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Review

Advancing Fruit Preservation: Ecofriendly Treatments for Controlling Fruit Softening

Sisanda Sibusiso Mthembu [1], Lembe Samukelo Magwaza [1,2,3], Samson Zeray Tesfay [1] and Asanda Mditshwa [1,*]

[1] Discipline of Horticultural Science, School of Agricultural, Earth and Environmental Sciences, University of KwaZulu-Natal, Private Bag X01, Pietermaritzburg 3209, South Africa; sibusisomthembu025@gmail.com (S.S.M.); lembe.magwaza@cranfield.ac.uk (L.S.M.); tesfay@ukz.ac.za (S.Z.T.)
[2] Plant Science Laboratory, Cranfield University, Cranfield MK43 AL, UK
[3] Department of Food Systems and Development, Faculty of Natural and Agricultural Sciences, University of Free State, Bloemfontein 9300, South Africa
* Correspondence: mditshwaa@ukzn.ac.za

Abstract: Textural softening is a major factor that limits the storage potential of fruit. Fresh produce markets incur severe financial losses due to excessive fruit softening. The application of preservation strategies aimed at mitigating fruit softening is crucial for optimising the marketability of fruit. Proposed preservation strategies include ecofriendly treatments, namely, hexanal, edible coatings, heat treatments, ozone and UV-C irradiation. These treatments optimise firmness retention by targeting the factors that affect fruit softening, such as ethylene, respiration rates, enzymes and pathogens. This review discusses the mechanisms by which ecofriendly treatments inhibit fruit softening, providing insights into their effect on ethylene biosynthesis, cell wall metabolism and disease resistance. Although ecofriendly treatments offer a promising and sustainable approach for delaying fruit softening, the optimisation of treatment application protocols is needed to improve their efficacy in retaining fruit firmness. Studies reporting on the molecular mechanisms by which ecofriendly treatments inhibit fruit softening are limited. Future studies should prioritise proteomic and transcriptome analyses to advance our understanding of the underlying molecular mechanisms by which ecofriendly treatments delay the fruit-softening process.

Keywords: ethylene biosynthesis; cell wall metabolism; gene expression; firmness; lignin synthesis

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1. Introduction

Fruit play an essential role in providing human nutrition by supplying nutrients vital for the maintenance of normal health. However, fruit are highly perishable and susceptible to rapid deterioration, which adversely affects both their storability and marketability [1]. One of the primary contributors to this perishability is textural softening, a physiological change driven by factors such as ethylene production, respiration rate and the action of cell wall-degrading enzymes (CWDEs) [2]. Furthermore, fruit softening is linked to a decrease in the hardness of the cell wall, which facilitates pathogen invasion into the cell, resulting in spoilage [3]. High softening rates exacerbate quality deterioration, leading to consumer rejection and severe economic losses [4]. Therefore, retaining fruit firmness is crucial for ensuring commercial viability, as it serves as a vital attribute that governs the saleability and shelf life of fruit.

Researchers have investigated various preservation strategies aimed at reducing postharvest losses by controlling fruit softening. Examples of these strategies include ecofriendly treatments such as heat treatments [5], ozone technology [6], ultraviolet C (UV-C) irradiation [7], edible coatings [8,9] and hexanal formulations [10]. Studies conducted on the listed treatments have demonstrated their capacity to optimise shelf life by regulating the factors that influence fruit softening. Furthermore, these treatments have been granted

Generally Recognized as Safe (GRAS) approval by the United States Food and Drug Administration (FDA), which is crucial for ensuring market access and building consumer confidence amidst growing concerns about food safety and environmental health.

Despite the advancements in these ecofriendly preservation techniques, there is a scarcity of comprehensive reviews that specifically addresses their role in controlling fruit softening. Therefore, the current review addresses this gap by summarizing recent advances in the application of ecofriendly treatments to suppress fruit softening. Additionally, it explores the underlying mechanisms affecting fruit softening during postharvest storage, focusing on how these treatments inhibit softening by limiting gaseous exchange, suppressing enzymatic activities, downregulating softening-related genes and enhancing disease resistance. The aim of this review is to gain an understanding of the mechanisms by which ecofriendly treatments optimise firmness retention, encourage the adoption of these treatments in managing fruit softening and promote wide utilization in the fruit industry.

2. Factors Contributing to Fruit Softening

2.1. Ethylene

Ethylene is a naturally produced two-carbon gaseous ripening hormone that has numerous effects on the storage life of fruit [11]. Fruit ripening-related processes such as colour development, taste, flavour and tissue softening are regulated by ethylene. Apart from its beneficial effect on promoting fruit ripening, ethylene production can be detrimental by causing excessive softening of fruit. Ethylene production can accelerate fruit softening by triggering the action of enzymes involved in cell wall degradation [12]. Ethylene is synthesized from the amino acid methionine, which is converted to S-adenosyl methionine (SAM) via the enzyme SAM synthetase [13].

SAM is converted to the four-carbon compound 1-aminocyclopropane-1-carboxylic acid (ACC) by the enzyme ACC synthase (ACS) [14]. However, ACC can undergo one of two fates, either being converted to malonyl ACC (MACC), which is an inactive end product, or being converted to ethylene by the enzyme ACC oxidase (ACO) [15]. Hence, the rate-limiting step in ethylene production is the formation of ACC, which is catalysed by ACS [16]. Therefore, ethylene production can be reduced by downregulating the ethylene biosynthesis and perception of ethylene by the receptor at appropriate ripeness, leading to delayed ripening and fruit softening.

2.2. Respiration

Respiration is a fundamental metabolic process in fresh produce, playing a critical role in maintaining fruit vitality and supporting developmental changes. During respiration, stored organic materials such as carbohydrates, fats and proteins undergo oxidative catabolism, resulting in the production of energy, carbon dioxide (CO_2) and water [17]. This energy is essential for sustaining cellular functions and various physiological processes in the fruit. However, respiration also leads to the loss of stored energy and can contribute to the deterioration of fruit quality. As respiration progresses, fruit lose moisture through transpiration, leading to a decrease in firmness [18]. Additionally, high respiration rates are associated with increased metabolic activities and the production of respiration heat, which accelerates the degradation of fruit texture and overall quality [19]. Therefore, managing the respiration rate is crucial for maintaining fruit firmness and optimising storage life.

2.3. Cell Wall-Degrading Enzymes

Fruit firmness is dependent on the integrity of the cell wall, which is comprised of polysaccharides (pectin, cellulose and hemicellulose) and lignin, which are responsible for the mechanical strength of the cell wall [20,21]. The enzymatic degradation and solubilisation of cell wall polysaccharides (CWPs) causes alterations in the structure and composition of the cell wall, leading to textural changes resulting in fruit softening [22]. The degradation of CWPs is catalysed by enzymes such as pectin methyl esterase (PME), polygalacturonase (PG), pectin lyase (PNL), pectate lyase (PL), β-galactosidase (β-Gal) and cellulase (Cx). In

the cell wall, PME catalyses the removal of methyl ester groups from the polygalacturonic acid chain of pectin, resulting in the generation of demethylated pectin, which is further hydrolysed by PG [23].

PG hydrolyses the α-1,4-galacturonan linkages in the polygalacturonic acid chain of the demethylated pectin, causing the depolymerization and dissolution of pectin in the cell wall [24]. PNL specifically targets pectin with methyl ester groups, whereas PL acts primarily on demethylated pectin (specifically on pectate with free carboxyl groups) [25]. Both PNL and PL catalyse a β-elimination reaction, which breaks down the α-1,4-galacturonan linkages in their respective substrates, generating unsaturated galacturonic acid residues, thereby contributing to the depolymerization and solubilization of pectin [26]. β-Gal hydrolyses pectin and hemicellulose by breaking the galactosidic linkages in these polysaccharides [27]. Cx catalyses the hydrolysis of cellulose by breaking the β-1,4-glycosidic linkages within the cellulose chains [28,29]. Additionally, Cx is involved in the degradation of the β-1,4-glucan backbone of xyloglucan (a hemicellulosic polysaccharide) [30]. The depolymerization of pectin and hydrolysis of cellulose and hemicellulose weakens the structural integrity of the cell wall, leading to softening of the fruit tissues [31].

2.4. Fungal Pathogens

Necrotrophic pathogens are the most devastating fungal pathogens as they kill host tissue, resulting in rotting. Examples of necrotrophic fungi are *Botrytis cinerea*, *Sclerotinia sclerotiorum*, *Monilinia* spp., *Alternaria* spp., *Rhizopus* spp., *Penicillium* spp. and *Fusarium* spp. [32–36]. The manner in which necrotrophic fungi (exemplified by *B. cinerea*) cause fruit softening has been documented. *B. cinerea* can secrete extracellular enzymes such as pectinases (PG, PNL and PL) to promote cell wall degradation, making it easier for fungal spores to penetrate the host tissues [37,38]. Additionally, *B. cinerea* has the capacity to secrete oxalic acid, which lowers the pH of host tissues, thereby stimulating the production and activity of extracellular enzymes [38]. Furthermore, the accumulation of oxalic acid results in Ca^{2+} chelation, which diminishes the structure of pectin in the cell wall [39].

To mitigate the deleterious effects caused by fungal invasion, plants have developed a defence system that induces disease resistance against pathogens. Lignin is a phenolic polymer responsible for fruit firmness and provides protection against pathogens by strengthening the structural integrity of the cell wall, which forms a physical barrier that inhibits the penetration of pathogenic spores [40]. The activation of the phenylpropanoid and monolignol pathways stimulates the biosynthesis of lignin [41,42], which is crucial for minimising pathogenic infection since fruit become more susceptible to fungal decay as they soften.

Phenylalanine ammonia-lyase (PAL) is the key and rate-limiting enzyme in the phenylpropanoid metabolic pathway, involved in the biosynthesis of lignin [43]. PAL converts phenylalanine to cinnamic acid, which further undergoes a series of reactions catalysed by enzymes such as cinnamate 4-hydroxylase (C4H), 4-coumarate-CoA ligase (4CL), *p*-hydroxycinnamoyltransferase (HCT) and cinnamylalcohol dehydrogenase (CAD). These enzymatic reactions result in the production of monolignols such as coniferyl alcohol, sinapyl alcohol and *p*-coumaryl alcohol, which are the main precursors of lignin. Thereafter, the peroxidase (POD) and laccase (LAC) enzymes catalyse the polymerization of these monolignols to form lignin.

3. Effect of Ecofriendly Treatments on Factors Contributing to Fruit Softening

The inhibition of fruit softening by ecofriendly treatments such as hexanal formulations, edible coatings, heat treatment, ozone and UV-C irradiation occurs through a variety of mechanisms. These treatments generally function by limiting gaseous exchange, inhibiting CWDEs and their related genes or suppressing fungal growth by inducing disease resistance. The following sections provide a detailed discussion of how these mechanisms impact the various factors contributing to fruit softening.

3.1. Hexanal Formulations

3.1.1. Effect on Ethylene Production

Hexanal is a natural volatile compound, formed from linoleic acid via the lipoxygenase pathway during lipid peroxidation in plants [44]. Hexanal can be applied as vapour, spray or dip treatment in a formulation containing ethanol and Tween 20 [45]. Additionally, a modified version named "Enhanced Freshness Formulation (EFF)" incorporates antioxidants such as Vitamin C and E into the aforementioned formulation, which enhances hexanal's preservation efficacy [46]. As previously discussed in Section 2.1, the rate-limiting step in ethylene production is the formation of ACC, which is catalysed by ACS.

Hexanal has the capacity to limit ethylene production by downregulating a single ortholog of ACS [47]. Based on past research (Table 1), hexanal formulations have been proven to be effective at reducing ethylene production as well as delaying the climacteric peak of fruit. EFF applied to mango [48] and banana [49] exhibited a significant reduction in ethylene production compared to untreated fruit. Hexanal applied to oriental sweet melons [50] and mango [51] exhibited lower ethylene production than their untreated counterparts. These studies demonstrate the efficacy of hexanal treatments to reduce ethylene production.

3.1.2. Effect on Respiration Rates

The efficacy of hexanal formulations in reducing respiration rates has been shown by studies conducted on banana [49], mango [48] and strawberry fruit [52]. In contrast, the respiration rates of tomatoes [47,53] and sweet bell peppers [54] was heightened in response to EFF treatment. However, treated fruit maintained significantly higher firmness than the untreated fruit throughout the storage period. Hexanal is a potent inhibitor of Phospholipase D (PLD), a phospholipid-degrading enzyme [55]. PLD inhibition by hexanal leads to a reduction in the catabolism of free fatty acids liberated during the membrane phospholipid catabolism. This results in more carbon intermediates being channelled into the respiratory cycle, leading to an increase in CO_2 production due to the lowered demand for substrates to replace membrane phospholipids that are broken down by PLD action. This may explain the reason why hexanal-treated fruit had higher respiration rates.

3.1.3. Effect on Fruit Softening Enzymes

The capacity of hexanal formulations to inhibit the activity of CWDEs has been documented (Table 1). The preharvest application of EFF suppressed the activity of PME in guava [56] and table grapes [57], correlating with substantially higher pectin content and firmness than the untreated fruit. Hexanal applied as a postharvest dip inhibited the PME activity of apple fruit, leading to optimised firmness retention [58]. Furthermore, preharvest treatment with hexanal formulation significantly suppressed the PME and PG enzyme activities of mango fruit stored in both cold and ambient conditions [48,59]. The mechanism by which hexanal inhibits the action of cell-degrading enzymes (CWDEs) may be related to its capacity to downregulate the transcript levels of genes encoding PME, PG, β-Gal and Cx [47].

The findings of the study conducted by Anusuya et al. [48] showed that preharvest application of EFF treatment retained the firmness of mango (cultivar: Alphonso) during cold storage for 12 out of 21 days, whereas no significant effects were observed in ambient storage. However, for the Banganapalli cultivar, EFF did not significantly affect firmness of mango fruit stored in both ambient and cold conditions. The results obtained by Preethi et al. [59] showed that preharvest application of hexanal optimised firmness retention of mango fruit (cultivar: Neelum) during ambient storage. However, no significant differences between treatments were observed in cold storage. The findings from these studies demonstrate that hexanal formulations can delay fruit softening by suppressing the activities of CWDEs. However, the efficacy of hexanal formulations to effectively delay fruit softening varies with cultivar and storage conditions. The contradictory findings indicate that further research is needed to optimise treatment application protocols in order to improve the

efficacy of hexanal formulations to effectively delay fruit softening for various cultivars stored at varying storage conditions.

3.1.4. Effect on Pathogens

Pathogens can secrete extracellular enzymes such as PME, PG and Cx to impair the integrity of the cell wall, which facilitates penetration and spread in the host organ [60]. The impact of hexanal vapour on inhibiting the activities of extracellular enzymes was studied by Thavong et al. [61]. The authors found that the Cx activity of *Lasiodiplodia theobromae* fungi exposed to hexanal was reduced by more than 80%; however, PME and PG was not affected. Comparably, Zhang et al. [62] found that hexanal significantly suppressed the activities of PG, PL and Cx, produced by *Erwinia carotovora*. In vivo experiments have shown the effectiveness of hexanal to control disease development in inoculated fruit.

Hexanal vapour effectively reduced decay caused by *B. cinerea* in raspberry [63] and tomato fruit [64]. Additionally, the fungal growth of *Monilinia fructicola* and *Monilinia laxa* was significantly suppressed in peach fruit treated with hexanal vapour [63,65]. Despite the positive results obtained by prior studies, the inhibitory mechanism by which hexanal controls pathogen growth in fruit was not investigated. In a study conducted by Dhakshinamoorthy et al. [66], hexanal vapour reduced fungal decay caused by *Colletotrichum gloeosporioides* and *Lasiodiplodia theobromae* in inoculated banana fruit. The inhibition of fungal growth was attributed to the enhancement of PAL and POD enzyme activities in response to hexanal treatment.

Furthermore, the application of hexanal resulted in cell wall thickening of the treated fruit, which aided in reducing decay by impeding the penetration of fungal spores. This was illustrated by scanning electron micrographs, which showed that the surface of hexanal-treated fruit exhibited lignification and distorted hyphae. These findings therefore suggest that hexanal induces disease resistance by activating the phenylpropanoid and monolignol pathway, resulting in lignification, which improves defence against invading pathogens. This finding provides valuable insight into hexanal's role in optimising fruit firmness. The mechanism by which hexanal enhances the activities of defence-related enzymes may be attributed to its capacity to upregulate their associated gene expressions [67].

Table 1. Effect of hexanal formulations on factors affecting fruit softening and firmness retention.

Factor	Fruit	Cultivar	Treatment	Storage Condition	Key Findings	Author
Ethylene	Mango	Alphonso, Banganapalli	EFF	14 ± 1 °C, 85 ± 5% RH and 28 ± 2 °C	Significant reduction in C_2H_4	[48]
	Banana	Grand Nain	EFF	25 ± 1 °C, 60 ± 5% RH	Significant reduction in C_2H_4	[49]
	Mango	Neelum	Hexanal	25 ± 0.8 °C, 60 ± 10% RH	Significant reduction in C_2H_4	[51]
	Sweet melon	Jinheng No. 2	EFF	10 °C, 85% RH	Moderate reduction in C_2H_4	[50]
Respiration	Mango	Alphonso, Banganapalli	EFF	14 °C, 85% RH and 28 °C	Significant reduction in CO_2	[48]
	Banana	Grand Nain	EFF	25 ± 1 °C, 60 ± 5% RH	Significant reduction in CO_2	[49]
	Strawberry	Darselect	Hexanal	4 °C	Moderate reduction in CO_2	[52]
	Tomato	Rapsodie	EFF	15 °C and RT	Increased CO_2 production	[47]
	Tomato	De Ruiter	Hexanal	RT	Increased CO_2 production	[53]
	Sweet bell pepper	Felicitas	EFF	12 °C, 95% RH	Increased CO_2 production	[54]
Enzymes	Table grapes	Flame Seedless	EFF	0–2.2 °C, 90–95% RH	Significantly suppressed PME	[57]
	Mango	Neelum	Hexanal	13 °C, 90% RH and RT	Significantly suppressed PME and PG	[59]
	Guava	Allahabad Safeda	EFF	6–8 °C, 95% and 25 °C, 52% RH	Significantly suppressed PME	[56]
	Mango	Alphonso and Banganapalli	EFF	14 °C, 85% RH and 28 °C	Significantly suppressed PME and PG	[48]
	Apple	Royal Delicous	Hexanal	1–2 °C, 80–90% RH	suppressed PME	[58]
Firmness	Guava	Allahabad Safeda	EFF	6–8 °C, 95% RH	Retained firmness	[56]
	Banana	Grand nain	Hexanal	Ambient	Retained firmness	[68]
	Sweet cherry	Bing	Hexanal	4 °C, 95% RH	Retained firmness	[69]
	Sweet melon	Jinheng No. 2	EFF	10 °C, 85% RH	Retained firmness	[50]
	Sweet bell pepper	Felicitas	Hexanal	12 °C, 95% RH	Retained firmness	[54]

Relative humidity (RH), room temperature (RT), enhanced freshness formulation (EFF).

3.2. Edible Coatings

3.2.1. Effect on Ethylene Production

The findings from previous studies (Table 2) show that the application of rice starch-ι-carrageenan coating reduced the ethylene production of plum fruit stored for 21 days at 20 °C [70]. Similar findings were obtained by Shinga et al. [71] for banana fruit treated with *Opuntia ficus indica* mucilage edible coating stored at 23 ± 2 °C for 12 days. The monolayer application of an individual coating is constrained by factors such as poor adhesion ability, uneven distribution on fruit surfaces and low water vapour permeability, which reduce its performance [72]. Improved performance of edible coatings has been achieved by combining more than one coating using a layer-by-layer approach [73]. Coating lemons with beeswax and coconut oil [74] and treating pears with chitosan and alginate [75], resulted in substantially lower ethylene production compared to the untreated fruit.

The authors further showed that the application of a combined edible coating performed better than the monolayer application of an individual coating. Comparable findings were obtained by Guerreiro et al. [76] for fresh-cut apple coated with alginate and eugenol. As previously discussed in Section 2.1, the ACS enzyme converts SAM to ACC, which is subsequently converted to ethylene by ACO. Edible coatings repress ethylene evolution by providing a gas barrier between the fruit and the surrounding atmosphere, creating semi anaerobic conditions (an increase in CO_2 and a decrease in O_2) within the fruit. The semi anaerobic conditions formed inside the fruit decrease the catalytic activity of ACO, resulting in reduced ethylene production [77].

3.2.2. Effect on Respiration Rates

Sodium alginate lowered respiration and delayed the respiratory peak of coated peach fruit [78]. The respiration rate was substantially reduced in fresh-cut papaya treated with an *Aloe vera* gel-based coating over 12 days of cold (5 °C) storage [79]. Comparable findings were reported by Hu et al. [80] for sweet cherries coated with chitosan and stored for 24 days at 10 °C. Similar to the findings reported in Section 3.2.1, combining edible coatings improved their efficacy in reducing respiration rates [74,75]. Edible coatings reduce the CO_2 production of fruit by modifying gaseous exchange (an increase in CO_2 and a decrease in O_2) between the fruit and the surrounding atmospheric environment [81].

The tricarboxylic acid (TCA) cycle in plants is the second stage of cellular respiration, whereby living cells are involved in the catabolism of organic fuel molecules in the presence of oxygen, leading to CO_2 production [82]. Genes involved in the TCA cycle such as 2-oxogluratalate dehydrogenase, malate dehydrogenase and pyruvate dehydrogenase are associated with fruit ripening [83]. Transcriptome analysis demonstrated that the application of edible coatings substantially downregulated the expression levels of genes involved in the TCA pathway, namely, citrate synthase (ACLA-3, PCP002422), isocitrate dehydrogenase (CICDH, PCP012811), succinate dehydrogenase 6 (SDH6, PCP002115), malate dehydrogenase (MDH, PCP005199), 2-oxogluratalate dehydrogenase (OGDH, PCP027756) and pyruvate dehydrogenase E1 (PDH-E1α, PCP021728) [75]. This resulted in significantly lower respiration rates, leading to substantially higher firmness levels of treated fruit.

3.2.3. Effect on Fruit-Softening Enzymes

The application of carboxymethyl cellulose (CMC) significantly delayed the softening of banana fruit by suppressing PME, PG, β-glucosidase (β-Glu) and Cx enzyme activity [84]. Chitosan effectively reduced the PG and PME activity in plums stored at 5 °C for 20 days [85]. A study conducted by Panahirad et al. [86] demonstrated that CMC effectively suppressed PG activity in plum fruit stored at 4 °C. Similar findings were reported by Lo'ay and Taher [87], where chitosan/poly-vinyl-pyrrolidine coating reduced the enzyme activities of Cx and pectinase in guava fruit stored at 27 °C.

Gum Arabic coating inhibited the Cx, PG and PME enzyme activity in persimmon fruits [88]. It is noteworthy to highlight that the findings from prior studies demonstrate that edible coatings suppressed enzyme activities at low (≤5 °C) and high (≤27 °C) storage

temperatures. The activity of hydrolysing enzymes is dependent on the production of carbon dioxide and ethylene. An increase in carbon dioxide and ethylene production enhances the activity of CWDEs [89]. The ability of edible coatings to control O_2 availability by modifying internal gas composition lowers fruit respiration and ethylene production. This leads to a decrease in enzymatic activity, which delays the softening process of fruit [90,91].

The suppression of CWDEs in response to edible coating treatments may be due to the downregulation of genes encoding these enzymes. However, there is a scarcity of studies reporting the impact of edible coatings on the expression levels of genes encoding CWDEs. This gap in the literature raises questions about the precise mechanisms by which edible coatings regulate the activities of CWDEs. To address this, further research adopting a holistic approach that examines both the activities of CWDEs and the expression levels of their associated genes is necessary. Such research will provide a comprehensive understanding of the regulatory mechanism through which edible coatings inhibit these enzymes, broadening our knowledge of how edible coatings delay the fruit-softening process.

3.2.4. Effect on Pathogens

Hydroxypropyl methylcellulose beeswax (HPMC-BW) coatings significantly reduced the incidence and severity of *B. cinerea* in cherry tomatoes during cold storage at 5 °C [92]. However, the coatings did not prevent fungal decay and disease incidence, which reached 100% for all treatments when transferred to 20 °C to simulate shelf-life conditions. The prolonged period of shelf-life simulation (7 days) may have had an influence on lowering the performance of the coatings. This indicates that HPMC-BW coating loses its efficacy over time, especially with an increase in storage temperature. Candelilla wax effectively reduced the decay caused by *Rhizopus stolonifer* in strawberry fruit by more than 40% during six days of storage at 25 °C [93]. The application of sodium alginate reduced the decay caused by *Penicillium expansum* in peach fruit stored for 7 days at 28 ± 1 °C [78]. Moulds are strictly aerobic, and sodium alginate-based coatings have an effective barrier against gas exchange. This gives the coating the ability to slow down the growth of *Penicillium expansum* by creating an anaerobic environment.

Chitosan coating was demonstrated to significantly reduce infection caused by *B. cinerea*, *Rhizopus stolonifer* and *Aspergillus niger* on strawberry fruit [94]. This study revealed that storage temperature had a profound effect on the performance of chitosan in inhibiting fungal growth. Strawberry fruit stored at 24 °C exhibited a 90% and 75.55 ± 13.46% infection for *B. cinerea* and *Rhizopus stolonifer*, respectively. Fruit stored at 12 °C had 70 ± 17.32% and 75% infection for *B. cinerea* and *Rhizopus stolonifer*, respectively. At low temperatures, the pathogenicity of the fungi was weakened due to a decrease in the physiological processes of the fruit [95]. As a result of this weakening, strawberries stored at cold temperatures presented a lower percentage of *B. cinerea* infection.

In the case of *Rhizopus stolonifer*, a lower storage temperature contributed to a low dissemination capacity of this fungus. This is depicted by the lower percentage of infection for fruit stored at 12 °C in comparison to fruit stored at 24 °C. In contrast, strawberry fruit infected with *Aspergillus niger* exhibited a lower infection (18 ± 8%) at 24 °C and a higher infection (75 ± 15%) at 12 °C. According to Oliveira Junior et al. [96], chitosan gels tend to deposit on the surfaces of the hyphae. This results in shrunken hyphae and the loss of cytoplasmic material (empty hyphae). From these results, regarding disease incidence and severity, it is confirmed that the mode of action of edible coatings is fungistatic rather than fungicidal because fungal growth was only retarded but not completely inhibited.

Table 2. Effect of edible coatings on factors affecting fruit softening and firmness retention.

Factor	Fruit	Cultivar	Treatment	Storage Condition	Key Findings	Author
Ethylene	Apple	Bravo de Esmolfe	Alginate and eugenol	4 °C	Significant reduction in C_2H_4	[76]
	Banana	AAA group	*Opuntia ficus indica* mucilage	23 ± 2 °C, 85 ± 2% RH	Significant reduction in C_2H_4	[71]
	Plum	Doongara	Carrageenan	20 °C, 85% RH	Significant reduction in C_2H_4	[70]
	Lemon	Not reported	Coconut oil and beeswax	21 ± 2 °C, 50 ± 5% RH	Significant reduction in C_2H_4	[74]
	Pear	Kosui	Chitosan and alignate	20 °C	Significant reduction in C_2H_4	[75]
Respiration	Papaya	Not reported	*Aloe vera*	5 °C, 90% RH	Significant reduction in CO_2	[79]
	Sweet cherry	Summit	Chitosan	10 °C	Significant reduction in CO_2	[80]
	Peach	Baihua	Sodium alginate	28 ± 1 °C, 90% RH	Significant reduction in CO_2	[78]
	Pear	Kosui	Chitosan and alignate	20 °C	Significant reduction in CO_2	[75]
	Lemon	Not reported	Coconut oil and beeswax	21 ± 2 °C, 50 ± 5% RH	Significant reduction in CO_2	[74]
Enzymes	Banana	Basrai	Carboxymethylcellulose	20 ± 1 °C, 85 ± 2% RH	Significantly suppressed PME. PG, β-Glu and Cx	[84]
	Plum	Sanhuali	Chitosan	5 ± 1 °C, 90 ± 5% RH	Significantly suppressed PG and PME	[85]
	Plum	Golden Drop	Carboxymethylcellulose	4 °C, 80 ± 5% RH	Significantly suppressed PG	[86]
	Guava	Banati	Chitosan/poly-vinyl-pyrrolidine	27 ± 1 °C, 48 ± 2% RH	Significantly suppressed CEL, LOX and PT	[87]
	Persimmon	Fuyu	Gum arabic	15 ± 2 °C, 70–80% RH	Significantly suppressed CEL, PG and PME	[88]
Firmness	Papaya	Not reported	*Aloe vera*	25 ± 4°C, 82 ± 2% RH	Retained firmness	[97]
	Plum	Not reported	Carrageenan	20 °C, RH 55 ± 5% RH	Retained firmness	[70]
	Cherry	Summit	Chitosan	10 °C	Retained firmness	[80]
	Pear	Kosui	Chitosan and alignate	20 °C	Retained firmness	[75]

Relative humidity (RH).

3.3. Heat Treatment

3.3.1. Effect on Ethylene Production

HT substantially enhanced the ethylene production of apples [98] stored at 0 °C for a six-month period. In addition, the authors reported that increasing the exposure time (1, 2 and 4 days at 38 °C) of heat treatment further exacerbated ethylene production. Despite the elevated ethylene production, heat-treated apples exhibited significantly higher firmness levels compared to untreated apples. In a study conducted by Nair et al. [99], mango fruit were conditioned for 14 h at 38–40 °C followed by either hot water (HWT) or hot air treatment (HAT) at 46–48 °C for 10 min. The results illustrated that ethylene production was suppressed by the listed heat treatments. The heat treatments had a positive effect on firmness retention, as treated fruit registered a substantially higher firmness than untreated fruit.

HWT at 48 °C for 10 min and HAT at 38 °C for 3 h reduced the ethylene production of treated peach fruit [100]. As a result, the heat treatments enhanced the firmness retention of peach fruit after 35 days of storage at 4 ± 0.5 °C. Silva et al. [101] reported a higher initial ethylene emission rate for papayas subjected to HWT at 40 °C for 20 min. In addition, the results show a displacement of the climacteric peek, meaning that the treatment decreased the shelf life of fruit. Despite the higher initial ethylene production, treated fruit maintained lower ethylene production during storage. Ethylene synthesis of fruit subjected to heat treatments undergo a rapid loss of ACC oxidase activity [102]. This is primarily due to the decrease in ACC oxidase mRNA and cessation of enzyme synthesis, leading to the suppression of ethylene production [103]. Furthermore, Lurie [104] stated that heat treatment can inhibit endogenous ethylene production due to the inactivation of ethylene receptors. However, no information is available on the response of ethylene receptors to heat treatments.

3.3.2. Effect on Respiration Rates

HT substantially decreased the respiration rates of apple fruit, correlating with significantly higher firmness levels compared to their untreated counterparts [98]. Heat treatment at 40 °C for 20 min reduced the CO_2 production in papaya fruit [101]. In a study conducted by Huan et al. [100], peach fruit were subjected to HAT (48 °C for 10 min) and HWT (38 °C for 3 h). The HAT outperformed the HWT, characterised by lower CO_2 production and a delay in the respiratory peak. No significant differences were observed between HWT and untreated fruit. Regardless, both heat treatments suppressed fruit softening and registered significantly higher firmness levels compared to the untreated fruit.

Nair et al. [99] found that HT elevated the CO_2 production in mango fruit; however, treated fruit registered a substantially higher firmness than untreated fruit. Similar findings were reported by Hernández et al. [105], where avocado fruit subjected to HWT at 38 °C for 1 h exhibited a significantly higher CO_2 emission rate than the untreated fruit. The higher respiration rates caused by heat treatments may be attributed to the stress induced by exposure to a high temperature [106]. Furthermore, heat treatments induced high respiration rates without causing adverse effects on firmness retention, suggesting that respiration may not significantly contribute to fruit softening.

3.3.3. Effect on Fruit Softening Enzymes

The efficacy of HT to suppress softening enzymes has been documented (Table 3). Klein et al. [107] reported that heat treatment (4 days at 38 °C) had no effect on the PME enzyme activity of apple fruit during 5 months of storage at 0 °C. However, treated fruit registered substantially higher firmness levels compared to the untreated fruit. HWT (50 °C for 10 min) temporarily suppressed the enzyme activities of PG, PL and β-Gal and had little effect on PME and β-1,3 glucanase (β-Glu) in banana peels [108]. In this particular study, firmness was negatively correlated with PME, PG, PL and β-Gal activities, indicating that the suppression of these enzymes delayed the softening of treated banana peels. Hernández et al. [105] reported that HWT (38 °C for 1 h) had no effect on the PME and

PG enzyme activity of avocado fruit. The efficacy of HAT (3 h at 45 °C) in delaying the softening of strawberry fruit stored for 8 days at 4 °C, followed by 2 days at 20 °C, was investigated by Langer et al. [109]. The authors found that strawberries exposed to HT had reduced PG, β-Gal and β-xylosidase activity, which significantly optimised the firmness retention of treated fruit.

Further investigations by Amnuaysin et al. [108] and Langer et al. [109] revealed that the suppression of CWDEs in response to HT may be related to the treatment's capacity to downregulate the expression levels of their associated genes. Amnuaysin et al. [108] found that HWT inhibited the gene expression of PG (*MaPG*) PL (*MaPL*) and β-Gal (*MaGAL*); however, this effect was not consistent. Similarly, Langer et al. [109] showed that the gene expression levels of PG (*FaPG1*), β-Gal (*FaβGal4*), β-xylosidase (*FaβGal4*) and PL (*FaPLB* and *FaPLC*) were down-regulated in response to HAT. The mechanism by which HT suppressed the activities of PG, β-Gal and β-xylosidase was attributed to the capacity of HT to downregulate the expression of their respective genes. Additionally, the expression of pectate lyase genes (*FaPLB* and *FaPLC*) was also downregulated by HT. Although studies investigating the effect of HT on the expression levels of softening genes are limited, the findings obtained by Amnuaysin et al. [108] and Langer et al. [109] provide valuable insights into the possible regulatory mechanisms by which HT optimises fruit firmness retention.

3.3.4. Effect on Pathogens

The ability of HT to inhibit disease severity caused by fungal pathogens has been demonstrated by previous studies. HWT (52 °C, 2 min) suppressed the germination of *Penicillium italicum* on the pericarp of mandarin fruit stored at 12–16 °C for 60 days [110]. The authors observed that heat-treated fruit exhibited significantly higher firmness and lignin content than the untreated fruit. This indicates that HT induced the accumulation of lignin, which thickened the cell walls in the pericarp of mandarins and facilitated delaying pathogen invasion. Furthermore, the induced lignin accumulation in response to HT may be attributed to the capacity of HT to elevate PAL enzyme activity. Therefore, the higher firmness of treated fruit may be due to the thickened cell walls as a result of induced lignin accumulation. This finding expands our understanding of the role of HT in improving fruit firmness.

In a study conducted by Wang et al. [111], HAT (48 °C for 3 h) effectively suppressed the incidence of *Leptographium abietinum* by inducing POD enzyme activity in inoculated bayberry fruit. The capacity of HT to enhance the activity of POD may have reduced fungal growth by strengthening the fruit cell walls through lignification. However, lignin content or firmness was not measured in this particular study. HAT (3 h at 45 °C) reduced decay caused by *B. cinerea* in strawberry fruit [109]. The authors stated that the reduction in fungal decay in heat-treated fruits could be attributed to a well-preserved cell wall structure, characterised by significantly higher contents of CWPs, correlating with higher firmness retention. The well-maintained cell wall of strawberry fruit was attributed to the capacity of HT to suppress the activities of CWDEs by downregulating the expression levels of genes encoding these enzymes.

Table 3. Effect of heat treatment on factors affecting fruit softening and firmness retention.

Factor	Fruit	Cultivar	Treatment	Storage Condition	Key Findings	Author
Ethylene	Apple	Granny Smith	HAT	0 °C, 90% RH	Significant reduction in C_2H_4	[98]
	Mango	Kensington Pride	HWT and HAT	5 °C and 22 °C	Reduced C_2H_4 production	[99]
	Peach	Xiahui 5	HWT and HAT	4 ± 0.5 °C, 85 ± 5% RH	Moderate reduction in C_2H_4	[100]
	Papaya	Not reported	HWT	25 °C, 62% RH	Increased C_2H_4 production	[101]
Respiration	Apple	Granny Smith	HT	0 °C, 90% RH	Significant reduction in CO_2	[98]
	Peach	Xiahui 5	HAT	4 ± 0.5 °C, 85 ± 5% RH	Moderate reduction in CO_2	[100]
	Mango	Kensington Pride	HWT and HAT	5 °C and 22 °C	Increased CO_2 production	[99]
	Avocado	Hass	HWT	5 °C and 20 °C, 60 ± 10% RH	Increased CO_2 production	[105]
Enzymes	Banana	Hom Thong	HWT	25 ± 1 °C	Moderately suppressed PG and PL	[108]
	Strawberry	Aroma	HAT	4 °C + 2 days at 20 °C	Significantly suppressed PG, β-Gal and β-xylosidase	[109]
	Apple	Golden delicious	HT	0 °C	No effect on PME activity	[107]
	Avocado	Hass	HWT	5 °C and 20 °C, 60–70% RH	No effect on PME and PG activity	[105]
	Banana	Hom Thong	HWT	25 ± 1 °C	Retained firmness	[108]
Firmness	Peach	Xiahui 5	HWT and HAT	4 ± 0.5 °C 85 ± 5% RH	Retained firmness	[100]
	Apple	Granny Smith	HT	0C, 90% RH	Retained firmness	[98]
	Zucchini	Belle-308	HWT and HWFC	4 ± 0.5 °C, 85 ± 5% RH	Retained firmness	[23]
	Mango	Kensington Pride	HWT and HAT	5 °C and 20 °C	Retained firmness	[99]

Relative humidity (RH).

3.4. Ozone

3.4.1. Effect on Ethylene Production

Studies on the impact of ozone on ethylene production are listed in Table 4. Gaseous ozone treatment (0.15 ppm during the day and 0.3 ppm overnight) significantly reduced ethylene production of cantaloupe melon stored at 6 °C [112]. Similarly, Chen et al. [113] found that ozone treatment significantly reduced ethylene production in cantaloupes stored at 4 ± 0.5 °C for 42 days. One of the key findings in this study is that higher doses of ozone concentrations (6.432–15.008 mgm^{-3} for 1 h) exhibited greater ethylene suppression. In addition, increasing ozone concentrations resulted in greater firmness retention and pectin content in treated cantaloupe. Additionally, Triardianto and Bintoro [114] reported a similar trend for banana fruit, whereby ethylene production decreased with an increase in the concentration of ozone (0.3–0.5 ppm). Furthermore, the authors demonstrated that storage temperature had an effect on the efficacy of ozone in reducing ethylene production. Ethylene production increased with an increase in storage temperature, with the lowest ethylene production registered at 5 °C, followed by 15 °C and 27 °C.

Gaseous ozone application significantly reduced the ethylene production of kiwifruit [115]. The authors revealed that fruit exposed to ozone had lower concentrations of ethylene biosynthesis intermediates (ACC and MACC), alongside substantially lower ACS and ACO enzyme activities than the control. The effect of ozone on ethylene biosynthesis intermediates and enzyme activities may be the mechanism by which this treatment suppresses ethylene production. These findings indicate that the suppression of ACS activity reduced the formation of ACC, which may have lowered the activity of ACO, resulting in reduced ethylene production. Additionally, the continuous application of ozone may reduce the catalytic activity of ACO by limiting oxygen availability in the storage room.

3.4.2. Effect on Respiration Rates

Ozone treatment (10 µL/L for 10 min) had no effect on the respiration rate of tomatoes stored at 20 °C for nine days [116]. The firmness of ozone-treated tomato fruit in this study registered significantly higher firmness, despite the treatment having no effect on respiration rates. In a study conducted by Minas et al. [115], the respiration and softening rate of ozone-treated kiwifruit was substantially lower than that of the control. Chen et al. [113] illustrated that increasing the ozone concentration from 6.432 to 15.008 mgm^{-3}, resulted in greater suppression of CO_2 production in cantaloupes. Similarly, the capacity of ozone to retain firmness was more pronounced at higher doses of ozone. Phosphoenolpyruvate carboxykinase (PEPCK) is an enzyme involved in the gluconeogenesis pathway that converts oxaloacetate into phosphoenolpyruvate and carbon dioxide [117].

Enolase (ENO) is an enzyme in the glycolytic pathway (which is the first step of cellular respiration) that catalyses the conversion of 2-phosphoglycerate to phosphoenolpyruvate. Minas et al. [115] showed that ozone treatment suppressed respiration and the expression of PEPCK in the gluconeogenic (sucrose biosynthesis) pathway and ENO in the glycolytic (CO_2 production) pathway. Despite the findings from this particular study, the mechanism of how ozone reduces fruit respiration was still not clear. Therefore, further research on how ozone application affects the tricarboxylic acid cycle is needed in order to elucidate the mode of action by which ozone reduces the respiration rates of fruit.

3.4.3. Effect on Fruit Softening Enzymes

Ozone treatment had little effect on PG and PME enzyme activities but was effective at suppressing β-Gal activity in melons, resulting in significantly higher firmness than the control [112]. In this study, significant inhibition of PME and PG enzyme activities was only observed on the last day of storage. Comparable findings were obtained by Liu et al. [118], where aqueous ozone (1.4 mg/L for 30 min) inhibited the increase in β-Gal activity but had no effect on PG or PME in fresh-cut apples. In addition, ozone-treated apple fruit exhibited significantly higher contents of CWPs (pectin and cellulose), alongside

substantially higher firmness values. Gaseous ozone (1 mg/L for 10 min) significantly delayed the softening of treated kiwifruit by limiting the degradation of pectin and cellulose through the suppression of PG, β-Glu and Cx activity [119]. Gaseous ozone (0.3 µL/L) treatment had no significant effect on the enzyme activities of β-Gal but was effective at lowering the enzyme activities of PG and Glu in kiwifruit [120]. The inhibitory effects of ozone on fruit-softening enzymes led to a delay in the degradation of CWPs, which enhanced the firmness retention of treated fruit. Despite the positive results yielded by prior research, the information provided is still limited. Further work incorporating a holistic approach involving gene expression analysis and proteomic studies can address this gap by providing insights into the molecular mechanisms by which ozone regulates CWDEs.

3.4.4. Effect on Pathogens

The ability of ozone to suppress the disease incidence of fungal pathogens has been demonstrated by the previous studies. Ozone treatment (1.5, 2.5, 3.5 and 5.0 µL/L for 24 h) effectively suppressed the growth of *C. gloeosporioides* in papaya [121]. The authors found that ozone inhibited fungal growth by degrading the mitochondria of fungal spores. Furthermore, fruit exposed to higher concentrations of ozone (≥3.5 µL/L) had increased decay compared to the lower doses of ozone. This indicates that higher doses of ozone impaired fruit quality and exacerbated deterioration by reducing resistance to anthracnose.

Ozone treatment (1.6–60 mg kg^{-1}) suppressed the growth of *Penicillium digitatum* and *Penicillium italicum* in citrus [122] and reduced the fungal growth of *Penicillium expansum* in apple fruit [123]. Gaseous ozone (149.8 mg/m^3) enhanced disease resistance against *Fusarium hypha* by delaying the softening of cantaloupe fruit [124]. In this particular study, ozone delayed softening by inhibiting the degradation of CWPs (pectin, cellulose and hemicellulose) and the activities of CWDEs (PME, PG, β-Gal and Cx) and their relative gene expression levels, resulting in higher firmness and enhanced defence against fungal invasion.

The study by Luo et al. [125] showed that ozone treatment effectively inhibited fungal decay caused by *B. cinerea* and *Penicillium expansum* in inoculated kiwifruit. This effect was attributed to the enhancement of defence-related enzymes (PAL and POD). Furthermore, ozone-treated fruit had substantially higher firmness than untreated fruit. This effect may be due to the enhanced enzyme activities of PAL and POD, involved in strengthening the cell wall through the biosynthesis of lignin. However, lignin content was not measured in this study. Thus, further investigations evaluating the capacity of ozone to improve the structural integrity of the cell wall by stimulating the synthesis of lignin are warranted to validate this theory.

Table 4. Effect of ozone treatment on factors affecting fruit softening and firmness retention.

Factor	Fruit	Cultivar	Treatment	Storage Condition	Key Findings	Author
Ethylene	Kiwifruit	Hayward	0.3 μL L^{-1}	0 °C, 95% RH and 20 °C, 95%	Significant reduction in C_2H_4	[115]
	Cantaloupe	Caldeo	0.15 ppm and 0.3 ppm	6 ± 2 °C, 90 ± 5% RH	Significant reduction in C_2H_4	[112]
	Cantaloupe	Not reported	6.4, 10.7 and 15 mgm^{-3}	4 ± 0.5 °C, 90 ± 5% RH	Significant reduction in C_2H_4	[113]
	Banana	Kepok	0.3, 0.4, and 0.5 ppm	15 °C	Significant reduction in C_2H_4	[114]
Respiration	Tomato	Not reported	10 μL/L	20 °C, 90% RH	No effect on CO_2 production	[116]
	Kiwifruit	Hayward	0.3 μL L^{-1}	0 °C, 95% RH and 20 °C, 95%	Significant reduction in CO_2	[115]
	Cantaloupe	Not reported	6.4, 10.7 and 15 mgm^{-3}	4 ± 0.5 °C, 90 ± 5% RH	Significant reduction in CO_2	[113]
Enzymes	Apple	Fuji	1.4 mg L^{-1}	4 ± 1 °C, 90% RH	Significantly suppressed β-Gal	[118]
	Cantaloupe	Caldeo	0.15 ppm and 0.3 ppm	6 ± 2 °C, 90 ± 5% RH	Significantly suppressed β-Gal	[112]
	Kiwifruit	Hayward	1 mg L^{-1}	4 °C, 85–85% RH	Significantly suppressed PG, β-Glu and Cx	[119]
	Kiwifruit	Hayward	0.3 μL L^{-1}	0 °C, 95% RH and 20 °C, 90% RH	Significantly suppressed PME	[120]
Firmness	Tomato	Not reported	10 μL L^{-1}	20 °C, 90% RH	Retained firmness	[116]
	Kiwifruit	Hayward	0.3 μL L^{-1}	0 °C, 95% RH	Retained firmness	[115]
	Cantaloupe	Not reported	6.4, 10.7 and 15 mgm^{-3}	4 ± 0.5 °C, 90 ± 5% RH	Retained firmness	[113]
	Cantaloupe	Caldeo	0.15 ppm and 0.3 ppm	6 ± 2 °C, 90 ± 5% RH	Retained firmness	[112]
	Apple	Fuji	1.4 mg L^{-1}	4 ± 1 °C, 90% RH	Retained firmness	[118]

Relative humidity (RH).

3.5. UV-C

3.5.1. Effect on Ethylene Production

UV-C (4.1 kJ/m^2) treatment was effective at delaying ethylene production of tomatoes stored at 20 °C, which contributed to the retardation of fruit softening [126]. Similar results were reported by Mansourbahmani et al. [127] for UV-C-treated (1.5, 3 and 4.5 kJ m^{-2}) tomato fruit stored at 7 °C. The findings from this study showed that the efficacy of UV-C in suppressing ethylene production and softening rates was dose-dependent. The highest irradiation dose (4.5 kJ m^{-2}) resulted in the most significant suppression of ethylene production and softening rates. Similarly, Kan et al. [128] also found that the suppression of ethylene production in response to UV-C treatment (4 kJ/m^2) helped retain the firmness of peach fruit. The authors further showed that the expression of the ACS gene and the ethylene receptor was downregulated in UV-C-treated fruit.

This inhibitory effect on ethylene biosynthesis suggests that this may be the mechanism by which UV-C limits ethylene production in treated fruit. Contradictory results were obtained by Zhou et al. [129], who found that UV-C (4 kJ m^{-2}) significantly reduced ethylene production of peach fruit; however, there was no significant influence on the softening rate during the entire storage period. Kan et al. [128] stored UV-C-treated peach fruit (cv. Xiahui 5) at 10 °C for 9 days, whereas Zhou et al. [129] stored treated peach fruit (cv. Jinxiang) at 15 °C for 10 days. Hence, the contradictory findings could be due to differences in storage conditions and cultivar characteristics. Therefore, further research investigating the interactions between UV-C treatment, storage conditions and peach genotypes is warranted to optimise the postharvest preservation strategies of various cultivars.

3.5.2. Effect on Respiration Rates

UV-C (4.1 kJ/m^2) treatment was effective at suppressing the respiration rates of tomatoes, with treated fruit registering higher firmness retention [125]. UV-C irradiation significantly reduced the respiration rate of peaches [129]. In contrast, UV-C was not effective in suppressing the respiration rate of banana fruit [130]. In the mentioned study, UV-C-treated fruit exhibited a relatively higher value of firmness than control fruit. However, the inhibitory effect was lost as ripening progressed, characterised by no significant differences among treatments towards the end of the storage period.

3.5.3. Effect on Fruit Softening Enzymes

The effects of UV-C irradiation on the activity of CWDEs, as reported in past studies, are listed in Table 5. UV-C (5 kJ m^{-2} for 9 min) treatment suppressed PG, PL, β-Gal and Cx enzyme activities in jujube fruit [131]. In addition, the firmness of UV-C-treated jujube fruit was substantially higher than untreated fruit. UV-C-irradiated (4.2 kJ/m^{-2} for 8 min) tomato fruit exhibited significantly lower PG, PME and Cx enzyme activities, correlating with higher firmness than the untreated fruit [132]. Lu et al. [126] reported that UV-C irradiation delayed the solubilisation of pectin by inhibiting PME and PG activities of tomato fruit, which optimised the firmness retention of treated fruit. UV-C treatment significantly reduced PG and PME enzyme activity in tomato fruit, resulting in improved firmness retention [127]. UV-C irradiation effectively delayed the initiation of fruit softening in pineapple by suppressing PG, PME and Cx activity [133]. Repeated doses of UV-C irradiation reduced the activities of PG, PME and β-Glu in strawberry fruit, which in turn delayed fruit softening [134].

The suppressed catalytic activity of CWDEs in response to UV-C irradiation provides insights into the manner in which this treatment inhibits the fruit-softening process. However, in our extensive review of the literature, we found that there is a scarcity of studies reporting on the mechanism by which UV-C regulates the activities of CWDEs. Further research on transcriptome analysis examining the effect of UV-C on the gene expressions of CWDEs may generate novel findings that can potentially expand our understanding of the mode of action by which UV-C irradiation influences the softening process of fruit.

3.5.4. Effect on Pathogens

The ability of UV-C irradiation to inhibit fungal pathogen growth has been documented (Table 6). UV-C irradiation effectively suppressed the fungal growth of *B. cinerea*, anthracnose and *Alternaria alternata* in strawberry, mango and pear fruit, respectively [135–137]. The authors showed that UV-C irradiation induced disease resistance against fungal pathogens by enhancing the activities of defence-related enzymes in treated fruit, particularly PAL and POD. Further investigations by Pombo et al. [135] and Sripong et al. [136] revealed that the activation of defence enzyme activities in response to UV-C irradiation may be attributed to the upregulated expressions of their corresponding genes. Additionally, UV-C irradiation improved the firmness retention of mango fruit, which may have facilitated reducing the fruit's susceptibility to fungal invasion [136]. As previously discussed, PAL and POD are involved in the biosynthesis of lignin. UV-C irradiation induced resistance against *Rhizopus stolonifer* by enhancing PAL activity and the biosynthesis of lignin in nectarine fruit [138]. The accumulation of lignin strengthened the structural integrity of the cell wall, which may have facilitated in reducing decay by limiting the penetration of fungal spores.

Table 5. Effect of UV-C treatment on factors affecting fruit softening and firmness retention.

Factor	Fruit	Cultivar	Treatment	Storage Condition	Key Findings	Author
Ethylene	Tomato	Zheza 205	4.1 kJ/m^2	20 °C	Significant reduction in C_2H_4	[126]
	Tomato	Valouro	1.5, 3 and 4.5 kJ m^{-2}	7 °C, 90% RH	Significant reduction in C_2H_4	[127]
	Peach	Jinxiang	4 kJ m^{-2}	15 ± 2 °C, 75 ± 5% RH	Reduced C_2H_4 production	[129]
	Peach	Xiahui 5	4 kJ m^2	10 °C, 85% RH	Significant reduction in C_2H_4	[128]
	Tomato	Zheza 205	4.1 kJ/m^2	20 °C	Significant reduction in CO_2	[126]
Respiration	Peach	Jinxiang	4 kJ m^{-2}	15 ± 2 °C, 75 ± 5% RH	Significant reduction in CO_2	[129]
	Banana	Berangan	0.01 to 0.30 kJ m^{-2}	25 ± 2 °C, 85% RH	No effect on CO_2 production	[130]
	Jujube	Lingwu long	5 kJ s^{-1} m^{-2}	4 °C, 85~95% RH	Significantly suppressed PG, PL, β-Gal and Cx	[131]
Enzymes	Strawberry	Camarosa	4, 2 and 0.8 kJ/m^{-2}	0 °C	Significantly suppressed PG, PME and β-Glu	[134]
	Pineapple	Not reported	2, 4, 6 and 8 kJ/m^{-2}	25 °C, 85% RH	Significantly suppressed PG, PME and β-Glu	[133]
	Tomato	Zhenzhu1.	4.2 kJ/m^{-2}	18 °C, 95% RH	Significantly suppressed PG, PME and Cx	[132]
	Tomato	Zheza 205	4.1 kJ/m^2	20 °C	Significantly suppressed PG and PME	[126]
	Tomato	Valouro	1.5, 3 and 4.5 kJ m^{-2}	7 °C, 90% RH	Significantly suppressed PG and PME	[127]
	Tomato	Zheza 205	4.1 kJ/m^2	20 °C	Retained firmness	[126]
Firmness	Tomato	Valouro	1.5, 3 and 4.5 kJ m^{-2}	7 °C, 90% RH	Retained firmness	[127]
	Peach	Xiahui 5	4 kJ m^2	10 °C, 85% RH	Retained firmness	[128]
	Banana	Berangan	0.01 to 0.30 kJ m^{-2}	25 ± 2 °C, 85% RH	No effect on firmness	[130]
	Peach	Jinxiang	4 kJ m^{-2}	15 ± 2 °C, 75 ± 5% RH	No effect on firmness	[129]

Relative humidity (RH), ultraviolet C (UV-C).

Table 6. Studies conducted on pathogen inactivation in response to ecofriendly treatments.

Fruit	Cultivar	Treatment	Storage	Pathogen	Findings	Author
Banana	Grand Naine	Hexanal	Room temperature	*Colletotrichum gloeosporioides and Lasiodiplodia theobromae*	Inhibited hyphal growth	[66]
Peach and Raspberry	Red Haven and Encore, Red Wings, K81-6	Hexanal	0 °C and 20 °C	*Sclerotinia sclerotiorum*, *Alternaria alternata*, *Colletotrichum gloeosporioides*	Reduced mycelial growth	[63]
Peach	Chiripá	Hexanal	20 °C	*Monilinia fructicola*, *Monilinia laxa*	Suppressed pore germination	[65]
Tomato	Royale	Hexanal	20 ± 1 °C, 99% RH	*Botrytis cinerea*	Reduced growth of *B. cinerea*	[64]
Longan	Daw	Hexanal	5 °C	*Lasiodiplodia theobromae*	Reduced incidence severity	[61]
Tomato	Josefina	EC	5 °C and 20 °C, 85 ± 5% RH	*Botrytis cinerea*	Reduced incidence and severity	[92]
Strawberry	Albion	EC	25 °C	*Rhizopus stolonifer*	Reduced incidence and severity	[93]
Bayberry	Not reported	HT	1 °C and 20 °C, 90% RH	*Leptographium abietinum*	Suppressed mycelial growth	[111]
Mandarin	Kamei	HT	12 ± 4 °C, 90 ± 5% RH	*Penicillium italicum*	Inhibited fungal growth	[110]
Strawberry	Aroma	HT	4 °C and 20 °C	*Botrytis cinerea*	Suppressed mycelial growth	[109]
Papaya	Sekaki	Ozone	25 °C, 70% RH	*Colletotrichum gloeosporioides*	Suppressed fungal growth	[121]
Mandarin	Fortune and Ortanique	Ozone	5 °C and 20 °C	*Penicillium digitatum*, *Penicillium italicum*	Suppressed fungal growth	[122]
Orange	Navelate, Lanelate, Salustiana and Valencia	Ozone	5 °C and 20 °C	*Penicillium digitatum*, *Penicillium italicum*	Suppressed fungal growth	[122]
Kiwifruit	Hayward	Ozone	0 °C, 95% RH	*Botrytis cinerea*, *Penicillium expansum*	Inhibited spore germination	[125]
Apple	Golden delicious and Fuji	Ozone	1 ± 1 °C, 95% RH	*Penicillium expansum*	Suppressed fungal growth	[123]
Strawberry	Toyonoka	UV-C	20 °C	*Botrytis cinerea*	Suppressed fungal decay	[135]
Nectarine	Ruiguang 7	UV-C	25 ± 2 °C, 80–90% RH	*Rhizopus stolonifer*	Suppressed fungal growth	[138]
Mango	Chok-Anan	UV-C	13 °C, 85 ± 5% RH	*Colletotrichum gloeosporioides*	Reduced incidence	[136]

Relative humidity (RH), enhanced freshness formulation (EFF), edible coating (EC), heat treatment (HT), ultraviolet C (UV-C).

4. Instrumental Texture Profile Analysis (TPA)

Instrumental Texture Profile Analysis (TPA) is a method that mirrors consumer perception by simulating oral chewing to assess fruit texture, an important indicator of quality, marketability and consumer acceptability [139]. TPA quantifies key textural attributes such as hardness (the initial deformation force), chewiness (required energy to chew a solid food), gumminess (required energy to disintegrate a semisolid food), springiness (the rate at which deformed food reforms), adhesiveness (the adhesive ability to our palate, teeth and tongue during chewing) and cohesiveness (a measure of the bonds in the internal structure) [140]. These measurements provide a detailed profile of the fruit's texture, making TPA essential for understanding and monitoring textural changes, which are crucial for both perceived quality and consumer acceptance [141].

4.1. TPA in Ecofriendly Treatments

TPA can facilitate providing a comprehensive understanding of the impact various ecofriendly treatments have on fruit texture. The effects of these treatments on TPA attributes across different fruit are discussed below. Table 7 summarizes the impact of different ecofriendly treatments on the textural attributes of various fruits.

4.1.1. Edible Coatings

Past studies have shown that the application of edible coatings significantly influences the textural properties of fruit. Zhou et al. [142] reported that pears treated with shellac and CMC coating exhibited significantly greater hardness and chewiness than the control. Similarly, Benítez et al. [143] found that Aloe vera and chitosan-based coatings formulated with acetic or citric acid, effectively maintained higher adhesiveness, springiness and cohesiveness in kiwifruit during 12 days of storage at 4 ± 1 °C, resulting in optimised textural quality. In addition, Marghmaleki et al. [140] found that alginate-based coatings preserved the hardness, chewiness, gumminess and springiness of fresh-cut apples during 7 days of storage at 4 °C.

Sodium alginate coatings supplemented with hydroxyapatite/quercetin glucoside complexes (HA/QUE) significantly improved the hardness, cohesiveness, springiness, and chewiness of fresh-cut papaya [144]. These findings demonstrate the capacity of edible coatings to preserve the textural integrity of fruit, with their effectiveness being highly dependent on their formulation. Supplementing edible coatings with components such as acetic acid, citric acid and quercetin glycosides plays a crucial role in maintaining texture, necessitating the need for further research on the optimization of these coatings.

4.1.2. Heat Treatment

Heat treatment application has been shown to preserve the textural properties of fruit. Shao et al. [145] reported that HAT at 38 °C for 4 days improved the textural stability of 'Gala' and 'Golden Delicious' apples, which was characterised by substantially higher hardness, fracturability, cohesiveness and chewiness, compared to the control. Similarly, Belović et al. [146] found that subjecting tomatoes to HAT (60 °C for 1 min) resulted in significantly higher springiness, cohesiveness, gumminess and chewiness, which is indicative of a well-preserved texture. The capacity of heat treatment to preserve the textural quality of fruit may be attributed to the inactivation of CWDEs.

4.1.3. Ozone

Aqueous ozone treatment (0.075 mg/L) preserved the adhesiveness, springiness, cohesiveness and chewiness of strawberry fruit [147]. Similarly, Piechowiak et al. [148] demonstrated that gaseous ozone treatment (10 ppm) significantly improved springiness, adhesiveness, gumminess and cohesiveness in strawberries, with treated fruit exhibiting better mechanical properties than the control. Furthermore, the authors attributed the ability of ozone to preserve the texture of treated strawberry fruit to the inhibition of CWDEs, namely, polygalacturonase, β-galactosidase and β-hexosaminidase.

4.1.4. UV-C Irradiation

Gómez et al. [149] found that UV-C-treated apples (11.2 kJ/m^2 for 20 min) exhibited lower fracturability, hardness, cohesiveness, gumminess and chewiness compared to control fruit, though springiness was significantly higher. In contrast, Belović et al. [146] reported that UV-C irradiation (4 kJ/m^2) preserved hardness, gumminess and chewiness in tomatoes whilst reducing springiness and cohesiveness. These findings suggest that UV-C irradiation can have varied effects on fruit texture, with some parameters being preserved and others being negatively impacted. This implies that the influence of UV-C on fruit texture may differ depending on the specific fruit and treatment conditions. Thus, further research is necessary to optimize UV-C treatment protocols for different fruit types to effectively retain textural quality during storage.

Table 7. Effect of ecofriendly treatments on the textural attributes of fruit.

Treatment	Fruit	Cultivar	Parameters	Storage Condition	Key Findings	References
Edible coatings						
Shellac and CMC coatings	Pear	Huanghu	Hardness and chewiness	4 °C, 95% RH	Greater hardness and chewiness.	[142]
Aloe vera and chitosan-based coating	Kiwifruit	Hayward	Adhesiveness, springiness and cohesiveness	4 ± 1 °C, 75% RH	Optimised textural quality.	[143]
Sodium alginate with (HA/QUE)	Papaya	Formosa	Hardness, cohesiveness and springiness, chewiness	6 °C	Enhanced textural stability.	[144]
Alginate-based coating	Apple	Fuji	Hardness, chewiness gumminess and springiness	4 ± 1 °C	Preserved textural attributes	[140]
Heat treatment						
HAT at 38 °C for 4 days	Apple	Gala and Golden Delicious	Hardness, fracturability, cohesiveness and chewiness	0 °C cold storage, and 20 °C shelf life	Improved textural stability	[145]
HAT at 60 °C for 1 min	Tomato	Camry and Zouk	Springiness, cohesiveness, gumminess and chewiness	14.4 to 19.9 °C, 35–55% RH	Preserved textural properties	[146]
Ozone						
Aqueous ozone (0.075 mg/L)	Strawberry	Not specified	Adhesiveness, springiness, cohesiveness and chewiness	4 °C	Preserved textural attributes	[147]
Gaseous ozone (10 and 100 ppm)	Strawberry	Elkat	Springiness, adhesiveness, gumminess and cohesiveness	20–22 °C, 65–70% RH	Significantly improved mechanical properties	[148]
UV-C irradiation						
11.2 kJ/m^2 for 20 min	Apple	Granny Smith	Fracturability, hardness, cohesiveness, gumminess and chewiness, springiness	5 °C	Significantly higher springiness.	[149]
4 kJ/m^2 treated overnight	Tomato	Camry and Zouk	Hardness, gumminess, chewiness, springiness and cohesiveness	14.4 to 19.9 °C, 35–55% RH	Preserved hardness and gumminess	[146]

Relative humidity (RH).

5. Conclusions

This literature review discussed the effect of ecofriendly treatments on the factors affecting fruit softening, namely, ethylene production, respiration rate, CWDEs and fungal pathogens. The key finding is that ethylene regulates CWDEs by promoting the expression of genes encoding these enzymes, identifying ethylene as the primary factor that triggers fruit softening. Ecofriendly treatments can delay the onset of fruit softening by inhibiting ethylene production and the gene expression of CWDEs. This inhibition hinders the degradation of CWPs, thereby optimising fruit firmness retention. Despite the promising results, studies investigating the effect of ecofriendly treatments on the ethylene biosynthesis pathway and cell wall metabolism are scarce. This necessitates the need for more studies evaluating the impact of these treatments on the expression of genes involved in ethylene biosynthesis and cell wall metabolism. This will deepen our understanding of the underlying molecular mechanisms by which these treatments delay fruit softening.

Additionally, lignin biosynthesis contributed to maintaining fruit firmness and enhancing disease resistance. Hexanal, heat treatments and UV-C irradiation have been shown to stimulate the accumulation of lignin, which reinforces cell wall integrity and reduces susceptibility to decay. However, most studies have primarily focused on the capacity of these treatments to induce pathogen resistance by enhancing the activity of defence-related enzymes, disregarding the downstream impact on lignin accumulation. Therefore, further research is encouraged to elucidate how ecofriendly treatments optimise cell wall integrity and fruit firmness through lignin biosynthesis. In conclusion, the capacity of ecofriendly treatments to control the factors influencing fruit softening demonstrates their potential to improve the storability and marketability of fruit. While laboratory-scale studies provide strong evidence of their efficacy, further research is needed to evaluate the costs and practicality of large-scale applications in the agricultural industry.

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Advancing fruit preservation: ecofriendly treatments for controlling fruit softening

Mthembu, Sisanda Sibusiso; Magwaza, Lembe Samukelo; Tesfay, Samson Zeray; Mditshwa, Asanda

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