomposites have been used. Gold, silver, zinc, cerium, titanium dioxide (TiO_2), silica, silica–silver, alumina–silicate, and chitosan are nanoparticles used to control plant pathogens [130,131].

The fungicidal activity of TiO_2 nanoparticles has been proven against fungal pathogens *Venturia inaequalis* and *Fusarium solani* [132] and likewise manganese oxide (MnO_2) nanoparticles against the pathogens causing wilt diseases in watermelon, eggplant, and tomatoes [133]. The inhibition of pathogens *B. cinerea* and *P. expansum* by using nanoparticles of zinc oxide is due to the induction of reactive oxygen species [134]. A honeycomb-like structure of silica nanoparticles is used in the targeted delivery of DNA and chemicals into plants [135]. Similarly, growth suppression of *B. cinerea*, *C. gloeosporioides*, *Magnaporthe grisea*, and *Pythium ultimum* was shown in solution of silica–silver [136]. Mycotoxin determination of pathogens has been conducted using nanocarbon materials like carbon nanowires and nanotubes [137]. Spray drying, precipitation, ionic gelation, emulsion cross-linking, sieving, and reverse micellar are used to produce chitosan-based agronanochemicals [138]. Chitosan-based nanoparticles have been used to reduce postharvest decay [139,140] through an inhibitory effect against *Aspergillus* sp., *Fusarium* sp., and *Alternaria* sp. [141]. Nanomaterials with chitosan coating films can control mesophilic aerobic, yeast, and mold contaminations by modulating the ripening index and increasing enzyme activities [142]. The chitosan-AgNPs based-composite showed remarkably higher antifungal activity against *C. gloeosporioides* [143]. Nanocomposites of selenium and chitosan nanoparticles synthesized using pomegranate peel extracts and Fenneropenaeus indicus shells stimulated the deformation of *P. digitatum* hyphae [144]. Thyme oil in an edible coating based on chitosan nanoparticles showed complete inhibition of *C. gloeosporioides* of avocado [145]. Mango preservation using carrageenan-based coating with zinc nanoparticles was also satisfactory [146]. Similarly, chitosan-coated iron oxide nanoparticles inhibited *R. stolonifer* on peach fruits [147].

Decay and storage disorders of pomegranate fruit were reduced in nano bags containing a high level of carbon dioxide [148]. Biodegradable nanoparticles loaded with essential oils have been used to control fungal decay by damaging the integrity of the spore membrane, resulting in homeostatic imbalance and cell death [149]. Since nanoemulsions are kinetically stable encapsulation techniques, their extended-release dose is either sustained-release or controlled-release dosage [150,151]. Essential oil can be fixed by using nanoemulsions to increase the potential and delivery against various pathogens. Pongsumpun et al. (2020) reported that cinnamon oil nanoemulsions showed more efficacy than conventional emulsions against the fungi *A. niger*, *C. gloeosporioides*, *Rhizopus arrhizus*, and *Penicillium* sp. [152]. Sodium alginate coating with eugenol, carvacrol, and cinnamaldehyde nanoemulsion had a growth-inhibiting action on *P. digitatum* and caused better stability of the physical parameters of tangerine [153]. Thyme oil encapsulated in zein nanofiber significantly lowered total bacterial counts, fungi, and yeast, and maintained the total phenol content, antioxidant activity, and titratable acidity of strawberries [154].

2.4. Plant Growth Regulators (PGRs)

PGRs are factors affecting gene expression and related biological activities. As a short- to medium-term strategy, plant-derived natural compounds, such as plant hormones, associated with defense systems have been considered [155]. Melatonin (MT), as a signaling molecule and antioxidant [156], is vital in physiological processes [157], response to stresses [158], and resistance to pathogens [159]. Exogenous application of MT significantly increased disease resistance in strawberries [160], kiwi [161], plums [162], bananas [160],

and grapes [163] and reduced decay. The effects of synergism MT with NO and ROS induce disease resistance [164,165]. Induction of resistance by MT is associated with the expression of defense genes/proteins, such as POD, lipid transfer proteins (LTPs), chitinases, β-1,3-glucanases, and pathogenesis-related (PR) proteins [163,166]. MT and NO induce phytohormones such as SA, JA, and MAPK signaling pathways [167,168]. Exogenous melatonin stimulated endogenous melatonin production in the mesocarp and exocarp of plum, and total phenol and anthocyanin increased in the mesocarp [169]. A rise in JA and its precursor (oxo-phytodienoic acid (OPDA)) was detected in mesocarp by hormonal analysis [169]. Therefore, melatonin induces the JA signaling pathway to increase total phenol and anthocyanins. JA is involved in promoting the biosynthesis of phenylpropanoid compounds such as anthocyanins [170] by regulating the WD-repeat/bHLH/MYB complexes [171]. MeJA activates defense responses against stresses [172]. Sun et al. (2013) confirmed that methyl jasmonate (MeJA) stimulated enzymes and reduced hydrogen peroxide (H_2O_2) and malondialdehyde (MDA) in banana plants after Fusarium inoculation [173]. Exogenous melatonin increased disease resistance in apples, peaches, and kiwi by increasing the activity of CAT, POD, SOD, and ascorbate peroxidase (APX) [161,174].

Artificial inoculation of table grapes immersed in MT showed that MT did not significantly inhibit hyphae growth and spore germination but reduced the severity of gray mold disease [175]. MT reduces the MDA content and prevents the increase in cell membrane permeability by synthesizing and accumulating phenols and flavonoids. Simultaneously, the activity of defense enzymes such as SOD, POD, CAT, PAL, PPO, chitinase, and β-1,3 glucanase significantly increases [176]. Similarly, DPPH inhibition and activity of antioxidant enzymes SOD, POD, and APX strawberries immersed in melatonin increased, and *B. cinerea* decay decreased [177]. MT increases the activity of glucose-6-phosphate dehydrogenase, shikimate dehydrogenase, and PAL, which cause the accumulation of total phenol and endogenous SA, and thus is effective in inhibiting decay and increasing shelf life [178]. It seems that melatonin is involved in plant innate immunity against pathogens through SA/JA/ET and NO-dependent pathways [179].

SA is a natural phenolic molecule that facilitates signal transduction as a plant growth regulator [180]. SA induces defense genes, especially genes encoding pathogenesis-related (PR) proteins with antimicrobial activities [181,182]. Therefore, SA is involved in the induction of systemic acquired resistance (SAR) [183]. Disease inhibition in jujube inoculated with *A. alternata* was influenced by SA [174]. SA treatment of apple fruits before inoculation with *P. expansum* effectively inhibited blue mold [184]. SA increases resistance to *P. expansum* by increasing SOD activity [185]. Methyl salicylate (MeSA) vapors increased epicatechin, PAL, chitinase, β-1,3-glucanase activity and reduced anthracnose of avocado significantly [186]. Pre- and postharvest SA treatment increased the shelf life of pomegranate, mango, jujube, and strawberries by inhibiting decay [187–190]. Salicylic acid maintained the content of total phenol, total antioxidant, and activity of CAT, SOD, and POD and reduced papaya rot [191]. SA may have ability for induction of systemic or local acquired resistance (LAR) against pathogens to inhibit microbial decay [183].

SA and MeJA are critical in plant interactions to induce systemic defense against pathogenic microorganisms [191]. The activity of PPO and POD, increased proportionally to the content of SA and JA in citrus treated and infected with *P. italicum* and *P. digitatum*, resulted in inhibiting both molds [192]. Pan et al. (2020) reported that MeJA significantly reduced the diameter of the lesions caused by *B. dothidea* on kiwifruit [193]. MeJA significantly increased the activity of defense-related enzymes such as CAT, POD, SOD, PPO, chitinase, and β-1,3-glucanase. It also increased the accumulation of total phenolic compounds, while lipid oxidation decreased [193]. MeJA increased the activity of PAL and 4-coumarate-CoA ligase (4CL), total phenol, total flavonoid, lignin, individual phenols such as chlorogenic acid, neochlorogenic acid, and epicatechin in peach [194]. Furthermore, the increase of PpPAL and Pp4CL transcripts after inoculation with *R. stolonifer* indicates the induction of primary defense through phenylpropanoid pathway activation [194].

2.5. Edible Coatings

Natural films and coatings include polysaccharides (pectin, cellulose, starch, gums), lipids (fatty acids, acetylated glycerides, surfactants, waxes), proteins (fatty acids, collagen, gelatin, waxes, resins, whey), and composite polymers. The principal components for producing biodegradable films are film-forming biopolymers which include carbohydrates, proteins, solubilizing medium, and plasticizers [195]. The majority of the edible coating components are polysaccharides such as chitosan, alginate, cellulose, carrageenan, pectin, starch, and proteins such as whey and casein [196]. In addition to maintaining structural integrity due to the arrangement of hydrogen bonds, polysaccharide-based films have good barrier properties [197]. Protein-based coatings have lower moisture barrier properties than polysaccharide-based films [198]. Lipid-based coatings have very high moisture barrier properties due to the greater polarity difference [199]. Polysaccharides and proteins due to their hydrophilic nature are used for transport active components such as antioxidant and antimicrobial agents [200]. Starch and alginate are considered for bio-packaging due to their gelatinization properties [201] and the ability to form hydrogels and encapsulation barriers, respectively [202]. Chitosan has attracted attention due to its properties as a gelling agent and the ability to form hydrogen bonds and hydrophobic interactions [203]. Low gaseous permeability is an important property of edible coating in order to slow down the respiration and transpiration processes, thereby delaying ripening and senescence. Among other features is the control of the migration of oxygen, carbon dioxide, and moisture from the outside environment into the products, the inertness of coating substances, nature transparent, non-toxic, non-sticky, low viscous, economical and possessing a quick drying nature, digestible, and no change in sensory characteristics (taste, smell or color) of products [204]. Reduced water loss, microbial decay inhibition, protection against chilling damage, and appearance enhancement are among the benefits of coatings in food preservation [205]. The mechanical properties of edible films and coatings are highly influenced by the types of biopolymers, and also the addition of plasticizers and surfactants [206]. Chitosan is one of the principal edible coatings in postharvest disease management of fresh products [207]. Chitosan has shown significant antifungal activity inhibiting growth conidium and mycelium [208]. Transcriptional studies of chitosan interactions with pathogens indicate the effect of chitosan on metabolic pathways that lead to morphological and biochemical changes and inhibition of growth and germination [209]. The electrostatic interactions between chitosan and the phospholipids in the cell membrane, which increase the permeability of the fungal cell provide the antifungal ability of chitosan. In addition, the short chain of chitosan may penetrate through the membrane and cell wall and disrupt the function of DNA and RNA [209]. Chelation mechanisms (the reaction of amino groups with metal ions) reduce the availability of essential metals in enzymatic reactions and prevent pathogenesis [210]. Moreover, coatings transfer antioxidants and antimicrobial compounds to food [211]. Zheng et al. (2017) showed that chitosan induces CAT and SOD activity, ascorbate peroxidase gene expression, and total phenolic compounds of kiwifruit, and is involved in resistance to gray and blue molds [212]. Low molecular weight chitosan (LMWC) and high molecular weight chitosan (HMWC) significantly inhibited the growth of gray mold in kiwifruit. However, LMWC had higher antifungal activity [213]. Expression of chitin elicitor receptor kinase 1 (CERK1), mitogen-activated protein kinase 3 (MPK3), and pathogenesis-related gene 1 (PR1 and PR5) was due to induction by LMWC and HMWC. LMWC has tremendous penetration power in the epidermal cell wall, therefore induction is an appropriate defense response [205]. Recently, it has been shown that chitosan–silica nanocomposite polymers significantly reduce the decay of grape berries [214]. Chitosan edible coating on blackberries significantly inhibited the growth of *Mucor racemosus* [215]. The inhibitory efficiency of chitosan against *B. cinerea*, *A. niger*, and *R. stolonifer* was observed in grapes [216] and strawberries [217]. De Oliveira et al. (2014) reported that chitosan inhibits spore germination, radial growth, and germ tube elongation and causes morphological changes in spores and hyphae of *B. cinerea*, *P. expansum*, and *R. stolonifer* in strawberries and grapes [218,219]. Another defense response of grapes

was with the synthesis of organic metabolites, such as catechin, epigallocatechin gallate, quercetin, myristin, or resveratrol against *B. cinerea* [216]. Furthermore, chitosan-based edible coatings are used to stimulate the hormones JA and SA and their derivatives [220]. The resistance against *B. cinerea* depends on the function of chitosan in inducing JA and modulating oxidative stress [221]. Simultaneous use of chitosan and propolis inhibited the growth of mycelium of *C. gloeosporioides* in vitro and reduced the severity of anthracnose disease in vivo [222]. Studies show that chitosan causes the biosynthesis of arginine vaso-pressin (AVP), which protects the fruit of avocado against *C. gloeosporioides* [223]. Chitosan induces defense genes through the up-regulation of PAL and down-regulation of lipoxyge-nase (LOX) genes and it helps to control anthracnose by increasing the epicatechin content of exocarp [224].

Some natural components have been used to formulate edible coatings. Natural gums can induce defense reactions and reduce plant diseases. Gum arabic increased PPO activity in strawberries [225], and peach gum increased PPO, POD, PAL, and chitinase activity in blueberries [226]. Propolis extract significantly reduced the postharvest microbial decay of blueberries [227]. The application of propolis extract in an edible gelatin coating on raspberries had an inhibitory effect on *B. cinerea* and *P. digitatum* strains [228]. The traga-canth gum coating preserves the sensory and quality properties of apple fruit by reducing the microbial load [229]. Corn starch with papaya leaf extract significantly extended the shelf life and decreased the fruit spoilage percentage [230]. The incorporation of antioxi-dant, antifungal, and antimicrobial additives in bioactive bio-packaging is common [231]. Chitosan–polylactic acid films containing Melaleuca alternifolia essential oil improved the flexibility and elongation at break of the film and controlled postharvest diseases in mango [232]. Increasing the concentration of cinnamaldehyde in chitosan-graph-based edible films, in addition to improving the mechanical properties of elastic modulus, tensile strength, and elongation at break, had antifungal properties against *P. italicum* and *Rhizopus stolonifera* [233]. The hydroxyl group in the EO chain replaces the internal hydrogen bonds between the polymers by forming hydrogen bonds and leads to an increase in the free spaces between the molecules, thus reducing the stiffness and increasing the flexibility of the film [234]. The reaction between essential oil compounds and the cell membrane of microorganisms results in antimicrobial properties [235]. The bioactive film based on chitosan and gum arabic with the addition of cinnamon essential oil created an entangled structure and the water barrier properties increased in addition to the antioxidant poten-tial [236]. Pectin beeswax coating containing eugenol is a viable method to maintain the quality of citrus [237]. Although essential oils enhance antimicrobial properties, they may lead to low water-solubility and offensive odors from the edible coatings [238]. Therefore, the effectiveness of edible coatings was studied as a biological control strategy [239], and simultaneous use of edible coatings and probiotics was investigated for their antifungal activity [240]. As a result, wax-based edible coatings with *B. subtilis* as a biocontrol agent were developed [241]. These coatings increase resistance to *R. stolonifer* by producing biofilms, antibiotics, or siderophores and maintain strawberry quality [241]. Lactic acid bacteria (LAB) incorporated into edible coatings by producing hydrogen peroxide, organic acids, fatty acids, or cyclic dipeptides reduced the fungal rot of grapes [242]. Similarly, the probiotic bacterium *L. plantarum* incorporated into edible coatings reduces fungal rot caused by *B. cinerea* of grapes [243]. A combination of candellila wax and the probiotic bacterium *B. subtilis* completely inhibited the fungal rot caused by *R. stolonifera* in straw-berries [241]. Simultaneous use of edible coatings based on alginate/gelatin and inulin with *Lacticaseibacillus rhamnosus* bacteria reduced the decay of blueberries and strawber-ries [244,245]. Additives such as plasticizers or stabilizers are used to modify mechanical properties, ensure flexibility, and reduce the brittleness, and uniformity of the coating solution [201]. Hydrophilic plasticizers, such as glycerol promote elasticity and perme-ability in films, and sorbitol increases the percentage elongation of edible films [246]. To improve wettability and homogeneity of coatings certain emulsifiers or surfactants are added (oleic acid, tween 20 and 80) that significantly reduce the surface tension [247].

The simultaneous application of plasticizers and surfactants has better results in terms of wettability and permeability [248]. To overcome the side effects of the additives mentioned above, composite coatings (combination of hydrocolloids, lipids, acylglycerols, and waxes) are applied. In this way, lipids create a water barrier and hydrocolloids a respiratory gas barrier [249]. The composite film composed of pectin, sodium alginate, and xanthan gum had excellent tensile strength and minimized water vapor transmission [250] (Figure 2).
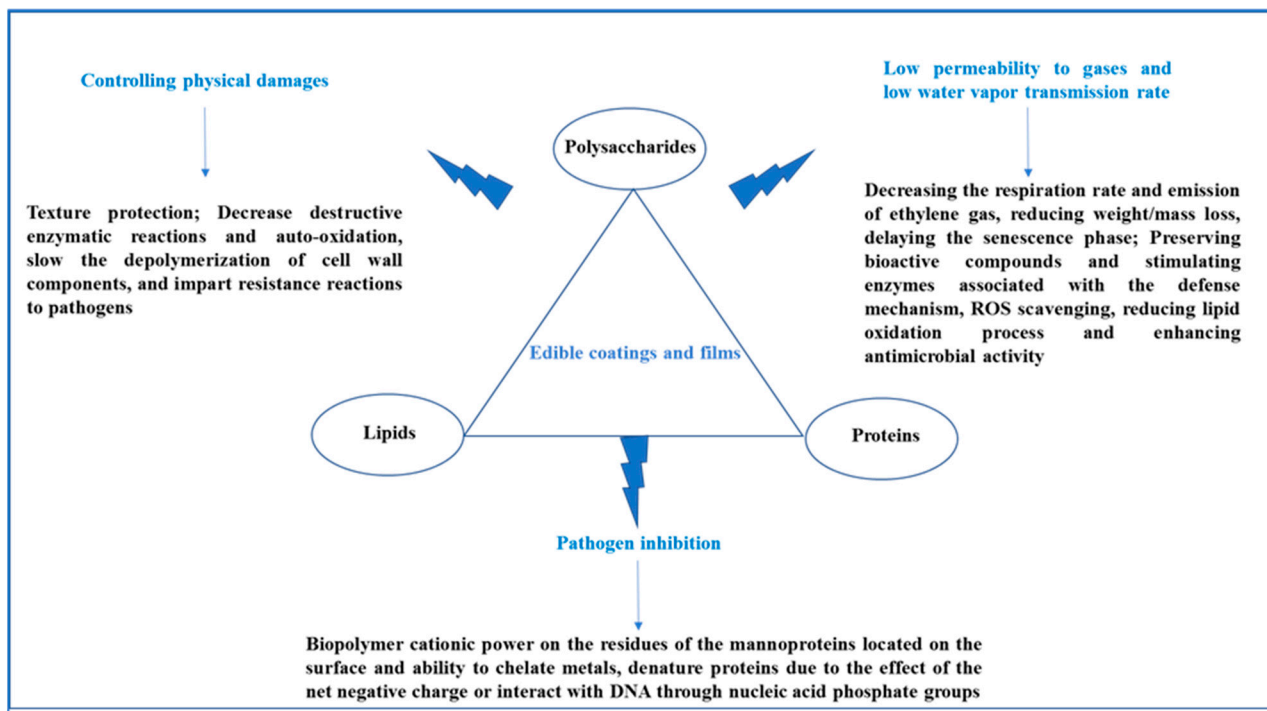
Figure 2. Proposed mechanisms of action of edible coatings against plant pathogens.

2.6. Essential Oils (EOs)

Applying EOs is an eco-friendly and sustainable method for postharvest disease management [251]. The function of EOs against postharvest fungi happens at the level of the cell membrane (disruption of the cell membrane integrity) or at the level of cell metabolism (dysfunction of mitochondria, vacuole, and inhibition of efflux pumps) [252] EOs often have a complex composition containing terpenes (monoterpenes, sesquiterpenes, diterpenes, norterpenes), phenylpropanoids, and sulfur and nitrogen compounds [253]. The synergistic effects of the constituents of EOs [254] reduce the possibility of pathogen survival or resistance [255]. It seems the presence of monoterpenes (hydrocarbon and oxygenated monoterpene) and sesquiterpenes (hydrocarbon, oxygenated sesquiterpenes) in EOs, is thought to produce antioxidant and antibacterial properties [256]. In fact, molecules with a phenolic structure, for example, thymol and carvacrol, or aldehydes, such as p-anisaldehyde and ketones, significantly inhibit pathogen growth [257]. Pomegranate peel phenolic extracts stimulate expression of PAL, chitinase, chalcone synthase (CHS), and mitogen-activated protein kinase kinase (MAPKK), which contribute to the activation of plant defenses for response to reactive oxygen species (ROS) [258] and therefore inhibits the germination of *P. italicum* and *P. digitatum* conidia [258]. Applying EOs to manage mango anthracnose showed that clove and thyme oils inhibited conidia germination and mycelia growth [259]. An assay growth inhibition of fungal strains and *Escherichia coli* showed that the inhibitory activity of cinnamon and clove oils was due to the bioactive compounds of cinnamaldehyde and eugenol, respectively [260]. Thymol fumigation reduced anthracnose in avocados [261]. Thymol fumigation increased the activity of chitinase and β-1,3-glucanase, which can hydrolyze fungal cell wall polymers and activate plant defense

systems [262]. Thymol inhibited citrus blue mold [263] and in addition to direct antifungal effects, it caused a rapid accumulation of hydrogen peroxide, leading to increased activity of defense enzymes such as β-1,3-glucanase, chitinase, PAL, POD, PPO, and LOX [263]. Thymol inhibits pomegranate fruit rot by disrupting the function of cell-wall-degrading enzyme fungi such as cellulase and pectinase [264]. Studies have proven the effectiveness of carvacrol against *Alternaria tomatophila*, *Podosphaera xanthii*, and *Xanthomonas perforans* [265] as well as eugenol and thymol against *B. cinerea* [265,266]. Chemical structures with isomerization of the double bond or nitro group on the aromatic ring were associated with the antifungal activity of phenylpropanoids derived from the compounds [266]. The structure of EOs determines their hydrophobicity and allows them to pass through cell walls and membranes, resulting in cell death or inhibiting sporulation and germination of fungi [252]. Studies have shown that hydrophobic compounds interact with ergosterol, a vital molecule that maintains cell integrity, viability, function, and growth [267]. Therefore, clove and thyme oils effectively inhibited ergosterol synthesis [267,268]. Changing cell membrane fluidity and permeability leads to ion leakage, proton pump disorder, and reduces membrane potential. Additionally, interactions of phenolic compounds and membrane proteins cause them to precipitate and leads to the leakage of intracellular constituents [269,270]. EOs inhibit certain enzymes such as mitochondrial ATP synthase, malate dehydrogenase, and succinate dehydrogenase, while reducing energy metabolism, eventually exerting their antifungal activity by mitochondrial dysfunction [271] (Figure 3).
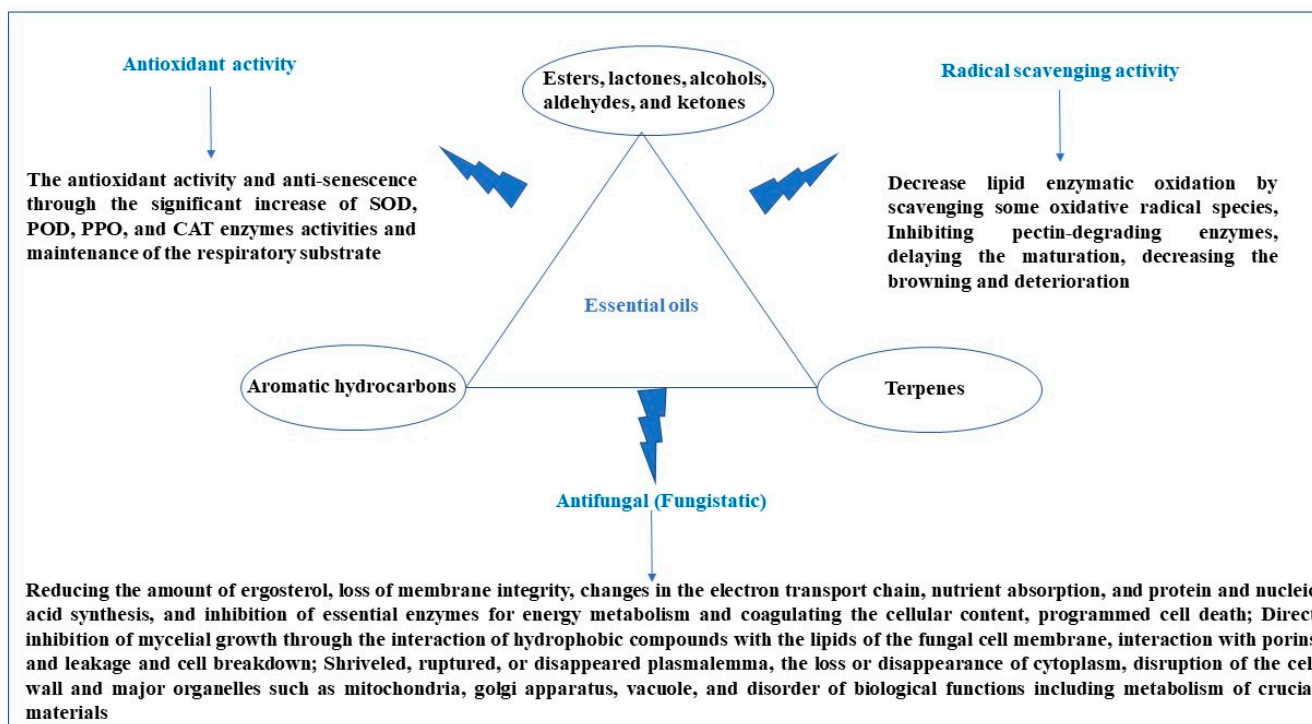
Figure 3. Proposed mechanisms of action of essential oils against plant pathogens.

3. Conclusions and Future Prospects

For pathogen control strategies to become generally recognized as safe (GRAS) and acceptable to the public, they must be cost-effective and sustainable. Concurrently, they must be compatible with the environment and have a low impact on the profile of nutritional and organoleptic compounds of products. Despite the careful selection of antagonists for disease control, biological control often raises safety concerns. Therefore, it is essential to have public knowledge of the advantages of using these techniques. The lack of sufficient information about the potential of biological control agents in orchards may be due to the lack of pre-harvest application information and the facts on the necessity of resistance of

biological control agents to radiation, extreme temperatures, water stress, nutrient limitation, and climate change. Accordingly, applied research is needed to identify resistant antagonists and overcome the barriers to the commercialization of biocontrol agents and promote sustainable agriculture. Biosensor technology must be evaluated at all stages of the production chain, transportation, and storage to ensure its effectiveness. Since the role of plant growth regulators in inhibiting postharvest decay and their relationship with each other is unclear, a detailed investigation is necessary with the goal of identifying the mechanisms involved in this process. The application of edible coatings containing active substances has been developed to control pathogens; however, other variables should be considered such as interference with sensory characteristics. Although plant extracts show potential for pathogenic agent control, there is a principal limitation in the availability and commercialization or formulation. In addition, the effects on changing nutrient compounds and organoleptic properties were discussed here. Future studies should not only have good agricultural practices, proper facilities, and controlled storage conditions, but also focus on the application of new and eco-friendly biological controls, nanomaterials, EOs, PGRs and their combinations which are essential to minimize postharvest diseases of fruits and vegetables.

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