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Review

Postharvest Melatonin Applications in Soft Fruits: Mechanisms and Factors Determining Treatment Efficacy

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Abstract

Soft fruits are highly perishable due to their delicate surface barriers, rapid cell-wall disassembly, turgor loss, oxidative imbalance, and tightly coordinated ripening and senescence processes that collectively accelerate water loss, softening, and decay after harvest. This review examines how melatonin (MLT) interacts with these deterioration processes in blueberries, raspberries, strawberries, grapes, and sweet cherries. Current evidence identifies redox regulation as the most consistent mechanism of MLT action, including modulation of reactive oxygen species, enhancement of antioxidant enzymes and the ascorbate–glutathione cycle, and maintenance of phenolic and other non-enzymatic antioxidants. These responses are linked with lower lipid peroxidation, reduced membrane leakage, delayed cell-wall degradation, and improved firmness, water retention, and decay resistance. More limited and species-specific evidence suggests that MLT may influence cuticular wax metabolism, endogenous MLT biosynthesis, H_2S signaling, GABA and polyamine metabolism, phenylpropanoid pathways, and host-defense responses. However, direct evidence for effects on cuticular permeability, cellular compartmentation, and hormonal signaling remains limited. Overall, MLT should be regarded as a context-dependent regulator of redox homeostasis, tissue integrity, ripening, and defense rather than as a universal anti-senescence treatment, because its effects vary with species, cultivar, concentration, maturity stage, and storage conditions and still require validation under commercial conditions.

Keywords: melatonin; soft fruits; postharvest quality; fruit senescence; oxidative stress

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1. Introduction

Soft fruits are small, fleshy fruits with delicate texture, thin skin, and high susceptibility to bruising, water loss, and microbial decay [1,2]. Although this grouping is not based on strict botanical classification, it is widely used in postharvest technology because these fruits share high metabolic activity, rapid quality deterioration, and short shelf life [3,4]. They generally include true berries such as blueberries (*Vaccinium* spp.) and currants (*Ribes* spp.), aggregate or accessory fruits like raspberries (*Rubus* spp.), strawberries (*Fragaria* × *ananassa*), as well as small fruits such as grapes (*Vitis vinifera*) and stone fruits like sweet cherry (*Prunus avium*) due to their similar postharvest behavior [1,5,6]. The rapid quality deterioration of soft fruits may result in substantial economic losses across high-value berry supply chains, highlighting the need for effective and residue-free preservation strategies. Changing consumer expectations, a focus on responsible purchasing, and

demand for minimally processed, clean-label foods heighten the challenge. Sustainability efforts to reduce food loss and energy use in the cold chain further complicate the study of soft fruits and the development of aligned postharvest strategies [7,8]. Against this backdrop, MLT emerges as a promising postharvest treatment to extend the shelf life of soft fruits [9–11].

MLT (N-acetyl-5-methoxytryptamine) is a natural hormone in animals, but also a phytohormone produced in plants [12,13], where it regulates growth, stress responses, and senescence [14,15]. Unlike synthetic fungicides or harsh chemicals, MLT is endogenously present in many edible plants [14]. Its synthesis, compartmentation, and signaling respond to environmental and hormonal cues, with abscisic acid (ABA)-linked signaling emerging as a prominent trigger under osmotic and other stresses, consistent with its integrative role in plant stress physiology [16–19]. In ripe soft fruits, endogenous MLT (phyto-melatonin) is present at low yet biologically active levels that vary with cultivar, developmental stage, stress exposure, and the quantification method (e.g., HPLC-ECD or HPLC-EMS) [20–22]. As a potent antioxidant with amphiphilic properties, MLT readily crosses biological membranes and has been shown to delay senescence and spoilage, mitigate chilling and oxidative injury, enhance disease resistance, and preserve sensory attributes across horticultural products [23–27]. Soft fruits concentrate precisely the vulnerabilities that MLT can counter: their cuticle-governed water relations and high pathogen susceptibility mean that even modest gains in barrier function or redox balance can translate into outsized shelf-life benefits [28–31].

Previous reviews have extensively examined the physiological effects and mechanisms of MLT in postharvest fruits and vegetables [32–35]. However, evidence for soft fruits remains fragmented, and the integration of their specific deterioration processes with MLT mechanisms and treatment efficacy has received limited attention. This soft-fruit-specific perspective distinguishes the present review from broader previous syntheses of MLT in postharvest horticulture. This review examines how MLT extends the shelf life of soft fruits by: (i) developing a mechanistic synthesis that links MLT-mediated redox regulation, defense activation, and preservation of membrane, cell-wall, and cuticular integrity with the main deterioration processes of soft fruits; (ii) consolidating the intrinsic and extrinsic factors that govern treatment efficacy, including species, cultivar, maturity stage, concentration, application method, exposure time, and storage conditions; and (iii) evaluating current application strategies, optimization approaches, and the main barriers to commercial implementation. The goal is not merely to summarize current findings, but to assess how MLT functions as a biopreservative, identify practical and scientific constraints, and delineate pathways for effective deployment—alone or in combination with other interventions—to reduce waste and maintain quality across soft-fruit supply chains.

2. Search Strategy

A targeted literature search was conducted in the Scopus, Web of Science, and PubMed databases on 18 February 2026 to identify relevant studies addressing the role of MLT in the postharvest physiology of soft fruits. This review was conducted as a narrative review supported by a structured literature search. The search strategy was applied to title, abstract, and keyword/topic fields, as appropriate for each database. The following Boolean query was used: (Melatonin OR phytomelatonin OR "N-acetyl-5-methoxytryptamine" OR "5-methoxy-N-acetyltryptamine") AND (postharvest OR "shelf life" OR storage OR "cold storage" OR chilling OR "quality maintenance" OR "decay control") AND ("soft fruit" OR berry OR berries OR strawberry OR "*Fragaria ananassa*" OR blueberry OR "*Vaccinium corymbosum*" OR raspberry OR "*Rubus idaeus*" OR blackberry OR "*Rubus fruticosus*" OR cherry OR "*Prunus avium*" OR "*Prunus cerasus*" OR blackcurrant OR "*Ribes nigrum*" OR

grape OR "*Vitis vinifera*") were used to capture studies within the 2016–2026 period. A summary of this search is presented in Table 1.

Table 1. Overview of the literature search conducted in databases like Scopus, Web of Science, and PubMed.

Document Type	Number of Records		
	Scopus	Web of Science	PubMed
Article	69	81	26
Review	4	9	3
Conference paper	2	2	0
Book	1	0	0
Total	76	92	29

Only peer-reviewed journal articles in English were considered, and after de-duplication, 123 unique records were retained. Titles, abstracts, and keywords were screened to identify studies meeting predefined relevance criteria: (i) MLT application in soft fruits (blueberries, raspberries, blackcurrants, grapes, strawberries, or sweet cherries); (ii) postharvest or storage context; (iii) measurable quality, antioxidant, or defense outcomes; and (iv) practical exogenous applications such as dipping, spraying, or coating. We excluded preharvest-only and developmental studies from the core postharvest evidence. Studies combining pre- and postharvest MLT applications, or MLT with another treatment, were considered when a postharvest MLT component was present, and its effects could be distinguished. Studies outside the defined soft-fruit group, minimally processed products not relevant to the review scope, and studies without relevant postharvest outcomes were excluded from the core evidence. Following this process, 48 studies were selected as the core literature for critical evaluation and synthesis. As this is a narrative review, we did not perform a formal risk-of-bias assessment. However, differences in cultivar, experimental design, MLT treatment conditions, storage conditions, and the level of mechanistic evidence were considered when interpreting the studies.

3. Soft-Fruit Biology Relevant to MLT Action

Postharvest deterioration in soft fruits is governed by a set of anatomical and physiological traits (Figure 1): (i) a delicate surface barrier controlling water loss, mechanical injury and microbial entry [28,36], (ii) rapid tissue softening and stress susceptibility, arising from the combined effects of cellular decompartmentalization, turgor loss, and accelerated cell-wall remodeling [37–39], (iii) oxidative and hormonal regulation of ripening and senescence [40,41], and (iv) flavor-related metabolic changes involving sugars, organic acids, volatile compounds, and other relevant constituents [42,43]. In the predominantly non-climacteric soft fruits considered in this review, these traits and physiological processes define the principal postharvest behavior of soft fruits, characterized by rapid water loss, shriveling, texture collapse, flavor changes, and susceptibility to decay. They identify the main biological interfaces through which MLT may act, including maintenance of barrier and membrane integrity, mitigation of oxidative stress, delayed softening, modulation of ripening-related signaling, and regulation of flavor-related metabolism. Developmental and preharvest studies are included in this section only to provide biological context for postharvest deterioration and potential MLT targets; evidence on exogenous MLT efficacy is addressed separately in the following sections.

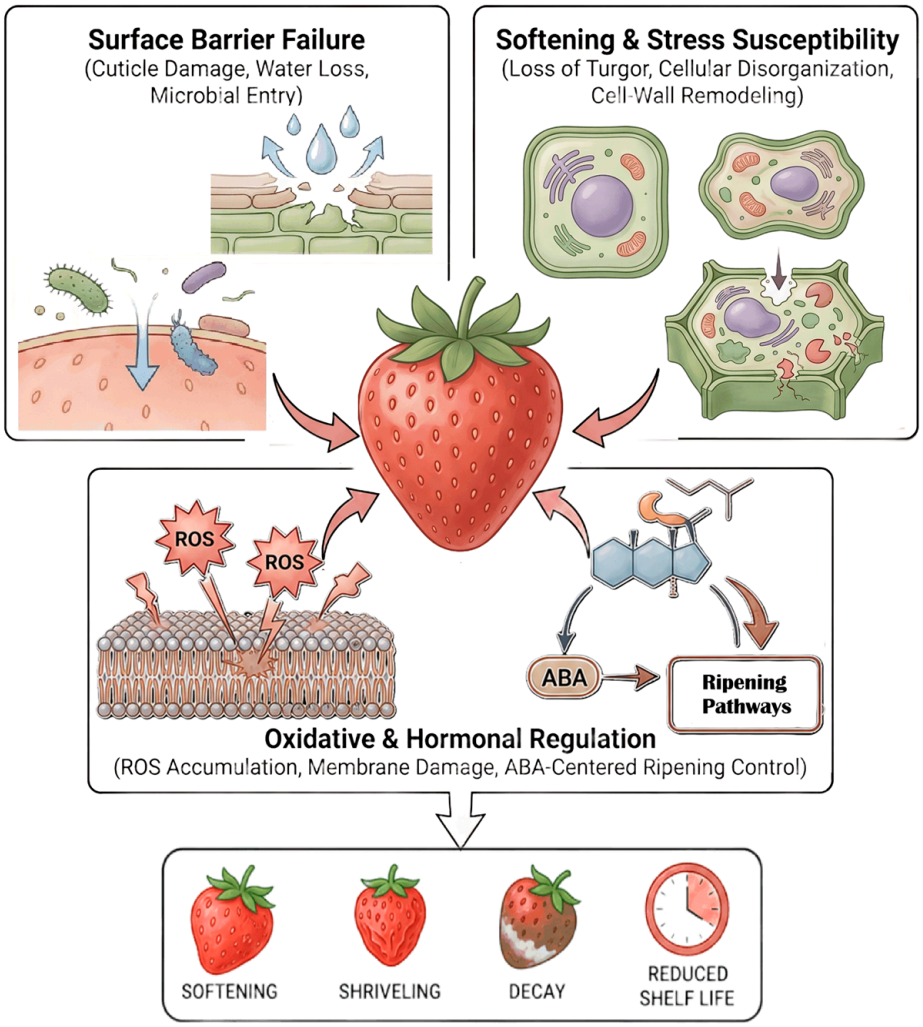


Figure 1. Main anatomical and physiological traits governing postharvest deterioration in soft fruits.

3.1. Surface Barrier Architecture

The skin of soft fruits consists of a polymeric cuticle membrane (CM) over a single layer of epidermis and, in some species, an underlying hypodermis. Structurally, CM is built on cutin and waxes [44,45]. Cutin forms the structural matrix of the cuticle, whereas intracuticular waxes embedded within this matrix and epicuticular waxes deposited on the surface contribute strongly to hydrophobicity, surface wettability, and water-barrier properties [46,47]. The structure mentioned is prevalent in soft fruits, although its composition and functional performance differ significantly among species. In strawberries, sweet cherries, and raspberries, cutin is dominated by 9(10),16-dihydroxy hexadecanoic acid [48–50], whereas in grapes, the major cutin monomer is 18-hydroxy-9(10)-epoxyoctadecanoic acid [51], and in blueberries, monocarboxylic fatty acids predominate [52]. Regarding wax composition, strawberry cuticular waxes are dominated by very-long-chain primary alcohols, together with alkanes and fatty acids [49].

In contrast, grape waxes are particularly rich in triterpenoids, especially oleanolic acid [53], while in sweet cherries, triterpenes, particularly ursolic acid, are the predominant wax constituents [50]. Blueberry waxes also contain substantial amounts of triterpenoids, including oleanolic and ursolic acids, together with β-amyrin and β-diketones that contribute to the characteristic wax bloom [47]. The compositional and structural differences are not merely descriptive; they strongly influence CM functions against water loss, pathogen infection, and mechanical damage [44,45]. Maintaining these functions requires an intact CM.

A major feature of soft-fruit surface biology, such as in cherries [50], grapes [54], and strawberries [55], is that CM deposition largely ceases early in development, so continued fruit expansion imposes tensile strain on a stretched cuticle. When CM extensibility cannot accommodate growth, failure occurs through microcrack formation, defined as minute fractures confined to the CM that do not penetrate underlying cellular layers [56]. Barrier performance is further compromised by additional surface discontinuities, including stem-scar pathways and abrasion damage during harvesting, which can increase water exchange and provide entrance points to pathogens, ultimately contributing to surface disorders and rots [28,57].

Once surface-barrier integrity is compromised, postharvest water loss progressively reduces cellular turgor and promotes weight loss, shriveling, texture deterioration, and accelerated senescence [36,58]. In blueberries, 55–69% of water loss has been estimated to occur through the cuticle, and both cuticular wax content and composition are associated with variation in water loss; accordingly, removal of the natural wax layer accelerates dehydration, decay, cellular deterioration, and senescence [47,59]. The stem scar also contributes to water loss, although its relative importance varies among and within cultivars, and sealing this pathway reduces dehydration-associated firmness loss during storage [46,57]. Overall, the soft-fruit surface barrier is a dynamic, mechanically stressed system rather than a static coating, and its postharvest performance depends on cuticle composition, developmental deposition, and structural defects.

3.2. Cellular Determinants of Softening

Beyond the surface barrier, softening in soft fruits reflects changes in tissue mechanical behavior linked to a coupled system that depends strongly on the integrity of the (i) internal cellular system, particularly cellular compartmentation, cell-to-cell adhesion, and (ii) turgor maintenance [60,61]. First, the enzymatic disassembly of cell-wall and middle-lamella networks during soft fruit ripening weakens cell-to-cell adhesion and tissue cohesion [5,62]. This process is driven by pectin solubilization and depolymerization, together with modifications in wall architecture and polymer interactions, which progressively weaken tissue cohesion and cell-to-cell adhesion [37,60]. In strawberries, suppression of polygalacturonase (*FaPG1*) and pectate lyase (*FaplC*) genes increased firmness [63,64]. In blueberries, firmness decline is associated with cell-wall disassembly and changes in calcium-related wall organization [65,66]. In raspberries and blackberries, tissue weakening during ripening is likewise accompanied by progressive pectin loss, depolymerization, and increased wall-modifying enzyme activity [38,67], with similar cell-wall remodeling trends also reported in grapes [68] and sweet cherries [69].

Second, turgor pressure, which acts as the hydraulic component of tissue, modulates the extent to which tissues remain firm, cohesive, and resistant to deformation or fracture [37,61,70]. Softening therefore reflects not only cell wall disassembly but also changes in cellular water relations. Hence, dehydration may affect fruit firmness by decreasing stiffness, enlarging intercellular spaces, and altering tissue failure mode [71]. In grapes and sweet cherries, this relationship is especially evident: in grapes, flesh-cell turgor contributes to tensile stress in the skin and thereby to splitting susceptibility [72], whereas in sweet cherries, turgor directly contributes to skin stiffness and fracture resistance, and its loss promotes cell-wall relaxation and reduced resistance to failure [61]. In strawberries and blueberries, softening is largely linked to decreased internal turgor [73,74], whereas in raspberries and blackberries, changes in turgidity are reflected in texture and bruise susceptibility [75]. At advanced levels of dehydration, increased mass loss is accompanied by reduced hardness and chewiness, loss of cellular integrity, and cellular collapse, indicating

that water loss can become a major determinant of texture even when postharvest cell-wall modifications remain limited [36,73].

As ripening progresses, fruit softening increases susceptibility to permanent damage under water-related, oxidative, and biotic challenges, as well as mechanical stress, including bruising during harvesting and other mechanically induced disorders [70,76]. For instance, bruised blueberry tissues, even without any visible injuries, could also exhibit weight loss, cell membrane damage, quality deterioration, and shortened shelf life, with lipid-related metabolites responding strongly to impact [66]. In this context, MLT may be especially relevant if it helps preserve membrane integrity, cellular water relations, vacuolar homeostasis, and cell wall stability, thereby delaying both texture loss and the broader rise in postharvest susceptibility.

3.3. Oxidative and Hormonal Regulation During Ripening

Oxidative metabolism plays a pivotal role in ripening and postharvest deterioration in soft fruits [77]. After harvest, reactive oxygen species (ROS), such as hydrogen peroxide (H_2O_2), superoxide anion ($O_2\bullet^-$), and hydroxyl radicals (•OH), accumulate in fruit tissues due to ongoing metabolism and stress responses. When ROS production exceeds antioxidant capacity, oxidative imbalance promotes lipid peroxidation, membrane integrity loss, malondialdehyde (MDA) accumulation, and senescence activation. This oxidative imbalance accelerates pigment degradation, tissue softening, browning, and decay susceptibility during storage [77]. In strawberries, a model for non-climacteric fruit, ripening involves significant changes in antioxidant and redox-related proteins, including increased superoxide dismutase (SOD) and glutathione transferase (GT), along with decreased dehydroascorbate reductase, catalase (CAT), and L-ascorbate peroxidase (APX), reflecting a shift in ROS homeostasis as the fruit approaches senescence [78]. For instance, ripening onset at color change in grapes is associated with an oxidative accumulation of H_2O_2 and a burst of lipoxygenase (LOX) mediated peroxidation of membrane galactolipids, indicating that ROS production is developmentally regulated and closely linked to membrane remodeling rather than being only a symptom of senescence [79]. While the mechanistic evidence for oxidative imbalance is stronger in strawberries and grapes than in other soft fruits, similar trends may still be expected.

Among hormones, ABA is a major, and often dominant, regulator of ripening in most of the non-climacteric soft fruits addressed here. ABA rises at ripening onset and regulates anthocyanin accumulation, sugar metabolism, cell-wall remodeling, and other ripening-related processes through both canonical and non-canonical signaling pathways [40,41]. During softening, particularly in strawberries, enhanced ABA signaling is accompanied by reduced auxin activity and stage- and cultivar-dependent changes in gibberellins, cytokinins, strigolactones, ethylene, and polyamines [40,80,81]. Functional studies link ABA to firmness loss through the regulation of cell-wall-remodeling genes, including *FaRGL1*, *FaXyl1*, *FaXTH1*, *FaCx*, and *FaPL*, whose products contribute to pectin and hemicellulose modification and the progressive loss of tissue cohesion [80,81]. Experimental attenuation of ABA biosynthesis or perception delays ripening and softening in strawberries, whereas ABA-promoted softening has also been reported in ~~the~~ blueberries [80,82]. Nevertheless, evidence for the contribution of other hormones to softening remains largely correlational and varies with species, cultivar, developmental stage, and the specific hormone examined [40,81].

Importantly, evidence from strawberries [41], grapes [83], and sweet cherries [84] indicates that ABA does not act independently but rather operates within a broader redox-regulated network. In this network, ABA and ROS participate in interconnected signaling processes that link ripening progression with oxidative status and membrane

remodeling [79,83]. In grapes, this network extends into phenolic metabolism and late-ripening stress responses [85], whereas in blueberries, available evidence also supports an ABA-centered but context-dependent role during ripening and storage, likely interacting with ethylene-mediated responses [86]. The ABA-centered network also interacts with auxin, ethylene, jasmonates, gibberellins, and polyamines, indicating that ripening outcomes depend on hormonal balance and developmental context rather than ABA alone [87]. These findings suggest that the ABA–ROS–membrane interaction is crucial for connecting ripening and postharvest deterioration, making it a potential target for MLT action.

3.4. Flavor-Related Metabolic Changes During Ripening and Senescence

Flavor in non-climacteric soft fruits depends on interactions among sugars, organic acids, volatile compounds, and specialized metabolites, which together shape sweetness, acidity, aroma, bitterness, and astringency [42,88,89]. Because flavor perception results from interactions among volatile and non-volatile compounds, individual metabolite concentrations do not directly predict sensory perception. During postharvest storage, continued respiration and substrate catabolism alter soluble solids, sugars, organic acids, and the sugar–acid balance, contributing to flavor-related changes as ripening progresses toward senescence [42,43]. Such changes have been reported in sweet cherries, strawberries, grapes, blueberries, and raspberries, although their magnitude and direction depend on species, cultivar, maturity, treatment, and storage conditions [25,90–93].

Postharvest senescence also affects phenolics, flavonoids, proanthocyanidins, amino acids, and volatile profiles that may contribute to flavor quality [21,92–94]. However, relationships between these metabolites and sensory attributes are often nonlinear and context-dependent [89], and evidence for volatile-related effects remains comparatively limited, although changes in terpene metabolism have been reported in blueberries [59]. Therefore, these pathways represent a potential interface through which MLT may modulate postharvest quality, but changes in physicochemical or biochemical markers should be interpreted as alterations in flavor-related constituents rather than confirmed changes in perceived flavor unless supported by direct sensory evidence.

4. Mechanisms of MLT Action in Soft Fruits

In soft fruits, MLT has been increasingly described as a postharvest modulator capable of delaying deterioration through multiple, interconnected physiological responses. Unless otherwise indicated, the mechanistic evidence discussed in this section refers to MLT applied after harvest. Reported effects commonly converge on redox buffering and membrane-related responses, with downstream effects on ripening- and senescence-related changes in firmness, water status, leakage, and decay susceptibility [35]. Accordingly, this section synthesizes the mechanistic evidence explaining how MLT may modulate the deterioration processes outlined in Section 3, focusing on (i) regulation of redox homeostasis and antioxidant defenses, which is supported across several fruit species; (ii) membrane-related responses, cell-wall metabolism, water loss, leakage, and cuticular wax traits, although direct evidence for cuticular regulation remains more limited; and (iii) ripening- and stress-related signals, including ABA–ROS interactions and other hormonal pathways, for which evidence is more limited and species-specific. Because MLT responses may vary with species, cultivar, concentration, maturity stage, and storage conditions, the evidence is interpreted as a set of context-dependent mechanisms rather than as a uniform postharvest response.

4.1. Regulation of Redox Homeostasis

Studies on postharvest MLT treatments in blueberries, raspberries, grapes, strawberries, and sweet cherries commonly identify redox regulation as the strongest and most widely replicated mechanism associated with quality preservation in soft fruits. Across these studies, MLT is generally associated with reduced oxidative damage, lower lipid peroxidation, enhanced antioxidant enzyme activity, and preservation or stimulation of non-enzymatic antioxidant pools, including phenolics, flavonoids, anthocyanins, ascorbic acid (AsA), and glutathione. However, ROS levels and antioxidant responses vary among species, cultivars, treatment concentrations, and storage conditions, indicating that MLT acts as a context-dependent redox modulator rather than as a uniform ROS suppressor (Table 2).

Mechanistically, SOD first converts $O_2\bullet^-$ into H_2O_2, which is then removed by CAT, POD, and APX [77]. In the APX-dependent pathway, AsA acts as an electron donor, and it is regenerated through the ascorbate–glutathione cycle (AsA–GSH) by dehydroascorbate reductase (DHAR), monodehydroascorbate reductase (MDHAR), and glutathione reductase (GR), thereby maintaining AsA and GSH availability and sustaining antioxidant buffering during storage [77,95]. This metabolic pathway provides a biochemical basis through which MLT can reduce oxidative injury while maintaining ROS at levels compatible with signaling and stress adaptation. This redox-regulatory pattern was observed in blueberries [10], raspberries [93], grapes [11], strawberries [25,96], and sweet cherries [90], where MLT enhanced ROS-scavenging enzyme activity and AsA–GSH antioxidant recycling, thereby improving ROS detoxification. These responses are generally associated with lower membrane lipid peroxidation, cellular leakage, pigment degradation, browning, and senescence-associated softening. Consequently, MLT contributed to maintaining firmness, color, and overall postharvest quality.

However, MLT-mediated redox regulation should not be interpreted as a simple or uniform suppression of ROS in every fruit system. In the strawberry cv. Selva, immersion in 100 μM MLT increased SOD but lowered CAT and APX, resulting in higher H_2O_2 accumulation rather than immediate H_2O_2 removal. This response coincided with increased PAL activity, total phenols, anthocyanins, antioxidant capacity, and GABA (γ-aminobutyric acid) transaminase activity, suggesting a link between redox signaling, phenylpropanoid metabolism, and GABA-related stress response [97]. Thus, under certain conditions, MLT may promote a controlled H_2O_2 signal that activates antioxidant and defense metabolism before critical oxidative damage occurs. This positions MLT as a redox modulator rather than just a ROS scavenger. Depending on factors like species, dosage, and storage, MLT can enhance ROS detoxification to delay senescence or enable selective redox signaling that stimulates defense pathways. In both cases, MLT may contribute to quality preservation by limiting oxidative injury or by activating protective metabolism before irreversible senescence-associated damage occurs.

MLT-associated antioxidant buffering is also linked to the preservation or stimulation of non-enzymatic antioxidant pools, particularly phenolics, flavonoids, anthocyanins, ascorbic acid, and glutathione across soft fruits, as summarized in Table 2. These compounds contribute directly to radical-scavenging capacity and help maintain color, nutritional value, and oxidative stability during storage [98]. Importantly, phenolic metabolism can connect antioxidant protection with structural and antimicrobial defense through phenylpropanoid-derived compounds involved in cell-wall reinforcement, lignin-related barriers, and pathogen resistance [99]. The phenylpropanoid pathway is crucial for this response, with PAL catalyzing phenylalanine into trans-cinnamic acid, thereby directing carbon flow into phenylpropanoid metabolism; cinnamate 4-hydroxylase (C4H), 4-coumarate-CoA ligase (4CL), and chalcone synthase (CHS) extend this pathway, and downstream

enzymes support the synthesis of phenolic acids, flavonoids, anthocyanins, and lignin-related compounds [100]. Within this network, POD links phenolic metabolism with redox control by using H_2O_2 to oxidize phenolics, contributing to defense or lignification but also potentially to browning when oxidation is excessive or poorly controlled. Consistent with this, MLT has been reported to modulate phenylpropanoid-related enzymes, including PAL, C4H, 4CL, CAD, PPO, and POD, together with phenols, flavonoids, anthocyanins, and lignin in blueberries [92], raspberries [93], sweet cherries [101], and grapes [21]. Evidence also indicates that MLT upregulated genes associated with the phenylpropanoid pathway [94] and its downstream branches, particularly flavonoid and anthocyanin biosynthesis [23,102,103].

Overall, the evidence supports MLT as a redox modulator in soft fruits, coordinating ROS detoxification, antioxidant recycling, phenolic antioxidant accumulation, and, in some cases, controlled redox signaling. This redox regulation provides the biochemical basis for limiting oxidative injury, but its effects on visible quality depend on how ROS metabolism is coupled to membranes, cell walls, surface barriers, and ripening-related signaling during storage.

Table 2. Comparative effects of exogenous postharvest MLT on oxidative stress, membrane-related indicators, antioxidant defense, and phenolic metabolism across soft-fruit species. The MLT concentration corresponds to that at which the reported biochemical and physiological responses were evaluated and does not necessarily represent the only concentration assessed in the corresponding study.

Fruit	Cultivar	MLT (μM)	Oxidative Stress/ Membrane-Related Indicator	Antioxidant Defense/ Redox Status	Phenolic-Related Response	Reference
blueberry	Duke	100	-	antioxidant capacity maintained	↑ total polyphenols; anthocyanins maintained	[104]
	Berkley	1000	↓ MDA, H_2O_2; ↓ PPO, POD, LOX-related browning	↑ SOD, ↑ CAT, APX activities; ↑antioxidant activity; higher AsA retention	↑ total polyphenols, flavonoids, anthocyanins	[10]
	-	300	↓ LOX activity, lipid peroxidation, and membrane permeability	↑ antioxidant capacity; reduced AsA degradation	↑ anthocyanins;	[92]
	Powder blue	300	-	↑ POD activity	↑ PAL, C4H, 4CL, CAD activities; ↑ total phenolics, flavonoids, anthocyanins, and lignin; ↑ expression of *VaPAL*, *VaC4H*, *Va4CL*, *VaCAD*, *VaPPO*, and *VaPOD*	[30]
	Powder blue	50	↓ ROS and lipid peroxidation;	↑ APX, GST activities; higher AsA retention ↑ expression of *VcAPX* and *VcGST*	Maintained anthocyanins and total phenolics; ↑ PAL activity and *VcPAL* expression	[105]
raspberry	Driscoll's variety	100		antioxidant capacity maintained	anthocyanins and total phenolics maintained	[104]
	Sanctus	10		↑ CAT activity ↑antioxidant capacity	↑ PAL activity, total phenolics, flavonoids, anthocyanins	[93]
grape	Cuibao Seedless	100	↓ MDA and browning index; ↓ PPO, POD-related browning	↑ SOD, CAT activities	↑ total phenolics and flavonoids; ↑ expression of *VvPAL*, *VvCHI*, *VvF3H2*, and *VvAN*	[102]
	Shine Muscat	200	↓ MDA and $O_2\bullet^-$	↑ hydroxyl radical and antioxidant capacity; ↑ SOD and CAT activities; ↓ PPO and moderate POD activities	↑ total phenolics and flavonoids; ↑PAL, 4CL, and C4H activities	[106]
	Shine Muscat	10	↓ lipid peroxidation, MDA-related damage	↑ SOD, CAT, APX activities	-	[107]

Table 2. *Cont.*

Fruit	Cultivar	MLT (μM)	Oxidative Stress/ Membrane-Related Indicator	Antioxidant Defense/ Redox Status	Phenolic-Related Response	Reference
grape	Kyoho	100	-		↑ phenolics, flavonoids, and anthocyanins	[27]
	Muscat Hamburg	200	↓ MDA and membrane permeability	↑ SOD, POD, CAT activities	↑ PAL, ↑ PPO activities; ↑ total phenolics and flavonoids	[108]
	Crimson Seedless	100	↓ H_2O_2, $O_2\bullet^-$;	↑ POD, ↑ CAT activities	-	[109]
	Fengzao	500	↓ MDA, H_2O_2, $O_2\bullet^-$	↑ SOD, CAT, APX activities; higher AsA retention	-	[11]
	Kyoho	200	-	↑ CAT activity	↑ PAL activity, total phenolics; ↑expression of 12 phenolic and amino-acid pathway genes	[21]
strawberry	Albion	100	-	antioxidant capacity maintained	↑ total polyphenols; anthocyanins maintained	[104]
	Rubygem	500	↓ MDA	↑ CAT, APX, POD, SOD activities; ↑ AsA retention; ↑ antioxidant capacity	-	[96]
	Camino Real	100	-	↑ SOD, CAT, APX, POD activities; ↑ antioxidant capacity	-	[26]
	Hongyan	50–100	-	-	↑ anthocyanins; ↑ expression of *FaPAL*, *FaC4H*, *Fa4CL* and anthocyanin-biosynthesis genes	[103]
	Luca	100	-	-	↑ total phenolics and anthocyanins	[110]
	Hongyan	100 or 1000	↓ H_2O_2, MDA	↑ antioxidant capacity; ↓AsA content	↑ total phenolics and flavonoids	[25]
	Selva	100	↑ H_2O_2 accumulation as a defense signal	↑ SOD and ↓CAT and APX activities as a defense signal; ↑ DPPH scavenging	↑ PAL activity, total phenolics, and anthocyanins	[97]
sweet cherry	Lapins	100	-	antioxidant capacity maintained	anthocyanins and total polyphenols maintained	[104]
	Samba	500	-	↑ APX activity; ↑ lipophilic antioxidant activity	anthocyanins and flavonoids maintained	[111]
	Sweetheart	1000	-	↑ antioxidant activity; higher AsA retention	Maintained total phenolics and anthocyanins	[112]
	Siah Mashhad	100	↓ MDA and H_2O_2; ↓ PLD, LOX, and PPO-related browning	↑ SOD, CAT, APX, and GR activities	↑ phenolics, flavonoids, and anthocyanins; ↑ PAL and CHS activities	[101]
	Ferrovia	500	-	-	↑ phenolic acids, flavan-3-ols, procyanidins and anthocyanins; ↑ *PaC4H* and *Pa4CL* expression	[23]
	Santina and Royal Rainier	100	↓ MDA;	↑expression of genes encoding CAT, SOD, APX, MDHAR, DHAR, and GR	↑ total anthocyanins; up-regulation of genes *DFR* and *UFGT*	[113]
	Sunburst	100	↓ $O_2\bullet^-$, H_2O_2, MDA and membrane permeability;	↑ SOD, CAT, APX, DHAR, GR, MDHAR activities; ↑ AsA and GSH contents	-	[90]

MLT—melatonin; ↑—increased, enhanced or up-regulated; ↓—decreased, inhibited or down-regulated; "-"—not reported or not directly measured. MDA—malondialdehyde; H_2O_2—hydrogen peroxide; $O_2\bullet^-$—superoxide anion; ROS—reactive oxygen species; LOX—lipoxygenase; PLD—phospholipase D; PPO—polyphenol oxidase; SOD—superoxide dismutase; CAT—catalase; APX—ascorbate peroxidase; POD—peroxidase; GR—glutathione reductase; DHAR—dehydroascorbate reductase; MDHAR—monodehydroascorbate reductase; GST—glutathione S-transferase; AsA—ascorbic acid; DHA—dehydroascorbic acid; GSH—reduced glutathione; GSSG—oxidized glutathione; PAL—phenylalanine ammonia-lyase; C4H—cinnamate 4-hydroxylase; 4CL—4-coumarate-CoA ligase; CAD—cinnamyl alcohol dehydrogenase; CHS—chalcone synthase; CHI—chalcone isomerase; DFR—dihydroflavonol 4-reductase; UFGT—UDP-glucose flavonoid 3-O-glucosyltransferase; Vc—*Vaccinium* gene prefix; Va—*Vaccinium ashei* gene prefix; Fa—*Fragaria* × *ananassa* gene prefix; Pa—*Prunus avium* gene prefix; Vv—*Vitis vinifera* gene prefix.

4.2. Barrier, Membrane, and Cell-Wall Integrity

In contrast to the broad evidence supporting MLT-mediated redox buffering in soft fruits, direct evidence for its effects on structural traits remains limited. Nevertheless, available studies suggest that MLT may help maintain postharvest quality by influencing both the external cuticular barrier and internal cell-wall metabolism [114]. This structural protection may contribute to the reduced water loss frequently observed after MLT treatment, although evidence linking water retention to cuticular preservation is currently limited mainly to blueberries. In rabbiteye blueberries, postharvest MLT treatment delayed the decline in total cuticular wax and altered wax composition in a cultivar-dependent manner, with reported water loss reductions of 35.61% in 'Baldwin' and 62.90% in 'Garden Blue' by day 35 of cold storage [31]. Similarly, other studies reported that MLT maintained the rod-like morphology of cuticular wax, delayed wax degradation, and selectively modified wax metabolism, including the retention of triterpenoids and long-chain saturated fatty acids [114,115]. Together, these findings suggest that, at least in blueberries, MLT-mediated postharvest protection extends beyond internal biochemical defenses to include preservation of cuticular wax properties, which was associated with reduced water loss during storage. However, changes in wax amount, composition, or morphology do not directly demonstrate reduced cuticular permeability, and comparable evidence for cuticle or wax preservation remains scarce in other soft fruits, so this mechanism should not yet be generalized across the entire group.

At the tissue level, cell-wall stability and membrane integrity provide complementary structural links between biochemical responses and postharvest quality. Evidence suggests that MLT can decrease enzymatic cell-wall disassembly [92]. In blueberries, MLT inhibited pectin methylesterase (PME), polygalacturonase (PG), cellulase (Cx), β-glucosidase, and β-galactosidase activities and downregulated cell-wall metabolism genes, including *VcPE*, *VcPG*, *VcBG6*, and *VcGAL*. These changes maintained higher protopectin and cellulose contents, indicating that the treatments slowed the conversion of insoluble wall polymers into more soluble forms associated with softening [92,114]. By limiting cell-wall disassembly and preserving tissue structure, these responses may also indirectly support tissue hydration and turgor, thereby complementing the effects of MLT on postharvest water retention. A similar pattern was observed in *B. cinerea*-inoculated blueberries, accompanied by lower water-soluble pectin accumulation, better firmness retention, and improved resistance to gray mold [115]. In table grapes, MLT also reduced PME, Cx, β-galactosidase, and PG activity, which was associated with better maintenance of firmness during refrigerated storage [109,116,117].

In parallel, the reductions in MDA, lipid peroxidation, membrane permeability, LOX, and phospholipase D (PLD) reported in several studies (Table 2) provide indirect evidence of reduced membrane damage following MLT treatments. These membrane-related indicators link the redox effects described in Section 4.1 with postharvest quality outcomes, as lower lipid peroxidation and leakage are consistent with better preservation of cellular compartmentation and turgor, and may therefore support tissue water status and turgor-dependent texture [92,101,107]. However, firmness retention should not be attributed to membrane protection alone, because it also depends on cell-wall architecture, pectin solubilization, tissue hydration, and cultivar-specific anatomy [60,62].

Overall, although direct structural evidence remains limited, current findings support that MLT contributes to texture and water-balance maintenance through three interconnected levels: maintenance of surface wax properties where measured, suppression of enzymatic cell-wall degradation, and indirect evidence of improved membrane integrity. These structural and biochemical changes are associated with quality outcomes, such as reduced leakage, slower softening, better water retention, and lower decay susceptibility. Together, these responses are associated with improved postharvest performance in soft fruits and highlight the need for more direct measurements of cuticle permeability, microcracking, epidermal integrity, and cellular compartmentation in future studies.

4.3. Ripening, Senescence, Hormonal Crosstalk and Defense Signaling

Beyond the redox and structural mechanisms discussed above, postharvest MLT also appears to regulate broader ripening- and senescence-associated networks. Evidence shows that MLT does not act through a single anti-ripening pathway; its effects vary by species, cultivar, concentration, developmental stage, and storage conditions. Direct evidence for hormonal crosstalk remains comparatively limited and is derived partly from developmental studies. For example, in developing strawberries, MLT delays ripening by reducing H_2O_2, lowering ABA content, and downregulating *NCED* genes [118]. Conversely, in developing grapes, MLT promotes ripening by increasing ABA, and H_2O_2 levels, and enhancing ethylene signaling [119]. Further evidence of MLT–ethylene interaction was observed in blueberries, where inhibition of ethylene action by 1-MCP reduced terpene accumulation, while MLT partially counteracted this response, indicating that both signals participate in regulating terpene metabolism [59]. These contrasting responses indicate that MLT participates in hormone–redox crosstalk, particularly involving ABA and ethylene, rather than acting as a universal inhibitor of ripening.

MLT may also modulate flavor-related metabolism during postharvest storage. In strawberries and grapes, MLT maintained higher TSS and titratable acidity during storage, resulting in a higher taste index, although its effect on aroma was selective [27,110]. In 'Luca' strawberries, the overall volatile profile remained largely unchanged, while individual aroma-active esters, including ethyl hexanoate and ethyl 2-methylbutanoate, were altered [110]. In 'Kyoho' grapes, MLT altered the volatile profile, increasing esters, aldehydes, and alcohols while reducing terpene accumulation during prolonged storage [27]. More direct mechanistic evidence indicates regulation of aroma-biosynthetic pathways. In 'Shine Muscat' grapes, MLT upregulated the expression of genes involved in fatty-acid and terpenoid metabolism, including *FAD*, *HMGR*, and *VvTPS12* [107]. In blueberries, MLT enhanced terpene biosynthesis through increased expression of *VcDXS*, *VcHDR*, *VcGGPS*, and *VcTPS* [59]. Thus, MLT-mediated flavor responses appear to involve modulation of both primary taste components and volatile biosynthesis.

Evidence for exogenous MLT-mediated regulation of MLT metabolism is limited mainly to sweet cherries and grapes, where exogenous MLT increased fruit MLT content, altered the expression of MLT-biosynthetic genes, and modulated ripening-related quality changes [21,22,101]. In sweet cherries, MLT increased fruit MLT content and upregulated genes involved in MLT biosynthesis, including *PaSNAT*, *PaT5H*, and *PaASMT*, suggesting activation of endogenous MLT biosynthesis, although the contribution of absorbed exogenous MLT to the measured MLT content cannot be excluded [22]. Sharafi et al. (2021) [101] further showed that MLT promoted endogenous hydrogen sulfide (H_2S) accumulation through greater L-cysteine desulfhydrase (LCD) and D-cysteine desulfhydrase (DCD) expression and activity, suggesting that MLT-mediated senescence delay may involve interaction between MLT metabolism and H_2S-related signaling during cold storage, together with stronger antioxidant and phenylpropanoid responses. In table grape,

MLT reduced berry abscission and rot index while increasing amino acid accumulation, fruit MLT content, and the expression of MLT-biosynthetic genes such as *VvTDC*, *VvT5H*, *VvSNAT*, and *VvASMT* [21]. Thus, MLT may modulate postharvest senescence through coordinated changes in MLT metabolism, redox metabolism, H_2S-related signaling, and phenolic accumulation rather than through a single anti-senescence pathway, although evidence for H_2S-related responses remains largely limited to sweet cherries.

Limited evidence suggests that MLT may also participate in stress-response regulation through defense signaling and amino acid–related metabolic pathways. In strawberry cv. Selva, MLT enhanced GABA-shunt activity, which was associated with reduced decay and maintenance of nutritional quality, suggesting that GABA-related metabolism may contribute to postharvest stress tolerance during cold storage [97]. In grapes, proteomic evidence showed that MLT upregulated proteins associated with arginine (Arg) and proline (Pro) metabolism and polyamine biosynthesis, including upregulation of *VvADC*, *VvODC*, *VvNAC*, *VvSPDS*, and *VvCuAO*, together with higher Arg, Pro, GABA, putrescine, spermidine, and spermine contents. These metabolites are commonly associated with osmotic adjustment, cellular tolerance, membrane stabilization, redox balance, and stress adaptation [94]. These amino acid- and polyamine-related responses provide an additional bridge between metabolic stress tolerance and the tissue integrity mechanisms described in Section 4.2. However, evidence for GABA- and polyamine-related responses remains limited to individual studies and should therefore be considered emerging in soft fruits.

In pathological terms, studies found that MLT enhanced disease resistance [92,108]. In grapes, MLT reduced gray mold development caused by *Botrytis cinerea*. The response did not involve a direct effect of MLT on spore germination or mycelial growth, indicating that disease suppression was mainly associated with host defense activation rather than a direct antifungal effect [108]. Hormonal crosstalk also appears to contribute to MLT-mediated defense responses. In blueberries, MLT enhanced disease resistance in association with jasmonic acid-related signaling and phenylpropanoid metabolism, upregulating genes related to jasmonic acid synthesis (*VaLOX*, *VaAOS*, and *VaAOC*), pathogenesis-related proteins (*VaGLU* and *VaCHT*), and accumulation of defense-associated metabolites [30]. This host-defense interpretation is consistent with the redox and phenylpropanoid responses described above: controlled ROS signaling, phenolic metabolism, and pathogenesis-related enzymes may reinforce resistance to decay without requiring MLT to act directly as an antimicrobial compound.

Overall, as summarized in Figure 2, MLT-mediated quality preservation in soft fruits is best understood as a context-dependent network response rather than the result of a single protective mechanism. Within this network, redox homeostasis has the strongest and most consistent support across soft-fruit species, while membrane- and cell-wall-related responses are supported by a more restricted body of evidence. In contrast, cuticular wax-related responses, polyamine metabolism, hormone–redox crosstalk involving ABA and ethylene, jasmonic acid-related defense signaling, MLT-related metabolism, H_2S signaling, GABA-related responses, and other host-defense pathways remain comparatively limited and species-specific. Together, these responses may contribute, to different extents, to ROS control, cellular integrity, and postharvest stress tolerance, thereby slowing deterioration during storage.

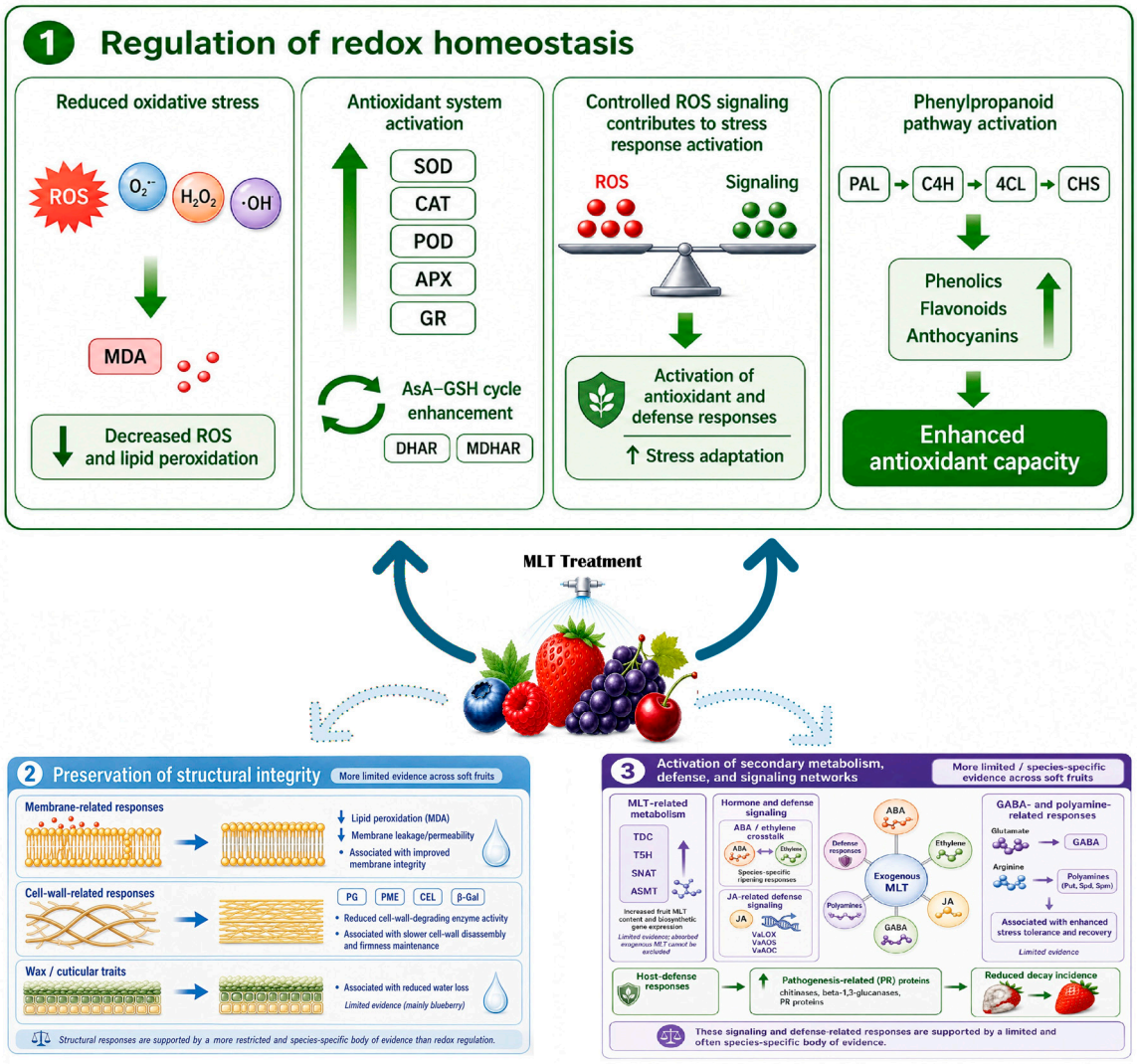


Figure 2. Summary of the proposed mechanisms underlying melatonin-mediated postharvest quality preservation in soft fruits: (1) regulation of redox homeostasis, (2) preservation of structural integrity, and (3) activation of secondary metabolism, defense, and signaling networks. Solid arrows indicate more consistently supported mechanisms, whereas dashed arrows indicate mechanisms supported by more limited or species-specific evidence.

5. Efficacy Determinants, Quality Responses, and Application Strategies

A single factor does not determine the efficacy of MLT treatments for soft fruits; rather, it is the interaction between extrinsic treatment conditions and intrinsic fruit characteristics. This section examines those factors, the resulting effects on fruit quality, and the main application strategies used to optimize treatment outcomes.

5.1. Extrinsic Efficacy Determinants

Among the extrinsic determinants, treatment concentration is one of the most important; however, the available evidence does not support a simple "higher-dose-is-better" interpretation. Effective concentrations range from low µM to mM levels depending on the commodity, cultivar, and measured quality response (Table 3). In blueberries, effective responses ranged from 5 to 300 µM during cold- and room-temperature storage, affecting decay control and delaying postharvest senescence [30,115]. In grapes, the most effective treatments range from 10 to 1000 µM, with 100 µM being the most used concentration among cultivars during cold storage. These treatments not only help maintain fruit quality

but also protect various components related to aroma and flavor [27,107,116]. In strawberries, a more common favorable response was observed with 100 μM, which was effective in reducing postharvest fungal decay, maintaining fruit physicochemical traits, and regulating membrane deterioration [26,97]. Similarly, in sweet cherries, a concentration of 100 μM was effective during long-term cold storage, maintaining sensory and quality attributes, while treatments at 1000 μmol L^{-1} maintained quality [90,112]. Overall, MLT concentration should be optimized for each fruit–cultivar–storage system rather than transferred directly across studies.

Application methods are important extrinsic determinants of treatment outcome because dipping, immersion, soaking, spraying, and coating differ in contact efficiency, uptake potential, surface wetting, mechanical risk, and drying requirements. Immersion was the most commonly reported application method (Table 3), although spraying and coating treatments also showed promising results [104,120]. Another critical MLT efficacy determinant is the treatment exposure duration. Postharvest MLT applications shown in Table 3 used contact periods ranging widely from 3 to 360 min, indicating substantial variation in treatment duration among commodities and experimental protocols [91,115]. In grapes, exposure times were generally the longest (>20 min) (Table 3), while in strawberries, treatments were generally 5 min except in 'Camino Real' [26] and 'Hongyan' [103] strawberries; these marked differences possibly reflect differences in surface properties, wax coverage, or treatment objective.

Treatment timing is also an important determinant of MLT efficacy. While the postharvest treatments summarized in Table 3 were applied to harvest-ripe fruit, some studies evaluated combined pre- and postharvest applications, particularly in sweet cherries. In 'Ferrovia', 500 μM MLT was applied as foliar sprays 2 and 1 weeks before harvest, as a 10 min postharvest immersion, or as a combination of both treatments. The combined treatment produced firmer fruit after cold storage and resulted in the greatest accumulation of several phenolic compounds and expression of phenylpropanoid-related genes [23]. More recently, 'Sunburst' cherries received two preharvest foliar applications of 500 μM MLT, at pit hardening and the beginning of anthocyanin biosynthesis, followed by a 15 min postharvest dip in the same concentration and storage for 21 days at 2 °C. Single pre- or postharvest treatments increased endogenous MLT but tended to stabilize or attenuate phenolic accumulation, whereas the combined treatment produced the highest endogenous MLT and phenolic concentrations, including an approximately 29% increase in total anthocyanins relative to harvest values, suggesting a cumulative or synergistic effect of prolonged MLT exposure [121]. Overall, combined pre- and postharvest applications appear promising for enhancing MLT-related responses; however, the available evidence remains limited to a single soft-fruit species.

Co-application of MLT with other phytohormones may represent an additional factor influencing postharvest efficacy, although evidence in soft fruits remains very limited. In 'Shine Muscat' grapes, 200 μM MLT combined with 5 μM 24-epibrassinolide (EBR), a brassinosteroid, more effectively maintained firmness and cell-wall integrity than either treatment alone by limiting cellulose and protopectin degradation, soluble pectin accumulation, and the activities of cell-wall-degrading enzymes [106]. The combined treatment also reduced MDA accumulation and enhanced antioxidant-related responses. However, although the combined treatment generally outperformed the individual applications, statistical synergy cannot be established because an MLT × EBR interaction effect was not reported. A factorial analysis of interaction effects would be needed to determine whether the combined response is additive or synergistic.

Storage conditions further determine whether MLT responses translate into meaningful postharvest benefits. Most studies have been conducted under cold storage, commonly

between 0 and 5 °C, where MLT generally delayed softening, decay, water loss, oxidative injury, or senescence symptoms (Table 3). However, ambient or high-temperature studies are also important because they better simulate distribution, retail display, and interruptions in the cold chain. In 'Shine Muscat' grapes, MLT maintained quality under both 4 °C and 35 °C storage, suggesting a role in temperature-stress tolerance as well as conventional cold-storage protection [107]. Room-temperature studies in blueberries [104,115], raspberries [104], strawberries [97], grapes [11,91,108], and sweet cherries [22] also indicate that MLT may reduce weight loss, browning, abscission, and quality deterioration under non-refrigerated conditions. Thus, MLT efficacy should be evaluated in relation to the intended postharvest scenario, whether continuous refrigeration, interrupted cold chain, ambient marketing, dehydration stress, fresh-cut handling, or pathogen challenges.

5.2. Intrinsic Efficacy Determinants and Quality Responses

Intrinsic fruit characteristics are equally important in explaining variability among studies (Table 3). Soft fruits differ markedly in fruit size, surface morphology, wax load, trichomes, epidermal permeability, cluster structure, pedicel retention, and susceptibility to handling damage [1,53,57]. These differences occur not only among species but also among cultivars within the same species. Therefore, cultivar specificity should also be considered as a source of experimental variation, as was observed in MLT-treated blueberries and sweet cherries [31,113]. Treatment efficacy is also likely to depend on fruit maturity and physiological status at application because ripening involves substantial changes in hormone balance, antioxidant metabolism, surface properties, firmness, and susceptibility to senescence and decay [52,63].

These intrinsic differences may influence which postharvest limitations are most relevant in each fruit and, consequently, which quality responses are most frequently associated with MLT treatment. In blueberries, responses were closely associated with surface and structural traits, including cuticular wax properties, water loss, softening, and susceptibility to gray mold and other pathogens [31,114,115]. In grapes, relevant postharvest limitations included berry abscission, rachis or cluster browning, decay, water loss, firmness loss, and changes in aroma or phenolic composition [21,27,107,122]. Strawberry studies mainly emphasized fungal decay, firmness, color, soluble solids, acidity, and possible aroma-related trade-offs [25,26,97,110]. In sweet cherries, MLT studies have focused on firmness, respiration, weight loss, browning, pitting, phenolics, anthocyanins, sensory quality, and cultivar-dependent cold-storage responses [90,111,113,120,123]. This variability highlights how MLT interacts with the unique postharvest biology of each fruit.

Beyond the directional responses summarized in Table 3, available quantitative evidence indicates that MLT can produce substantial reductions in decay and weight loss and improve firmness retention, although differences in endpoints and experimental conditions limit direct comparisons among studies [21,26,114]. For example, MLT reduced rotten index by 58.37% and berry abscission by 37.50% in 'Kyoho' grapes [21], while final weight loss in strawberries decreased from 22.60% to 12.11%, corresponding to an approximate 46.4% relative reduction [26]. Across studies, however, differences in cultivar, concentration, storage conditions, evaluation time, and reporting methods prevent direct ranking of treatment efficacy. These limitations highlight the need for standardized control-based measures such as relative decay or weight-loss reduction, firmness retention, marketable-life extension, and saleable-fruit percentage.

Table 3. Application conditions and main postharvest effects of MLT treatments in soft fruits. Where available, quantitative changes are expressed as percentage differences relative to the corresponding control and were obtained from values explicitly reported in the text or tables of the original studies.

Fruit	Cultivar	Application Method	MLT Treatment	Storage	Main Postharvest Effects	Reference
blueberry	Berkley	Immersion	0 and 100 µM Time: 30 min MET: 100 µM	5 °C, 85–90% RH, 21 d	↓ weight loss (44%), browning; ↑ TA (25%), maintained overall quality	[10]
	-	Immersion	0, 100, 300 and 500 µM Time: 3 min MET: 300 µM	0 °C, 80 d	maintained firmness, TSS and TA, ↓ respiration rate (7%) and decay rate (57%)	[92]
	Powder blue	Immersion	0, 100, 300 and 500 µM Time: 3 min MET: 300 µM	0 °C, 80 d,	↓ postharvest decay by resistance induction	[30]
	L25	Immersion	5, 10, 20 and 50 µM Time: 3 min MET: 5 µM	22–25 °C, 85–95% RH, 10 d	↓ gray mold, ↓ disease incidence, ↓ weight loss, ↑ firmness, maintenance of luminosity/color, ↑ TA (21%), ↑ AsA (4%), ↓ TSS (19%) associated with maturation delay, ↓ PE, ↓ PG, ↓ Cx, ↓ β-Gal, ↓ α-L-Af	[115]
	Duke	sprayed by nebulization	0 and 100 µM MET: 100 µM	Room temperature until 70% decay	↓ postharvest decay and, ↓ weight loss	[104]
	Powder blue	sprayed	0, 10, 50 and 250 µM Time: 3 min MET: 50 µM	4 °C, 42 d	↓ weight loss, ↓ decay, ↑ firmness, maintenance of TSS and TA	[105]
raspberry	Sanctus	Immersion	0, 1, 10, and 100 µM Time: 5 min MET: 1 µM	4 °C, 90–95% RH	↓ decay (37%); prolonged shelf life; maintained TSS and TA	[93]
	Driscoll's variety	sprayed by nebulization	0 and 100 µM MET: 100 µM	Room temperature until 70% decay	↓ postharvest decay (~20%) and severity (up to 70%), ↓ weight loss, ↑ firmness, maintenance of luminosity/color	[104]
grape	Kabarcık (bunches)	Immersion	0, 25, 250 µM Time: 180 and 360 min MET: 250 µM-180 min	23 °C, 15 d	↓ weight loss (25%), ↑ shelf life, ↑ pH, maintenance/modulation of titratable acidity during storage.	[91]
	Cuibao Seedless (bunches)	Immersion	0 and 100 µM Time: 20 min MET: 100 µM	5 °C, 85–90% RH, 20 d	↓ browning index, ↓ weight loss, and preserved the contents of ascorbic acid TSS, and soluble proteins	[102]
	Shine Muscat	Immersion	0 and 10 µM Time: 30 min MET: 10 µM	4 °C, 21 d; 35 °C, 6 d	↓ weight loss (30%), decay (60%) and browning; maintenance of firmness, TSS and TA, ↓ cell damage; ↑ visual quality and aroma	[107]
	Kyoho (bunches)	Immersion	0, 50 and 100 µM Time: 30 min MET: 100 µM	4 °C, 25 d	↓ rachis browning index (40%), weight loss, decay (100%), berry abscission (77%), respiration rate (21%), maintained TSS, protected the antioxidant compounds and several aroma volatile components	[27]
	Red Globe (bunches)	Immersion	0 and 100 µM Time: 5 min MET: 100 µM	4 °C, 56 d	↓ firmness loss (27%); ↑ TSS (4%) and TA (11%); maintenance of glucose, fructose and organic acids, ↑ cuticular wax (26%); ↓ PME, PG (24%) and β-Gal (13%)	[117]
	Muscat Hamburg	Immersion	0, 20, 200 and 2000 µM Time: 20 min MET: 200 µM	21 °C, 95% RH, 8 d	↓ gray mold incidence and severity	[108]
	Crimson Seedless (bunches)	Immersion	0, 50, and 100 µM Time: 30 min MET: 100 µM	0 °C, 90% RH; 35 d	↓ weight loss; maintenance of TSS, TA, firmness and berry-rachis adhesion; ↑ shelf life	[109]

Table 3. *Cont.*

Fruit	Cultivar	Application Method	MLT Treatment	Storage	Main Postharvest Effects	Reference
grape	Fengzao	Immersion	0, 50, 100, 500, and 1000 µM Time: 2 h MET: 500 µM	24 °C, 15 d	maintained firmness, TSS and shelf life; ↓ weight loss	[11]
	Crimson Seedless	Immersion	0, 100, 1000 and 10,000 µM MET: 1000 µM	1 °C, 35 d	↓ weight loss (34%), maintained color, berry quality and bioactive compounds	[116]
	Kyoho (bunches)	Immersion	0 and 200 µM Time: 25 min MET: 200 µM	4 °C, 85–90% RH, 25 d	↓ berry abscission/detachment (38%), ↓ decay (58%), no effect on TSS and TA	[21]
strawberry	Albion	sprayed by nebulization	0 and 100 µM MET: 100 µM	Room temperature until 70% decay	↓ postharvest decay (20%) and severity (up to 30%), ↓ weight loss, ↑ firmness, maintenance of luminosity/color, ↓ TA	[104]
	Rubygem	Immersion	0, 200, and 500 µM Time: 5 min MET: 500 µM	4 °C, 90–95% RH, 18 d	↓ weight loss, ↓ decay incidence (71%), delay in TSS, TA, ascorbic acid and firmness changes	[96]
	Camino Real	Immersion	0 and 100 µM Time: 15 min MET: 100 µM	25 °C, 80–85% RH, 6 d	↓ *B. cinerea* infection (81%), ↓ weight loss (46%), ↑ firmness, maintenance of brightness/color, maintenance of TA, lower TSS increase	[26]
	Hongyan	Immersion	0, 50, and 100 µM Time: 30 min MET: 50 µM	4 °C, 9 d	↑ melatonin, better visual appearance, ↓ deterioration, ↓ decay/softening compared to control	[103]
	Luca	Immersion	0, 50 and 100 µM Time: 5 min MET: 100 µM	4 °C, 90% RH, 12 d	↓ weight loss (60%) and decay (50%), maintenance of TSS, TA and taste index; slight alteration of two key aromatic compounds	[110]
	Hongyan	Immersion	0, 10, 100, 1000, and 10,000 µM Time: 5 min MET: 100 or 1000 µM	4 °C, 90% RH, 12 d	↓ decay (75%), ↓ decay severity, ↓ weight loss, ↑ firmness (19%), color maintenance, senescence delay	[25]
	Selva	Immersion	0, 1, 10, 100, and 1000 µM Time: 5 min MET: 100 µM	4 °C, 90–95% RH, 12 d + 20 °C, 2 d shelf life	↓ decay (55%), ↑ unsaturated/saturated fatty acids (unSFA/SFA) ratio	[97]
sweet cherry	Lapins	sprayed by nebulization	0 and 100 µM MET: 100 µM	Room temperature until 70% decay	↓ postharvest decay (~30%) and severity (20–30%), ↓ weight loss, ↑ firmness	[104]
	Samba	Immersion	0, 100, 300 and 500 µM Time: 10 min MET: 500 µM	1 °C and 94% RH, 21 d	↓ weight loss, ↑ firmness (19%), ↑ respiration rate, ↑sensory qualities (color, sourness, and acceptance)	[111]
	Sweetheart	Immersion/ coating	0, 1000, and 1000 µM +0.5% chitosan Time: 5 min MET: 1000 µM + 0.5% chitosan	0–1 °C and 90–95% RH, 28 d	↓ weight loss, respiration, and decay, maintained firmness, TSS, TA, storability, and sensory quality	[112]
	Siah Mashhad	Immersion	0, 1, 10, 100 and 1000 µM Time: 5 min MET: 100 µM	0 °C, 90% RH, 45 d +20 °C, 3 d shelf life	↓ flesh browning (56%), ↓ decay incidence (65%); ↑ melatonin by expression of *TDC*, *T5H*, *SNAT*, and *ASMT*, greater membrane integrity, and senescence delay	[101]
	Van	Immersion	0 and 100 µM Time: 30 min MET: 100 µM	20 °C, 80–90% RH, 9 d	↓ weight loss (17%), ↓ membrane permeability, ↑ firmness (25%), maintenance of L*, C*, TSS and TA, better visual appearance, ↑ endogenous melatonin	[22]

Table 3. *Cont.*

Fruit	Cultivar	Application Method	MLT Treatment	Storage	Main Postharvest Effects	Reference
sweet cherry	Santina and Royal Rainier	Immersion	0 and 100 µM Time: 5 min MET: 100 µM	0 °C, 90% RH, 21 d	↓ weight loss (63% in Santina and 95% in Royal Rainier); maintained color, TSS, storability, respiration and overall quality	[113]
	Sunburst	Immersion	0, 50, 100, and 150 µM Time: 5 min MET: 100 µM	0 °C, 90–95% RH, 63 d	↓ decay incidence (69%), ↓ weight loss (48%), ↓ respiration, ↑ firmness (23%), maintenance of TSS, TA, L*, C*, and h°, ↑ endogenous melatonin, senescence delay, and better-quality maintenance	[90]

MET—selected MLT treatment with the most favorable responses among the evaluated conditions. ↑—increase or higher value; ↓—decrease or lower value; TSS—total soluble solids; TA—titratable acidity; AsA—ascorbic acid; PE—pectin esterase; PME—pectin methylesterase; PG—polygalacturonase; Cx—cellulase; β-Gal—β-galactosidase; α-L-Af—α-L-arabinofuranosidase; *B. cinerea*—*Botrytis cinerea*; unSFA/SFA—ratio of unsaturated to saturated fatty acids; *TDC*—tryptophan decarboxylase; *T5H*—tryptamine 5-hydroxylase; *SNAT*—serotonin N-acetyltransferase; *ASMT*—N-acetylserotonin O-methyltransferase; L*—lightness; C*—chroma; h°—hue angle.

5.3. Scale-Up, Optimization, and Implementation Gaps

The available evidence supports MLT as a promising postharvest treatment for soft fruits; however, most studies remain at the laboratory or controlled-storage scale. Conventional aqueous treatments, particularly immersion, dominate the evidence because they allow relatively simple concentration control and experimental application. Commercial translation will nevertheless require optimization of concentration, exposure time, solution stability, treatment uniformity, water use, sanitation, drying conditions, and compatibility with existing packing-line operations. A major methodological gap is the limited use of multivariable optimization approaches in soft fruits. Most studies compare a small number of discrete MLT concentrations under fixed application and storage conditions, which identifies the best treatment tested but not necessarily the true optimum. Response surface methodology could be used to model interactions among MLT concentration, exposure time, and storage conditions [124].

Edible coatings, active films, and combined delivery systems represent another promising direction because they may integrate the physiological effects of MLT with physical protection against moisture loss and microbial contamination. In sweet cherry, a chitosan coating enriched with MLT reduced weight loss, respiration, and decay while maintaining firmness, biochemical quality, storability, and sensory attributes [120]. More recently, an MLT-functionalized gellan gum–chitosan composite film was developed for blueberry preservation, extending shelf life and maintaining anthocyanin content during storage [125]. These findings indicate that MLT can be incorporated into coating and packaging systems, although the limited number of studies, differences in formulations, and lack of direct comparisons prevent these technologies from being considered commercially mature.

Implementation is also constrained by limited information on economic feasibility, sensory acceptance, residue behavior, regulatory requirements, treatment stability, packaging interactions, and performance under interrupted cold-chain or commercial handling conditions. Safety and residue behavior are particularly underexplored. Although MLT occurs naturally in edible fruits, this alone does not establish the safety of exogenous postharvest applications, and the reviewed studies did not provide direct measurements of treatment-derived MLT residues or formal dietary exposure assessments. Moreover, increases in fruit MLT after treatment may reflect both absorption of applied MLT and

changes in endogenous metabolism and therefore should not be interpreted as residue measurements [21,25,101]. Future studies should therefore address residue distribution, dissipation during storage, removal by washing, and relevant toxicological and regulatory requirements, while also combining mechanistic measurements with commercially relevant outcomes, including marketable-life extension, saleable-fruit percentage, decay incidence, firmness and water-loss thresholds, sensory acceptance, treatment cost, and compatibility with commercial storage and packaging systems. Integrating multivariable optimization with semi-commercial validation will be essential for translating MLT from proof-of-concept studies into reliable postharvest technologies.

6. Conclusions and Future Perspectives

Melatonin has emerged as a promising postharvest treatment for soft fruits, acting primarily as a context-dependent redox and stress-response modulator. Across studies, MLT is linked to enhanced antioxidant defenses, decreased lipid peroxidation and membrane leakage, and improved maintenance of firmness, water content, color, nutritional quality, and decay resistance. More limited evidence also supports involvement of phenylpropanoid metabolism, cell-wall regulation, MLT metabolism, H_2S, GABA, polyamines, and host-defense pathways. However, MLT does not act through a universal anti-ripening or anti-senescence mechanism, and its effects vary with fruit, cultivar, maturity stage, concentration, and storage conditions. In addition, relatively few studies have directly measured cuticular permeability, microcracking, cellular compartmentation, hormone concentrations, or signaling-related gene expression. Consequently, a decrease in weight loss, deterioration, or softening should not be immediately viewed as proof of direct surface-barrier, hormonal, or structural control.

Future research should prioritize direct and coordinated measurements of redox metabolism, membrane lipids, cell-wall architecture, water relations, cuticular properties, hormone signaling, endogenous MLT metabolism, and pathogen-defense responses. Research comparing different cultivars, maturity levels, and treatment conditions is also required to elucidate dose-dependent responses and assess whether shared mechanisms function among soft fruits. Although optimization and commercial scale-up still require validation, mechanistic findings should increasingly be linked with marketable life, saleable-fruit percentage, firmness and water loss thresholds, visual and sensory quality, and actual reductions in postharvest losses. Addressing these gaps will strengthen the biological basis and practical reproducibility of MLT-based postharvest treatments.

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