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Phytomelatonin: From Intracellular Signaling to Global Horticulture Market

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ABSTRACT

Melatonin (*N*-acetyl-5-methoxytryptamine), a well-known mammalian hormone, has been having a great relevance in the Plant World in recent years. Many of its physiological actions in plants are leading to possible features of agronomic interest, especially those related to improvements in tolerance to stressors and in the postharvest life of fruits and vegetables. Thus, through the exogenous application of melatonin or by modifying the endogenous biosynthesis of phytomelatonin, some change can be made in the functional levels of melatonin in tissues and their responses. Also, acting in the respective phytomelatonin biosynthesis enzymes, regulating the expression of tryptophan decarboxylase (*TDC*), tryptamine 5-hydroxylase (*T5H*), serotonin *N*-acetyltransferase (*SNAT*), *N*-acetylserotonin *O*-methyltransferase (*ASMT*), and caffeic acid *O*-methyltransferase (*COMT*), and recently the possible action of deacetylases on some intermediates offers promising opportunities for improving fruits and vegetables in postharvest and its marketability. Other regulators/effectors such as different transcription factors, protein kinases, phosphatases, miRNAs, protein–protein interactions, and some gasotransmitters such as nitric oxide or hydrogen sulfide were also considered in an exhaustive vision. Other interesting aspects such as the role of phytomelatonin in autophagic responses, the posttranslational reprogramming by protein-phosphorylation, ubiquitylation, SUMOylation, PARylation, persulfidation, and nitrosylation described in the phytomelatonin-mediated responses were also discussed, including the relationship of phytomelatonin and several plant hormones, for chilling injury and fungal decay alleviating. The current data about the phytomelatonin receptor in plants (CAND2/PMTR1), the effect of UV-B light and cold storage on the postharvest damage are presented and discussed. All this on the focus of a possible new action in the preservation of the quality of fruits and vegetables.

Abbreviations: 13-LOX, 13-lipoxygenase; 3-OHM, cyclic 3-hydroxy melatonin; 4CL, ligase; 5GT, anthocyanin 5-O-glucosyltransferase; 5-MT, 5-methoxytryptamine; 6PGDH, 6-phosphogluconate dehydrogenase; 9-LOX, 9-lipoxygenase; AA, ascorbic acid; AAO, abscisic aldehyde oxidase; AAT, alcohol acyltransferase; AA/GSH, ascorbate/glutathione; ABA, abscisic acid; ABA1, xanthoxin dehydrogenase; ABF, ABA-responsive element-binding factor; ABTS, 2,2-azino-bis-3-ethylbenzothiazoline-6-sulfonic acid; ACC, 1-aminocyclopropane-1-carboxylic acid; ACO, ACC oxidase; ACS, ACC synthase; ACX, acyl-CoA oxidase; ADC, arginine decarboxylase; ADH, alcohol dehydrogenase; ADP, adenosine diphosphate; ADT, arogenate dehydratase; AFB1, aflatoxin B1; H_3NBH_3, ammonia borane (ammoniotrihydroborate); AMP, adenosine monophosphate; ANR, anthocyanidin reductase; AnS, anthranilate synthase; AOC, allene oxide cyclase; AOMT, anthocyanidin 3′-methyltransferase; AOS, allene oxide synthase; AOX, alternative oxidase; AP2/ERF, APETALA2/ethylene-responsive element-binding factor; APX, ascorbate peroxidase; APY1, apyrase 1; ARF, auxin response factor; ARG, arginase; ASDAC, N-acetylserotonin deacetylase; *ASMT*, *N-acetylserotonin methyltransferase*; ATG, AuTophaGy-related; ATG8-PE, ATG8-phosphatidylethanolamine; ATHB, homeobox-leucine zipper protein; ATP, adenosine triphosphate; ATPase, ATP synthase; ATP-CL, ATP-citrate lyase; AV, acid value; BA, benzoic acid; BA2H, benzoic acid-2-hydroxylase; BRs, brassinosteroids; BSO, L-buthionine-sulfoximine; bZIP, basic leucine zipper; C2H2, cysteine 2/histidine 2; C4H, cinnamic acid 4-hydroxylase; CA, controlled atmosphere; Ca^{2+}/CaM, calcium/calmodulin; $CaCl_2$, calcium chloride; CAD, cinnamate dehydrogenase; CaMs, calmodulins; CAND2, candidate G protein-coupled receptor 2; CAO, chlorophyll a oxygenase; CAT, catalase; CBB, cassava bacterial blight; CBF1, binding factors; CBLs, calcineurin B-like; CBR; NYC1, chlorophyll b reductase; CCO, cytochrome c oxidase; CCR, cinnamoyl-CoA reductase; CCR, cinnamoyl-CoA reductase; CCT, choline-phosphate cytidylyltransferase; CC-NBS-LRR, coiled-coil nucleotide-binding site leucine-rich repeat; CDPKs or CPKs, calcium-dependent protein kinases; Cel, cellulase; Cer, ceramides; CER1, eceriferum 1; cGMP, guanosine 3′; 5′-cyclic monophosphate; CHI, chalcone isomerase; CHI, chalcone isomerase; Chlase, chlorophyllase; CHS, chalcone synthase; CH-M, chitosan-based melatonin edible coating; CKs, cytokinins; CKX, cytokinin oxidase/dehydrogenase; ClO_2, chlorine dioxide; CMC-Gel-M, carboxymethyl cellulose-gelatin-melatonin edible coating; CMLLA, chitosan-based melatonin layer-by-layer assembly; CMLs, calcium-binding protein; CMLs, calcium-binding protein; CMV, cassava common mosaic virus; CNGCs, cyclic nucleotide-gated ion channels; CO, carbon monoxide; CoA, 4-coumaric acid:coenzyme A; COLD1, chilling tolerance divergence 1; *COMT*, *caffeic acid O-methyltransferase*; COP1, constitutively photomorphogenic1; CrHYD1, hydrogenase1 gene from *Chlamydomonas reinhardtii*; CRTISO, carotenoid isomerase; CRT/DRE, C-repeat/dehydration-responsive element.

1 | Introduction

Melatonin (*N*-acetyl-5-methoxytryptamine), an indole derivative of tryptophan and a well-known animal hormone, is related to the regulation of different rhythms such as sleep/wakefulness, endocrine, mood, corporal temperature, and others, and also studied in several dysfunctions such as neurological, cancer, and viral therapies [1–8]. Melatonin was discovered in cows in 1958, in humans in 1959 [9, 10], and surprisingly in plants in 1995 by three teams simultaneously [11–13]. Currently, it has been presented as a new plant hormone and as an exciting plant master regulator [14, 15]. In plants, melatonin, so-called phytomelatonin, is a pleiotropic molecule with relevant actions in multiple physiological aspects such as seed germination, stem and root growth, rooting, photosynthesis and stoma regulation, leaf senescence, parthenocarpy, fruit set, ripening and senescence of fruits, among others [14–21]. In addition, it plays an essential role in regulating abiotic stress situations (drought, salinity, extreme temperatures, soils contaminated by heavy metals or pesticides, UV radiation, etc.) and biotic stress (mainly bacteria, fungi, and viruses) [22–34]. Phytomelatonin can regulate the redox network in plants, restoring the redox homeostasis state in stressful situations, detoxifying both reactive oxygen species (ROS) and reactive nitrogen species (RNS), activating the ascorbate/glutathione (AA/GSH) cycle and the detoxification enzyme system including GSH-related enzymes [22, 35]. These antioxidant and detoxifying capacities of melatonin are in addition to their regulatory activity as a hormone-regulating hormone in plants. Thus, melatonin can modulate the levels and action of phytohormones such as auxin, gibberellin (GAs), cytokinins (CKs), abscisic acid (ABA), and ethylene, also from jasmonic acid (JA), salicylic acid (SA), and brassinosteroids (BRs) in stressful situations [21, 36, 37]. All these melatonin-mediated effects imply significant changes at the transcriptional level acting on primary and secondary metabolism elements as described [15, 35].

Owing to health-promoting bioactive phytochemicals exhibiting ROS scavenging potential, horticultural crops exhibit commercial value, nutritional worthiness, and health benefits. Horticultural crop consumption is favorable for ensuring human health by confining chronic diseases such as cancer, cardiovascular, and neurodegenerative diseases in industrial countries [38]. During postharvest life, qualitative and quantitative deterioration of horticultural crops as highly perishable commodities imposes significant economic losses to horticultural industries. Elucidating physiological, biochemical, and molecular regulatory mechanisms governing postharvest storability will enable us to advance strategies for improving horticultural crop marketability. Low-temperature storage has been employed extensively to extend the postharvest life of horticultural crops. However, horticultural crops suffer from chilling injury and fungal decay, which confine low-temperature storage. In addition to conferring tolerance to chilling injury and fungal decay, attempts to introduce safe, eco-friendly strategies for ameliorating stresses, postponing senescence, and preserving horticultural crops' organoleptic and nutritional quality have emerged in recent years [39–41]. In recent years, melatonin has emerged as a universal biostimulator and signaling biomolecule with great potential in the horticultural industry. Insights into physiological, biochemical, and molecular mechanisms employed by exogenous melatonin application will give us a worthy economic

CS, citrate synthase; CTR, constitutive triple response; CuAO, copper binding diamine oxidase; CUPRAC, cupric reducing antioxidant power; CV, chloroplast vesiculation; CYP707A, ABA 8′-hydroxylase; Cyt c, cytochrome c; Cyt c/a, cytochrome c/a; DAO, diamine oxidase; DCD, D-cysteine desulfhydrase; DES1, L-cysteine desulfhydrase 1; DFR, dihydroflavonol reductase; DG, diacylglycerol; DHA, dehydroascorbate; DHAR, dehydroascorbate reductase; DORN1/P2K1, does not respond to nucleotides 1; DPPH, 2,2-diphenyl picrylhydrazyl; DREB1, dehydration-responsive element-binding protein 1; EDS1, enhanced disease susceptibility 1; EGase, endo-1,4-β-glucanase; eIF2, eukaryotic initiation factor 2; eIF4F, eukaryotic initiation factor 4F; EIL5, ethylene insensitive like5; EIN2, ethylene insensitive; EPT, ethanolaminephosphotransferase; ER, endoplasmic reticulum; Er4P, erythrose-4-phosphate; ERF, ethylene response factor; ERL3, ethylene insensitive 3; ETR, ethylene receptor; EXP, expansin; F3H, flavanone 3-hydroxylase; F3′ H, flavonoid 3′-hydroxylase; FAD3 and FAD7, fatty acid desaturase 3 and 7; FK, fructokinase; FLS, flavonol synthase; FRAP, ferric reducing antioxidant power; Fv/Fm, photosynthetic efficiency; G6PDH, glucose-6-phosphate dehydrogenase; GA20ox, GA 20-oxidase; GA2ox, GA $_2^-$oxidase; *GABA*, *γ-aminobutyric acid*; *GABA-T*, *γ-aminobutyric acid transaminase*; *GAD*, *glutamate decarboxylase*; GAs, gibberellin; GC, guanylate cyclase; GDH, glutamate dehydrogenase; GGGT, GDP-L-galactose guanylyltransferase; GLDH, L-galactono-1,4-lactone dehydrogenase; GME, GDP-D-mannose-3′,5′-epimerase; GMPH, mannose-1-phosphate guanylyltransferase; GOGAT, glutamate synthase; GPAT4/8, glycerol-3-phosphate acyltransferase 4/8; GPCR, G protein-coupled receptor; GPP, L-galactose-1-phosphate phosphatase; GPX, glutathione peroxidase; GR, glutathione reductase; GRX, glutaredoxin; GS, glutamine synthetase; GSH, glutathione; GSNOR, S-nitrosoglutathione reductase; GSSG, oxidized glutathione; GST, Glutathione S-transferase; Gt1, rice seed storage protein glutelin; GTs, glycosyltransferases; GWD, α-glucan water dikinase; G/T/M, glutenin/tamarind gum/melatonin bioactive film; G/T-M-E, glutenin/tamarind gum loaded with the binary microemulsion of melatonin/pummelo essential oil; Gα; GPA1, heterotrimeric G protein α subunit; H_2, molecular hydrogen; H_2O_2, hydrogen peroxide; H_2S, hydrogen sulfide; HDA9, histone deacetylase 9; HK, hexokinase; HO1, heme oxygenase 1; HOS1, high expression of osmotically responsive gene1; HPL, hydroperoxide lyase; HRW, hydrogen-rich water; HSE, GAANNTTC, heat shock elements; Hsf20, heat stress transcription factor 20; HSP40, heat shock protein 40 kDa; HY5, elongated hypocotyl 5; HYD, β-carotene hydroxylase; IAA, indole-3 acetic acid; ICDH, isocitrate dehydrogenase; ICE1, inducer of CBF expression 1; ICS, isochorismate synthase; ICS, isochorismate synthase; IDO, indoleamine 2,3-dioxygenase; InsP3, inositol 1,4,5-triphosphate; INV, invertase; IPL, isochorismate pyruvate lyase; JA, jasmonic acid; KAO, ent-kaurenoic acid oxidase; KO, ent-kaurene oxidase; KS, ent-kaurene synthase; LAC, laccase; LacCer, lactosylceramides; LAH, lipolytic acyl hydrolase; LAR, leucoanthocyanidin reductase; LCD, L-cysteine desulfhydrase; LD, luzindole; LOG, LONELY GUY; LPA, lysophosphatidic acid; LPC, lysophosphatidylcholine; LPE, lysophosphatidylethanolamine; LPI, lysophosphatidylinositols; LPS, lipase; LUT1/5, lutein-deficient 1/5; M2H, melatonin 2-hydroxylase; M3H, melatonin 3-hydroxylase; MA1, melatonin biosynthesis 1; MAPK, mitogen-activated protein kinase; MDA, malondialdehyde; MDC; SGR/NYE1, Mg-dechelatase; MDHAR, monodehydroascorbate reductase; MeJA, methyl jasmonate; MET1, DNA (cytosine-5)-methyltransferase 1; MOF-MEL, melatonin-loaded UiO-66 metal-organic framework nanoparticles; MPTP, mitochondrial permeability transition pores; MSRA/B, methionine sulfoxide reductase; MVK, mevalonate kinase; MYO, myrosinase; NADH-CWP, NADH-dependent cell wall peroxidase; NADK, NAD kinase; NADP-IDH, NADP-dependent isocitrate dehydrogenase; NAS, N-acetylserotonin; NCA, N-carbamoylputrescine amidase; NCED, 9-cis-epoxycarotenoid dioxygenase; NDH, NADH dehydrogenase; NO, nitric oxide; NOA1, NO-associated 1; NOS, nitric oxide synthase; NP, nanoparticles; NR, nitrate reductase; NTR1, NADPH-dependent thioredoxin reductase; N-INV, neutral invertase; O_2^-, superoxide anion; OAT, ornithine aminotransferase; ODC, ornithine decarboxylase; OGDH, 2-oxoglutarate dehydrogenase; OPDA, oxophytodienoic acid; OPDAR, OPDA reductase; P5CR, pyrroline-5-carboxylate reductase; P5CS, pyroline 5-carboxylate synthetase; PA, phosphatidic acid; *PAL*, *phenylalanine ammonia-lyase*; PaO, pheophorbide a oxygenase; PaO, pheophorbide a oxygenase; PAP, phosphatidate phosphatase; PC, phosphatidylcholine; PCD, programmed cell death; PCM, phase change material; PDC, pyruvate decarboxylase; PDH, pyruvate dehydrogenase; PDS, phytoene desaturase; PE, phosphatidylethanolamine; PEP, phosphoenolpyruvate; PEPC, phosphoenolpyruvate carboxylase; PEPCK, phosphoenolpyruvate carboxykinase; PG, phosphatidylglycerol; PGI, phosphoglucoisomerase; phyB2, phytochrome B2; PhytoCer, phytoceramides; PI, phosphatidylinositol; PI3K, phosphatidylinositol 3-kinase; PIF4, phytochrome interacting factors; PIP, aquaporins; PIP, aquaporins; PIP2-PLC, phosphatidylinositol 4,5-bisphosphate (PIP2)-dependent phospholipase C; PLA1, phospholipase A1; PLA2, phospholipase A2; PLC, phospholipase C; PLD, phospholipase D; PLP, pyridoxal 5-phosphate; PME, pectin methylesterase; POD, peroxidase; PP2C12, protein phosphatase 2C 12; PPD, postharvest physiological deterioration; PPH, pheophytinase; PPO, polyphenol oxidase; PR1, pathogenesis-related gene 1; ProDH, proline dehydrogenase; PRPP, 5-phosphoribosyl 1-pyrophosphate; PRX, peroxiredoxin; PS, phosphatidylserine; PsbO, protein 1 PsbO1 in PSII; PSKR1, phytosulfokine receptor 1; PSKα, phytosulfokine α; PSY, phytoene synthase; PTI, pattern-triggered immunity; Put, putrescine; PV, peroxide value; PYL, ABA-receptor protein; p-CPA, p-chlorophenylalanine; RAPTOR1, regulatory-associated protein of TOR; RBOH, respiratory burst oxidase homologs; RBOH; NADPH oxidase, respiratory burst oxidase homologues; RCCR, red chlorophyll catabolite reductase; RGA1, rice G-protein α subunit 1; RNAi, RNA interference; RNS, reactive nitrogen species; ROS, reactive oxygen species; RUP1 and RUP2, UV-B photomorphogenesis 1 and 2; SA, salicylic acid; SAM, S-adenosyl-L-methionine; SAMDC, S-adenosylmethionine decarboxylase; SAMS, S-adenosylmethionine synthase; SAM-MTase, SAM-dependent methyltransferase; SCL, succinate–CoA ligase; SCW, secondary cell wall; SDH, succinate dehydrogenase; SERT, serotonin reuptake transporter; SKDH, shikimate dehydrogenase; SKK, shikimate kinase; *SNAT*, *serotonin N-acetyltransferase*; SNO, S-nitrosothiol; SnRK1α1/KIN10, SNF1-related protein kinase catalytic subunit alpha KIN10; SnRKs, sucrose nonfermenting-1 (SNF1)-related protein kinases; SOD, superoxide dismutase; SorDH, sorbitol dehydrogenase; SOX, sorbitol oxidase; Spd, spermidine; SPDS, spermidine synthase; Sph, sphingosine; Spm, spermine; SPS, sucrose-phosphate synthase; SSADH, succinic semialdehyde dehydrogenase; STS, stilbene synthase; SuSy, sucrose synthase; SuSy-C, sucrose synthase cleavage; SuSy-S, sucrose synthase synthesis; SUT2, sugar transporter/sucrose carriers; SWEET10, sugars will eventually be exported transporter; *T5H*, *tryptamine 5-hydroxylase*; TA, titratable acidity; TAL, tyrosine ammonia lyase; tCA, trans-cinnamic acid; *TDC*, tryptophan *decarboxylase*; TEAC, Trolox equivalent antioxidant capacity; TG, triacylglycerols; TGase, transglutaminase; TOR, target of rapamycin; TPP, trehalose-phosphate phosphatase; TPS, trehalose phosphate synthase; TrpS, tryptophan synthase; Trx2, thioredoxins; TSS, total soluble solids; TyrDC, tyrosine decarboxylase; UCP, mitochondrial uncoupling protein; UFGT, UDP glucose-flavonoid-3-O-glycosyltransferase; unSFA/SFA, unsaturated/saturated fatty acids; UVR8, UV resistance locus 8; VDE, violaxanthin de-epoxidase; WSD1, wax-ester synthase; XET, xyloglucan endotransglucosylase; XTH, xyloglucan endotransglucosylase/hydrolase; YUC, yucca flavin monooxygenase; YUCCA, indole-3-pyruvate monooxygenase; ZAT10, zinc finger protein 10; ZAT2/6/12, zinc finger; ZDS, ζ-carotene desaturase; ZEP, zeaxanthin epoxidase; β-1,3-Glu, β-1,3-glucanase; β-GAL, β-galactosidase; β-Glu, β-glucosidase; ε-LCY and β-LCY, lycopene cyclase; ΔΨm, mitochondrial membrane potential.

attractive opportunity for ameliorating stresses, postponing senescence, and preserving the organoleptic and nutritional quality of horticultural crops during postharvest life. Recently, considerable research has been invested in improving the postharvest marketability of horticultural crops by exogenous melatonin application or endogenous phytomelatonin accumulation. Owing to environmental and human health risks, exogenous melatonin application as an environmentally friendly strategy or developing plants to extend shelf life by manipulating endogenous phytomelatonin accumulation would be highly economically attractive [16, 42, 43].

In this review, we have elucidated the physiological, biochemical, and molecular mechanisms employed by exogenous melatonin for ameliorating stresses, postponing senescence, and preserving the organoleptic and nutritional quality of horticultural crops as a worthy attractive economic opportunity for improving horticultural crops' marketability. Thus, a detailed analysis of the role of phytomelatonin in postharvest physiology of fruits and vegetables is presented, with emphasis on situations of stress. Thus, the most relevant studies on the biosynthesis of phytomelatonin and its regulation by different transcription factors and protein kinases, among others, the current knowledge about the phytomelatonin receptor in plants, and several studies on melatonin and the effect of UV-B light, the effect of cold storage and the postharvest damage are presented and discussed, including the relationships of melatonin with the plant hormones involved in postharvest physiology. All this on the focus of a possible new action in the preservation of the quality of fruits and vegetables.

2 | Phytomelatonin Biosynthesis and Its Genetic and Epigenetic Regulation

2.1 | Phytomelatonin Biosynthesis and Its Intracellular Homeostasis

Phosphoenolpyruvate (PEP) provided from the glycolysis (EMP) pathway and erythrose 4-phosphate (Er4P) provided by oxidative pentose phosphate (OxPP) pathway, shikimic acid pathway represented by NADPH-dependent shikimate dehydrogenase (SKDH) and ATP-dependent shikimate kinase (SKK) enzymes are responsible for endogenous tryptophan, tyrosine and phenylalanine biosynthesis [39, 44]. The shikimic acid pathway provides sufficient intracellular tryptophan. In plants, tryptophan decarboxylase (TDC) is accountable for tryptamine biosynthesis from tryptophan in the cytosol, while tryptamine 5-hydroxylase (T5H) is accountable for serotonin biosynthesis from tryptamine in the endoplasmic reticulum. Then, serotonin *N*-acetyltransferase (SNAT) in chloroplast and mitochondria is responsible for *N*-acetylserotonin biosynthesis from serotonin or melatonin biosynthesis from 5-methoxytryptamine (5-MT). *N*-acetylserotonin *O*-methyltransferase (ASMT) or caffeic acid *O*-methyltransferase (COMT) is accountable for melatonin biosynthesis from *N*-acetylserotonin or 5-methoxytryptamine biosynthesis from serotonin in the cytosol, chloroplast and mitochondria [14, 42, 45, 46]. In plants, pyruvate dehydrogenase (PDH) dependent acetyl-CoA supplies prevalent ROS-generating chloroplasts and mitochondria organelles for facilitating SNAT activity for melatonin biosynthesis [47]. In chloroplast, SNAT is accountable for acetyl-CoA-dependent serotonin acetylation into NAS, while N-acetylserotonin deacetylase (ASDAC) in rice (HDAC10) and Arabidopsis (HDAC14) is responsible for N-acetylserotonin deacetylating into serotonin (Figure 1). Therefore, SNAT and HDAC activity might be accountable for preserving chloroplast serotonin status for melatonin biosynthesis during senescence and stress [48]. By evolving COMT from ASMT during plant terrestrialization with gene duplication, COMT acquired UV-protective monolignols such as p-coumaryl alcohol and coniferyl alcohol biosynthesis capacity, as well as melatonin as a relevant ROS/RNS scavenging molecule [49]. Tsunoda et al. [50] reported that transgenic tomato fruits overexpressing the TDC1 gene displayed higher serotonin biosynthesis. In addition, exogenous serotonin application or endogenous serotonin biosynthesis by TDC1 gene overexpressing is accountable for accelerating fruit ripening by activating colorless non-ripening (SPL-CNR) transcription factor and its downstream ACC oxidase 1 (*ACO1*) and ACC synthase 2/4 (*ACS2/4*) expression [50]. Yang et al. [51] reported that transgenic rice overexpressing *TDC1* gene driven by rice seed storage protein glutelin (Gt1) promoter displayed higher endogenous serotonin biosynthesis in rice endosperm (rice endosperm serotonin fortification), which was accompanied by higher grain quality and promising agronomical traits. Higher endogenous serotonin biosynthesis was associated with higher endogenous lysine accumulation in rice endosperm in transgenic rice overexpressing the *TDC1* gene, which may be favorable for health and nutrition.

Wang et al. [52] reported that transgenic apple and Arabidopsis ectopically overexpressing mouse serotonin reuptake transporter (*MmSERT*) gene displayed higher endogenous phytomelatonin accumulation, which was associated with lower superoxide anion (O_2^-) generation and hydrogen peroxide (H_2O_2) accumulation, thus protecting membrane integrity, evidenced by lower electrolyte leakage and malondialdehyde (MDA) accumulation, under salinity stress. In plants, plasma membrane-localized MmSERT is crucial for reuptakes extracellular serotonin for intracellular phytomelatonin accumulation, which not only is accountable for improving salt resistance of transgenic apple and Arabidopsis by activating the expression of salt-responsive genes but also diminishes the sensitivity of transgenic apple and Arabidopsis to ABA [52]. Indoleamine 2,3-dioxygenase (IDO) activity in plants is accountable for cytosolic AFMK production from melatonin [53]. In the cytosol, melatonin 2-hydroxylase (M2H) activity is responsible for 2-hydroxy melatonin production from melatonin, while melatonin 3-hydroxylase (M3H) activity is accountable for cyclic 3-hydroxy melatonin (3-OHM) production from melatonin in the chloroplast [54–57]. Phytomelatonin biosynthesis genes *TDC*, *T5H*, *SNAT*, *ASMT*, and *COMT* expression regulatory mechanisms have been illustrated in Figure 2.

2.2 | Phytomelatonin Biosynthesis Regulation by Histone Deacetylase (HDAs)

During cassava bacterial blight (CBB) development, cassava plants displayed higher histone deacetylase 9 (HDA9) gene expression [58]. Zhao et al. [58] reported that cassava plants overexpressing HDA9 displayed lower tolerance to CBB, which

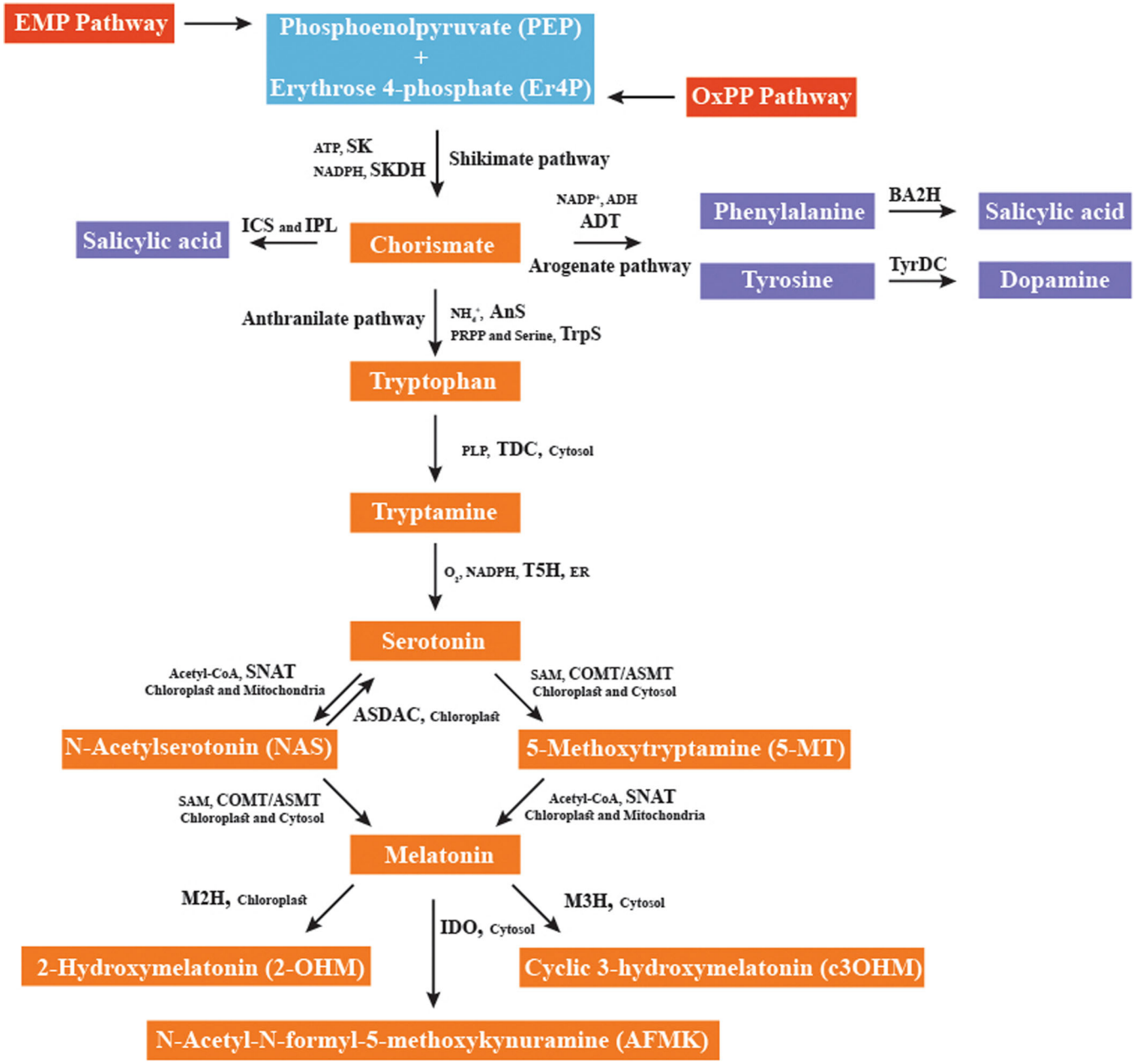

FIGURE 1 | Phytomelatonin biosynthesis pathway in plants. TDC, T5H, SNAT, ASMT, and COMT enzymes are responsible for phytomelatonin biosynthesis from shikimate pathway dependent tryptophan in cytosol, chloroplast and mitochondria. In addition, M2H enzyme in chloroplast and M3H and IDO enzymes in cytosol are responsible for melatonin metabolism. SNAT and ASDAC enzymes are responsible for endogenous serotonin homeostasis maintenance.

was associated with lower endogenous phytomelatonin biosynthesis by lower *TDC2*, *T5H*, *SNAT*, and *ASMT2* expression, while HDA9 virus-induced gene silencing cassava plants displayed higher tolerance to CBB, which was associated with higher endogenous phytomelatonin biosynthesis by higher *TDC2*, *T5H*, *SNAT*, and *ASMT2* expression. This demonstrates that HDA9 negatively regulates cassava disease resistance. These authors reported that HDA9 binds to the promoters of TDC2, T5H, SNAT, and ASMT2 and represses their expression via lysine 5 of histone 4 (H4K5) deacetylation, thus suppressing endogenous phytomelatonin biosynthesis. Also, HDA9 physically interacted with protein phosphatase 2C 12 (PP2C12) in vivo and in vitro, and PP2C12 negatively regulates CBB resistance by interacting with HDA9 through suppressing endogenous phytomelatonin accumulation (Figure 2C).

2.3 | Phytomelatonin Biosynthesis Regulation by Transcription Factors (TFs)

By promoting ROS accumulation under bacterial blight infection, RAV1 and RAV2 transcription factors are responsible for conferring cassava resistance front bacterial blight by activating endogenous phytomelatonin biosynthesis. ROS-responsive RAV1 and RAV2 transcription factors directly bind to the CAACA motif in the promoters of TDC2, T5H, and ASMT1,

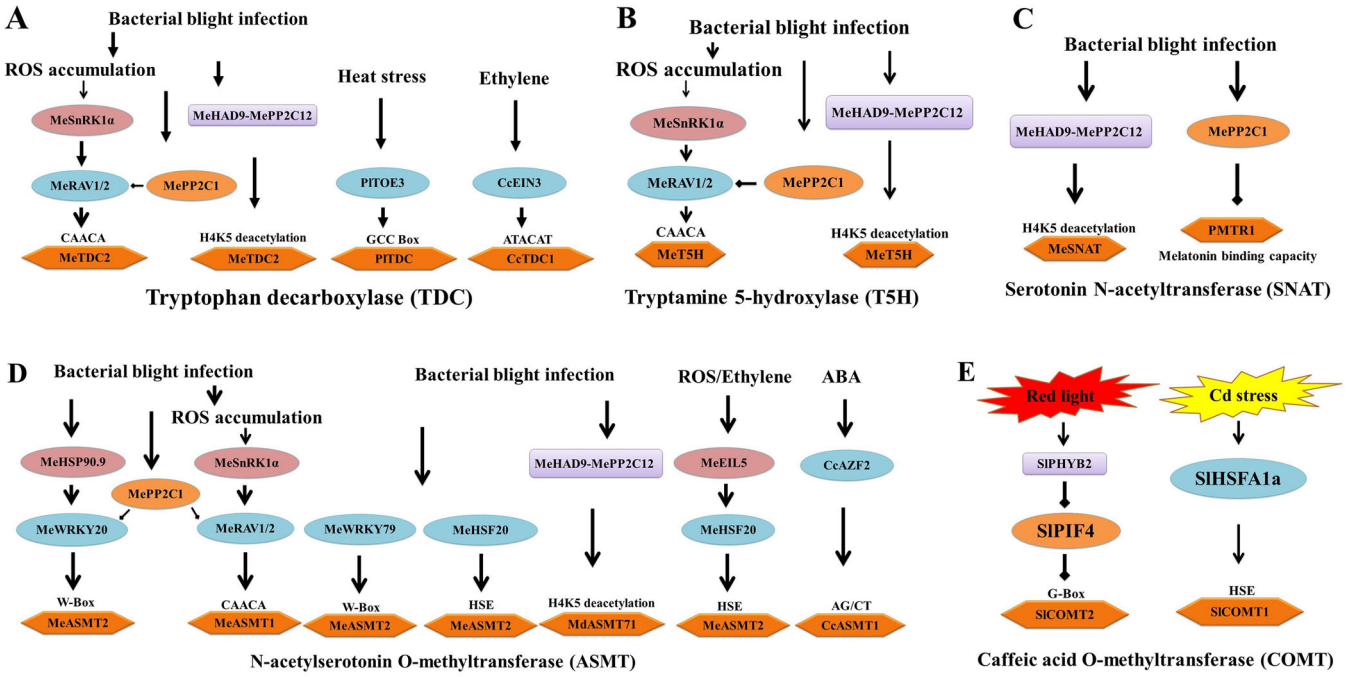

FIGURE 2 | Phytomelatonin biosynthesis genes *TDC* (A), *T5H* (B), *SNAT* (C), *ASMT* (D), and *COMT* (E) expression regulatory mechanisms. In plants, SnRK1-RAV1/2, TOE3, and EIN3 transcription factors are responsible for regulating *TDC* gene expression. SnRK1-RAV1/2 transcription factor and histone deacetylase 9 HDA9 are responsible for regulating *T5H* gene expression. In addition, histone deacetylase 9 (HDA9) is responsible for regulating *SNAT* gene expression while protein phosphatase 1 PP2C1 is responsible for PMTR1 melatonin binding capacity. HSP90.9-WRKY20, SnRK1-RAV1/2, WRKY79, HSF20, EIL5-HSF20, and AZF2 transcription factors and HDA9 are responsible for regulating *ASMT* gene expression. HSFA1a and PHYB2-PIF4 transcription factors are responsible for regulating *COMT* gene expression.

thereby activating their expression and boosting endogenous phytomelatonin biosynthesis for enhancing cassava resistance against bacterial blight [59] (Figure 2A,B,D).

In addition to RAV1 and RAV2 transcription factors, the heat-shock factor A1a (HsfA1a) transcription factor regulates plant melatonin biosynthesis. Cai et al. [60] reported that the HsfA1a transcription factor is responsible for conferring cadmium (Cd) stress tolerance to tomato plants by promoting endogenous phytomelatonin biosynthesis. By Cd stress, the HsfA1a transcription factor is responsible for activating *COMT1* expression via direct binding to heat shock elements (HSE, GAANNTTC) in the promoter of COMT1 and enhancing its expression (Figure 2E). Chen et al. [61] reported that the ethylene-responsive transcription factor EIN3 directly binding to EIN3-binding sites (ATACAT, ATGTAT, ATGTAC, or CTACAT) in the promoter of TDC1, triggers *TDC1* expression. Additionally, they reported that the ABA-responsive transcription factor AZF2 directly binds to the A (G/C)T-box in the promoter of ASMT1 and triggers *ASMT1* expression. These authors found that the transcription factors EIN3 (response to ethylene) and AZF2 (response to abscisic acid) play a role in activating the expression of *TDC1* and *ASMT1*, respectively, which accelerated endogenous phytomelatonin biosynthesis in hickory nuts. Wei et al. [62] demonstrated that WRKY79 and heat-shock transcription factor 20 (Hsf20) transcription factors directly binding to heat-shock elements (HSE, GAANNTTC) and W-box elements (TTGACC/T) in the promoter of ASMT2, respectively, activating *ASMT2* expression, ultimately enhancing tolerance to CBB through increased endogenous phytomelatonin accumulation. Zhang et al. [63] reported that the APETALA2/ethylene-responsive element-binding factor (AP2/ERF) transcription factor, TOE3, directly binds to the promoter of TDC and activating its expression, enhancing high-temperature stress tolerance by promoting endogenous phytomelatonin biosynthesis in herbaceous peony. By bacterial cassava blight infection, promoting endogenous ROS burst-dependent ethylene biosynthesis and signaling could be responsible for improving immune response. By ethylene signaling, ethylene-responsive transcription factor ethylene insensitive like5 (EIL5) could be accountable for promoting endogenous melatonin biosynthesis by interaction with heat stress transcription factor 20 (Hsf20) in the nucleus and promoting its transcriptional activation activity for activating *ASMT2* expression, thereby promoting endogenous melatonin biosynthesis [64]. EIL5 enhances the transcriptional activation of the melatonin biosynthesis gene *ASMT2* by Hsf20 without binding to its promoter. EIL5 interacts with Hsf20 to promote the expression of *ASMT2* independently of ethylene. In addition, EIL5 could improve the antibacterial activity of pathogen-related gene 3 (PR3) by promoting the physical interaction of Hsf20 and PR3. Hsf20 interacted with PR3 to improve its antibacterial activity. In addition, the antibacterial activity of PR3–Hsf20 was higher than that of PR3 alone, and the antibacterial activity of EIL5–PR3–Hsf20 was higher than that of PR3–Hsf20. These results showed that Hsf20 enhances the antibacterial activity of PR3 and that EIL5 enhances the antibacterial activity of Hsf20 and PR3. Therefore, EIL5 exhibits dual roles in fine-tuning melatonin accumulation and antibacterial activity by employing Hsf20, which illustrates the ethylene-

responsive EIL5 as the integrator of ethylene and melatonin signals in the immune response in cassava [64]. Wei et al. [65] showed that HSP90.9 interacts with WRKY20, which facilitates WRKY20's transcriptional activation on ASMT2 by binding to W-box elements in the ASMT2 promoter and activating *ASMT2* expression to confer tolerance to CBB by increasing endogenous phytomelatonin biosynthesis or suppressing auxin biosynthesis (Figure 2D).

2.4 | Phytomelatonin Biosynthesis Regulation by Protein Kinases and Phosphatases

As well as RAV1 and RAV2 transcription factors, ROS-responsive SNF1-related protein kinase catalytic subunit alpha KIN10 (SnRK1α1/KIN10) is responsible for physical interaction with and phosphorylation of Serine 45 in RAV1 and Serine 44 in RAV2 which promotes transcriptional activation of CAT6 and CAT7 by RAV1/2. Phosphorylation of RAV1/2 by SnRK1 (KIN10) under oxidative stress accelerated the direct binding of RAV1/2 to CACCTG and CAACA motifs in CAT6 and CAT7 promoters and activated their expression, which is essential for oxidative stress resistance in cassava as evidenced higher *CAT6* and *CAT7* expression and CAT activity, lower ROS accumulation favorable for preserving membrane integrity [66]. RAV1/2 was located in the nucleus, whereas KIN10 was located in both the nucleus and the cytoplasm. Therefore, cytoplast into the nucleus translocation of KIN10 might be crucial for the phosphorylation of RAV1/2 during oxidative stress [67]. In addition to activating *CAT6* and *CAT7* expression, phosphorylation of RAV1/2 by SnRK1 (KIN10) under oxidative stress accelerated endogenous phytomelatonin biosynthesis. Wei et al. [68] reported that coat protein is accountable for the pathogenicity determinant of cassava common mosaic virus (CMV) casual of cassava mosaic disease by direct interaction with RAV1/2 transcription factors, which interferes with the interaction of KIN10 with RAV1/2 transcription factors. Wei et al. [68] reported that coat protein inhibits RAV1/2 transcription factors phosphorylation at Serine 45 and Serine 44 by competitively binding to RAV1/2 with KIN10 thereby inhibits transcriptional activation activity of RAV1/2 on melatonin biosynthetic *TDC2*, *T5H*, and *ASMT1* genes along with ROS scavenging *CAT6* and *CAT7* genes. Therefore, coat protein is accountable for attenuating cassava's antiviral responses by suppressing endogenous phytomelatonin biosynthesis and repressing ROS-scavenging CAT activity. KIN10 improves cassava resistance against CMV via interaction with and phosphorylation of RAV1/2 transcription factors at Serine 45 and Serine 44, thereby promoting transcriptional activation activity of RAV1/2 on melatonin biosynthetic *TDC2*, *T5H*, and *ASMT1* genes along with ROS scavenging *CAT6* and *CAT7* genes, which enhances endogenous phytomelatonin biosynthesis along with promotes ROS scavenging CAT activity [68]. Therefore, SnRK1 might be liable for boosting endogenous phytomelatonin biosynthesis and ROS scavenging activity by employing RAV1 and RAV2 transcription factors. In addition to SnRK1 kinase, mitogen-activated protein kinase (MAPK or MAP kinase) also is crucial for regulating endogenous phytomelatonin biosynthesis. Song et al. [69] reported that WRKY17 directly binds to the W-box cis-element in the ASMT7 promoter, which activates *ASMT7* expression, enhancing endogenous phytomelatonin biosynthesis and conferring drought tolerance in apple plants. Also, ASMT7 is a plasma membrane-localized enzyme accountable for melatonin biosynthesis from NAS. Exogenous melatonin application or biotic/abiotic stressors boosts mitogen-activated protein kinases (MPK3 and MPK6) activity, which might be liable for WRKY17 phosphorylation, which enhances WRKY17 transcription factor binding to the ASMT7 promoter and activates endogenous phytomelatonin biosynthesis by activating *ASMT7* expression. The authors proposed that boosting MPK3 and MPK6 kinase activity by melatonin receptor PMTR1 under melatonin treatment or endogenous phytomelatonin biosynthesis could be crucial for regulating melatonin biosynthesis through the MPK3/6–WRKY17–ASMT7 signaling pathway, which could serve as a promising procedure for producing transgenic melatonin-fortify apples [69]. More research is needed to clarify the role of protein kinases such as calcium-dependent protein kinases (CDPKs) and the target of rapamycin (TOR) in the regulation of phytomelatonin biosynthesis (Figure 2D).

In addition to SnRK1 and MPK3/6, protein phosphatases are also involved in regulating plants' melatonin biosynthesis. In cassava, melatonin biosynthesis 1 (MA1) encodes type 2C protein phosphatase 1 (PP2C1), a negative regulator of endogenous phytomelatonin biosynthesis and signaling. Bai et al. [70] reported that PP2C1 physically interacts with RAV1/2 and WRKY20 in the nucleus. In addition, PP2C1 dephosphorylates RAV1/2 at serine35/34 and WRKY20 at serine176, suppressing RAV1/2 transcriptional activation activity on ASMT1, TDC2, and T5H, as well as WRKY20 transcriptional activation activity on ASMT2 [70]. In addition to suppressing melatonin biosynthesis, PP2C1 interacts with phytomelatonin receptor PMTR1 at the plasma membrane and dephosphorylates phytomelatonin receptor PMTR1 at serine 11, inhibiting melatonin binding and downstream melatonin signaling [70].

2.5 | Phytomelatonin Biosynthesis Regulation by Protein–Protein Interactions (PPIs)

PPI reported for melatonin biosynthesis enzymes has been illustrated in Figure 3. Wei et al. [71] reported that WRKY20 and WRKY75 interaction with TDC2, ASMT2, and ASMT3 enzymes not only promotes the transcriptional activity of WRKY20/75 on W-box elements (TTGACC/T) but also triggers endogenous melatonin biosynthesis by enhancing TDC2 and ASMT2/3 activity. Therefore, melatonin biosynthetic TDC2, ASMT2, and ASMT3 enzymes can employ WRKY20/75 transcription factors at the nucleus for promoting endogenous melatonin biosynthesis along with the transcriptional activity of WRKY20/75 on the W-box [71]. Wei et al. [72] reported that TDC2, ASMT2, and ASMT3 interaction with ATG8b/8c/8e promoted endogenous melatonin biosynthesis and enhanced autophagic activity and autophagosome accumulation. In addition, PP2C1 interaction with ASMT2 is responsible for interfering interaction between ASMT2 and PR1. By CBB infection, activating *ASMT2* and *PR1* expression was associated with suppressing

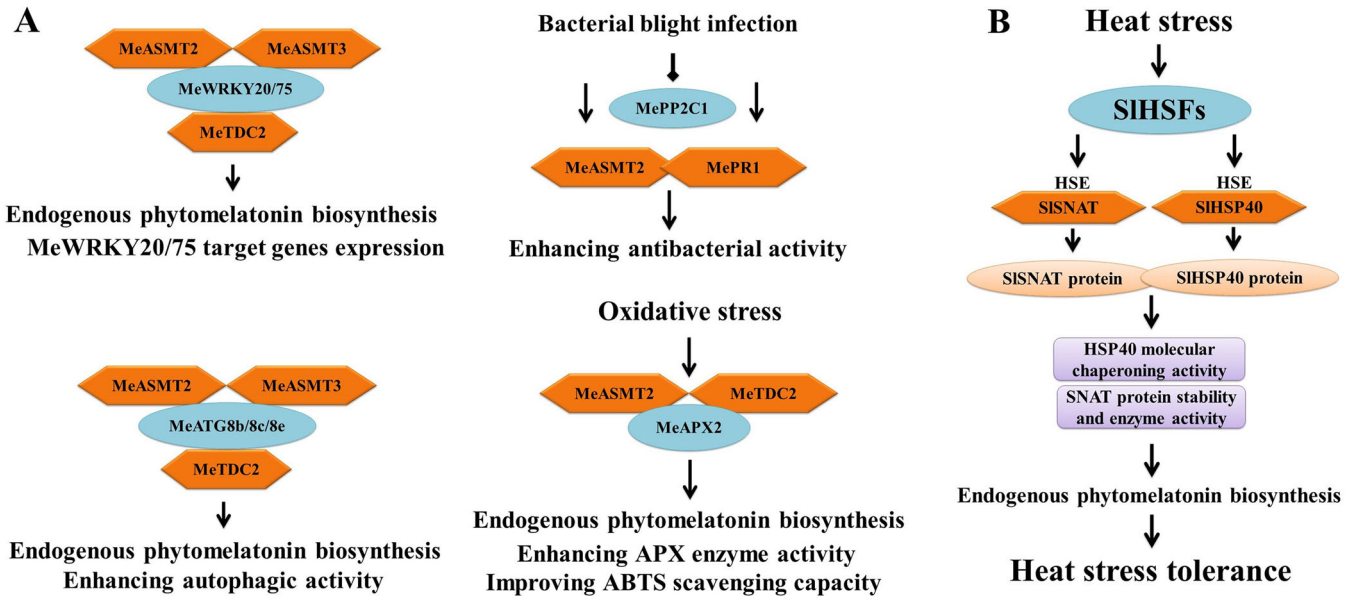

FIGURE 3 | Protein–protein interaction (PPI) reported for melatonin biosynthesis enzymes. ASMT2/3–WRKY20/75–TDC2 interaction is responsible for promoting endogenous phytomelatonin biosynthesis and WRKY20/75 target expression. ASMT2–PR1 interaction is responsible for enhancing antibacterial activity. ASMT2/3–ATG8b/8c/8e–TDC2 interaction is responsible for promoting endogenous phytomelatonin biosynthesis and enhancing autophagy activity. ASMT2–APX2–TDC2 interaction is responsible for improving ROS scavenging capacity. SNAT–HSP40 interaction is responsible for improving SNAT protein stability and promoting endogenous phytomelatonin biosynthesis.

PP2C1 expression. By suppressing PP2C1, ASMT2 releasing from PP2C1, promoted ASMT2 interaction with PR1, thereby promoting the antibacterial activity of PR1 without promoting ASMT2 activity for melatonin biosynthesis, which confers disease resistance [73]. Bai et al. [74] observed that the interaction of $ASMT_2$−APX2 and TDC_2−APX2 promotes APX activity, which is accompanied by endogenous phytomelatonin biosynthesis, thus enhancing 2,2-azino-bis-3-ethylbenzothiazoline-6-sulfonic acid (ABTS) radical scavenging activity (Figure 3A). By functioning as a molecular chaperone, heat shock protein 40 kDa (HSP40) interaction with SNAT in chloroplasts maintains SNAT enzyme stability which supports endogenous phytomelatonin biosynthesis during heat stress, according to Wang et al. [75] (Figure 3B).

2.6 | Phytomelatonin Biosynthesis Regulation by Posttranscriptional miRNAs and Posttranslational Persulfidation (H_2S)

Recently, posttranscriptional regulation of melatonin biosynthesis genes by miRNAs has been reported by Bhowal et al. [76] *TDC5* and *ASMT18* expression in rice seedlings is regulated by miR6249a and miR-1846e, respectively. During light/dark regimes and environmental stress, the opposite expression of osa–miR6249a–OsTDC5 and osa–miR1846e–OsASMT18 pairs has been validated by qRT-PCR [76]. In addition, posttranslational persulfidation of melatonin biosynthesis enzymes has been reported by Wang et al. [77]. Exogenous hydrogen sulfide (H_2S) application conferred osmotic stress resistance in Arabidopsis by activating L-cysteine desulfhydrase 1 (*DES1*) expression, boosting endogenous H_2S biosynthesis, enhancing endogenous phytomelatonin biosynthesis resulting from the activation of the expression of *ASMT*, *SNAT*, and *COMT1* genes and S-sulfhydration or persulfidation of ASMT and SNAT proteins.

3 | Melatonin, TOR/SnRK1 Signaling and Autophagic Activity

By external environmental stimuli and internal developmental cues, triggering autophagy (AuTophaGy; *ATG*) expression is responsible for autophagosome formation and autophagic activity in plants, which serves as a protective strategy for maintaining cellular homeostasis and promoting plant growth or survival. In plants, *ATGs* expression regulation at transcriptional, posttranscriptional, translational, and posttranslational levels have emerged as potential strategies for orchestrating autophagy. In addition, nuclear DNA methylation, histone methylation, and acetylation could be employed for epigenetically regulating *ATG*s expression for cytoplasmic autophagosome formation and autophagy activation in plants. By external environmental stimuli and internal developmental cues, transcriptional factors could be used by ROS and phytohormones signaling pathways for triggering *ATGs* expression, thereby cytoplasmic autophagosome formation and autophagic activation in plants [78]. By external environmental stimuli and internal developmental cues, TOR and SnRK1 could orchestrate autophagy by posttranslational phosphorylation of ATGs in plants. By sufficient sugars and energy supply, TOR serves as a negative regulator of cytoplasmic autophagosome formation and autophagic activation by ATG13 phosphorylation, while SnRK1 serves as a positive regulator of cytoplasmic autophagosome formation and autophagic activation under sugars and

energy deficiency by ATG6 phosphorylation [78, 79]. Insufficient intracellular sucrose supply means lower trehalose-6-phosphate biosynthesis could be responsible for SnRK1 activation, thereby promoting autophagy by TOR-dependent or independent pathway [80]. In addition, higher endogenous ABA accumulation under an unfriendly environment could be responsible for promoting autophagy by the SnRK2/TOR signaling pathway. By sufficient intracellular sucrose supply, higher trehalose-6-phosphate biosynthesis could be accountable for SnRK1 inhibition, thereby suppressing autophagy by TOR signaling pathway [81–83].

By activating autophagy under senescence and stresses, fatty acids, amino acids, and sugars supplied from macromolecule degradation could be responsible for intracellular energy and carbon skeletons supplying and avoiding intracellular ROS accumulation. In addition to intracellular energy homeostasis, autophagy activation could be responsible for chloroplast, peroxisome, and mitochondria maintaining and clearance [80, 84–86]. By nutrient or energy deficiency in Arabidopsis, SnRK1 is responsible for autophagy induction by suppressing TOR activity, demonstrating that SnRK1 acts upstream of TOR in the activation of autophagy in Arabidopsis [87]. Recently, Belda-Palazón et al. [88] proposed that promoting growth while suppressing stress response by SnRK2 kinases could be ascribed to nuclear $SnRK_2$—PP2C-SnRK1 repressor molecular machinery formation which by enabling TOR kinase activity allow growth during low intracellular ABA accumulation. By higher intracellular ABA accumulation during stresses, ABA binding to PYR1/PYL/RCARs promotes PP2C sequestration, which allows SnRK2 and SnRK1 releasing from $SnRK_2$—PP2C–SnRK1 repressor molecular machinery. SnRK2 and SnRK1 trigger stress responses and inhibit growth by accelerating TOR kinase phosphorylation [88, 89]. By ABA accumulation during stress, nuclear to cytoplasm translocation of SnRK1 could be responsible for phosphorylation and suppressing cytoplasmic TOR activity while promoting stress response [90].

In addition to the regulatory function of SnRK1α1/KIN10 in endogenous phytomelatonin biosynthesis, SnRK1α1/KIN10 and TOR kinases could be employed by exogenous melatonin application for conferring stress tolerance in plants. Supriya et al. [91] reported that melatonin treatment by seed priming improved drought stress tolerance in cotton seedlings by boosting endogenous phytomelatonin accumulation accompanied by boosting *SOD*, *CAT*, *APX*, monodehydroascorbate reductase (*MDHAR*), dehydroascorbate reductase (*DHAR*), and *GR* expression and activity along suppressing respiratory burst oxidase homologues D (*RBOHD*; NADPH oxidase) expression, which might be liable for higher endogenous AA and GSH accumulation, lower endogenous O_2^- generation and H_2O_2 accumulation, thereby stabilizing membrane integrity. As well as ROS homeostasis, endogenous phytomelatonin accumulation was associated with higher glutamine synthetase (*GS*) and glutamate synthase (*GOGAT*) expression and activity (GS/GOGAT pathway), which might be liable for boosting proline, GSH, and γ-aminobutyric acid (GABA) accumulation by endogenous glutamate providing. By endogenous phytomelatonin biosynthesis, suppressing the *TOR* expression might be liable for boosting autophagy activity by activating *ATG2*, *ATG9*, *ATG18a*, *ATG5*, *ATG12*, *ATG7*, *ATG8c*, and *ATG8i* expression and boosting ATG8-phosphatidylethanolamine (ATG8-PE) protein accumulation [91]. Recently, Supriya et al. [92] reported that cotton seeds priming with melatonin conferred drought stress tolerance in cotton plants, which was associated with higher endogenous phytomelatonin accumulation along with lower endogenous ABA accumulation through suppressing 9-*cis*-epoxycarotenoid dioxygenase (*NCED3*) expression. In addition, lower endogenous glucose accumulation through activating sugars will eventually be exported transporter (*SWEET10*) and sugar transporter/sucrose carriers (*SUT2*) expression was associated with lower endogenous trehalose 6-phosphate accumulation through suppressing trehalose phosphate synthase (*TPS63*) expression along with activating trehalose phosphate phosphatase (*TPP22*) expression. By cotton seeds priming with melatonin, activating *MPK6* expression and promoting MPK6 protein accumulation in cotton plants under drought stress could be responsible for activating *SnRK2.6* expression along with enhancing SnRK1 (*KIN10*) expression and protein accumulation. By activating *SnRK2* and *SnRK1* expression, suppressing regulatory-associated protein of TOR (*RAPTOR1*) expression could be responsible for promoting autophagic activity by activating *ATG8c* and *ATG8f expression along with enhancing* ATG8 lipidation by phospholipid phosphatidylethanolamine (higher ATG8-PE accumulation). Therefore, MAPK activation by melatonin could be responsible for ABA-independent SnRK2–SnRK1 signaling pathway activation and TOR signaling pathway inactivation, contributing to drought stress tolerance by promoting autophagy activity [92].

4 | Phytomelatonin Signaling by CAND2/PMTR1 Receptor

The first melatonin receptor discovered in plants was called AtCAND2/AtPMTR1 by Prof. Qi Chen's group in Arabidopsis [93], which functions as a G protein-coupled receptor boosting its direct interaction with the heterotrimeric G protein α subunit (Gα; GPA1) leads to enhanced production of ROS by activating NADPH oxidase. This activation boosts Ca^{2+} influx and promotes K^+ efflux, ultimately facilitating stomatal closure [93]. Later, in 2021, plasma membrane phytomelatonin receptor 1 (ZmPMTR1) was also described in maize plants [94], where the stimulation of the ROS scavenging system provides osmotic and drought stress tolerance. Li et al. [95] have shown that Arabidopsis can benefit from drought resistance because of the daily rhythmicity of melatonin generation and signaling. Daytime enhanced expression of the *PMTR1* gene was linked to melatonin signaling, which in turn was mediated by higher melatonin biosynthesis, *ASMT*, *SNAT1*, and *COMT1* expression. Throughout the day, activating stomatal closure at night and transmitting signals in darkness may be attributed to ROS signaling initiated by melatonin through PMTR1. By maintaining ROS dynamics, this rhythmicity helps to reduce water loss and improve water-use efficiency [95].

Exogenous melatonin accelerates stomatal closure via PMTR1, GPA1 melatonin receptor, and signaling-dependent ROS production by NADPH oxidase activation in tobacco plants. As well as melatonin treatment, endogenous phytomelatonin biosynthesis in guard cells of transgenic tobacco overexpressing

soybean SNAT1 could be responsible for accelerating stomatal closure via PMTR1 and GPA1 melatonin receptor and signaling ROS production by NADPH oxidase activation [96]. Melatonin treatment or endogenous phytomelatonin biosynthesis by overexpressing soybean SNAT1 suppressing phenylalanine ammonia-lyase (*PAL*), chalcone isomerase (*CHI*), chalcone synthase (*CHS1*), flavonol synthase (*FLS2*), and dihydroflavonol reductase (*DFR*) expression might be liable for lower flavonoid biosynthesis leading to higher ROS accumulation in transgenic tobacco guard cells accelerating stomatal closure [96]. In this system, exogenous kaempferol application or boosting endogenous kaempferol biosynthesis by overexpressing FLS2 might be accountable for suppressing stomatal closure by repressing ROS accumulation; flavonols exhibiting potent ROS scavenging activity that inhibit stomatal closure by impeding ROS signaling. The authors proposed that melatonin biosynthesis and signaling by PMTR1 and GPA1 interfere with flavonol biosynthesis to promote ROS accumulation for accelerating stomatal closure in tobacco plants [96]. Wang et al. [97] reported that PMTR1 is indispensable for endogenous phytomelatonin signaling by the PMTR1-GPA1 pathway for promoting NADPH-dependent ROS accumulation. By ROS accumulation, nitrate reductase (NR) and NO-associated 1 (NOA1) dependent NO biosynthesis are accountable for accelerating stomatal closure in Arabidopsis.

Panax notoginseng and *Arabidopsis thaliana* seedlings displayed higher SNAT1 and COMT1 expression in melatonin treatments, followed by higher *PMTR1* expression. By activating PMTR1-dependent melatonin signaling, promoting MPK3/6 and GPA1-independent signaling pathways might boost stomatal immunity by serving as a plant pattern-triggered immunity (PTI) response [98]. As well as the MPK3/MPK6 signaling pathway, PMTR1 interaction with GPA1 facilitates stomatal closure by activating NADPH oxidase-dependent ROS generation and boosting Ca^{2+} signaling independently of the MAPK signaling pathway [98]. By PMTR1/MAPKs and PMTR1/GPA1 signaling pathway, facilitating stomatal closure is crucial for preventing water loss and bacterial infection during nighttime [99, 100].

Zhang et al. [101] reported that transmembrane candidate G protein-coupled receptor 2 (CAND2) protein serves as a melatonin receptor in cotton. By melatonin treatment, enhancing *CAND2* expression in cotton plants is accountable for conferring salt tolerance. By melatonin receptor gene CAND2 silencing using virus-induced gene silencing (VIGS) technology, cotton plants displayed higher salt stress sensitivity as shown by higher H_2O_2 accumulation resulting from lower SOD activity. By the melatonin signaling pathway, G protein-coupled receptor GCR1 as melatonin receptor CAND2/PMTR1 interaction with GPA1 might be liable for phosphatidylinositol 4,5-bisphosphate (PIP2)-dependent phospholipase C (PIP2-PLC) activation boosting second messenger inositol 1,4,5-triphosphate (Ins3P) accumulation which promotes cytosolic Ca^{2+} accumulation [101]. Also, in CAND2 silencing, cotton plants displayed lower melatonin signal transduction responsible genes *GCR1*, *GPA1*, *PLC*, *ITPK* expression, and lower ROS scavenging activity conferring high salt stress sensitivity [101]. Barman et al. [102] reported that the melatonin receptor of rice, OsPMTR, is a plasma membrane-localized seven-transmembrane protein equivalent to the G-protein coupled receptor. Barman et al. [102] confirmed the interaction of PMTR with rice G-protein α subunit 1 (RGA1) and chilling tolerance divergence 1 (COLD1). By melatonin treatment, rice seedlings displayed higher abiotic stress tolerance responsive interacting proteins partners (RGA1 and COLD1) along with transcription factors (TGA2.1, WRKY90, DREB6/ERF60 and TCP5) were significantly induced by exogenous melatonin treatment. Phytomelatonin signaling and its possible actions for improving fruits and vegetables quality have been illustrated in Figure 4.

5 | Phytomelatonin and Light Signaling Pathways

5.1 | UV-B Light Signaling Regulation by Melatonin

To improve UV-B stress resistance, melatonin as a ROS and RNS scavenger regulates UV resistance locus 8 (UVR8)-constitutively photomorphogenic 1 (COP1)-elongated hypocotyl 5 (HY5) signaling pathway [103]. In Arabidopsis, UV-B light promotes endogenous phytomelatonin biosynthesis by activating *SNAT*, *ASMT*, and *COMT* expression through the UVR8–COP1–HY5 signaling pathway. Melatonin treatment conferred oxidative stress tolerance during UV-B light by enhancing CAT and APX activity and declining H_2O_2 and MDA accumulation. Exogenous melatonin delays repressor of UV-B photomorphogenesis 1 and 2 (*RUP1* and *RUP2*) expression while boosting *COP1* and *HY5* expression, thereby employing the UV-B signaling pathway for improving antioxidant systems for the stabilizing of Arabidopsis leaves from UV-B stress [33, 103]. Therefore, melatonin employs the UV-B signaling pathway by delaying *RUP1/2* expression for boosting UVR8–COP1–HY5 signaling pathway activity. As well as exogenous melatonin, endogenous phytomelatonin biosynthesis by SNAT gene overexpression employed the UV-B signaling pathway by boosting UVR8–COP1–HY5 transcriptional activity for higher *CAT*, *APX*, and *SOD* expression, lower O_2^- generation, and H_2O_2 accumulation, and stabilizing membrane integrity [33, 103]. By UV-B application and UVR8 gene VIGS silencing, Jiang et al. [104] reported that UV-B light signaling by UVR8 receptor might be liable for palliating chilling injury in tomato fruits by activating *SOD* and *CAT* expression and activity, inhibiting O_2^- generation and H_2O_2 accumulation, and stabilizing membrane integrity.

Gao et al. [105] reported that melatonin treatment or endogenous phytomelatonin accumulation in apple plants overexpressing ASMT9 confers tolerance to nitrogen deficiency accompanied by improving photosynthesis efficiency. By quantitative proteomics analysis, Gao et al. [105] reported that apple plants overexpressing ASMT9 displayed higher glycolysis along with higher GABA shunt proteins, which was associated with higher sucrose, glucose and fructose accumulation along with higher arginine, glutamate, histidine, lysine, threonine, and aspartate accumulation. By melatonin treatment or endogenous phytomelatonin accumulation in apple plants overexpressing *ASMT9*, activating *HY5* expression might be liable for directly binding to the nitrate transporters (NRT2.1 and NRT2.4) promoters, thereby activating their expression [105]. By melatonin treatment or increased phytomelatonin accumulation in apple plants overexpressing ASMT9, improving photosynthetic efficiency and boosting NO_3^-

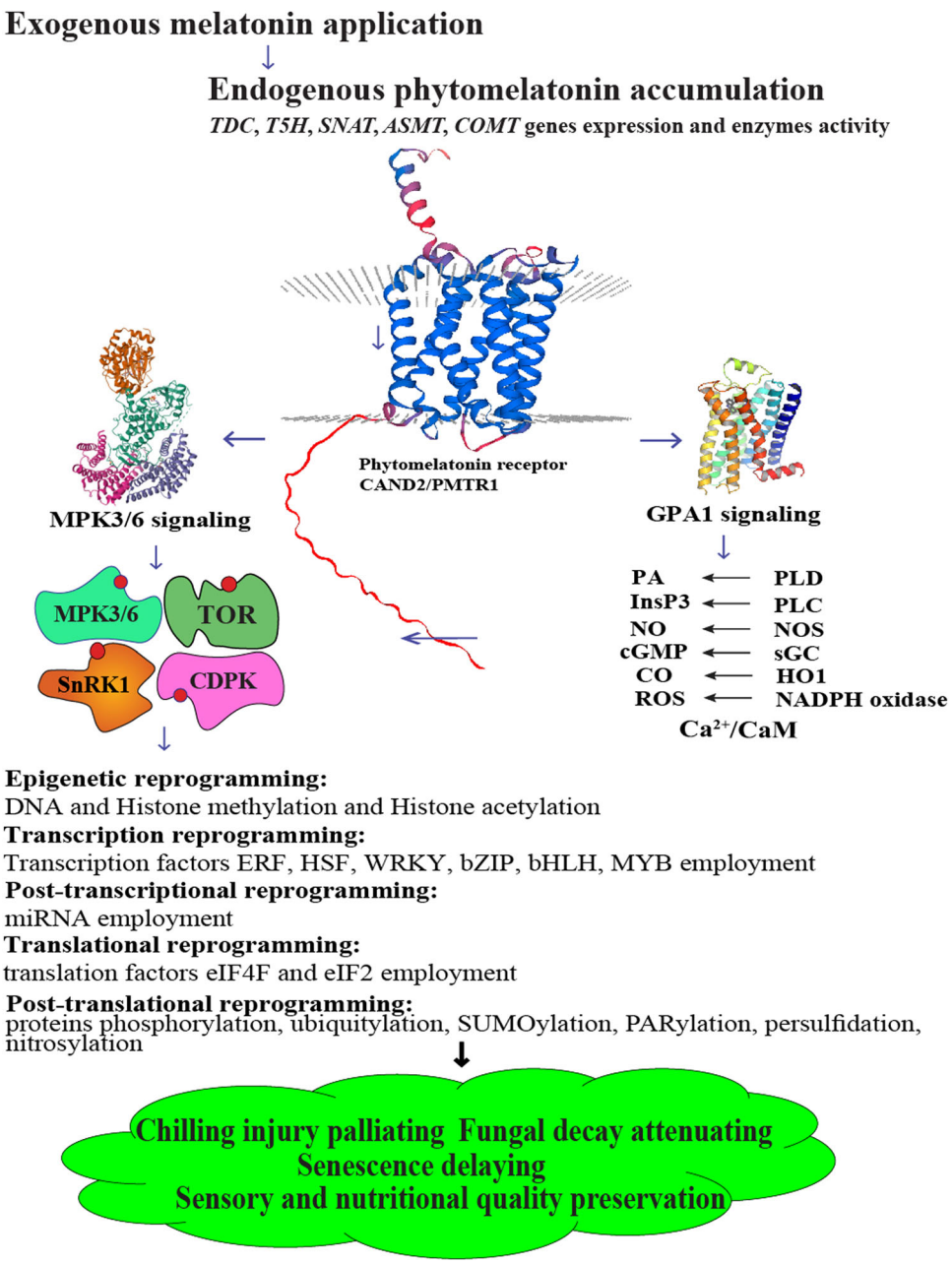

FIGURE 4 | Phytomelatonin signaling and its possible actions for improving fruits and vegetables quality. By exogenous melatonin application and endogenous phytomelatonin biosynthesis, CAND2/PMTR1 dependent MPK3/6 and GPA1 signaling pathways could be responsible for employing SnRKs, TOR, and CDPK signaling cascade for attenuating chilling injury and fungal decay, delaying senescence and preserving organoleptic and nutritional quality of horticultural products by activating epigenetic and genetic mechanisms.

uptake might be liable for enhancing TCA activity, which promotes amino acid metabolism conferring nitrogen deficiency. Gao et al. [105] proposed that the ASMT9–HY5–NRT2.1/NRT2.4 signaling pathway is accountable for conferring tolerance to nitrogen deficiency in apple plants and improving nitrogen use efficiency (NUE) [29].

5.2 | Phytomelatonin Biosynthesis Regulation by Light Signaling

By UV-B light, rice basic leucine zipper (bZIP) transcription factor bZIP18 as a functional ortholog of Arabidopsis HY5 might be liable for boosting tryptophan, tryptamine, and serotonin biosynthesis by directly binding to the ACE/G-box *cis*-elements and upregulating rice *TDC1*, *TDC3*, and *T5H* expression (UVR8–COP1–HY5 signaling pathway). By exogenous serotonin application or bZIP18 gene overexpressing, higher O_2^- generation, and H_2O_2 accumulation in rice seedlings revealed that higher endogenous serotonin accumulation exacerbates UV-B stress [106]. Melatonin interplay with UV-B light signaling in plants has been illustrated in Figure 5.

Rice plants displayed higher endogenous phytomelatonin accumulation, resulting in higher *TDC* and *COMT* expression

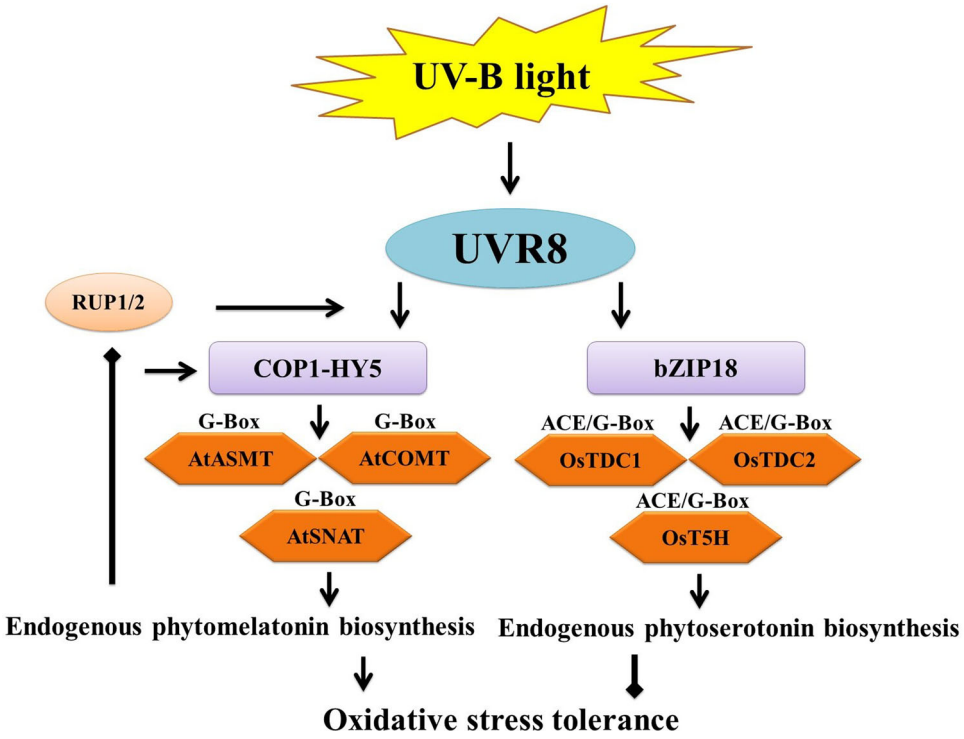

FIGURE 5 | Melatonin interplay with UV-B light signaling in plants. By UV-B light perception and UVR8 activation, COP1–HY5 signaling pathway is responsible for *SNAT*, *ASMT*, and *COMT* expression and promoting endogenous phytomelatonin biosynthesis while COP1–bZIP18 signaling pathway is responsible for *TDC1/2* and *T5H* expression and promoting endogenous phytoserotonin biosynthesis.

by red/blue light application, which is photosynthetically active radiation. Red/blue light perception by phytochromes and cryptochromes boosts PSI and PSII photosystems, and electron transport system activity might be liable for ROS production resulting from electron leakage. Therefore, boosting melatonin biosynthesis in chloroplasts by ROS may be favorable for overcoming oxidative stress [107]. Double chromatic red/blue light in rice seedlings promotes phytomelatonin biosynthesis by activating *TDC* and *COMT* expression [107]. By suppressing *CRY* expression by RNA interference (RNAi), rice plants displayed lower phytomelatonin biosynthesis arising from lower *TDC* expression [108].

Zhang et al. [109] reported that the lower phytomelatonin biosynthesis in leaves and flower buds is crucial for activating flower bud formation in apple trees. Lower phytomelatonin biosynthesis may arise from lower blue and far-red light intensity during spring, leading to lower *ASMT9* and *SNAT5* expression. Blue and far-red light application in apple trees before flowering promotes phytomelatonin biosynthesis by activating *ASMT9* and *SNAT5* expression, suppressing flower bud formation. Also, these authors reported that the melatonin treatment delayed flower bud formation in apple trees by boosting phytomelatonin biosynthesis, resulting in higher *ASMT9* and *SNAT5* expression and protein accumulation. Also, melatonin treatment at 200 μM promotes flower bud formation rate, but melatonin treatment at 1000 μM represses flower bud formation in apple trees. Delaying flower bud formation in apple trees in response to melatonin treatment may arise from activating gibberellin and vernalization pathways and suppressing autonomous and photoperiod pathways. Therefore, activating phytochromes and cryptochromes signaling pathway by blue and far-red light application might be liable for boosting the COP1–HY5 transcriptional signaling pathway for activating melatonin biosynthetic *ASMT9* and *SNAT5* expression and protein accumulation in apple plants [109].

Wang et al. [110] reported that the HY5 transcription factor directly binding to the G-box of the promoter of the SNAT6 gene is accountable for suppressing the *SNAT6* expression and preventing phytomelatonin accumulation. During darkness, COP1 translocation from cytoplasm to nuclear is responsible for boosting HY5 degradation by 26S proteasome. By HY5 degradation, enhancing *SNAT6* expression promoted phytomelatonin accumulation and delayed cotyledon opening in Arabidopsis. Delaying cotyledon opening by transgenic Arabidopsis seedlings overexpressing HY5 and SNAT6 while boosting cotyledon opening by Arabidopsis seedlings CRISPR/Cas9 silencing HY5 and SNAT6 demonstrated regulatory roles of HY5 and SNAT6 in phytomelatonin biosynthesis [110].

Li et al. [111] reported that monochromatic red light promotes phytomelatonin biosynthesis, but monochromatic blue light suppresses phytomelatonin biosynthesis in tomato fruits. In addition, promoting tomato ripening by double chromatic red/blue light (75% red light and 25% blue light) was associated with higher phytomelatonin biosynthesis. By double chromatic red/blue light, phytochromes and cryptochrome signaling pathways synergistically operation could be responsible for promoting phytomelatonin biosynthesis, which promotes tomatoes ripening by enhancing ethylene biosynthesis through upregulating ACC synthase (*ACS2* and *ACS4*) and ACC oxidase (*ACO1*)

expression and accompanying by an increased in lycopene biosynthesis through upregulation of phytoene synthase (*PSY1*) and carotenoid isomerase (*CRTISO*) expressions [111]. Higher phytomelatonin biosynthesis and lower H_2O_2 and MDA accumulation in tomato fruits under double chromatic red/blue light demonstrated that melatonin provides a ROS scavenging mechanism for delaying fruit senescence and accelerating fruit ripening [111]. Recently, Shan et al. [112] reported that accelerating tomato fruit ripening by exogenous melatonin application could be ascribed to regulating DNA methylation of CpG islands (CGIs) of ethylene biosynthesis and signaling genes. By exogenous melatonin application, DNA methylation levels of the CpG island of ACC synthase (ACS10) and ethylene response factor 1 (ERF1) were decreased, and the DNA methylation level of the CpG island of CTR1 was increased. In addition, exogenous melatonin application increased *ACS10* and *ERF1* expression and inhibited *CTR1* expression [112].

Zhang et al. [113] reported that ASMT5 and COMT2 are responsible for the *N*-acetylserotonin pathway of melatonin biosynthesis, while ASMT7 is accountable for the 5-methoxytryptamine pathway of melatonin biosynthesis. By red light treatment, tomato fruits displayed higher phytomelatonin levels during fruit ripening, which might be attributed to boosting the *N*-acetylserotonin pathway via upregulating *COMT2* and *ASMT5* expression. Also, phytochrome interacting factors (PIF4) transcription factor directly bind to the G-box elements of the COMT2 promoter, inhibiting *COMT2* expression for suppressing phytomelatonin biosynthesis in tomato fruit. In addition, phytochrome B2 (phyB2) interaction with PIF4 facilitates the degradation of PIF4 through the 26S proteasome pathway. These authors reported that the $phyB_2$–PIF4–COMT2 signaling pathway is accountable for boosting phytomelatonin biosynthesis in tomato fruit during ripening by red light application. PIF4 ubiquitination-dependent degradation by phyB2 was confirmed by employing proteasome inhibitor MG132. Enrichment of tomato fruit with exogenous melatonin enhances its agronomic traits and provides health benefits. Therefore, editing the PIF4 recognition site on COMT2 by gene-editing strategy CRISPR/Cas9 can be employed for engineering new melatonin-enriched health-boosting tomato fruits [113] (Figure 2E).

6 | Phytomelatonin Potential in Postharvest Management of Fruits and Vegetables

6.1 | Chilling Injury Alleviating

During cold storage, the cell membrane's physical phase transition from flexible liquid-crystalline to solid–gel structure is accountable for increasing cellular electrolyte leakage. By H^+-ATPase and Ca^{2+}-ATPase activity deterioration under cold stress, cytoplasmic acidification is associated with cytosolic Ca^{2+} accumulation. By Ca^{2+}/CaM activation, boosting phosphatidylinositol 3-kinase (PI3K), phospholipase D (PLD), phosphatidate phosphatase (PAP), and lipolytic acyl hydrolase (LAH) activity is responsible for free linolenic acid releasing for 9-lipoxygenase (9-LOX) or ROS-dependent peroxidation during cold stress, which is relevant to membrane integrity deterioration during cold stress. In addition, electron transport elements such as NADH dehydrogenase (NDH), succinate dehydrogenase (SDH), cytochrome C reductase (CCR), and cytochrome C oxidase (CCO), and the deterioration in mitochondria not only is responsible for increasing electron leakage and ROS accumulation but also for hampering intracellular ATP accumulation (FoF1 ATP synthase). In plants, electrolyte leakage and MDA accumulation have been considered physiological indicators of membrane integrity [39, 40, 114–117].

The results reported by researchers regarding the attenuating chilling injury of horticultural products by exogenous melatonin application during postharvest have been summarized in Table 1. Exogenous melatonin treatments conferring chilling tolerance in horticultural products could be ascribed to promoting signaling H_2O_2 accumulation [120, 125, 158], boosting phytomelatonin accumulation [120, 139, 141], $SlZAT2/6/1_2$–CBF1–arginine pathway activation giving rise to boosting endogenous nitric oxide (NO), proline, polyamines and GABA accumulation [119, 121, 124, 129, 130, 133, 138, 141, 146, 147, 152, 158], promoting endogenous polyamines accumulation by activating MYB44 transcription factor dependent arginine decarboxylase (*ADC*), ornithine decarboxylase (*ODC2*), and spermidine synthase (*SPDS5*) expression [123], sufficient intracellular energy ATP providing [118, 134] along with sufficient intracellular reducing power NADPH providing [126, 140, 146], boosting shikimate pathway activity responsible for sufficient intracellular phenylalanine, tryptophan, and tyrosine providing [126, 146], enhancing phenylpropanoid pathway activity for boosting phenols, flavonoids and anthocyanins accumulation leading to improving ABTS, 2,2-diphenyl picrylhydrazyl (DPPH), and ferric reducing antioxidant power (FRAP) radical scavenging capacity [120, 131, 141, 146, 148, 158], suppressing polyphenol oxidase (*PPO*) expression and activity by activating *miR528* expression [142] or promoting DNA hypermethylation [127], boosting endogenous SA accumulation while enhancing SA signaling responsive pathogenesis proteins (*PRs*) expression [126, 151], promoting thioredoxins (Trx) activation by NADPH-dependent thioredoxin reductase (*NTR*) expression for enhancing oxidized protein repairing methionine sulfoxide reductase (*MSR*) system activity [139, 140], promoting endogenous sucrose accumulation [147], suppressing phospholipase C (*PLC*), phospholipase D (*PLD*) and lipoxygenase (*LOX*) expression and activity accompanying by activating fatty acid desaturases (*FADs*) expression responsible for improving membrane unsaturated/saturated fatty acids (unSFA/SFA) accumulation [118, 143, 145, 148, 154], protecting membrane fluidity and integrity revealed by lower electrolyte leakage and MDA accumulation [119, 134, 135, 154, 158], preserving membrane lipid homeostasis by accelerating membrane lipidome (phospholipids, lysophospholipids, sphingolipids, and glycerides) remodeling by suppressing PLD, PLC, and LOX activity [132], promoting ROS avoiding alternative oxidase (*AOX*) expression and activity accompanying by enhancing ROS scavenging system activity giving rise to lower O_2^- generation and H_2O_2 accumulation [131, 142, 144, 148, 149, 152] accompanying by higher AA/DHA and GSH/GSSG accumulation [150, 151, 153, 158], improving cell wall structure and stability along with harmonizing cell wall pectin de-esterification and depolymerization [134, 141, 152, 159], promoting GABA shunt pathway activity responsible for sufficient intracellular energy and carbon skeletons providing accompanying by avoiding ROS accumulation [120], promoting endogenous ascorbic acid accumulation by activating ascorbic acid biosynthetic

TABLE 1 | Chilling injury alleviation by exogenous melatonin application in horticulture products during cold storage.

Plant material	Treatments	Molecular and biochemical effects	References
Tomato fruits (*Solanum lycopersicum*)	MEL 100 μM	Higher intracellular ATP supplying, higher H^+-ATPase, Ca^{2+}-ATPase, CCO, and SDH activity, higher unSFA/SFA accumulation, higher linoleic (18:2) and linolenic (18:3) acids accumulation, lower palmitic (16:0), stearic (18:0) and oleic (18:1) acids accumulation, higher *FAD3* and *FAD7* expression, lower *PLD* and *LOX* expression and activity.	[118]
	MEL 100 μM	Higher *ZAT2/6/12* transcription factors expression, higher *CBF1* transcription factor expression, higher *arginase* expression and activity, higher endogenous polyamines Put, Spd and Spm accumulation, higher *ODC* and *ADC* expression and activity, higher endogenous proline accumulation, higher *P5CS* and *OAT* expression and activity, lower *ProDH* expression and activity, higher endogenous NO accumulation, higher *NOS* expression and activity, lower electrolyte leakage and MDA accumulation.	[119]
	MEL 100 μM	Signaling H_2O_2 accumulation, higher endogenous phytomelatonin accumulation, higher *TDC*, *T5H*, *SNAT*, and *ASMT* expression, lower endogenous GABA accumulation, higher GAD, GABA-T, and SSADH activity, higher *PAL* expression and activity, higher phenols accumulation, higher DPPH scavenging capacity.	[120]
Cucumber fruits (*Cucumis sativus* L.)	MEL 100 μM	Lower electrolyte leakage, higher chlorophyll accumulation, lower Chlase activity, higher endogenous polyamines Put, Spd and Spm accumulation, higher *ADC* and *ODC* expression and activity, higher endogenous proline accumulation, higher *P5CS* and *OAT* expression and activity, lower *ProDH* expression and activity, higher endogenous GABA accumulation, higher *GAD* and *GABA-T* expression and activity.	[121]
	MEL 100 μM	Lower electrolyte leakage and MDA accumulation, higher endogenous AA accumulation, higher endogenous proline accumulation, lower O_2^- generation and H_2O_2 accumulation, lower weight loss and respiratory intensity.	[122]
	MEL 100 μM	Lower electrolyte leakage and MDA accumulation, higher MYB44 transcription factor expression, higher *ADC*, *ODC2* and *SPDS5* expression, higher endogenous polyamines Put, Spd, and Spm accumulation.	[123]
Peach fruits (*Prunus persica*)	MEL 100 μM	Higher endogenous polyamines Put, Spd and Spm accumulation, higher *ADC* and *ODC* expression, higher endogenous proline accumulation, higher *P5CS* and *OAT* expression, lower *ProDH* expression, higher endogenous GABA accumulation, higher *GAD* and *PAO* expression.	[124]
	MEL 100 μM	Signaling H_2O_2 accumulation, lower MDA accumulation, higher *SOD*, *CAT*, *APX*, *GR*, *MDHAR*, and *DHAR* expression, higher *GMPH*, *GME*, *GGGT*, *GPP*, *GDH*, and *GLDH* expression, higher AA and GSH accumulation, lower O_2^-generation and H_2O_2 accumulation.	[125]
	MEL 100 μM	Lower MDA accumulation, higher unSFA/SFA accumulation, higher linoleic (18:2) and linolenic (18:3) acids accumulation, lower palmitic (16:0), stearic (18:0) and oleic (18:1) acids accumulation, lower LOX activity, higher G6PDH activity, higher SKDH activity, higher phenols accumulation, higher PAL activity, lower PPO activity, higher endogenous SA accumulation.	[126]

(Continues)

TABLE 1 | (Continued)

Plant material	Treatments	Molecular and biochemical effects	References
	MEL 100 μM	Higher methylase and demethylase activity, higher chlorogenic acid, neochlorogenic acid, catechin, quercetin-3-glucoside, kaempferol-3-rutinoside and caffeic acid accumulation, lower DNA methylation (CpG methylation) along with higher expression of *PAL* gene, higher DNA methylation (CpG methylation) along with lower expression of *PPO* and *POD* genes.	[127]
	MEL 100 μM	Higher SUMO E3 ligase *SIZ1* expression.	[128]
Mango fruits (*Mangifera indica* L.)	MEL 100 μM	Lower MDA accumulation, higher endogenous AA accumulation, higher endogenous proline accumulation, higher P5CS and OAT activity, lower ProDH activity, lower ethylene production, weight loss and respiratory intensity.	[129]
	MEL 100 μM	Higher endogenous polyamines Put, Spd and Spm accumulation, higher ADC and ODC activity, lower DAO and PAO activity, higher endogenous GABA accumulation, higher GAD activity, lower GABA-T activity.	[130]
	MEL 100 μM	Higher endogenous phytomelatonin accumulation, higher PAL and TAL activity, higher phenols and flavonoids accumulation, higher DPPH, TEAC, FRAP and CUPRAC scavenging capacity, higher SOD, CAT, APX, GR and DHAR activity, lower O_2^- generation and H_2O_2 accumulation.	[131]
	MEL 500 μM	Lower electrolyte leakage and MDA accumulation, lower PLD, PLC and LOX activity, higher PLA2 activity, higher PC, PE, and PI accumulation, lower PA accumulation, higher LPC, LPE and LPI accumulation, lower LPA accumulation, lower Cer, PhytoCer, LacCer and Sph accumulation, lower TG accumulation, higher DG accumulation.	[132]
	MEL 100 μM	Higher endogenous proline accumulation, higher *P5CS*, *P5CR*, and *OAT* expression and activity, lower *ProDH* expression and activity.	[133]
	MEL 100 μM	Higher firmness, lower PG, PME, and EGase activity, lower PLD and LOX activity, lower palmitic and stearic acids accumulation, higher oleic, linoleic, and linolenic acids accumulation, higher unSFA/SFA accumulation, higher ATP and ADP and lower AMP accumulation, higher H^+-ATPase, Ca^{2+}-ATPase, SDH, and CCO activity.	[134]
Plum fruits (*Prunus salicina*)	MEL 100 μM	Higher SAMDC activity, higher endogenous polyamines Spd and Spm accumulation, higher TGase activity, higher plasma membrane covalently enrichment with Put and Spd, higher plasma membrane hydrogen and ionic bonding enrichment with Spd and Spm, lower electrolyte leakage and MDA accumulation, higher membrane proteins sulfhydryl (-SH) accumulation.	[135]
	MEL 1000 μM	Lower fresh-reddening, lower ethylene burst, lower phenols and anthocyanins accumulation, lower vanillic acid, caffeic acid, ferulic acid, epicatechin, rutin, dihydroquercetin, kaempferol, and cyanidin-3-glucoside accumulation, higher carotenoids accumulation, higher intracellular ATP supplying, lower *PAL*, *DFR* and *UFGT* expression, higher *CRTISO*, *ZEP*, *VDE*, and *ZDS* expression, lower *PG*, *β-GAL* and *XET* expression, lower *ACO*, *ETR* and *EFR* expression, higher *SDH*, *CCO*, and *ATPase* expression, lower *MYB124* transcription factor expression.	[136]
	MEL 100 μM	Higher SAMDC and TGase activity, higher endogenous polyamines Spd and Spm accumulation, higher plasma	[137]

(Continues)

TABLE 1 | (Continued)

Plant material	Treatments	Molecular and biochemical effects	References
		membrane covalently enrichment with Put and Spd, higher mitochondrial and vacuolar membranes covalently enrichment with Put, higher plasma membrane, mitochondrial and vacuolar membranes hydrogen and ionic bonding enrichment with Spd and Spm, lower electrolyte leakage and MDA accumulation, higher membrane proteins sulfhydryl (-SH) accumulation.	
Litchi fruits (*Litchi chinensis*)	MEL 400 μM	Lower electrolyte and MDA accumulation, higher anthocyanins accumulation, higher intracellular ATP supplying, higher H^+-ATPase, Ca^{2+}-ATPase, SDH, and CCO activity, higher endogenous proline accumulation, higher P5CS and OAT activity, lower ProDH activity.	[138]
	p-CPA 150 μM	Lower endogenous serotonin and melatonin accumulation, lower TDC, T5H, and SNAT expression, higher electrolyte and MDA accumulation, higher O_2^- generation and H_2O_2 accumulation, higher LOX activity, lower phenols and anthocyanins accumulation, higher PPO activity, lower SOD, CAT, APX, MDHAR, DHAR and GR activity, lower *MsrA1*, *MsrA2*, *MsrB1*, and *MsrB2* expression.	[139]
	MEL 500 μM	Higher endogenous NO accumulation, higher NR and NOS activity, lower electrolyte and MDA accumulation, lower O_2^- generation and H_2O_2 accumulation, higher SOD, CAT, APX, MDHAR, DHAR, and GR activity, higher AA and GSH accumulation, higher intracellular NADPH supplying, higher *NTR1* and *Trx2* expression, higher *MsrA1*, *MsrA2*, *MsrB1*, and *MsrB2* expression.	[140]
Eggplant fruits (*Solanum melongena* L.)	MEL 100 μM	Higher endogenous phytomelatonin accumulation, higher *TDC*, *T5H*, *SNAT*, *ASMT,* and *COMT* expression, higher *ZAT2/6/12* transcription factors expression, higher *CBF1* transcription factor expression, higher endogenous polyamines accumulation, higher *ODC* and *ADC* expression, higher anthocyanins accumulation, higher *PAL*, *CHS*, *CHI*, *DFR*, *F3H*, *F3′ H*, *UFGT*, and *ANS* expression, higher SOD and CAT expression, lower H_2O_2 accumulation, lower *PG*, *PME* and *Cel* expression and activity, lower electrolyte leakage and MDA accumulation.	[141]
Banana fruits (*Musa acuminate* L.)	MEL 200 μM	Lower electrolyte leakage and MDA accumulation, higher phospholipids and unSFA accumulation, lower O_2^- generation and H_2O_2 accumulation, higher SOD and CAT activity, higher *miR528* expression, lower *PPO1*, *PPO2*, and *PPO3* expression, lower PPO activity.	[142]
	MEL 200 μM	Lower electrolyte leakage and MDA accumulation, higher phenols and flavonoids accumulation, lower O_2^- generation and H_2O_2 accumulation, higher CAT activity, lower LOX activity, lower AAO activity, higher endogenous proline accumulation, higher phospholipids and unSFA accumulation, higher *omega-3/6 fatty acid desaturase* expression.	[143]
Green horn peppers (*Capsicum annuum* L.)	MEL 100 μM	Lower electrolyte leakage and MDA accumulation, lower O_2^- generation and H_2O_2 accumulation, higher SOD, CAT, APX, MDHAR, DHAR and GR activity, higher intracellular ATP supplying, higher AA/DHA and GSH/GSSG accumulation, higher phenols and flavonoids accumulation, higher chlorophyll accumulation, lower weight loss, and respiratory intensity.	[144]
Green bell peppers	MEL 100 μM	Lower electrolyte leakage and MDA accumulation, higher endogenous proline accumulation, lower *PLD* and *LOX* expression and activity, higher PC and PE accumulation, lower	[145]

(Continues)

TABLE 1 | (Continued)

Plant material	Treatments	Molecular and biochemical effects	References
(*Capsicum annuum* L.)		PA accumulation, lower *NAC1* transcription factor expression, higher *SOD*, *CAT*, and *APX* expression, higher linoleic (18:2) and linolenic (18:3) acids accumulation, lower palmitic (16:0), stearic (18:0) and oleic (18:1) acids accumulation. Higher PC and PE enrichment with unSFA.	
Pear fruits (*Pyrus bretschneideri*)	MEL 100 μM	Lower electrolyte leakage and MDA accumulation, lower LOX activity, higher endogenous proline accumulation, higher P5CS and OAT activity, lower ProDH activity, higher phenols accumulation, higher 6PGDH activity, higher SKDH activity, higher PAL, C4H, and 4CL activity, lower PPO activity, higher phenols accumulation.	[146]
	MEL 5 mM	Higher endogenous proline accumulation, higher *P5CS* and *OAT* expression and activity, lower *ProDH* expression and activity, higher endogenous GABA accumulation, higher *GAD*, *GABA-T* and *SSADH* expression and activity, higher AA accumulation, higher *APX*, *MDHAR*, and *DHAR* expression and activity, lower *AAO* expression and activity, higher sucrose accumulation, lower glucose and fructose accumulation, lower *NI* expression and activity, higher *SuSy* and *SPS* expression and activity.	[147]
Pomegranate fruits (*Punica granatum* L.)	MEL 100 μM	Lower electrolyte leakage and MDA accumulation, higher CAT, SOD, APX and GR activity, lower H_2O_2 accumulation, lower PLD and LOX activity, higher phenols accumulation, higher DPPH scavenging capacity, higher PAL activity, lower PPO activity.	[148]
	MEL 100 μM	Lower electrolyte leakage, higher phenols accumulation, higher DPPH scavenging capacity, higher PAL activity, lower PPO activity, lower H_2O_2 accumulation, higher SOD, CAT, and APX activity.	[149]
Kiwifruits (*Actinidia deliciosa*)	MEL 100 μM	Lower electrolyte leakage and MDA accumulation, lower lignin accumulation, lower *PAL*, *C4H*, and *4CL* expression and activity, lower O_2^- generation and H_2O_2 accumulation, higher *SOD*, *CAT*, *APX*, and *GR* expression and activity, higher AA and GSH accumulation.	[150]
	MEL 50 μM	Lower electrolyte leakage and MDA accumulation, lower O_2^- generation and H_2O_2 accumulation, higher SOD, CAT, and APX activity, higher AA and GSH accumulation, higher endogenous phytomelatonin accumulation, higher endogenous SA and tCA accumulation, lower endogenous BA accumulation, higher PAL and BA2H activity, higher *PAL* and *ICS* expression, higher *PR1* expression.	[151]
Zucchini fruits (*Curcurbita pepo*. L.)	MEL 200 μM	Lower electrolyte leakage and MDA accumulation, lower O_2^- generation and H_2O_2 accumulation, higher SOD, CAT, and APX activity, higher chlorophyll accumulation, higher endogenous glutamate and GABA accumulation, higher GAD activity, lower GABA-T activity, higher endogenous proline accumulation, higher P5CS and OAT activity, lower ProDH activity, lower PG, β-GAL, Cel, and PME activity.	[152]
Squash fruits (*Cucurbita pepo*)	MEL 200 μM	Lower O_2^- generation and H_2O_2 accumulation, higher SOD, CAT, APX, MDHAR, DHAR and GR activity, higher AA/DHA and GSH/GSSG accumulation.	[153]
Sapota fruits (*Achras zapota*)	MEL 90 μM	Lower electrolyte leakage and MDA accumulation, lower O_2^- generation and H_2O_2 accumulation, higher SOD and CAT activity, higher endogenous proline accumulation, lower PLD and LOX activity, higher endogenous GABA accumulation.	[154]

(Continues)

TABLE 1 | (Continued)

Plant material	Treatments	Molecular and biochemical effects	References
Apple fruits (*Malus domestica*)	MEL 100 μM	Higher SAMDC and TGase activity, higher endogenous polyamines Spd and Spm accumulation, higher plasma membrane covalently enrichment with Put and Spd, higher plasma membrane hydrogen and ionic bonding enrichment with Spd and Spm, lower electrolyte leakage and MDA accumulation, higher plasma membrane protein sulfhydryl (-SH) accumulation.	[155]
Apricot fruits (*Prunus armeniaca* L.)	MEL 100 μM	Higher SAMDC and TGase activity, higher endogenous polyamines Spd and Spm accumulation, higher plasma membrane covalently enrichment with Put and Spd, higher plasma membrane hydrogen and ionic bonding enrichment with Spd and Spm, lower electrolyte leakage and MDA accumulation, higher plasma membrane protein sulfhydryl (-SH) accumulation.	[156]
Loquat fruits (*Eriobotrya japonica*)	MEL 50 μM	Lower electrolyte leakage and MDA accumulation, higher sucrose accumulation, lower glucose and fructose accumulation, higher chlorogenic acid and neochlorogenic acid accumulation, higher malic acid, oxalic acid, and tartaric acid accumulation, higher ABTS, DPPH, and FRAP scavenging capacity, lower lignin accumulation, lower PAL, 4CL, CAD, and POD activity.	[157]
Cut anthurium flowers (*Anthurium andraeanum*)	MEL 100 μM	Lower electrolyte leakage and MDA accumulation, higher NADPH oxidase activity, higher signaling H_2O_2 accumulation, higher endogenous proline accumulation, higher P5CS and OAT activity, lower ProDH activity, higher phenols accumulation, higher PAL activity, lower PPO activity, higher DPPH scavenging capacity, higher AOX expression, lower damaging H_2O_2 accumulation, higher SOD, CAT, APX, and GR activity, higher AA/DHA and GSH/GSSG accumulation.	[158]

L-galactose (Gal) pathway activity [125], accelerating biomembranes enrichment with polyamines for stabilizing corresponding membranes conformations giving rise to lower membrane lipids peroxidation as shown by lower MDA accumulation accompanying by lower membrane proteins peroxidation as shown by lower sulfhydryl accumulation [135, 137, 155, 156], suppressing lignification by lower lignin and cellulose accumulation [150, 157]. As well as epigenetic and genetic mechanisms, melatonin treatment might be liable for palliating chilling injury in fruits and vegetables by boosting proteins posttranslational SUMOylation by SUMO E3 ligase (*SIZ1*) expression and activity and proteins posttranslational S-nitrosylation by NO and persulfidation by H_2S [128, 140].

6.2 | Fungal Decay Attenuating

As well as chilling damage, fungal infection is confining for postharvest management of fresh fruits and vegetables. Fungal elicitors are responsible for plasma membrane receptor-dependent extracellular ROS generation accelerated by NADH-dependent cell wall peroxidase (NADH-CWP). In addition, elicitors-receptor-dependent heterotrimeric G-protein activation might be liable for Ca^{2+} influx, activating CDPK. CDPK-dependent phosphorylation boosts plasma membrane NADPH oxidase activity and increases extracellular ROS accumulation. By extracellular ROS generation from NADH-CWP and plasma membrane NADPH oxidase activity, intracellular ROS signaling might be liable for boosting phenylpropanoid pathway responsible for cell wall fortification by phenolics incorporation, as well as hormone signaling such as SA and JA, which are essential for attenuating fungal decay in fruits and vegetables [99, 160, 161].

In recent years, exogenous melatonin has been employed for conferring gray mold decay resistance caused by *Botrytis cinerea* in tomato [162–164], apple [165], grape berries [166, 167], and strawberry fruits [168], blue mold decay by *Penicillium expansum* in apple fruits [169], anthracnose decay by *Colletotrichum musae* in banana fruits [170], anthracnose decay by *Colletotrichum gloeosporioides* and *Colletotrichum brevisporum* in papaya fruits [171], food-borne *Bacillus cereus*, *Bacillus licheniformis*, and *Bacillus subtilis* in cherry tomato fruits [172], ginger rhizome decay by *Fusarium oxysporum* and *Penicillium brevicompactum* [173], *Alternaria alternata*, *B. cinerea*, and *C. gloeosporioides* decay in blueberries fruits [174], Aspergillus decay by *Aspergilllus flavus* in pistachio fruits [175], soft rot decay by *Botryosphaeria dothidea* in kiwifruits [176], ring rot decay by *B. dothidea* in pear fruits [177] and downy blight caused by *Peronophythora litchii* in litchi fruits [178].

The results reported by researchers regarding the attenuating fungal decay of horticultural products by exogenous melatonin application during postharvest management have been summarized in Table 2. By exogenous melatonin treatments, attenuating fungal decay in fruits and vegetables might be attributed to boosting signaling O_2^- generation and H_2O_2 accumulation

TABLE 2 | Fungal decay attenuation by exogenous melatonin application in horticulture products during cold storage.

Plant material	Treatments	Molecular and biochemical effects	References
Papaya fruits (*Carica papaya* L.)	MEL 400 μM	Lower anthracnose decay caused by *Colletotrichum gloeosporioides* and *Colletotrichum brevisporum*, higher NADH oxidase activity, higher signaling H_2O_2 accumulation, higher SOD, CAT, APX and GR activity, higher PAL, 4CL and C4H activity, higher phenolic and flavonoid accumulation, lower LPS and LOX activity, lower MDA accumulation, higher CHI and β-1,3-Glu activity.	[171]
Table grape fruits (*Vitis vinifera* L.)	MEL 200 μM	Lower gray mold caused by *Botrytis cinerea*, higher phenols and flavonoids accumulation, lower electrolyte leakage and MDA accumulation, higher SOD and CAT activity, higher PAL and PPO activity, higher CHI, and β-1,3-Glu activity.	[166]
Cherry tomato fruits (*Solanum lycopersicum*)	MEL 100 μM	Lower gray mold caused by *B. cinerea*, higher endogenous phytomelatonin accumulation, higher signaling O_2^- generation and H_2O_2 accumulation, higher endogenous SA accumulation, higher PAL, 4CL, and POD activity, higher phenols, flavonoids and lignin accumulation, higher CHI and β-1,3-Glu activity.	[163]
	MEL 100 μM	Lower *Bacillus cereus*, *Bacillus licheniformis* and *Bacillus subtilis* incidence, lower *FtsZ*, *FtsA*, and *divIB* expression participating in bacterial cell division, lower *FlgB* expression participating in bacterial flagellum formation, lower *CybB* and *AtpI* expression exhibiting bacterial NADPH oxidase and ATP synthase activity, and lower *YikB* and *YukE* expression participating in bacterial ATP-dependent transportation and secretion processes, lower swimming motility and biofilm formation by *B. cereus*, *B. licheniformis* and *B. subtilis*, higher fruit ethylene accumulation and signaling *ACO1* and *ERF6* expression, higher fruit nitric oxide biosynthesis and signaling *NOS* and *E3 ubiquitin-protein ligase CSU1* expression, lower fruit ROS/O_2^- accumulation by higher fruit *POD18* and *SOD1* expression, higher fruits phenols and flavonoids accumulation, higher fruit ABTS scavenging capacity, higher fruit PRs expression.	[172]
	MEL 100 μM	Lower gray mold caused by *B. cinerea*, higher endogenous phytomelatonin accumulation, higher *TDC*, *T5H*, *SNAT* and *ASMT* expression, lower endogenous NO accumulation, lower *NOS* expression and activity, higher signaling O_2^- generation and H_2O_2 accumulation, higher *NADPH oxidase* expression and activity, higher endogenous SA accumulation, higher *PAL* and *ICS* expression, higher PAL and BA2H activity, higher *EDS1* and *PAD4* expression, higher *NPR1*, *TGA2/5* and *WRKY70* expression, higher *PR1/2/5* expression, higher *CHI* and *β-1,3-Glu* expression and activity.	[179]
	MEL 100 μM	Lower gray mold caused by *B. cinerea*, higher signaling O_2^- generation and H_2O_2 accumulation, higher *NADPH oxidase* expression and activity, higher *CDPK* expression, higher endogenous SA accumulation and signaling pathway, higher *WRKY70*, *PAD4*, *NPR1*, *TGA5*, *PR1*, *PR2* and *PR5* expression, higher CHI and β-1,3-Glu expression and activity, higher phenols and lignin accumulation, higher *PAL*, *C4H*, *4CL* and *POD* activity, higher *PAL*, *C4H*, *4CL*, *CCR*, *CAD* and *COMT* expression.	[164]
Tomato fruits (*Solanum lycopersicum*)	MEL 50 μM	Lower gray mold caused by *B. cinerea*, lower H_2O_2 accumulation, higher SOD and APX activity, higher CHI, β-1,3-Glu, PPO, and PAL activity, higher endogenous MeJA accumulation, higher *LOX* and *AOC* expression, lower *MYC2* and *JAZ1* expression.	[162]

(Continues)

TABLE 2 | (Continued)

Plant material	Treatments	Molecular and biochemical effects	References
Strawberry fruits (*Fragaria ananassa*)	MEL 100 μM	Lower gray mold caused by *B. cinerea*, higher signaling H_2O_2 accumulation, higher SOD activity, lower CAT and APX activity, higher PAL activity, higher total phenols and anthocyanins accumulation, higher DPPH scavenging capacity, higher GAD and GABA-T activity, lower endogenous GABA accumulation, higher intracellular ATP supplying, higher acids unSFA/SFA accumulation, lower palmitic (16:0), stearic (18:0) and oleic (18:1) acids accumulation, higher linoleic (18:2) and linolenic (18:3) acids accumulation.	[180]
Jujube fruits (*Zizyphus jujuba*)	MEL 200 μM	Lower Alternaria rot caused by *Alternaria alternata*, higher SOD, CAT, and APX activity, lower O_2^- generation and H_2O_2 accumulation, higher AA and GSH accumulation, lower electrolyte leakage and MDA accumulation.	[181]
Pistachio fruits (*Pistacia vera*)	MEL 1000 μM	Lower Aspergillus decay caused by *Aspergillus flavus*, lower endogenous AFB1 accumulation, higher phenols and flavonoids accumulation, higher DPPH scavenging capacity, higher PAL activity, higher linoleic and linolenic acids accumulation, lower H_2O_2 and MDA accumulation, lower LOX activity.	[175]
Blueberry fruits (*Vaccinium corymbosum*)	MEL 300 μM	Lower *Alternaria alternata*, *B. cinerea*, and *C. gloeosporioides* decay, higher *LOX*, *AOS* and *AOC* expression, higher endogenous JA accumulation and signaling, higher *PAL*, *C4H*, *4CL*, and *CAD* expression and activity, higher phenols, flavonoids, anthocyanins, and lignin accumulation, higher *CHI* and *β-1,3-Glu* expression.	[182]
Litchi fruits (*Litchi chinensis*)	MEL 250 μM	Lower downy blight caused by *Peronophythora litchii*, higher PAL, C4H and 4CL activity, higher phenols and flavonoids accumulation, higher G6PDH and 6PGDH activity, higher intracellular NADPH supplying, higher H^+-ATPase, Ca^{2+}-ATPase, SDH and CCO activity, higher intracellular ATP supplying.	[178]
Apple fruits (*Malus domestica*)	MEL 100 μM	Lower gray mold caused by *B. cinerea*, higher biocontrol efficacy of *Meyerozyma guilliermondii* Y-1, higher population growth and colonization of *Meyerozyma guilliermondii* Y-1, higher *PDF1.2* and *COI1* expression, higher SOD and CAT activity, higher phenols and lignin accumulation, higher PAL and PPO activity, higher *PR1*, *PR5*, *β-1,3-Glu*, and *CHI* expression.	[165]
	MEL 50 μM	Lower blue mold caused by *Penicillium expansum*, higher PAL, C4H, and 4CL activity, higher LAC and PPO activity, higher PGI and G6PDH activity, higher endogenous phenylalanine, tyrosine, and tryptophan accumulation, higher phenols, flavonoids, and lignin accumulation, higher endogenous caffeic acid, p-coumaric acid, ferulic acid, and erucic acid accumulation.	[169]
Ginger rhizomes (*Zingiber officinale*)	MEL 100 μM	Lower ginger rhizome decay caused by *Fusarium oxysporum* and *Penicillium brevicompactum*, higher *β-1,3-Glu*, *PAL*, and *CC-NBS-LRR* expression, higher β-1,3-Glu and PAL activity, higher phenols accumulation.	[173]
Guava fruits (*Psidium guajava* L.)	MEL 600 μM	Lower anthracnose decay caused by *C. gloeosporioides*, higher phenols and flavonoids accumulation, higher 4CL, C4H and PAL activity, lower O_2^- generation and H_2O_2 accumulation, higher AA accumulation, higher CAT, SOD, GR, and APX activity, lower MDA accumulation, lower LPS, PLD and LOX activity, higher CHI and β-1,3-Glu activity.	[183]

(Continues)

TABLE 2 | (Continued)

Plant material	Treatments	Molecular and biochemical effects	References
Pear fruits (*Pyrus bretschneideri*)	MEL 100 μM	Lower ring rot disease caused by *Botryosphaeria dothidea*, higher endogenous phytomelatonin accumulation, lower O_2^- generation and H_2O_2 accumulation, higher AA/DHA and GSH/GSSG accumulation, higher SOD and CAT activity, higher sugars fructose and glucose accumulation, higher organic acids oxalic, quininic, malic, shikimic, and citric acids accumulation, higher autophagosome formation, higher autophagic activity, higher *ATG1*, *ATG5*, *ATG8c*, and *ATG10* expression.	[177]
Grape berry fruits (*Vitis vinifera* L.)	MEL 100 μM	Lower gray mold caused by *B. cinerea*, higher endogenous phytomelatonin accumulation, higher flavonoids accumulation, lower DNA methylation (CpG methylation) along with higher expression of *PAL1*, *STS1*, *EDS1* and *CML41*, lower *MET1* and *SAM-MTase* expression.	[167]
Wax apple fruits (*Syzygium samarangense*)	MEL 800 μM	Higher endogenous JA and SA accumulation, higher *CAT*, *APX*, *SOD* and *GR* expression and activity giving, lower O_2^- generation and H_2O_2 accumulation, lower *LOX* expression and activity, lower MDA accumulation, higher *GLDH* expression, higher AA accumulation, lower *PG* and *Cel* expression, higher *GAD*, *GABA-T*, and *SSADH* expression.	[184]

along with activating cytosolic Ca^{2+} accumulation which is responsible for *CDPK* and *MAPK* expression [163, 164, 171, 179, 180], boosting phytomelatonin accumulation [179], sufficiently intracellular NADPH and erythrose-4-phosphate (Er4P) providing [169, 178], promoting shikimic acid pathway accountable for higher phenylalanine, tyrosine, and tryptophan accumulation [169], boosting phenolic, flavonoid, and anthocyanin accumulation inducing FRAP, ABTS, and DPPH radical scavenging activities [163–166, 169, 171, 173, 175, 178, 182, 183], boosting lignin accumulation [163, 182], boosting endogenous SA accumulation and signaling [163, 179, 184], boosting endogenous JA biosynthesis and signaling [162, 165, 182], boosting endogenous NO accumulation [179], activating coiled-coil nucleotide-binding site leucine-rich repeat (*CC-NBS-LRR*) expression [173] associated with activating PRs such as chitinase (*CHI*) and β-1,3-glucanase (*β-1,3-Glu*) expression [163, 164, 166, 171, 173, 183], sufficiently intracellular ATP providing [178, 180], boosting *SOD*, *CAT*, *APX*, and *GR* expression and activity leading to lower O_2^- generation and H_2O_2 accumulation favorable for protective membrane integrity [165, 166, 171, 183], boosting GABA shunt pathway activity [180], improving membrane unSFA/SFA accumulation [171, 175, 180, 183] and protective cell wall stability [184].

Wang et al. [177] reported that melatonin treatments confer resistance to ring rot disease caused by *B. dothidea* in pear fruits by boosting phytomelatonin biosynthesis accompanied by lower O_2^- generation and H_2O_2 accumulation along with higher AA/DHA and GSH/GSSG accumulation resulting from higher SOD and CAT activity, higher fructose and glucose levels, and also in oxalic, quininic, malic, shikimic, and citric acid accumulation. Also, autophagosome formation is boosted by autophagic *ATG1*, *ATG5*, *ATG8c*, and *ATG10* expression. By phytomelatonin biosynthesis, suppressing *TOR* expression or promoting *SnRK1* expression might be liable for boosting autophagy activity by activating *ATG2*, *ATG9*, *ATG18a*, *ATG5*, *ATG12*, *ATG7*, *ATG8c*, and *ATG8i* expression and boosting ATG8-phosphatidylethanolamine (ATG8-PE) accumulation [91]. By exogenous melatonin and DNA methylation inhibitor 5-azacytidine (5-azaC) application, Gao et al. [167] reported that lessening DNA methylation by suppressing DNA methyltransferase (*MET1*) expression activating resveratrol biosynthesis, SA biosynthesis, Ca^{2+} signaling, being MAPK signaling involved in grape berries disease resistance.

Lin et al. [185] reported that the citrus fruits under response to postharvest *Penicillium digitatum* infection exhibit higher H_2O_2 accumulation giving rise to higher endogenous melatonin accumulation. Higher H_2O_2 accumulation in *P. digitatum* in citrus fruits may be crucial for attenuating green mold decay caused by *P. digitatum* infection during postharvest life by promoting cell wall strengthening and triggering defense strategies such as *HSP90* expression. Also, the authors reported that the exogenous melatonin application aggregates green mold decay caused by *P. digitatum* infection in citrus fruits by triggering endogenous melatonin accumulation giving rise to lowering H_2O_2 accumulation by decreasing SOD enzyme activity or scavenging endogenous H_2O_2 accumulation, leading to hampering cell wall strengthening and impeding defense strategies operation such as *HSP90* expression. By green mold decay caused by *P. digitatum* infection, citrus fruits exhibited higher endogenous H_2O_2 accumulation, while exogenous H_2O_2 application attenuated green mold decay caused by *P. digitatum* infection in citrus fruits. In addition, exogenous *N*-acetylcysteine application as a potent ROS scavenger aggregates green mold decay caused by *P. digitatum* infection in citrus fruits. Also, it suggested that signaling H_2O_2 accumulation is responsible for conferring resistance to green mold in citrus fruits via cell wall strengthening and defense genes expression, while exogenous melatonin application conferred susceptibility to green mold by scavenging signaling H_2O_2 in citrus fruits [185].

6.3 | Senescence Delaying and Quality Preservation

During postharvest senescence, organoleptic and nutritional quality deterioration of fruits and vegetables restricts their global marketing, which imposes economic loss. This organoleptic and nutritional quality deterioration flows into plant food losses, which impacts global food security, environmental sustainability, and human health [41, 186]. During postharvest management, senescence-associated browning of fresh fruits and vegetables might be attributed to insufficient intracellular energy availability along with ineffective ROS scavenging activity and irrepressible PLD and LOX activities, provoking damage in cell membranes, losing fluidity and integrity evidenced by lower unSFA/SFA ratio. By membrane fluidity and integrity loss, interrupting intracellular compartmentalization might be accountable for accelerating browning arising from PAL-dependent phenolic accumulation in contact with the PPO enzyme [187–189].

During carbon starvation or darkness, α-glucan water dikinase (*GWD*) expression is implied in the increased leaf senescence in tomato plants, boosting starch degradation. Consequently, transgenic tomato plants overexpressing GWD promoted leaf senescence by enhancing starch degradation [190]. GWD is a direct target of miR171b, and its overexpression delays leaf senescence by suppressing starch degradation in tomato plants. Melatonin treatments upregulated the *miR171b-GWD* expression, which delayed leaf senescence by suppressing starch degradation and improving energy use efficiency under carbon starvation [190]. In tomato plants, chloroplast vesiculation (CV) is related to boosting leaf senescence by physical interaction with oxygen-evolving enhancer protein 1 PsbO1 in PSII (PsbO) in thylakoids membrane, which its disruption triggers free electrons combination with O_2 and promotes O_2^- accumulation. In addition, the physical interaction of CV with catalase 3 (CAT3), inhibits CAT3 activity and promotes H_2O_2 accumulation [191]. By *M3H* gene overexpression, lower endogenous phytomelatonin accumulation might be liable for increasing leaf senescence in tomato plants. M3H and CV were localized to the cytoplasm and chloroplasts, respectively. Delaying leaf senescence in tomato plants by melatonin treatment or phytomelatonin accumulation might be attributed to suppressing *CV* expression and inhibiting CV physical interaction with PsbO and CAT3, which not only impedes O_2^- generation in chloroplasts but also promotes H_2O_2 scavenging in peroxisomes, preserving ROS homeostasis. By employing the terminal deoxynucleotidyl transferase dUTP nick end labeling (TUNEL) assay, suppressing *CV* expression and inhibiting its interaction with PsbO and CAT3 might be advantageous for stabilizing chloroplast integrity and preventing programmed cell death (PCD) in tomato leaves by melatonin treatment or endogenous phytomelatonin accumulation via senescence-dependent autophagy and vacuolar-independent pathways [191].

The results reported by researchers regarding the delaying senescence and preserving quality in horticultural products by exogenous melatonin application have been summarized in Table 3. By exogenous melatonin application, delaying senescence and preserving organoleptic and nutritional quality of fruits and vegetables could be attributed to promotion of signaling O_2^- generation and H_2O_2 accumulation [272, 282], promotion of endogenous phytomelatonin accumulation [236, 241, 245, 246, 272, 292], promoting endogenous NO accumulation [217, 269, 282], promoting endogenous H_2S accumulation [245], boosting endogenous GABA accumulation [262], inhibiting ethylene accumulation [264, 268, 269, 281], suppressing endogenous ABA accumulation [244, 264], enhancing intracellular ATP supplying [228, 279], ensuring sufficient intracellular NADPH and Er4P supplying [225], boosting *SOD*, *CAT*, *APX*, and *GR* expression and activity resulting in lower O_2^- generation and H_2O_2 accumulation imply in fluidity and integrity of membranes [245, 247, 248, 253, 254, 261, 262, 284–286, 288, 289, 302], promotion of endogenous AA accumulation by activating AA biosynthetic L-galactose (Gal) pathway [258, 279], improving membrane unSFA/SFA accumulation [245, 265, 289], enhancing phenylpropanoid pathway activity for boosting phenolic, flavonoid, and anthocyanin accumulation leading to improving ABTS, DPPH, and FRAP radical scavenging capacity [242, 245, 246, 248, 271, 272, 288, 303], upregulating *ACS1* expression and ethylene biosynthesis through MYB14 transcription factor and enhancing secondary metabolites, including flavonoids, phenolic acids, stilbenes, and flavonols accumulation [237, 239], enhancing phenylpropanoid accumulation by activating *AOX* expression which ensures reducing power NADPH and carbon skeletons PEP and Er4P supply by increasing glycolysis, OxPP and shikimate pathways turn-over [225, 304], enhancing oxidized protein repairing systems as MSR activity [227, 230], preserving protein stability by enhancing heat shock proteins (*HSPs*) expression acting as molecular chaperones [281], suppressing cell wall-degrading genes expression and enzymes activity [240, 250, 251, 257, 264, 268, 274, 302, 305], preventing weight and water loss by enhancing waxes biosynthesis by activating eceriferum 1 (*CER1*) expression along with promoting cutin biosynthesis upregulating glycerol-3-phosphate acyltransferase 4/8 (*GPAT4/8*) expression responsible for cuticle integrity maintenance, suppressing plasma membrane water channels plasma membrane intrinsic protein aquaporins (*AQPs*) expression for impeding water transport from fruit cuticle, avoiding peel microcracks [244, 249, 251, 252, 306], promoting endogenous sucrose accumulation along with suppressing sorbitol decomposition [238, 259, 280], preserving flavors by regulating citric acid metabolism through enhancing TCA and glyoxylate cycles, GABA shunt, and acetyl-CoA catabolism [283], inhibiting alcoholic off-flavor formation via suppressing ethanol fermentation by lower ethylene responsive factor (*ERF*) transcription factors expression [255], and improving aroma quality by enhancing lactones and esters biosynthesis along with suppressing alcohols and aldehydes biosynthesis [235, 270, 290, 307].

In the horticulture industry, pesticide (fungicide, bactericide, insecticide, etc.) applications have instigated public concerns regarding human, animal, and environmental health. Concerning the pesticide uses in postharvest management, melatonin treatments of jujube fruits exhibited lower endogenous malathion, chlorothalonil, and glyphosate accumulation during postharvest storage. By employing p-chlorophenyl alanine (p-CPA, melatonin biosynthesis inhibitor) and L-buthionine-sulfoximine (BSO, GSH accumulation inhibitor), Deng et al. [275] reported that melatonin treatment promotes endogenous phytomelatonin accumulation which enhances GR activity and improves endogenous GSH accumulation, boosting glutathione

TABLE 3 | Senescence delaying and quality preserving by exogenous melatonin application in horticulture products during cold storage.

Plant material	Treatments	Molecular and biochemical effects	References
Pak choi leaves (*Brassica rapa* subsp. chinensis)	MEL 100 μM	Delaying leaf yellowing, higher endogenous phytomelatonin accumulation, higher chlorophyll accumulation, higher chlorophyll fluorescence (F_v/F_m), lower respiration intensity, lower *PGI*, *SDH* and *CCO* expression and activity, higher *6PGDH* expression and activity, lower ethylene production, lower *ACS* and *ACO* expression and activity.	[192]
	MEL 500 μM	Delaying leaf yellowing, higher chlorophyll accumulation, higher chlorophyll fluorescence (F_v/F_m), lower *Chlase*, *PPH* and *MDC*, *CBR*, and *CAO* expression, lower Chlase, PPH and MDC activity, lower *LOX* expression and activity, higher *SOD*, *APX* and *CAT* expression and activity, lower O_2^- generation and H_2O_2 accumulation, lower weight loss and respiration intensity, higher AA/DHA and GSH/GSSG accumulation, lower electrolyte leakage and MDA accumulation.	[193]
	MEL 100 μM	Delaying leaf yellowing, higher chlorophyll accumulation, lower PaO, MDC, and PPH activity, lower *CBR*, *MDC*, *PPH* and *PaO* expression, higher endogenous IAA accumulation, higher *AUX1* and *PIN3* expression, lower endogenous ABA and JA accumulation, lower *ABA2*, *AAO3*, and *NCED3* expression, lower *JAR1* expression, lower *NAC41* and *NAC87* transcription factors expression.	[194]
	MEL 100 μM	Delaying leaf yellowing, higher chlorophyll a, chlorophyll b, chlorophyllide a, chlorophyllide b, pheophytin a, and pheophorbide a accumulation, higher cytosolic cGMP accumulation, higher *GC1* expression and activity, lower *CBR*, *MDC*, *PPH* and *PaO* expression, lower Chlase, PaO, MDC, and PPH activity.	[195]
Broccoli florets (*Brassica oleracea* L. var. italic)	MEL 200 μM	Delaying florets yellowing, higher endogenous melatonin, SA, and ABA accumulation, lower endogenous JA accumulation, higher NR, GS, GOGAT, and GDH activity, higher endogenous glutamate supplying, higher chlorophyll accumulation, lower endogenous sucrose supplying, higher SuSy-S and NI activity, lower SuSy-C and SPS activity, lower carotenoids accumulation.	[196]
	MEL 1 μM	Delaying florets yellowing, higher chlorophyll accumulation, lower carotenoids accumulation, higher AA and phenols accumulation, higher FRAP scavenging capacity, higher aliphatic glucosinolates glucoraphanin and glucoerucin accumulation, higher indolic glucosinolates glucobrassicin, glucobrassicin, neoglucobrassicin, and 4-methoxy glucobrassicin accumulation, lower aliphatic glucosinolates sinigrin and progoitrin accumulation, higher *CYP79F1* and *CYP79B2* expression, higher *MYB28* and *MYB34* transcription factors expression.	[197]
	MEL 100 μM	Delaying florets yellowing, higher chlorophyll accumulation, higher endogenous phytomelatonin accumulation, higher TDC, T5H, SNAT and ASMT activity, lower carotenoids (β-carotene, β-cryptoxanthin, zeaxanthin and lutein) accumulation, lower *PSY*, *PDS*, *ZDS*, *CRTISO*, *ε-LCY* and *β-LCY*, *VDE*, *ZEP*, *LUT1/5*, and *HYD* expression, lower endogenous ABA accumulation, lower *NCED* expression.	[198]
	LUZ 10 μM	Hastening florets yellowing, lower endogenous phytomelatonin accumulation, lower chlorophyll a, chlorophyll b, chlorophyllide a, chlorophyllide b, pheophytin a, and pheophorbide a accumulation, higher Chlase, PPH and MDC activity, higher *Chlase* and *PPH* expression, higher ethylene production, higher *ACS1*, *ACS2*, *ACS3* and *ACO1*, *ACO2*, and *ACO3* expression and activity.	[199]

(Continues)

TABLE 3 | (Continued)

Plant material	Treatments	Molecular and biochemical effects	References
	MEL 100 μM	Delaying florets yellowing, higher endogenous phytomelatonin accumulation, higher chlorophyll a, chlorophyll b, chlorophyllide a, chlorophyllide b, pheophytin a, and pheophorbide a accumulation, lower Chlase, PPH and MDC activity, lower *Chlase* and *PPH* expression, lower ethylene production, lower *ACS1*, *ACS2*, *ACS3* and *ACO1*, *ACO2*, and *ACO3* expression and activity.	[199]
	MEL 100 μM	Delaying florets yellowing, higher chlorophyll accumulation, lower Chlase, PPH, PaO and RCCR activity, lower *NYC1*, *NOL*, *HCAR*, *Chlase*, *PPH*, *PaO*, *RCCR*, and *SGR1* expression.	[200]
	MEL 80 μM	Higher chloroplasts and mitochondria integrity, higher chlorophyll accumulation, lower *PPH*, *PaO* and *MDC* expression, lower mitochondria O_2^- generation and H_2O_2 accumulation, higher mitochondrial APX, CAT, and SOD activity, higher mitochondrial membrane permeability, lower mitochondrial MDA accumulation, higher *AOX* expression and activity, higher *CCO* expression and activity, lower mPTP opening, higher ΔΨm, lower mitochondria-cytosol Cyt c translocation, higher mitochondrial Cyt c/a accumulation, delaying PCD.	[201]
	MEL 100 μM	Longer shelf life, higher fresh weight, higher hue angle, higher chlorophyll and lower carotenoid accumulation.	[202]
Fresh-cut broccoli florets(*Brassica oleracea* L. var. italic)	MEL 100 μM	Higher glucoraphanin accumulation, higher Elong, *CYP83A1*, *UGT74B1*, and *FMOGS-OX1* expression, higher MYB28 transcription factor expression, higher *MYO* expression and activity, lower *AOP2* expression, higher sulforaphane accumulation.	[203]
	MEL 50 μM	Longer shelf life, lower weight loss, higher hue angle, higher chlorophyll and lower carotenoid accumulation, higher phenolic, and flavonoid accumulation, lower MDA accumulation, higher ABTS scavenging capacity.	[204]
	MEL 100 μM	Delaying florets yellowing, higher endogenous phytomelatonin accumulation, higher alternative electron transporting system activity, higher intracellular ATP supplying, higher chlorophyll, ascorbic acid, phenols, and flavonoids epicatechin, rutin and quercetin accumulation, higher DPPH, ABTS, and FRAP scavenging capacity, lower O_2- generation and H_2O_2 accumulation, higher SOD, CAT and APX activity, lower MDA accumulation.	[205]
Fresh-cut cauliflower (*Brassica oleracea* var. botrytis)	MEL 100 μM	Delaying cauliflower floret yellowing, higher endogenous phytomelatonin accumulation, lower *PG* and *LOX* expression and activity, higher phenols, ascorbic acid and glucosinolates accumulation, higher DPPH scavenging capacity, lower mitochondria swelling, higher autophagic activity.	[206]
Chinese flowering cabbage (*Brassica rapa* ssp. parachinensis)	MEL 100 μM	Delaying leaf senescence, higher endogenous phytomelatonin accumulation, higher *TDC2*, *TDC3*, *TDC4*, *T5H*, *ASMT* and *SNAT* expression, lower transcriptional activators *ABF1*, *ABF4*, and *ABI5* expression, lower endogenous ABA accumulation, lower *NCED3* and *AAO3* expression, higher chlorophyll accumulation, lower *NYC1*, *NOL*, *PPH*, *PaO*, *RCCR*, *SGR1*, and *SGR2* expression, lower electrolyte leakage.	[207]
	MEL 100 μM	Delaying leaf senescence, lower respiratory intensity, higher intracellular ATP and ADP supplying, lower intracellular AMP supplying, higher ATPase activity, lower ATP synthase expression, lower *AOX1/2* expression, higher NADK activity, higher	[208]

(Continues)

TABLE 3 | (Continued)

Plant material	Treatments	Molecular and biochemical effects	References
		intracellular $NADP^+$ supplying, higher *G6PDH* and *6PGDH* expression and activity, higher intracellular NADPH supplying, lower *PHI*, *SDH*, *CCO*, and *AAO* expression and activity, higher phenols and flavonoids accumulation, higher ascorbic acid accumulation.	
	MEL 100 μM	Delaying leaf senescence, lower *RBOHB*, *RBOHC*, *RBOHD*, and *RBOHE* expression, higher *SOD*, *CAT*, *APX*, *GR*, *MDHAR*, and *DHAR* expression and activity, higher AA/DHA and GSH/GSSG accumulation, lower $O_{2\cdot}$ generation and H_2O_2 accumulation, higher $O_2^{\bullet-}$, $OH^{\bullet}$, and DPPH radicals scavenging capacity, lower MDA accumulation, higher chlorophyll accumulation, lower *PaO* and *MDC* expression.	[209]
	MEL 100 μM	Delaying leaf senescence, higher chlorophyll accumulation, lower *NYC1*, *NOL*, *PaO*, *RCCR*, *HCAR*, *MCS*, *PPH1*, *PPH2*, *SGR1*, *SGR2*, and *SGR3* expression, lower ethylene production, lower *SAMS2*.1, *SAMS2*.2, *ACS5* and *ACS10* and *ACO2* and *ACO5* expression, higher flavonoid accumulation, higher *PAL3*, *C4H*, *4CL*, *FLS1*, *FLS2*, *FLS3* and *FLS4* expression, lower *ERF2* and *ERF109* transcription factor expression.	[210]
	MEL 100 μM	Delaying leaf senescence, higher chlorophyll accumulation, lower *NYC1*, *PPH*, *PaO*, and *SGR1/2* expression, lower endogenous ABA, ethylene, and JA accumulation.	[211]
Spinach leaves (*Spinacia oleracea* L.)	MEL 0.20 mg/mL	Delaying leaf yellowing, lower weight loss, higher chlorophyll accumulation, lower MDA accumulation, higher SOD, CAT and POD activity, higher AA accumulation.	[212]
Baby mustard (*Brassica juncea*)	MEL 100 μM	Buds yellowing delaying, lower weight loss and higher chlorophyll accumulation, higher FRAP and ABTS scavenging capacity, higher phenols and AA accumulation, higher aliphatic glucosinolates sinigrin, gluconapin, progoitrin and glucoiberin accumulation, higher indolic glucosinolates glucobrassicin, neoglucobrassicin, 4-methoxyglucobrassicin and 4-hydroxyglucobrassicin accumulation, higher aromatic glucosinolate gluconasturtiin accumulation.	[213]
White button mushrooms (*Agaricus bisporus*)	MEL 100 μM	Cap browning alleviating, lower weight loss and higher firmness, higher signaling H_2O_2 accumulation, higher endogenous phytomelatonin accumulation, higher *TDC*, *T5H*, *SNAT*, and *ASMT* expression, higher phenols accumulation, higher *PAL* expression and activity, lower *PPO* expression and activity, higher AA accumulation, higher DPPH scavenging capacity, lower electrolyte leakage and MDA accumulation.	[214]
	MEL 100 μM	Cap browning alleviating, higher hardness, fracturability, chewiness and lower adhesiveness, lower caps opening and off-flavor and higher overall acceptability, lower chitinase and PPO activity, lower mitochondrial electron leakage (O_2^- generating), higher endogenous phytomelatonin accumulation, higher intracellular ATP supplying, higher SOD, CAT, APX and GR activity, higher AA and GSH accumulation, higher NDH and CCR expression and activity, lower mitochondria-cytosol Cyt c translocation, higher mitochondrial Cyt c/a accumulation.	[215]
Lotus seeds (*Nelumbo nucifera*)	MEL 100 μM	Lotus pods and seeds browning attenuating, higher endogenous phytomelatonin accumulation, higher intracellular ATP and ADP supplying, lower intracellular AMP supplying, higher intracellular NAD^+ and NADH supplying, higher H^+-ATPase and Ca^{2+}-ATPase, SDH and CCO activity, higher oleic, linoleic and linolenic	[216]

(Continues)

TABLE 3 | (Continued)

Plant material	Treatments	Molecular and biochemical effects	References
		acids accumulation, lower palmitic and stearic acids accumulation, lower LPS, PLD and LOX activity, higher unSFA/SFA accumulation, lower O_2^- generation and H_2O_2 accumulation, lower electrolyte leakage and MDA accumulation.	
	LUZ 10 μM	Lotus pods and seeds browning acceleration, lower endogenous phytomelatonin accumulation, lower intracellular ATP and ADP supplying, higher intracellular AMP supplying, lower intracellular NAD^+ and NADH supplying, lower H^+-ATPase and Ca^{2+}-ATPase, SDH and CCO activity, lower oleic, linoleic and linolenic acids accumulation, higher palmitic and stearic acids accumulation, higher LPS, PLD and LOX activity, lower unSFA/SFA accumulation, higher $O_2^{\cdot -}$ generation and H_2O_2 accumulation, higher electrolyte leakage and MDA accumulation.	[216]
	MEL 100 μM	Lotus pods and seeds browning attenuating, higher intracellular and mitochondrial NO accumulation, higher intracellular NOS activity, higher ΔΨm, higher mitochondrial oxygen consumption capacity, lower mitochondrial ROS and MDA accumulation, higher mitochondrial SOD and CAT activity, higher intracellular ATP and ADP supplying, lower intracellular AMP supplying, higher mitochondrial H^+-ATPase, Ca^{2+}-ATPase, SDH, and CCO activity.	[217]
Fresh-cut lotus roots (*Nelumbo nucifera*)	MEL 150 μM	Fresh-cut lotus root browning attenuating, higher *MYB5*, *MYB6*, and *MYB308* transcription factors expression, lower *PAL*, *4CL*, *C4H*, and *CHS* expression and activity, lower *CHI*, *COMT*, *HCT* and *DFR* expression, lower *PPO* expression and activity, lower H_2O_2 accumulation, higher SOD, CAT, APX, DHAR and GR activity, lower phenols and flavonoids accumulation, higher DPPH scavenging capacity, lower MDA accumulation.	[218]
Cassava roots (*Manihot esculenta*)	MEL 500 mg L^{-1}	PPD progression delaying, lower intracellular and mitochondrial H_2O_2 accumulation, higher *Cu/ZnSOD*, *CAT1*, *APX2*, *DHAR*, *GR*, *GPX*, *POD3*, and *GST* expression, higher SOD, CAT and GR activity.	[219]
	MEL 100 μM	PPD progression delaying, lower vascular streaking and vascular discoloration, higher ROS-responsive genes calcium signaling-, phospholipase signaling-, MAPK cascades-, NADPH oxidase-, and WRKY, NAC, ZAT, and HSF transcription factors expression, higher *SOD*, *APX*, *MDAR*, *CAT*, *PRX* and *GRX* expression, lower *sucrose synthase*, *glucose phosphomutase*, and *ADP-glucose pyrophosphorylase* expression, higher *starch phosphorylase*, *α-amylase*, and *β-amylase* expression, lower H_2O_2 accumulation, higher CAT and APX activity, lower *PLC* and *PLD* expression, higher *CDPK* expression.	[220]
Bamboo shoots (*Bambusa vulgaris*)	MEL 1 mM	Bamboo shoot lignification delaying, lower hardening and yellowing, lower lignin and cellulose accumulation, lower PAL and POD activity, higher SOD, CAT and APX activity, lower NAC family *SND2* and *KNAT7* transcription factors expression, lower MYB family *MYB20* and *MYB85* transcription factors expression.	[221]
	MEL 500 μM	Bamboo shoot lignification delaying, lower lignin and cellulose accumulation, higher phenols and AA accumulation, lower PAL, CAD and POD activity, lower NAC family *NAC1*, *NAC2*, *NAC3* and *NAC4* transcription factors expression, lower MYB family *MYB1* and *MYB2* transcription factors expression, lower *PAL1*, *PAL2*, *PAL3*, *PAL4*, *CAD1*, *CAD2* expression.	[222]

(Continues)

TABLE 3 | (Continued)

Plant material	Treatments	Molecular and biochemical effects	References
	MEL 500 μM	Bamboo shoot lignification delaying, lower lignin and cellulose accumulation, higher *H^+-ATPase1/2/3*, *Mg^{2+}-ATPase1/2/3*, *Ca^{2+}-ATPase1/2/3*, *SDH1/2/3* and *CCO1/2* expression and activity, higher intracellular ATP and ADP supplying, lower intracellular AMP supplying, higher *NADK1/2* expression and activity, higher intracellular $NADP^+$ and NADPH supplying.	[223]
Fresh-cut bamboo shoots	UV-C + MEL 1 mM	Bamboo shoot lignification delaying, lower cellulose and lignin accumulation, lower PAL, POD, CAD and 4CL activity.	[224]
Pomegranate fruits (*Punica granatum* L.)	MEL 100 μM	Higher intracellular NADPH supplying, higher G6PDH and 6PGDH activity, higher AOX expression, higher CAT, APX, SOD and GR activity, lower AAO activity, lower H_2O_2 accumulation, higher AA and GSH accumulation, higher phenols, and anthocyanins accumulation, higher DPPH scavenging capacity, higher PAL activity, lower PPO activity.	[225]
	MEL 100 μM	Lower weight loss, lower PPO activity, higher phenols, anthocyanins and AA accumulation, higher DPPH scavenging capacity, lower bacterial and fungal infections.	[226]
Litchi fruits (*Litchi chinensis*)	MEL 400 μM	Pericarp browning alleviating, lower O_2^- generation and H_2O_2 accumulation, lower electrolyte leakage and MDA accumulation, higher endogenous phytomelatonin accumulation, higher phenols, flavonoids, and anthocyanins accumulation, higher SOD, CAT, APX, and GR activity, lower PPO activity, higher *MsrA1*, *MsrA2*, *MsrB1*, and *MsrB2* expression.	[227]
	MEL 400 μM	Pericarp browning alleviating, lower electrolyte leakage, lower LPS, PLD, and LOX activity, higher PC accumulation, lower PA accumulation, higher unSFA/SFA accumulation, higher oleic, linoleic and linolenic acids accumulation, lower palmitic and stearic acids accumulation, higher intracellular energy supplying, higher H^+-ATPase, Ca^{2+}-ATPase, SDH, and CCO activity.	[228]
	MEL 400 μM	Pericarp browning alleviating, higher chromaticity L*, a*, and b* value. Higher endogenous phytomelatonin accumulation, lower endogenous ABA accumulation, higher PUB protein, RING-H2 finger protein, phosphatase 2C, and F-box expression, lower bHLHs transcription factor expression, lower miR858 expression, higher MYB251 and TT2 transcription factors expression, higher *PAL*, *4CL*, *CHS*, *CHI*, *DFR*, *ANS*, and *UFGT* expression, higher anthocyanins accumulation, lower miR160 expression, higher ARF transcription factor expression, lower *XTH*, *EGase*, and *EXP* expression, higher *ZAT10* and *DREB1* expression, higher NAC transcription factor expression, higher *AOX* expression, lower *AAO* expression, higher AA accumulation, higher BON association protein 1 expression, lower accelerated cell death 6 and formin protein 18 expression, higher E3 ubiquitin-protein ligase expression, higher *PLA1* and *MYC2* expression, higher *UCP5* expression, higher H^+-ATPase, Ca^{2+}-ATPase, and pyruvate kinase expression, higher *NADP-malic enzyme* expression, higher 3-ketoacyl-CoA synthase expression, higher *GAD1*, *CaM*, and *CMLs* expression, lower *TPP* expression.	[229]
	MEL 600 μM	Pericarp browning alleviating, higher endogenous phytomelatonin accumulation, lower weight loss, lower O_2^- generation and H_2O_2 accumulation, lower electrolyte leakage and MDA accumulation, lower protein carbonyl accumulation, higher phenols, flavonoids and anthocyanins accumulation, higher SOD, CAT and GR activity, lower PPO expression and activity, higher *MsrA1*, *MsrA2*, *MsrB1*, and *MsrB2* expression.	[230]

(Continues)

TABLE 3 | (Continued)

Plant material	Treatments	Molecular and biochemical effects	References
	MEL 500 μM	Pericarp browning alleviating, lower weight loss, higher phenols, anthocyanins and AA accumulation, higher CUPRAC scavenging capacity, lower *PPO* and *LAC* expression, lower PPO activity, higher *DFR* and *UFGT* expression.	[231]
Table grape fruits (*Vitis vinifera* L.)	MEL 200 μM	Lower berry abscission and rotten index, lower electrolyte leakage and MDA accumulation, higher endogenous proline, GABA, arginine, Put, Spd, and Spm accumulation, higher N-carbamoyl putrescine amidase, *SPDS*, and *ALDH* proteins expression, higher *ARG*, *ODC*, *ADC*, *NCA*, *SPDS*, and *CuAO* expression.	[232]
	MEL 200 μM	Higher flavonoids and anthocyanins accumulation, higher *4CL*, *CHS*, *F3′ H*, *FLS*, and *UDPG* expression.	[233]
	MEL 100 μM	Higher CAT, APX, and SOD activity, lower H_2O_2 and MDA accumulation, higher AA accumulation, lower DNA methylation, higher DNA demethylase expression.	[234]
	MEL 100 μM	Lower rachis browning and berry abscission, lower weight loss rate and respiration intensity, higher phenols, flavonoids and anthocyanins accumulation, higher esters, aldehydes, and alcohols accumulation, lower terpenes accumulation.	[235]
	MEL 200 μM	Lower berry abscission and decay incidence, higher endogenous cysteine, methionine, phenylalanine, arginine, tryptophan and GABA accumulation, lower endogenous glutamic acid and proline accumulation, higher TDC2, TDC3, TDC4, T5H1, T5H2, T5H3, T5H4 and T5H5, ASMT1, ASMT2, ASMT3, ASMT4 and SNAT1 and SNAT3 expression, higher endogenous NAS, 5-MT and melatonin accumulation, higher phenols, flavonoids, and anthocyanins accumulation, higher PAL, CHI, F3H1, F3H2, F3′ H, LAR, ANR, F3′5′ H, 5GT, and AOMT expression.	[236]
	MEL 100 μM	Higher phenols, flavonoids, and anthocyanins accumulation, higher chlorogenic acid, gallic acid, epicatechin and malvidin-3,5-glucose accumulation, higher DPPH, ABTS, and FRAP scavenging capacity, higher STS and PAL expression, higher endogenous phytomelatonin accumulation.	[237]
	MEL 100 μM	Higher endogenous phytomelatonin accumulation, higher anthocyanins accumulation, higher PAL, CHS, CHI, F3H, F3′ H, F3′5′ H, DFR, LDOX, and UFGT expression, higher MYBA1 and MYBA2 transcription factors expression, higher sucrose accumulation, higher SPS activity, higher mineral nutrients N, K, Cu, Fe, and Zn absorption and accumulation.	[238]
	MEL 50 μM	Higher endogenous phytomelatonin accumulation, higher transcription factor MYB14 expression, higher ACS1 expression, higher ethylene accumulation, higher phenols, flavonoids, stilbenes, and flavonols accumulation, higher STS1, F3′H, LAR2, and DFR expression.	[239]
	MEL 100 μM	Lower weight loss and higher TSS, TA, berry adherence strength, and firmness, lower PME and PG activity, lower $O_{2\cdot}$ generation and H_2O_2 accumulation, higher CAT and APX activity.	[240]
Strawberry fruits (*Fragaria ananassa*)	MEL 100 μM	Higher endogenous phytomelatonin accumulation, higher *TDC*, *T5H*, *SNAT*, and *ASMT* expression, lower weight loss and higher firmness, higher AA accumulation, lower MDA accumulation, lower H_2O_2 accumulation, higher phenols and flavonoids accumulation, higher DPPH and ABTS scavenging capacity, higher L* value, higher hue angle.	[241]

(Continues)

TABLE 3 | (Continued)

Plant material	Treatments	Molecular and biochemical effects	References
	MEL 100 μM	Higher endogenous phytomelatonin accumulation, higher anthocyanin accumulation, higher cyanidin 3-glucoside, pelargonidin-3-O-glucopyranoside and pelargonidin-3-malonylglucoside accumulation, higher *PAL*, *C4H*, *4CL*, *CHI*, *CHS*, *F3H*, *DFR*, *ANS*, *3GT*, and *UFGT* expression.	[242]
Sweet cherry fruits (*Prunus avium*)	MEL 100 μM	Lower respiration intensity, and weight loss, higher firmness, lightness, saturation, hue angle, titratable acidity, and total soluble solids content, lower electrolyte leakage and MDA accumulation, lower O_2^- generation and H_2O_2 accumulation, higher endogenous phytomelatonin accumulation, higher SOD, CAT, APX, DHAR, MDHAR, and GR activity, higher AA/DHA and GSH/GSSG accumulation.	[243]
	MEL 100 μM	Lower respiration intensity, and ethylene production, higher firmness, higher anthocyanins accumulation, lower MDA accumulation, lower weight and water loss, improving cuticle integrity, higher *CER1* and *GPAT4/8* expression, lower water channels *PIP1;4* and *PIP2;7* expression, higher endogenous ABA accumulation, higher *NCED1* expression. Higher *Cu/Zn-SOD*, *Mn-SOD*, *CAT*, *APX*, *MDHAR*, *DHAR*, and *GR* expression, higher *DFR* and *UFGT* expression.	[244]
	MEL 100 μM	Lower flesh browning and decay incidence, higher endogenous phytomelatonin accumulation, higher *TDC*, *T5H*, *SNAT*, and *ASMT* expression, higher endogenous H_2S accumulation, higher *LCD* and *DCD* expression and activity, higher phenols, flavonoids and anthocyanins accumulation, higher PAL and CHS activity, lower PPO activity, higher ABTS, DPPH, and FRAP scavenging capacity, higher SOD, CAT, APX and GR activity, lower H_2O_2 accumulation, lower PLD and LOX activity, lower MDA accumulation.	[245]
	MEL 100 μM	Higher lightness (L*), chromaticity (C*), TSS and TA, lower weight loss, lower electrolyte leakage, higher firmness, higher endogenous phytomelatonin accumulation, higher endogenous phenylalanine, tyrosine, tryptophan, alanine, valine, leucine, glutamine, glutamate, histidine, arginine, GABA, proline, aspartate, asparagine, threonine, isoleucine and methionine accumulation, higher *TDC*, *T5H*, *SNAT*, and *ASMT* expression, higher anthocyanins, procyanidins and flavonoids accumulation, higher *PAL*, *C4H*, *4CL*, *CHS*, *F3H*, *F3′H*, *DFR*, *ANS*, and *UFGT* expression,	[246]
Blueberry fruits (*Vaccinium corymbosum*)	MEL 50 μM	Higher firmness, lower decay incidence and weight loss, higher phenols and anthocyanins accumulation, higher *PAL* expression and activity, higher *APX* and *GST* expression and activity, higher ascorbic acid accumulation, lower O_2^- generation and H_2O_2 accumulation, lower LOX activity, lower MDA accumulation.	[247]
	MEL 1000 μM	Lower flesh browning, higher phenols, flavonoids and anthocyanins accumulation, lower PPO activity, lower H_2O_2 and higher AA accumulation, higher SOD, CAT and APX activity, lower LOX activity, lower electrolyte leakage and MDA accumulation.	[248]
	MEL 100 μM	Lower water loss, higher cuticular wax accumulation, higher cuticular wax enrichment with diketone, triterpenoid, oleanolic, and hexadecenoic acids.	[249]
	MEL 300 μM	Lower electrolyte leakage and MDA accumulation, lower LOX activity, higher anthocyanins and AA accumulation, lower PME, PG, Cel, and β-Glu activity, higher protopectin and cellulose accumulation.	[250]

(Continues)

TABLE 3 | (Continued)

Plant material	Treatments	Molecular and biochemical effects	References
	MEL 50 μM	Lower water loss, lower cuticular wax degradation, higher cuticular wax enrichment with triterpenoids ursolic acid, α-amyrin, and β-amyrin accumulation, lower cuticular wax saturated fatty acids octadecanoic, eicosanoic, and triacontanoic acid oxidation metabolic degradation, lower PG, β-Gal, PME and Cel expression and activity.	[251]
	MEL 100 μM	Higher cuticular wax accumulation, higher cuticular wax enrichment with alkanes and triterpenoids β-amyrin, α-amyrin, ursolic acid, oleanolic acid, lupeol, and betulinic acid, lower water loss.	[252]
Blackberry fruits (*Rubus fruticosus* L.)	MEL 100 μM	Lower anthocyanin degradation dependent red drupelet reversion, lower PPO activity, higher phenols, flavonoids and anthocyanins accumulation, higher GSH and AA accumulation, higher DPPH scavenging capacity, higher SOD, GR, CAT, MDHAR, DHAR and APX activity, lower H_2O_2 accumulation, lower MDA accumulation.	[253]
Raspberry fruits (*Rubus idaeus*)	MEL 200 μM	Lower weight loss and disease incidence, higher phenols, flavonoids and anthocyanins accumulation, DPPH scavenging capacity, lower H_2O_2 accumulation, lower MDA accumulation, lower PPO activity, lower LOX activity, higher AA and GSH accumulation, higher CAT, SOD, APX, DHAR, MDHAR and GR activity.	[254]
Kiwifruits (*Actinidia deliciosa*)	MEL 100 μM	Lower ethylene production and respiration intensity, higher firmness, lower *ERF4*, *ERF74*, and *ERF75* expression, lower *PDC1* and *PDC2* and *ADH1* expression and activity, lower endogenous pyruvate accumulation, lower endogenous ethanol and acetaldehyde accumulation, lower alcoholic off-flavor.	[255]
	MEL 100 μM	Higher phenols and flavonoids accumulation, higher DPPH, FRAP, and ABTS scavenging capacity, lower MDA accumulation.	[256]
	MEL 100 μM	Higher firmness, lower *PME*, *PG*, *Cel*, and *β-Gal* activity, lower MDA accumulation, higher pectin, cellulose, and hemicellulose accumulation, higher ascorbic acid accumulation.	[257]
	MEL 100 μM	Higher *GME2*, *GalDH*, *GalLDH*, *PMI2*, *PMM*, *GMP1*, *GME1*, and *GGP1* expression, higher *APX1*, *GR*, *MDHAR1*, *MDHAR2*, and *DHAR* expression, lower *AAO* expression, higher endogenous AA accumulation.	[258]
Kiwiberry fruits (*Actinidia arguta*)	MEL 100 μM	Higher chlorophyll, carotenoid, and AA accumulation, lower softening and weight loss, higher sucrose, glucose, and fructose accumulation, higher starch accumulation, lower amylase activity, higher *HK* and *FK* expression, higher *AI*, *NI*, *SPS* and *SuSy-S* expression and activity.	[259]
Papaya fruits (*Carica papaya* L.)	MEL 1.5 mM	Higher TA and AA accumulation, lower TSS and weight loss, higher phenols accumulation, higher DPPH scavenging capacity, higher SOD and CAT activity, lower H_2O_2 accumulation, lower MDA accumulation.	[260]
Peach fruits (*Prunus persica*)	MEL 100 μM	Lower weight loss, decay incidence and respiration intensity, higher firmness, total soluble solids and AA accumulation, higher SOD, CAT, and APX activity, lower O_2^- generation and H_2O_2 accumulation, lower LOX activity, lower MDA accumulation.	[261]
	MEL 100 μM	Lower H_2O_2 accumulation, lower MDA accumulation, higher DPPH and ABTS scavenging capacity, higher SOD, CAT, and APX activity, higher endogenous glutamate and GABA accumulation, higher *GAD1* and *GAD4* expression, lower *GABA-T* expression.	[262]

(Continues)

TABLE 3 | (Continued)

Plant material	Treatments	Molecular and biochemical effects	References
Mango fruits (*Mangifera indica* L.)	MEL 100 μM	Lower weight loss and higher firmness, higher phenols and flavonoids accumulation, lower PPO activity, higher AA accumulation, higher CAT activity, higher DPPH scavenging capacity.	[263]
	MEL 500 μM	Higher firmness, lower chromaticity b*, lower β-carotene accumulation, lower climacteric ethylene production, lower ACS and ACO activity, lower endogenous ACC accumulation, lower endogenous ABA accumulation, lower NCED activity, lower PG, β-Gal and PME activity.	[264]
	MEL 100 μM	Lower softening, respiration intensity, and chlorophyll degradation, higher PC and PI accumulation, lower PS and PA accumulation, higher unSFA accumulation, lower saturated fatty acids (lauric acid, myristic acid, palmitic acid and stearic acid) accumulation, higher unsaturated fatty acids (linoleic acid and linolenic acid), lower H_2O_2 accumulation, lower MDA accumulation.	[265]
	MEL 1000 μM	Lower weight loss and higher firmness, lower respiration intensity, lower *PG*, *PME*, *Cel*, and *β-Glu* expression and activity, higher AA and GSH accumulation, higher GR activity, lower $O_{2\cdot-}$ generation and H_2O_2 accumulation.	[266]
	MEL 1000 μM	Lower fungicide prochloraz phytotoxicity, lower endogenous fungicide prochloraz accumulation, lower $O_{2\cdot-}$ generation and H_2O_2 accumulation, lower electrolyte leakage and MDA accumulation, higher ΔΨm, lower DNA damage and protein carbonylation, higher SOD, CAT, APX, MDHAR, DHAR and GR activity, higher AA and GSH accumulation, higher cytochrome P450, GST and GT activity.	[267]
Pear fruits (*Pyrus bretschneideri*)	MEL 100 μM	Lower water soaking and core browning physiological disorders, lower ethylene production, lower *ACS1* and *ACO1* expression, higher fruit firmness, lower *PG1* and *Cel* expression, higher *SOD* and *DHAR* expression and activity, lower *LOX* expression and activity.	[268]
	MEL 100 μM	Lower respiration intensity and ethylene production, higher endogenous NO accumulation, higher *NOS* expression and activity, lower *ACS1*, *ACO1* and *ACO2* expression, fruit firmness, lower *PG* and *Cel* expression.	[269]
	MEL 150 μM	Lower ethylene production, higher long-chain *acyl-CoA synthetase* expression, higher ethers, aldehydes and alcohols accumulation, lower ketones accumulation.	[270]
	MEL 200 μM	Higher anthocyanin accumulation, higher *RBOHF* expression, higher signaling $O_{2\cdot-}$ generation and H_2O_2 accumulation, higher *MYB10* transcription factor expression, higher *UFGT* expression.	[271]
	MEL 200 μM	Higher endogenous phytomelatonin accumulation, higher *TDC*, *T5H*, *SNAT* and *ASMT* expression, higher anthocyanin accumulation, higher *PAL*, *CHS*, *CHI*, *F3H*, *ANS*, and *UFGT* expression, higher *MYB10*, *MYB114*, *bHLH* and *WD40* transcription factors expression, higher anthocyanins and flavonols accumulation, lower hydroxycinnamate and flavanol accumulation.	[272]
Fresh-cut pear fruits (*Pyrus bretschneideri*)	MEL 150 μM	Lower enzymatic browning, higher *PAL* and *CHS* expression and activity, higher phenols accumulation, higher DPPH and ABTS scavenging capacity, lower *PPO1* and *PPO5* expression and activity, lower MDA and H_2O_2 accumulation, higher AA accumulation, lower *LOX* expressing.	[273]

(Continues)

TABLE 3 | (Continued)

Plant material	Treatments	Molecular and biochemical effects	References
Jujube fruits (*Zizyphus jujuba*)	MEL 25 μM	Lower respiratory intensity and ethylene production, lower weight loss and higher firmness, higher AA and GSH accumulation, higher APX, MDHAR and GR activity, lower PME, PG, Cel and β-Glu activity.	[274]
	MEL 100 μM	Lower weight loss and decay incidence, higher firmness, higher endogenous phytomelatonin accumulation, higher GR activity, higher endogenous GSH accumulation, higher GST activity, lower endogenous pesticides chlorothalonil, malathion, and glyphosate accumulation, higher FRAP scavenging capacity, higher phenols and ascorbic acid accumulation.	[275]
	MEL 100 μM	Higher endogenous phytomelatonin accumulation, higher *PAL*, *C4H*, *CHS*, *CHI*, *F3H*, *ANS*, *DFR*, *LAR*, *FLS*, and *ANR* expression, higher caffeic acid, catechin, epicatechin, rutin, ferulic acid, p-hydroxybenzoic acid, and chlorogenic acid accumulation.	[276]
	MEL 100 μM	Lower weight loss, higher titratable acid and ascorbic acid accumulation, higher firmness, higher protopectin, cellulose, and hemicellulose accumulation, lower *PG*, *Cel*, *β-Glu*, and *β-Gal*, and *LOX* expression and activity.	[277]
Fresh-cut sweetpotato (*Ipomoea batatas*)	MEL 500 μM	Lower enzymatic browning, lower O_2^- generation and H_2O_2 accumulation, lower MDA accumulation, higher ascorbic acid and α-tocopherol accumulation, lower PAL and PPO activity, higher phenols accumulation, lower LOX expression and activity, higher SOD, CAT, APX, and GR activity, higher *SOD1*, *SOD2*, *CAT1*, *APX1*, *APX3*, *GR1*, *GR2* and *DHAR* expression.	[278]
Chestnut rose fruits (*Rosa roxburghii*)	MEL 50 μM	Higher *GME*, *GGP*, *GMP*, and *GalDH* expression, higher *SOD*, *CAT*, *APX*, *GR*, *DHAR* and *MDHAR* expression and activity, lower MDA accumulation, lower H_2O_2 accumulation, higher AA and GSH accumulation, higher H^+-ATPase, Ca^{2+}-ATPase, SDH and CCO activity, higher intracellular ATP supplying.	[279]
Apple fruits (*Malus domestica*)	MEL 50 μM	Lower respiratory intensity and ethylene production, higher firmness, soluble sugars, and AA accumulation, lower AI and NI activity, lower SorDH, SOX, and SuSy-C activity, higher SuSy-S and SPS activity.	[280]
	MEL 1 mM	Lower weight loss and physical disorder black necrotic spots incidence, lower ethylene production and signaling, lower *ACS1*, *ACO1*, and *ACO3*, and *ERF109* expression, lower MDA accumulation, higher SOD and CAT activity, higher *HSP11* expression.	[281]
Potato tubers (*Solanum tuberosum*)	MEL 50 μM	Higher tubers wound healing, higher *NR* and *NOS* expression, higher endogenous NO accumulation, higher *NADPH oxidase* expression, higher signaling $O_{2\cdot}$ generation and H_2O_2 accumulation, higher suberin polyphenol and lignin accumulation, lower weight loss and disease incidence, higher *PAL*, *4CL*, and *CAD* expression and activity, higher POD activity.	[282]
Orange fruits (*Citrus sinensis*)	MEL 200 μM	Higher *PEPC1/2/4* and *CS1* expression, lower endogenous citrate accumulation, higher cytosolic *ACO2/3*, *NADP-IDH2/3*, *GAD5* and *GABP* expression, higher cytosolic *ATP-CL2*, *PEPCK1* and *FBPase2* expression.	[283]
Navel orange fruits (*Citrus sinensis*)	MEL 200 μM	Lower respiration intensity and weight loss, higher firmness, TSS, and TA, lower H_2O_2 and MDA accumulation, higher *CAT*, *SOD*, *APX* and *GR* expression and activity, higher AA and GSH accumulation, higher phenols accumulation.	[284]

(Continues)

TABLE 3 | (Continued)

Plant material	Treatments	Molecular and biochemical effects	References
Physalis fruits (*Physalis peruviana*)	MEL 200 μM	Lower weight loss, higher firmness, lower respiration intensity, higher phenols and carotenoid accumulation, higher CAT, SOD and APX activity, higher DPPH scavenging capacity, higher PAL activity.	[285]
Passion fruits (*Passiflora edulis*)	MEL 200 μM	Lower shrinkage and browning, lower weight loss, lower ethylene production and respiration intensity, higher firmness, lower electrolyte leakage and MDA accumulation, higher phenols, flavonoids and AA accumulation, higher CAT and SOD activity.	[286]
Hami melon fruits (*Cucumis melo* var. saccharinus)	MEL 500 μM	Lower softening, weight loss, and respiratory intensity, lower $O_{2\cdot}$ generation and H_2O_2 accumulation, lower MDA accumulation, higher SOD, CAT and APX activity, higher phenols, flavonoids and AA accumulation, higher DPPH and ABTS scavenging capacity, lower LPS, LOX, and PLD activity	[287]
Rambutan fruits (*Nephelium lappaceum*)	MEL 125 μM	Lower pericarp browning, lower $O_{2\cdot}$ generation and H_2O_2 accumulation, lower electrolytes leakage and MDA accumulation, higher phenols, flavonoids, and anthocyanins accumulation, lower PPO activity, higher SOD, CAT, APX, MDHAR, DHAR and GR activity, higher AA/DHA and GSH/GSSG accumulation.	[288]
Apricot fruits (*Prunus armeniaca* L.)	MEL 100 μM	Lower pericarp browning, lower softening, decay incidence, and weight loss, higher AA, phenols, and flavonoid accumulation, higher SOD and CAT activity, lower MDA accumulation, lower LOX activity, higher DPPH, ABTS and OH scavenging capacity, lower H_2O_2 accumulation, lower PPO and higher PAL activity.	[289]
	MEL 2 mM	Higher firmness and TSS, lower ethylene production and respiration intensity, lower LOX, HPL, and ADH activity, lower alcohols and aldehydes accumulation, higher ACX and AAT activity, higher lactones and esters accumulation.	[290]
Plum fruits (*Prunus salicina*)	MEL 100 μM	Higher firmness, lower respiration intensity and ethylene production, lower weight loss and decay incidence, higher PAL, 4CL, 4CH and POD activity, higher phenols and lignin accumulation.	[291]
Cherry tomato fruits (*Solanum lycopersicum*)	MEL 100 μM	Higher endogenous phytomelatonin accumulation, higher *TDC*, *T5H*, *SNAT* and *ASMT* expression, lower weight loss, fruit decay, and TA, higher firmness, TSS as well as TSS/TA, lower electrolyte leakage and MDA accumulation, higher GR, and APX activity, higher AA and GSH accumulation.	[292]
Longan fruits (*Dimocarpus Longan*)	MEL 400 μM	Lower pericarp browning, higher lightness and h° value, lower a* value, lower electrolyte leakage and MDA accumulation, lower PPO and POD activity, lower $O_{2\cdot}$ generation and H_2O_2 accumulation, higher phenols, flavonoids and GSH accumulation, higher APX and SOD activity.	[293]
Okra fruits (*Abelmoschus esculentus*)	MEL 100 μM	Higher endogenous phytomelatonin accumulation, higher *TDC*, *T5H1-3*, *SNAT* and *COMT1-3* expression, higher endogenous IAA and GA accumulation, higher endogenous GABA accumulation, lower endogenous ABA accumulation.	[294]
Pepper fruits (*Capsicum annuum*)	MEL 100 μM	Lower $O_{2\cdot}$ generation and H_2O_2 accumulation, lower MDA accumulation, higher *CAT* expression and activity, lower *NAC1* transcription factor expression, lower *PLD* and *LOX* expression, higher AA/DHA and GSH/GSSG accumulation, higher firmness, lower *PG* and *EGases* expression.	[295]
Cut peony flowers (*Paeonia lactiflora* Pall.)	MEL 500 μM	Higher endogenous phytomelatonin accumulation, higher *TDC* and *COMT1* expression, higher stems strength, higher S-lignin and G-lignin accumulation (higher S/G lignin accumulation), higher *PAL*, *CCR*, *CAD*, *COMT* and *POD* expression.	[296]

(Continues)

TABLE 3 | (Continued)

Plant material	Treatments	Molecular and biochemical effects	References
Cut rose flowers (*Rosa hybrida*)	MEL 200 μM	Longer vase life, lower stomatal aperture, higher phenols and GSH accumulation, higher CAT, APX and GR activity, lower H_2O_2 accumulation, lower electrolyte leakage and MDA accumulation, higher DPPH scavenging capacity.	[297]
Cut tuberose flowers (*Polianthes tuberosa* L.)	MEL 100 μM	Longer vase life, higher SOD and CAT activity, lower H_2O_2 and MDA accumulation.	[298]
Cut carnation flowers (*Dianthus caryophyllus* L.)	MEL 100 μM	Longer vase life, higher fresh weight and water uptake, lower respiration intensity and ethylene production, lower electrolyte leakage, higher chlorophyll and phenols accumulation, higher ABTS scavenging capacity.	[299]
	MEL 1 mg/L	Longer vase life, lower H_2O_2 and MDA accumulation, higher SOD and POD activity, lower procyanidins, catechin and epicatechin accumulation, lower endogenous SA and ABA accumulation, higher endogenous JA accumulation, higher L-phenylalanine, p-hydroxycinnamic acid, p-coumaric acid, perillyl alcohol, p-coumaryl alcohol, and cinnamic acid accumulation.	[300]
Cut peony flowers (*Paeonia lactiflora* Pall.)	MEL 50 μM	Delaying senescence and extending vase life, improving stem water balance, lower electrolyte leakage and MDA accumulation, higher SOD and CAT activity.	[301]

S-transferase (GST) activity degrading pesticides, which displays worthy potential to improve healthy food for human consumption. Hu et al. [267] reported that melatonin treatment attenuates fungicide prochloraz phytotoxicity in mango fruits, exhibiting lower endogenous fungicide accumulation, which could be attributed to higher cytochrome P450, GST and glycosyltransferases (GTs) enzyme activities along with higher SOD, CAT, APX, MDHAR, DHAR, and GR antioxidative enzyme activities, with higher endogenous AA and GSH accumulation along with lower O_2^- generation, H_2O_2, and MDA accumulation, and lower electrolyte leakage, showing higher mitochondrial membrane potential ($\Delta\Psi_m$), and lower DNA damage and protein carbonylation index. Melatonin could be a promising strategy for detoxifying pesticides in fruits and vegetables during postharvest. Therefore, melatonin exhibits great potential to improve food safety for human consumption [267, 275].

By exogenous melatonin application, delaying senescence and preserving organoleptic and nutritional quality of vegetables crops could be attributed to promoting endogenous melatonin accumulation [198, 207], preventing chlorophyll degradation [193, 195, 199, 200, 210, 211], inhibiting ethylene biosynthesis [192, 199, 210], suppressing endogenous ABA accumulation [207], inhibiting carotenoid accumulation [198], promoting cyclic guanosine 3′,5′-monophosphate (cGMP) signaling pathway [195], suppressing transcriptional activators ABFs responsive ABA biosynthesis and chlorophyll degradation genes expression [207], suppressing ERF2/ERF109 transcription factors inhibitory on flavonoid biosynthesis [210], promoting glucoraphanin and sulforaphane biosynthesis by enhancing glucoraphanin-sulforaphane system activity [197], suppressing PCD by maintaining mitochondrial biogenesis function [201], intracellular reducing power NADPH and carbon skeletons Er4P supplying [208], enhancing intracellular ATP supplying [208], promoting endogenous SA and IAA biosynthesis and signaling along with suppressing endogenous JA biosynthesis and signaling [194, 196, 211], enhancing endogenous glutamate supplying by promoting GS and GOGAT activities [196], inhibiting O_2^- generation and H_2O_2 accumulation along with enhancing AA/DHA and GSH/GSSG accumulation responsible for protective membrane integrity [193, 209, 212] and enhancing phenylpropanoid pathway activity for boosting phenols, flavonoids, and anthocyanins accumulation leading to improving ABTS, DPPH, and FRAP radical scavenging capacity [208, 209, 213, 214, 308]. By exogenous melatonin application, alleviating bamboo shoot lignification could be ascribed to suppressing secondary cell wall (SCW) formation by inhibiting cellulose, hemicellulose, and lignin biosynthesis *PAL*, *CAD*, and *POD* expression and activity arising from lower NACs and MYBs transcription factors expression, enhancing intracellular ATP supplying by enhancing *H^+-ATPase*, *Mg^{2+}-ATPase*, *Ca^{2+}-ATPase*, *SDH*, and *CCO* expression and activity accompanying by enhancing intracellular NADPH supplying by promoting NADK activity [221–223].

In addition, packaging films and edible coatings enrichment with melatonin has been designed in different strategies including chitosan-based melatonin layer-by-layer assembly (CMLLA) [309], melatonin in combination with phase change materials (PCMs) [310], glutenin/tamarind gum/melatonin bioactive film (G/T/M) [311], glutenin/tamarind gum loaded with the binary microemulsion of melatonin/pummelo essential oil (G/T-M-E) [312, 313], melatonin-loaded UiO-66 metal-organic framework nanoparticles (MOF-MEL) [314], carboxymethyl cellulose-gelatin-melatonin edible coating (CMC-Gel-M) [315], and chitosan-based melatonin edible coating (CH-M) [316–318] have been employed with exciting results for alleviating chilling injury and fungal decay, delaying senescence and preserving organoleptic and nutritional quality [43] (Table 4).

TABLE 4 | Packaging films and edible coatings enrichment with melatonin for improving postharvest storability of fruits and vegetable.

Plant material	Treatments	Molecular and biochemical effects	References
Fresh-cut broccoli florets (*Brassica oleracea* L. var. italic)	CMLLA	Higher packaging film DPPH radical scavenging capacity and antibacterial activity, lower weight loss and chlorophyll degradation, higher firmness and sugar/acid ratio.	[309]
White button mushrooms (*Agaricus bisporus*)	PCM + MEL	Cap browning attenuating, higher endogenous phytomelatonin accumulation, higher *T5H*, *SNAT*, and *AMST* expression, lower weight loss and higher firmness, lower electrolyte leakage and MDA accumulation, lower O_2^- generation and H_2O_2 accumulation, higher phospholipids and unSFA accumulation, higher *PAL* expression and activity, lower *PPO* expression and activity, higher phenols accumulation, higher FRAP scavenging capacity, higher intracellular ATP and ADP supplying, lower intracellular AMP supplying, higher H^+-ATPase and Ca^{2+}-ATPase activity, higher SOD, APX and GR activity.	[310]
	G/T/M packaging film	Cap browning attenuating, higher SOD, CAT, APX, GR, DHAR, MDHAR activity, higher AA/DHA and GSH/GSSG accumulation, lower O_2^- generation and H_2O_2 accumulation, lower MDA accumulation, lower PPO activity.	[311]
	G/T-M-E packaging film	Cap browning attenuating, higher hardness, fracturability, chewiness and lower adhesiveness, lower caps opening and off-flavor, higher overall acceptability, lower respiration intensity, lower MDA accumulation.	[312]
	G/T-M-E packaging film	Higher firmness, lower cap opening, weight loss, respiration intensity, lower electrolytic leakage, higher SDH and CCO activity, higher intracellular ATP supplying, lower O_2^- generation and H_2O_2 accumulation, lower PPO activity, higher SOD and CAT activity.	[313]
Spinach (*Spinacia oleracea* L.)	UiO-66 MOF-M packaging film	Delaying leaf yellowing, lower weight loss, higher chlorophyll accumulation, lower MDA accumulation, higher SOD, CAT and POD activity, lower O_2^- generation and H_2O_2 accumulation.	[314]
Longkong fruit (*Lansium domesticum*)	CMC-Gel-M edible coating	Chilling injury attenuation, lower pericarp browning, weight loss, and respiration intensity, lower PLD and LOX activity, lower electrolyte leakage and MDA accumulation, lower H_2O_2, OH^-, O_2^- accumulation, higher PAL activity, lower PPO activity, higher phenols accumulation, higher DPPH and ABTS scavenging capacity,	[315]
Pomegranate aril (*Punica granatum* L.)	CH-M edible coating	Lower aril browning, lower weight loss and respiration intensity, higher AA and anthocyanins accumulation, higher DPPH and FRAP scavenging capacity.	[318]
Sweet cherry fruits (*Prunus avium*)	CH-M edible coating	Lower weight loss and respiration intensity, higher firmness, higher AA, phenols and anthocyanins accumulation, higher DPPH scavenging capacity.	[317]
Banana fruits (*Musa acuminate* L.	CH-M edible coating	Lower pericarp browning, lower electrolyte leakage, higher AA, phenols and flavonoids accumulation, lower PPO activity, higher DPPH scavenging capacity, lower PG, α-amylase and xylanase activity, higher firmness.	[316]

7 | Plant Hormones and Gas Transmitters Imply Phytomelatonin Biosynthesis

By exogenous ATP application, white mushrooms exhibited higher endogenous phytomelatonin accumulation. Aghdam et al. [319] suggested that the extracellular ATP signaling by does not respond to nucleotides 1 (DORN1/P2K1) could be liable for boosting endogenous phytomelatonin biosynthesis. By boosting endogenous phytomelatonin accumulation resulting from extracellular ATP signaling, activating *AOX* expression could be liable for avoiding ROS accumulation and ensuring sufficient ATP and carbon skeletons supply, which protect membrane integrity represented by lower MDA accumulation, delays mushroom senescence represented by lower cap browning and preserve white mushroom nutritional quality by boosting higher phenol accumulation and higher DPPH scavenging capacity through phenylpropanoid pathway activity evidenced by enhancing PAL activity along with suppressing PPO activity [319]. By exogenous ATP application, extracellular ATP signaling could be liable for boosting shikimic acid pathway activity, as represented by higher SKDH activity, for sufficient tryptophan supply and support for melatonin accumulation. By serving as an extracellular ATP receptor, plasma membrane purinoreceptor DORN1/P2K1 is responsible for activating NADPH oxidase, activating ROS and Ca^{2+} signaling, and boosting NADPH/Ca^{2+}-CaM/arginine-dependent NOS/NO system activity [40, 114, 320]. DORN1-dependent NO biosynthesis could be liable for activating soluble guanylate cyclase (sGC) enzyme and cytosolic cGMP accumulation [114]. By silencing mevalonate kinase (*MVK*) expression using CRISPR/Cas9 technology, Cho et al. [321] revealed that the direct phosphorylation of MVK by DORN1 may be responsible for higher phenylalanine and tryptophan accumulation, reinforcing plant innate immunity [321].

By exogenous phytosulfokine α (PSKα) application, delaying senescence, attenuating decay, and preserving the nutritional quality of strawberry fruits could be ascribed to activating the endogenous PSKα signaling pathway. By serving as a moonlighting protein, PSKα receptor (PSKR1) exhibited particulate guanylyl cyclase (pGC) activity for producing cGMP. PKG could be liable for target proteins or transcription factors phosphorylation for cytosolic cGMP signaling. In addition to PKG, boosting cytosolic Ca^{2+} accumulation by cyclic nucleotide-gated ion channels (CNGCs) opening could be liable for cytosolic cGMP signaling by calcium/calmodulin (Ca^{2+}/CaM) or CDPK [40, 114, 322]. By exogenous PSKα application, cytosolic cGMP signaling could be liable for boosting endogenous phytomelatonin accumulation resulting from activating *TDC*, *T5H*, *SNAT*, and *ASMT* expression. By endogenous phytomelatonin accumulation, boosting intracellular ATP supply resulting in higher SDH and CCO activity was accompanied by activating extracellular ATP signaling evidenced by higher extracellular ATP accumulation resulting in lower apyrase 1 (*APY1*) expression, preserving intracellular ATP and ROS homeostasis by regulating TOR/SnRK1 signaling pathways, boosting NADPH oxidase activity and signaling H_2O_2 accumulation, activating posttranslational proteins SUMOylation SUMO E3 ligase (*SIZ1*) expression concomitant with suppressing NAD^+ dissipating poly-ADP-ribose polymerase 1 (*PARP1*) expression, enhancing ROS scavenging system activity, improving OxPP and folate pathways activity for carbon skeletons and NADPH supplying, and boosting phenols, flavonoids, and anthocyanins accumulation by activating phenylpropanoid pathway [322–331]. According to ROS responsive ERF109 and ERF115 directly binding to phytosulfokine 2 (*PSK2*) gene promoter and ERF114 and ERF115 directly binding to *PSK5* gene promoter [332], and brassinosteroid responsive ERF115 directly binding to *PSK5* gene promoter [333], activating *PSKs* expression and signaling by ERFs transcription factors may be responsible for boosting endogenous phytomelatonin accumulation.

By employing EGTA, an endogenous Ca^{2+} chelator, Hu et al. [334] reported that exogenous $CaCl_2$ application promotes endogenous Ca^{2+} accumulation concomitant enhancing endogenous phytomelatonin accumulation by activating *TDC1*, *TDC2*, *T5H*, *ASMT1*, *ASMT2*, *ASMT3*, and *SNAT* expression, which could be responsible for delaying postharvest physiological deterioration (PPD) progression accompanied by promoting ascorbic acid and starch accumulation in cassava storage roots [334]. By exogenous methyl jasmonate (MeJA) and ethanol application, endogenous phytomelatonin accumulation by activating *TDC1*, *TDC2*, *T5H*, *ASMT1*, *ASMT2*, *ASMT3*, and *SNAT* expression could be liable for delaying PPD progression in cassava storage root through boosting endogenous gibberellin and ethylene accumulation accompanying by activating *APX2* and *GR* expression and boosting SOD and CAT activity leading to lower O_2^- and H_2O_2 accumulation and boosting ABTS scavenging capacity. In addition to delaying PPD, exogenous MeJA, and ethanol application preserves higher ascorbic acid, starch, and carotenoid accumulation and maintains quality in cassava storage roots [335, 336].

Yin et al. [337] reported that exogenous MeJA application promoted endogenous phytomelatonin biosynthesis in mustard sprouts by activating *TDC1*, *TDC2*, *T5H1*, *T5H2*, *SNAT1*, *SNAT2*, *SNAT3*, *SNAT4*, *ASMT1*, *ASMT2*, and *ASMT3* expression. By quantitative iTRAQ proteomic analysis, also, exogenous MeJA application promoted tryptophan biosynthetic pathway proteins expression and supported endogenous phytomelatonin accumulation in mustard sprouts.

Zhou et al. [338] reported that exogenous IAA treatment conferred chilling tolerance in peach fruit by promoting endogenous phytomelatonin biosynthesis arising from activating *TDC1*, *T5H1*, *T5H2*, *SNAT*, and *COMT* expression. By exogenous IAA treatment, higher endogenous phytomelatonin IAA and GABA accumulation was accompanied by lower endogenous GA and ABA accumulation.

Dong et al. [339] reported that hydrogen-rich water (HRW) application delayed senescence in okra fruits by boosting endogenous phytomelatonin biosynthesis resulting from activating *TDC*, *T5H1/2/3*, *SNAT,* and *COMT1/2* expression along with boosting endogenous GA and IAA accumulation accompanying by inhibiting endogenous ABA accumulation. Therefore, boosting melatonin/ABA, GA/ABA and IAA/ABA accumulation could be liable for delaying senescence in okra fruits by HRW application [339]. By employing ammonia borane (ammoniotrihydroborate; H_3NBH_3) or transgenic tomato and Arabidopsis expressing hydrogenase1 (*CrHYD1*) from *Chlamydomonas reinhardtii* for safe, efficient, stable, long-acting, and lower dosage

H_2 supplying, endogenous molecule hydrogen (H_2) accumulation is responsible for promoting lateral root branching in tomato and Arabidopsis plants [340]. By endogenous molecule hydrogen (H_2) accumulation, activating *TDC*, *T5H*, *SNAT*, *ASMT* and *COMT* expression promotes endogenous phytomelatonin biosynthesis. By pharmacologically inhibiting endogenous phytomelatonin biosynthesis by employing p-chlorophenylalanine (p-CPA) application or biotechnological suppressing endogenous phytomelatonin biosynthesis by *SNAT* and *COMT* genes silencing, Wang et al. [340] reported that endogenous phytomelatonin biosynthesis is indispensable for promoting lateral root branching in tomato and Arabidopsis by endogenous molecule hydrogen (H_2) accumulation arising from ammonia borane employing or *CrHYD1* expression (Table 5).

TABLE 5 | Endogenous phytomelatonin biosynthesis by employing postharvest technologies for improving postharvest storability of fruits and vegetable.

Plant material	Treatments	Molecular and biochemical effects	References
Fresh walnut fruit (*Juglans regia)*	CA + ClO_2	Higher endogenous phytomelatonin accumulation, higher POD activity, lower PAL and PPO activity, higher acid value, lower peroxide value and carbonyl value, lower mold incidence.	[341]
Strawberry fruits (*Fragaria ananassa*)	PSKα 150 nM	Higher endogenous phytomelatonin accumulation, higher *TDC*, *T5H*, *SNAT*, and *ASMT* expression, higher endogenous PSKα accumulation, higher *PSK3* and *PSK6* expression, higher *PSKR1* expression, higher endogenous Ca^{2+} accumulation, higher endogenous cGMP accumulation, higher phenols, flavonoids, and anthocyanins accumulation, higher ABTS and DPPH scavenging capacity, higher *PAL* and *CHS* expression and activity.	[322]
Table grape (*Vitis vinifera* L.)	SA 2 mM	Higher endogenous phytomelatonin accumulation, lower endogenous histamine and dopamine accumulation. Lower berry drop and decay incidence, higher rutin, cyanidin-3,5-diglucoside and 3-O-glycosidic delphinidin accumulation, higher chlorogenic acid and gallic acid accumulation,	[342]
Okra fruits (*Abelmoschus esculentus*)	HRW 220 μM	Higher endogenous phytomelatonin accumulation, higher *TDC*, *T5H1/2/3*, *SNAT*, and *COMT1/2* expression, higher endogenous GA accumulation, higher endogenous IAA accumulation, lower endogenous ABA accumulation.	[339]
Mustard sprout (*Brassica juncea*)	MeJA 100 mM	Higher endogenous phytomelatonin accumulation, higher *TDC1*, *TDC2*, *T5H1*, *T5H2*, *SNAT1*, *SNAT2*, *SNAT3*, *SNAT4*, *ASMT1*, *ASMT2*, and *ASMT3* expression, higher myrosinase 1, cytosolic sulfotransferase 16, and glutamate-glyoxylate aminotransferase 2 proteins expression.	[337]
Cassava roots (*Manihot esculenta*)	$CaCl_2$ 10 mM	Higher endogenous phytomelatonin accumulation, higher *TDC1*, *TDC2*, *T5H*, *ASMT1*, *ASMT2*, *ASMT3*, and *SNAT* expression, PPD progression delaying, higher *CaMs*, *CMLs*, *CPKs* and *CBLs* expression, higher endogenous Ca^{2+} accumulation, higher AA and starch accumulation.	[334]
	MeJA 10 mM	Higher endogenous phytomelatonin accumulation, higher *TDC1*, *TDC2*, *T5H*, *ASMT1*, *ASMT2*, *ASMT3*, and *SNAT* expression, PPD progression delaying, higher endogenous GA3 accumulation, higher SOD and CAT activity, lower O_2^- generation and H_2O_2 accumulation, higher ascorbic acid, starch, and carotenoids accumulation.	[335]
	Ethanol 50%	Higher endogenous phytomelatonin accumulation, higher *TDC1*, *TDC2*, *T5H*, *ASMT1*, *ASMT2*, *ASMT3*, and *SNAT* expression, PPD progression delaying, higher SOD and CAT activity, lower O_2^- generation and H_2O_2 accumulation, higher ascorbic acid, starch, anthocyanin and carotenoids accumulation, higher ABTS scavenging capacity, higher *APX2*, *GR* and *Cu/ZnSOD* expression, higher endogenous ethylene production.	[336]

(Continues)

TABLE 5 | (Continued)

Plant material	Treatments	Molecular and biochemical effects	References
White button mushrooms (*Agaricus bisporus*)	ATP 750 μM	Higher endogenous phytomelatonin accumulation, Cap browning attenuating, higher signaling H_2O_2 accumulation, higher NADPH oxidase activity, higher *AOX* expression, higher phenol accumulation, higher DPPH scavenging capacity, higher PAL activity, lower PPO activity, higher SKDH activity, lower MDA accumulation.	[319]
Tomato (*Solanum lycopersicum*) and Arabidopsis (*Arabidopsis thaliana*)	Ammonia borane or *CrHYD1* gene overexpressing	Higher endogenous phytomelatonin accumulation, higher *TDC*, *T5H*, *SNAT*, *ASMT* and *COMT* expression, higher endogenous H_2 accumulation, higher lateral root branching.	[340]
Peach fruits (*Prunus persica*)	IAA 500 μM	Higher endogenous phytomelatonin and GABA accumulation, lower endogenous ABA and GA accumulation, higher *TDC1*, *T5H1*, *T5H2*, *SNAT*, and *COMT* expression.	[338]

8 | Conclusion and Future Perspectives

The different aspects presented in this work point to a spectacular increase in information on phytomelatonin in a few years. It is noteworthy that in the period 2009–2017 there was a number of publications related to melatonin of 33 per year, and in 2018–2020 there was an exponential increase (388 articles, with an average of 130 per year), while in 2023 more than 500 articles were published. Of the aspects analyzed here, we must point out that:

- The biosynthetic pathway of phytomelatonin is well established in higher plants, knowing the enzymes involved and the sites of biosynthesis in the cell. However, some aspects remain unelucidated, such as the detection in many cases of 5-hydroxytryptophan without having detected or identified the enzyme responsible for its formation from tryptophan. Little or nothing is known about the biosynthesis of phytomelatonin in other groups of plants beyond those of agronomic interest.
- We have presented the multiple factors and regulatory elements of the gene expression of phytomelatonin biosynthetic enzymes, being diverse, complex and with aspects of intervention of interest in the postharvest improvement of fruits and vegetables.
- Other aspects analyzed with special interest have been the configuration and mode of action of the plant melatonin receptor (CAND2/PMTR1), less evolved than that of mammals but with common points. And the interesting role of melatonin in autophagic activity, an aspect of maximum interest in melatonin studies in humans and animals.
- Undoubtedly, the improvement in plant tolerance to stressors (resilience) is one of the responses mediated by melatonin of great basic and applied significance. In this work, two of the stressors most directly involved with the postharvest quality of fruits and vegetables have been exposed, such as UV-B light and chilling injury, although multiple examples of water stress and biotic stress (fungal decay) applied to the improvement of postharvest quality and its improvement in the marketing of these products have also been given.
- Possibly one of the aspects that still requires more research is the metabolic, regulatory and signaling interconnections between phytomelatonin and the various plant hormones involved in the ripening and senescence of fruits and vegetables, mainly GAs, ABA, ethylene, SA and JA, as well as auxin and others. The hormonal plant network is clearly modulated by melatonin, which is why it was attributed the role of *plant master regulator*. There is sufficient knowledge to apply it in postharvest improvement that extends the commercial life of agro-products using also the challenges of new materials (new functional packaging, bioactive films) and the globalized refrigerated transport and conservation.

With regard to future perspectives, today, we have enough data and knowledge about the functions of phytomelatonin in higher plants and ways to modulate or alter its endogenous content in tissues to be able to face challenges with direct application in agriculture. Among the most interesting action points where melatonin could play a role in improving physiological processes would be: seed germination, rooting of cuttings, improvement of rhizobiome, vegetative growth, resilience of seedlings against stressors, photosynthesis, CO_2 intake, improvement in primary metabolism, especially in C, N, P and S; improvement of secondary metabolism, regulating the production of polyphenols and terpenoids, mainly; modulation of reproductive processes, affecting flowering, parthenocarpy and ripening, with special emphasis on the postharvest quality of fruits and vegetables. All these possible actions can and should converge in agronomic actions, especially in seedbeds, improving the resilience of seedlings against stress, obtaining seedlings with a better capacity to adapt to the seedbed-field transition, with better rooting capacity, improve plant growth in contaminated soils or in situations of thermal, saline and water stress, among others; improving the quality of functional foods, rich in functional groups such as antioxidants and others, and improving the postharvest of fruit and vegetables, extending their shelf life and ensuring their organoleptic qualities. In addition to preharvest spraying or postharvest dipping, bioactive films and coatings enriched with melatonin-nanoparticles formulations can be considered as promising approaches for improving the postharvest marketability of fruits and vegetables.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

Data sharing is not applicable to this article as no new data were created or analyzed in this study.

References

1. G. Di Bella, F. Mascia, L. Gualano, and L. Di Bella, "Melatonin Anticancer Effects: Review," *International Journal of Molecular Sciences* 14, no. 2 (2013): 2410–2430.

2. M. B. Arnao and J. Hernández-Ruiz, "Melatonin: Synthesis From Tryptophan and its Role in Higher Plants," in *Amino Acids in Higher Plants*, ed. J. D' Mello (Boston, MA: CAB International, 2015), 390–435.

3. Z. Xie, F. Chen, W. A. Li, et al., "A Review of Sleep Disorders and Melatonin," *Neurological Research* 39, no. 6 (2017): 559–565.

4. B. S. Alghamdi, "The Neuroprotective Role of Melatonin in Neurological Disorders," *Journal of Neuroscience Research* 96, no. 7 (2018): 1136–1149.

5. C. Blume, M. Angerer, M. Raml, et al., "Healthier Rhythm, Healthier Brain? Integrity of Circadian Melatonin and Temperature Rhythms Relates to the Clinical State of Brain-Injured Patients," *European Journal of Neurology* 26, no. 8 (2019): 1051–1059.

6. A. I. Socaciu, R. Ionuţ, M. A. Socaciu, et al., "Melatonin, an Ubiquitous Metabolic Regulator: Functions, Mechanisms and Effects on Circadian Disruption and Degenerative Diseases," *Reviews in Endocrine and Metabolic Disorders* 21, no. 4 (2020): 465–478.

7. D.-X. Tan and R. J. Reiter, "Melatonin Reduces the Mortality of Severely-Infected COVID-19 Patients," *Melatonin Research* 4, no. 4 (2021): 613–616.

8. E. S. Lauritzen, U. Kampmann, M. G. B. Pedersen, et al., "Three Months of Melatonin Treatment Reduces Insulin Sensitivity in Patients with Type 2 Diabetes—A Randomized Placebo-Controlled Crossover Trial," *Journal of Pineal Research* 73, no. 1 (2022): e12809.

9. A. B. Lerner, J. D. Case, and R. V. Heinzelman, "Structure of Melatonin," *Journal of the American Chemical Society* 81, no. 22 (1959): 6084–6085.

10. A. B. Lerner, J. D. Case, Y. Takahashi, T. H. Lee, and W. Mori, "Isolation of Melatonin, the Pineal Gland Factor That Lightens Melanocytes," *Journal of the American Chemical Society* 80, no. 10 (1958): 2587.

11. R. Dubbels, R. J. Reiter, E. Klenke, et al., "Melatonin in Edible Plants Identified By Radioimmunoassay and By High Performance Liquid Chromatography-Mass Spectrometry," *Journal of Pineal Research* 18, no. 1 (1995): 28–31.

12. A. Hattori, H. Migitaka, M. Iigo, et al., "Identification of Melatonin in Plants and Its Effects on Plasma Melatonin Levels and Binding to Melatonin Receptors in Vertebrates," *Biochemistry and molecular biology international* 35, no. 3 (1995): 627–634.

13. J. Kolar, I. Machackova, H. Illnerova, E. Prinsen, W. van Dongen, and H. A. van Onckelen, "Melatonin in Higher Plant Determined By Radioimmunoassay and Liquid Chromatography-Mass Spectrometry," *Biological Rhythm Research* 26 (1995): 406–409.

14. M. B. Arnao and J. Hernández-Ruiz, "Melatonin: A New Plant Hormone and/or a Plant Master Regulator?" *Trends in Plant Science* 24, no. 1 (2019): 38–48.

15. M. B. Arnao, A. Cano, and J. Hernández-Ruiz, "Phytomelatonin: An Unexpected Molecule with Amazing Performances in Plants," *Journal of Experimental Botany* 73, no. 17 (2022): 5779–5800.

16. M. B. Arnao and J. Hernández-Ruiz, "Melatonin: Plant Growth Regulator and/or Biostimulator during Stress?" *Trends in Plant Science* 19, no. 12 (2014): 789–797.

17. M. B. Arnao and J. Hernández-Ruiz, "Growth Activity, Rooting Capacity, and Tropism: Three Auxinic Precepts Fulfilled By Melatonin," *Acta Physiologiae Plantarum* 39, no. 6 (2017): 127.

18. M. B. Arnao and J. Hernández-Ruiz, "The Multi-Regulatory Properties of Melatonin in Plants," in *Neurotransmitters in Plants*, eds. A. Ramakrishna and V. V. Roshchina (Boca Raton, FL: CRC Press, 2018), 448.

19. M. B. Arnao and J. Hernández-Ruiz, "Melatonin in Flowering, Fruit Set and Fruit Ripening," *Plant Reproduction* 33, no. 2 (2020): 77–87.

20. M. B. Arnao and J. Hernández-Ruiz, "Melatonin As a Plant Biostimulant in Crops and during Postharvest: A New Approach is Needed," *Journal of the Science of Food and Agriculture* 101, no. 13 (2021): 5297–5304.

21. M. B. Arnao and J. Hernández-Ruiz, "Regulatory Role of Melatonin in the Redox Network of Plants and Plant Hormone Relationship in Stress," in *Plant in Challenging Environments. Hormones and Plant Response*, eds. D. K. Gupta and F. J. Corpas (Cham: Springer International Publishing, 2021), 235–272.

22. J. Hernández-Ruiz and M. B. Arnao, "Relationship of Melatonin and Salicylic Acid in Biotic/Abiotic Plant Stress Responses," *Agronomy* (2018). 8, 33. 4.

23. R. Sharif, C. Xie, H. Zhang, et al., "Melatonin and Its Effects on Plant Systems," *Molecules* 23, no. 9 (2018): 2352.

24. M. B. Arnao and J. Hernández-Ruiz, "Melatonin and Reactive Oxygen and Nitrogen Species: A Model for the Plant Redox Network," *Melatonin Research* 2, no. 3 (2019): 152–1168.

25. M. B. Arnao and J. Hernández-Ruiz, "Melatonin Against Environmental Plant Stressors: A Review," *Current Protein & Peptide Science* 22, no. 5 (2021): 413–429.

26. M. Moustafa-Farag, A. Almoneafy, A. Mahmoud, et al., "Melatonin and Its Protective Role against Biotic Stress Impacts on Plants," *Biomolecules.* 10, no. 1 (2019): 54.

27. M. Moustafa-Farag, A. Mahmoud, M. B. Arnao, et al., "Melatonin-Induced Water Stress Tolerance in Plants: Recent Advances," *Antioxidants* 9, no. 9 (2020): 809.

28. M. Moustafa-Farag, A. Elkelish, M. Dafea, et al., "Role of Melatonin in Plant Tolerance to Soil Stressors: Salinity, pH and Heavy Metals," *Molecules* 25, no. 22 (2020): 5359.

29. M. B. Arnao, J. Hernández-Ruiz, and A. Cano, "Role of Melatonin and Nitrogen Metabolism in Plants: Implications under Nitrogen-Excess or Nitrogen-Low," *International Journal of Molecular Sciences* 23, no. 23 (2022): 15217.

30. M. Giraldo Acosta, A. Cano, J. Hernández-Ruiz, and M. B. Arnao, "Melatonin As a Possible Natural Safener in Crops," *Plants* 11, no. 7 (2022): 890.

31. M. Giraldo-Acosta, C. Martínez-Andújar, P. A. Martínez-Melgarejo, A. Cano, J. Hernández-Ruiz, and M. B. Arnao, "Protective Effect

(Safener) of Melatonin on *Vigna Radiata* L. Seedlings in the Presence of the Fungicide Copper Oxychloride," *Journal of Plant Growth Regulation* 42, no. 8 (2023): 4918–4934.

32. S. Menhas, X. Yang, K. Hayat, et al., "Exogenous Melatonin Enhances Cd Tolerance and Phytoremediation Efficiency by Ameliorating Cd-Induced Stress in Oilseed Crops: A Review," *Journal of Plant Growth Regulation* 41, no. 3 (2022): 922–9935.

33. A. Cano, J. Hernández-Ruiz, and M. B. Arnao, "Melatonin in Plants Under UV Stress Conditions," in *Melatonin: Role in Plant Signaling, Growth and Stress Tolerance: Phytomelatonin in Normal and Challenging Environments*, eds. S. Mukherjee and F. J. Corpas (Cham: Springer International Publishing, 2023), 263–277.

34. J. Hernández-Ruiz, M. Giraldo-Acosta, A. El Mihyaoui, A. Cano, and M. B. Arnao, "Melatonin As a Possible Natural Anti-Viral Compound in Plant Biocontrol," *Plants.* 12, no. 4 (2023): 781.

35. M. B. Arnao, J. Hernández-Ruiz, A. Cano, and R. J. Reiter, "Melatonin and Carbohydrate Metabolism in Plant Cells," *Plants* 10, no. 9 (2021): 1917.

36. M. B. Arnao and J. Hernández-Ruiz, "Melatonin As a Regulatory Hub of Plant Hormone Levels and Action in Stress Situations," *Plant Biology* 23, no. Suppl 1 (2021): 7–19.

37. M. B. Arnao and J. Hernández-Ruiz, "Melatonin and Its Relationship to Plant Hormones," *Annals of Botany* 121, no. 2 (2018): 195–207.

38. A. Arias, G. Feijoo, and M. T. Moreira, "Exploring the Potential of Antioxidants from Fruits and Vegetables and Strategies for Their Recovery," *Innovative Food Science & Emerging Technologies* 77 (2022): 102974.

39. M. S. Aghdam, J. M. Palma, and F. J. Corpas, "NADPH as a Quality Footprinting in Horticultural Crops Marketability," *Trends in Food Science & Technology* 103 (2020): 152–1161.

40. M. S. Aghdam, A. Jannatizadeh, Z. Luo, and G. Paliyath, "Ensuring Sufficient Intracellular ATP Supplying and Friendly Extracellular ATP Signaling Attenuates Stresses, Delays Senescence and Maintains Quality in Horticultural Crops during Postharvest Life," *Trends in Food Science & Technology* 76 (2018): 67–81.

41. M. S. Aghdam, E. J. Flaherty, and B. J. Shelp, "γ-Aminobutyrate Improves the Postharvest Marketability of Horticultural Commodities: Advances and Prospects," *Frontiers in Plant Science* 13 (2022): 884572.

42. M. S. Aghdam, S. Mukherjee, F. B. Flores, M. B. Arnao, Z. Luo, and F. J. Corpas, "Functions of Melatonin during Postharvest of Horticultural Crops," *Plant and Cell Physiology* 63, no. 12 (2022): 1764–1786.

43. S. Mukherjee, S. Roy, and M. B. Arnao, "Nanovehicles for Melatonin: A New Journey for Agriculture," *Trends in Plant Science* 29, no. 2 (2024): 232–2248.

44. Z. Yuxiao, Y. Guo, and S. Xinhua, "Comprehensive Insight into an Amino Acid Metabolic Network in Postharvest Horticultural Products: A Review," *Journal of the Science of Food and Agriculture* 103, no. 12 (2023): 5667–5676.

45. M. S. Aghdam, "Melatonin Language in Postharvest Life of Horticultural Crops," in *Melatonin: Role in Plant Signaling, Growth and Stress Tolerance: Phytomelatonin in Normal and Challenging Environments*, eds. S. Mukherjee and F. J. Corpas (Cham: Springer International Publishing, 2023), 173–215.

46. Y. Gao, H. Chen, D. Chen, and G. Hao, "Genetic and Evolutionary Dissection of Melatonin Response Signaling Facilitates the Regulation of Plant Growth and Stress Responses," *Journal of Pineal Research* 74, no. 2 (2023): e12850.

47. D.-X. Tan and R. J. Reiter, "An Evolutionary View of Melatonin Synthesis and Metabolism Related to Its Biological Functions in Plants," *Journal of Experimental Botany* 71, no. 16 (2020): 4677–4689.

48. K. Lee, H. Y. Lee, and K. Back, "Rice Histone Deacetylase 10 and Arabidopsis Histone Deacetylase 14 Genes Encode N-Acetylserotonin Deacetylase, Which Catalyzes Conversion of N-Acetylserotonin into Serotonin, a Reverse Reaction for Melatonin Biosynthesis in Plants," *Journal of Pineal Research* 64, no. 2 (2018): e12460.

49. D. Zhao, Z. Yao, J. Zhang, et al., "Melatonin Synthesis Genes N-Acetylserotonin Methyltransferases Evolved into Caffeic Acid O-Methyltransferases and Both Assisted in Plant Terrestrialization," *Journal of Pineal Research* 71, no. 3 (2021): e12737.

50. Y. Tsunoda, S. Hano, N. Imoto, et al., "Physiological Roles of Tryptophan Decarboxylase Revealed By Overexpression of SlTDC1 in Tomato," *Scientia Horticulturae* 275 (2021): 109672.

51. Q. Yang, Y. Tan, Y. Ye, D. Zhao, and Q. Liu, "Serotonin Enrichment of Rice Endosperm By Metabolic Engineering," *The Crop Journal* 11 (2023): 1943–1948.

52. X.-N. Wang, J.-C. Zhang, H.-Y. Zhang, X.-F. Wang, and C.-X. You, "Ectopic Expression of MmSERT, a Mouse Serotonin Transporter Gene, Regulates Salt Tolerance and ABA Sensitivity in Apple and Arabidopsis," *Plant Physiology and Biochemistry* 197 (2023): 107627.

53. M. Okazaki, K. Higuchi, A. Aouini, and H. Ezura, "Lowering Intercellular Melatonin Levels By Transgenic Analysis of Indoleamine 2,3-Dioxygenase from Rice in Tomato Plants," *Journal of Pineal Research* 49, no. 3 (2010): 239–247.

54. Y. Byeon and K. Back, "Molecular Cloning of Melatonin 2-Hydroxylase Responsible for 2-Hydroxymelatonin Production in Rice (*Oryza Sativa*)," *Journal of Pineal Research* 58, no. 3 (2015): 343–351.

55. Y. Byeon, D.-X. Tan, R. J. Reiter, and K. Back, "Predominance of 2-Hydroxymelatonin over Melatonin in Plants," *Journal of Pineal Research* 59, no. 4 (2015): 448–454.

56. G.-H. Choi and K. Back, "Suppression of Melatonin 2-Hydroxylase Increases Melatonin Production Leading to the Enhanced Abiotic Stress Tolerance against Cadmium, Senescence, Salt, and Tunicamycin in Rice Plants," *Biomolecules* 9, no. 10 (2019): 589.

57. K. Lee, A. Zawadzka, Z. Czarnocki, R. J. Reiter, and K. Back, "Molecular Cloning of Melatonin 3-Hydroxylase and Its Production of Cyclic 3-Hydroxymelatonin in Rice (*Oryza Sativa*)," *Journal of Pineal Research* 61, no. 4 (2016): 470–478.

58. H. Zhao, Z. Ge, M. Zhou, et al., "Histone Deacetylase 9 Regulates Disease Resistance through Fine-Tuning Histone Deacetylation of Melatonin Biosynthetic Genes and Melatonin Accumulation in Cassava," *Journal of Pineal Research* 74, no. 3 (2023): e12861.

59. Y. Wei, Y. Chang, H. Zeng, G. Liu, C. He, and H. Shi, "Rav Transcription Factors Are Essential for Disease Resistance Against Cassava Bacterial Blight Via Activation of Melatonin Biosynthesis Genes," *Journal of Pineal Research* 64, no. 1 (2018): e12454.

60. S. Y. Cai, Y. Zhang, Y. P. Xu, et al., "HsfA1a Upregulates Melatonin Biosynthesis to Confer Cadmium Tolerance in Tomato Plants," *Journal of Pineal Research* 62, no. 2 (2017): e12387.

61. W. Chen, J. Zhang, S. Zheng, et al., "Metabolite Profiling and Transcriptome Analyses Reveal Novel Regulatory Mechanisms of Melatonin Biosynthesis in Hickory," *Horticulture Research* 8, no. 1 (2021): 196.

62. Y. Wei, G. Liu, Y. Bai, F. Xia, C. He, and H. Shi, "Two Transcriptional Activators of N-Acetylserotonin O-Methyltransferase 2 and Melatonin Biosynthesis in Cassava," *Journal of Experimental Botany* 68, no. 17 (2017): 4997–5006.

63. T. Zhang, Y. Tang, Y. Luan, et al., "Herbaceous Peony AP2/ERF Transcription Factor Binds the Promoter of the Tryptophan Decarboxylase Gene to Enhance High-Temperature Stress Tolerance," *Plant, Cell & Environment* 45, no. 9 (2022): 2729–2743.

64. Y. Wei, B. Zhu, G. Ma, et al., "The Coordination of Melatonin and Anti-Bacterial Activity By EIL5 Underlies Ethylene-Induced Disease Resistance in Cassava," *The Plant Journal* 111, no. 3 (2022): 683–697.

65. Y. Wei, B. Zhu, W. Liu, et al., "Heat Shock Protein 90 Co-Chaperone Modules Fine-Tune the Antagonistic Interaction between Salicylic Acid and Auxin Biosynthesis in Cassava," *Cell Reports* 34, no. 5 (2021): 108717.

66. P. Wang, Y. Yan, Y. Bai, et al., "Phosphorylation of RAV1/2 by KIN10 is Essential for Transcriptional Activation of CAT6/7, Which Underlies Oxidative Stress Response in Cassava," *Cell Reports* 37, no. 11 (2021): 110119.

67. M. Ramon, T. V. T. Dang, T. Broeckx, et al., "Default Activation and Nuclear Translocation of the Plant Cellular Energy Sensor SnRK1 Regulate Metabolic Stress Responses and Development," *The Plant Cell* 31, no. 7 (2019): 1614–1632.

68. Y. Wei, H. Xie, L. Xu, et al., "Coat Protein of Cassava Common Mosaic Virus Targets RAV1 and RAV2 Transcription Factors to Subvert Immunity in Cassava," *Plant Physiol* 194, no. 2 (2024): 1218–1232.

69. H. Song, Y. Sun, D. Shan, et al., "MdMPK3 and MdMPK6 fine-tune MdWRKY17-Mediated Transcriptional Activation of the Melatonin Biosynthesis Gene MdASMT7," *Journal of Pineal Research* 75, no. 1 (2023): e12891.

70. Y. Bai, Y. Wei, H. Yin, et al., "PP2C1 Fine-Tunes Melatonin Biosynthesis and Phytomelatonin Receptor PMTR1 Binding to Melatonin in Cassava," *Journal of Pineal Research* 73, no. 1 (2022): e12804.

71. Y. Wei, G. Liu, Y. Chang, et al., "Melatonin Biosynthesis Enzymes Recruit WRKY Transcription Factors to Regulate Melatonin Accumulation and Transcriptional Activity on W-Box in Cassava," *Journal of Pineal Research* 65, no. 1 (2018): e12487.

72. Y. Wei, Y. Bai, X. Cheng, B. Zhu, R. J. Reiter, and H. Shi, "The Dual Roles of Melatonin Biosynthesis Enzymes in the Coordination of Melatonin Biosynthesis and Autophagy in Cassava," *Journal of Pineal Research* 69, no. 1 (2020): e12652.

73. J. Guo, Y. Bai, Y. Wei, et al., "Fine-Tuning of Pathogenesis-Related Protein 1 (PR1) Activity By the Melatonin Biosynthetic Enzyme ASMT2 in Defense Response to Cassava Bacterial Blight," *Journal of Pineal Research* 72, no. 2 (2022): e12784.

74. Y. Bai, J. Guo, R. J. Reiter, Y. Wei, and H. Shi, "Melatonin Synthesis Enzymes Interact with Ascorbate Peroxidase to Protect against Oxidative Stress in Cassava," *Journal of Experimental Botany* 71, no. 18 (2020): 5645–5655.

75. X. Wang, H. Zhang, Q. Xie, et al., "SlSNAT Interacts with HSP40, a Molecular Chaperone, to Regulate Melatonin Biosynthesis and Promote Thermotolerance in Tomato," *Plant and Cell Physiology* 61, no. 5 (2020): 909–921.

76. B. Bhowal, A. Bhattacharjee, K. Goswami, et al., "Serotonin and Melatonin Biosynthesis in Plants: Genome-Wide Identification of the Genes and Their Expression Reveal a Conserved Role in Stress and Development," *International Journal of Molecular Sciences* 22, no. 20 (2021): 11034.

77. Z. Wang, Y. Mu, X. Hao, et al., "H2S Aids Osmotic Stress Resistance by S-Sulfhydration of Melatonin Production-Related Enzymes in *Arabidopsis thaliana*," *Plant Cell Reports* 41, no. 2 (2022): 365–376.

78. C. Yang, M. Luo, X. Zhuang, F. Li, and C. Gao, "Transcriptional and Epigenetic Regulation of Autophagy in Plants," *Trends in Genetics* 36, no. 9 (2020): 676–688.

79. H. Qi, F.-N. Xia, and S. Xiao, "Autophagy in Plants: Physiological Roles and Post-Translational Regulation," *Journal of Integrative Plant Biology* 63, no. 1 (2021): 161–179.

80. Y. Pu, X. Luo, and D. C. Bassham, "TOR-Dependent and -Independent Pathways Regulate Autophagy in *Arabidopsis thaliana*," *Frontiers in Plant Science* 8 (2017): 1204.

81. H. C. Janse van Rensburg, W. Van den Ende, and S. Signorelli, "Autophagy in Plants: Both a Puppet and a Puppet Master of Sugars," *Frontiers in Plant Science* 10, no. 14 (2019): 14.

82. T. Su, X. Li, M. Yang, et al., "Autophagy: an Intracellular Degradation Pathway Regulating Plant Survival and Stress Response," *Frontiers in Plant Science* 11 (2020): 164.

83. M. S. Aghdam, F. Razavi, and H. Jia, "TOR and SnRK1 Signaling Pathways Manipulation for Improving Postharvest Fruits and Vegetables Marketability," *Food Chemistry* 456 (2024): 139987.

84. S. Signorelli, Ł. P. Tarkowski, W. Van den Ende, and D. C. Bassham, "Linking Autophagy to Abiotic and Biotic Stress Responses," *Trends in Plant Science* 24, no. 5 (2019): 413–430.

85. J. A. S. Barros, J. A. B. Siqueira, J. H. F. Cavalcanti, W. L. Araújo, and T. Avin-Wittenberg, "Multifaceted Roles of Plant Autophagy in Lipid and Energy Metabolism," *Trends in Plant Science* 25, no. 11 (2020): 1141–1153.

86. E. V. Tyutereva, A. V. Murtuzova, and O. V. Voitsekhovskaja, "Autophagy and the Energy Status of Plant Cells," *Russian Journal of Plant Physiology* 69, no. 2 (2022): 19.

87. J. Soto-Burgos and D. C. Bassham, "Snrk1 Activates Autophagy Via the Tor Signaling Pathway in *Arabidopsis thaliana*," *PLOS ONE* 12, no. 8 (2017): e0182591.

88. B. Belda-Palazón, M. Adamo, C. Valerio, et al., "A Dual Function of SnRK2 Kinases in the Regulation of SnRK1 and Plant Growth," *Nature Plants* 6, no. 11 (2020): 1345–1353.

89. P. Wang, Y. Zhao, Z. Li, et al., "Reciprocal Regulation of the TOR Kinase and ABA Receptor Balances Plant Growth and Stress Response," *Molecular Cell* 69, no. 1 (2018): 100–112.e6.e106.

90. B. Belda-Palazón, M. Costa, T. Beeckman, F. Rolland, and E. Baena-González, "ABA Represses TOR and Root Meristem Activity through Nuclear Exit of the Snrk1 Kinase," *Proceedings of the National Academy of Sciences of the United States of America* 119, no. 28 (2022): e2204862119.

91. L. Supriya, P. Durgeshwar, M. Muthamilarasan, and G. Padmaja, "Melatonin Mediated Differential Regulation of Drought Tolerance in Sensitive and Tolerant Varieties of Upland Cotton (*Gossypium Hirsutum* L.)," *Frontiers in Plant Science* 13 (2022): 821353.

92. L. Supriya, D. Dake, M. Muthamilarasan, and G. Padmaja, "Melatonin-Mediated Regulation of Autophagy Is Independent of ABA under Drought Stress in Sensitive Variety of *Gossypium Hirsutum* L," *Plant Physiology and Biochemistry* 207 (2024): 108409.

93. J. Wei, D.-X. Li, J.-R. Zhang, et al., "Phytomelatonin Receptor PMTR1-Mediated Signaling Regulates Stomatal Closure in *Arabidopsis thaliana*," *Journal of Pineal Research* 65, no. 2 (2018): e12500.

94. L. F. Wang, K. K. Lu, T. T. Li, et al., "Maize Phytomelatonin Receptor1 Functions in Plant Tolerance to Osmotic and Drought Stress," *Journal of Experimental Botany* 73, no. 17 (2022): 5961–5973.

95. D. Li, J. Wei, Z. Peng, et al., "Daily Rhythms of Phytomelatonin Signaling Modulate Diurnal Stomatal Closure via Regulating Reactive Oxygen Species Dynamics in Arabidopsis," *Journal of Pineal Research* 68, no. 3 (2020): e12640.

96. L. Xiao, W. Ma, J. Zhang, et al., "Phytomelatonin Interferes with Flavonols Biosynthesis to Regulate ROS Production and Stomatal Closure in Tobacco," *Journal of Plant Physiology* 284 (2023): 153977.

97. Z. Wang, L. Li, D. Khan, et al., "Nitric Oxide Acts Downstream of Reactive Oxygen Species in Phytomelatonin Receptor 1 (PMTR1)-Mediated Stomatal Closure in Arabidopsis," *Journal of Plant Physiology* 282 (2023): 153917.

98. Q. Yang, Z. Peng, W. Ma, et al., "Melatonin Functions in Priming of Stomatal Immunity in Panax Notoginseng and *Arabidopsis thaliana*," *Plant Physiology* 187, no. 4 (2021): 2837–2851.

99. X. Li, Z. Rengel, and Q. Chen, "Phytomelatonin Prevents Bacterial Invasion during Nighttime," *Trends in Plant Science* 27, no. 4 (2022): 331–334.

100. J. E. Moreno and M. L. Campos, "Waking up for Defense! Melatonin As a Regulator of Stomatal Immunity in Plants," *Plant Physiology* 188, no. 1 (2022): 14–15.

101. Y. Zhang, M. Dai, Z. Wu, et al., "Melatonin Receptor, GhCAND2-D5 Motivated Responding to NaCl Signaling in Cotton," *Plant Physiology and Biochemistry* 203 (2023): 108001.

102. D. Barman, M. N. Kumar, M. Dalal, et al., "Identification of Rice Melatonin Receptor OsPMTR and Its Comparative In Silico Analysis with Arabidopsis AtCAND2 Receptor," *South African Journal of Botany* 162 (2023): 813–829.

103. J.-W. Yao, Z. Ma, Y.-Q. Ma, et al., "Role of Melatonin in UV-B Signaling Pathway and UV-B Stress Resistance in *Arabidopsis thaliana*," *Plant, Cell & Environment* 44, no. 1 (2021): 114–129.

104. Z. Jiang, M. Xu, J. Dong, et al., "UV-B Pre-Irradiation Induces Cold Tolerance in Tomato Fruit By SLUVR8-Mediated Upregulation of Superoxide Dismutase and Catalase," *Postharvest Biology and Technology* 185 (2022): 111777.

105. T. Gao, X. Liu, S. Xu, et al., "Melatonin Confers Tolerance to Nitrogen Deficiency through Regulating MdHY5 in Apple Plants," *The Plant Journal* 117, no. 4 (2024): 1115–1129.

106. Y. Sun, B. Wang, J. Ren, et al., "OsbZIP18, a Positive Regulator of Serotonin Biosynthesis, Negatively Controls the UV-B Tolerance in Rice," *International Journal of Molecular Sciences* 23, no. 6 (2022): 3215.

107. O. J. Hwang, K. Kang, and K. Back, "Effects of Light Quality and Phytochrome Form on Melatonin Biosynthesis in Rice," *Biomolecules.* 10, no. 4 (2020): 523.

108. O. J. Hwang and K. Back, "Suppression of Rice Cryptochrome 1b Decreases Both Melatonin and Expression of Brassinosteroid Biosynthetic Genes Resulting in Salt Tolerance," *Molecules* 26, no. 4 (2021): 1075.

109. H. Zhang, L. Wang, K. Shi, et al., "Apple Tree Flowering is Mediated By Low Level of Melatonin under the Regulation of Seasonal Light Signal," *Journal of Pineal Research* 66, no. 2 (2019): e12551.

110. L. Wang, F. Zhou, X. Liu, et al., "Elongated Hypocotyl 5-Mediated Suppression of Melatonin Biosynthesis is Alleviated By Darkness and Promotes Cotyledon Opening," *Journal of Experimental Botany* 73, no. 14 (2022): 4941–4953.

111. Y. Li, C. Liu, Q. Shi, F. Yang, and M. Wei, "Mixed Red and Blue Light Promotes Ripening and Improves Quality of Tomato Fruit By Influencing Melatonin Content," *Environmental and Experimental Botany* 185 (2021): 104407.

112. S. Shan, Z. Wang, H. Pu, et al., "Dna Methylation Mediated By Melatonin Was Involved in Ethylene Signal Transmission and Ripening of Tomato Fruit," *Scientia Horticulturae* 291 (2022): 110566.

113. Y. Zhang, Z. Zhang, X. Zhang, et al. Understanding the Mechanism of Red Light-Induced Melatonin Biosynthesis Facilitates the Engineering of Melatonin-enriched Tomatoes. 2023.

114. M. S. Aghdam and Z. Luo, "Harnessing cGMP Signaling Pathways for Improving Fruits and Vegetables Marketability," *Scientia Horticulturae* 291 (2022): 110587.

115. K. Albornoz, J. Zhou, J. Yu, and D. M. Beckles, "Dissecting Postharvest Chilling Injury through Biotechnology," *Current Opinion in Biotechnology* 78 (2022): 102790.

116. M. S. Aghdam, L. Sevillano, F. B. Flores, and S. Bodbodak, "Heat Shock Proteins As Biochemical Markers for Postharvest Chilling Stress in Fruits and Vegetables," *Scientia Horticulturae* 160 (2013): 54–64.

117. M. S. Aghdam and S. Bodbodak, "Physiological and Biochemical Mechanisms Regulating Chilling Tolerance in Fruits and Vegetables under Postharvest Salicylates and Jasmonates Treatments," *Scientia Horticulturae* 156 (2013): 73–85.

118. A. Jannatizadeh, M. S. Aghdam, Z. Luo, and F. Razavi, "Impact of Exogenous Melatonin Application on Chilling Injury in Tomato Fruits during Cold Storage," *Food and Bioprocess Technology* 12, no. 5 (2019): 741–750.

119. M. S. Aghdam, Z. Luo, A. Jannatizadeh, et al., "Employing Exogenous Melatonin Applying Confers Chilling Tolerance in Tomato Fruits By Upregulating ZAT2/6/12 Giving Rise to Promoting Endogenous Polyamines, Proline, and Nitric Oxide Accumulation By Triggering Arginine Pathway Activity," *Food Chemistry* 275 (2019): 549–556.

120. Y. Sharafi, M. S. Aghdam, Z. Luo, et al., "Melatonin Treatment Promotes Endogenous Melatonin Accumulation and Triggers GABA Shunt Pathway Activity in Tomato Fruits during Cold Storage," *Scientia Horticulturae* 254 (2019): 222–2227.

121. M. P. Madebo, S. Luo, L. Wang, Y. Zheng, and P. Jin, "Melatonin Treatment Induces Chilling Tolerance By Regulating the Contents of Polyamine, γ-Aminobutyric Acid, and Proline in Cucumber Fruit," *Journal of Integrative Agriculture* 20, no. 11 (2021): 3060–3074.

122. Q. Liu, D. Xin, L. Xi, et al., "Novel Applications of Exogenous Melatonin on Cold Stress Mitigation in Postharvest Cucumbers," *Journal of Agriculture and Food Research* 10 (2022): 100459.

123. M. P. Madebo, S. U. F. Bokhary, W. You, et al., "Melatonin Improves Cold Storage Tolerance in Cucumber Via CsMYB44-Mediated Transcriptional Activation of the Polyamine Biosynthesis Gene Family," *Postharvest Biology and Technology* 213 (2024): 112937.

124. S. Cao, C. Song, J. Shao, K. Bian, W. Chen, and Z. Yang, "Exogenous Melatonin Treatment Increases Chilling Tolerance and Induces Defense Response in Harvested Peach Fruit during Cold Storage," *Journal of Agricultural and Food Chemistry* 64, no. 25 (2016): 5215–5222.

125. S. Cao, J. Shao, L. Shi, et al., "Melatonin Increases Chilling Tolerance in Postharvest Peach Fruit By Alleviating Oxidative Damage," *Scientific Reports* 8, no. 1 (2018): 806.

126. H. Gao, Z. Lu, Y. Yang, et al., "Melatonin Treatment Reduces Chilling Injury in Peach Fruit through Its Regulation of Membrane Fatty Acid Contents and Phenolic Metabolism," *Food Chemistry* 245 (2018): 659–666.

127. Z. Bao, Q. Zhou, Y. Yu, et al., "Melatonin Treatment Induces Dna Methylation to Alleviate Chilling Induced-Browning in Cold Stored Peach Fruit," *Postharvest Biology and Technology* 208 (2024): 112686.

128. J.-R. Shao, C.-B. Song, K. Bian, W. Chen, and Z.-F. Yang, "Expression Responses of Sumo E3 Ligase (Siz1) to Low Temperature Stress and Exogenous Melatonin in Postharvest Peach Fruit," *Acta Horticulturae Sinica* 43, no. 7 (2016): 1257.

129. R. Bhardwaj, S. Pareek, G. A. González-Aguilar, and J. A. Domínguez-Avila, "Changes in the Activity of Proline-Metabolising Enzymes is Associated with Increased Cultivar-Dependent Chilling Tolerance in Mangos, in Response to Pre-Storage Melatonin Application," *Postharvest Biology and Technology* 182 (2021): 111702.

130. R. Bhardwaj, S. Pareek, C. Saravanan, and E. M. Yahia, "Contribution of Pre-Storage Melatonin Application to Chilling Tolerance of Some Mango Fruit Cultivars and Relationship with Polyamines Metabolism and γ-Aminobutyric Acid Shunt Pathway," *Environmental and Experimental Botany* 194 (2022): 104691.

131. R. Bhardwaj, S. Pareek, J. A. Domínguez-Avila, G. A. Gonzalez-Aguilar, D. Valero, and M. Serrano, "An Exogenous Pre-Storage Melatonin Alleviates Chilling Injury in Some Mango Fruit Cultivars, By Acting on the Enzymatic and Non-Enzymatic Antioxidant System," *Antioxidants* 11, no. 2 (2022): 384.

132. P. Xu, D. J. Huber, D. Gong, et al., "Amelioration of Chilling Injury in 'Guifei' Mango Fruit By Melatonin is Associated with Regulation of Lipid Metabolic Enzymes and Remodeling of Lipidome," *Postharvest Biology and Technology* 198 (2023): 112233.

133. M. Kebbeh, J. Dong, C. Huan, Y. Liu, and X. Zheng, "Melatonin Treatment Alleviates Chilling Injury in Mango Fruit 'Keitt' By

Modulating Proline Metabolism under Chilling Stress," *Journal of Integrative Agriculture* 22, no. 3 (2023): 935–944.

134. R. Bhardwaj, M. S. Aghdam, M. B. Arnao, J. K. Brecht, O. A. Fawole, and S. Pareek, "Melatonin Alleviates Chilling Injury Symptom Development in Mango Fruit By Maintaining Intracellular Energy and Cell Wall and Membrane Stability," *Frontiers in Nutrition* 9 (2022): 936932.

135. H. Du, G. Liu, C. Hua, et al., "Exogenous Melatonin Alleviated Chilling Injury in Harvested Plum Fruit Via Affecting the Levels of Polyamines Conjugated to Plasma Membrane," *Postharvest Biology and Technology* 179 (2021): 111585.

136. R. Xu, L. Wang, K. Li, J. Cao, and Z. Zhao, "Integrative Transcriptomic and Metabolomic Alterations Unravel the Effect of Melatonin on Mitigating Postharvest Chilling Injury Upon Plum (cv.Friar) Fruit," *Postharvest Biology and Technology* 186 (2022): 111819.

137. H. Du, D. Liu, G. Liu, H. Liu, and R. Kurtenbach, "Polyamines Conjugated to the Bio-Membranes and Membrane Conformations Are Involved in the Melatonin-Mediated Resistance of Harvested Plum Fruit to Cold Stress," *Postharvest Biology and Technology* 204 (2023): 112480.

138. G. Liu, Y. Zhang, Z. Yun, et al., "Melatonin Enhances Cold Tolerance By Regulating Energy and Proline Metabolism in Litchi Fruit," *Foods.* 9, no. 4 (2020): 454.

139. J. Liu, J. Sun, Y. Pan, et al., "Endogenous Melatonin Generation Plays a Positive Role in Chilling Tolerance in Relation to Redox Homeostasis in Litchi Fruit during Refrigeration," *Postharvest Biology and Technology* 178 (2021): 111554.

140. J. Liu, W. Zhang, M. Hu, et al., "Nitric Oxide is Involved in Melatonin-Induced Cold Tolerance in Postharvest Litchi Fruit," *Postharvest Biology and Technology* 196 (2023): 112157.

141. L. Song, W. Zhang, Q. Li, et al., "Melatonin Alleviates Chilling Injury and Maintains Postharvest Quality By Enhancing Antioxidant Capacity and Inhibiting Cell Wall Degradation in Cold-Stored Eggplant Fruit," *Postharvest Biology and Technology* 194 (2022): 112092.

142. Z. Wang, H. Pu, S. Shan, et al., "Melatonin Enhanced Chilling Tolerance and Alleviated Peel Browning of Banana Fruit under Low Temperature Storage," *Postharvest Biology and Technology* 179 (2021): 111571.

143. Z. Wang, L. Zhang, W. Duan, et al., "Melatonin Maintained Higher Contents of Unsaturated Fatty Acid and Cell Membrane Structure Integrity in Banana Peel and Alleviated Postharvest Chilling Injury," *Food Chemistry* 397 (2022): 133836.

144. L. Wang, X. Shen, X. Chen, Q. Ouyang, X. Tan, and N. Tao, "Exogenous Application of Melatonin to Green Horn Pepper Fruit Reduces Chilling Injury during Postharvest Cold Storage By Regulating Enzymatic Activities in the Antioxidant System," *Plants* 11, no. 18 (2022): 2367.

145. X. Kong, W. Ge, B. Wei, et al., "Melatonin Ameliorates Chilling Injury in Green Bell Peppers during Storage By Regulating Membrane Lipid Metabolism and Antioxidant Capacity," *Postharvest Biology and Technology* 170 (2020): 111315.

146. H. Sun, M. Luo, X. Zhou, Q. Zhou, and S. Ji, "Influence of Melatonin Treatment on Peel Browning of Cold-Stored "Nanguo" Pears," *Food and Bioprocess Technology* 13, no. 8 (2020): 1478–1490.

147. L. Liu, A. Huang, B. Wang, H. Zhang, Y. Zheng, and L. Wang, "Melatonin Mobilizes the Metabolism of Sugars, Ascorbic Acid and Amino Acids to Cope with Chilling Injury in Postharvest Pear Fruit," *Scientia Horticulturae* 323 (2024): 112548.

148. A. Jannatizadeh, "Exogenous Melatonin Applying Confers Chilling Tolerance in Pomegranate Fruit during Cold Storage," *Scientia Horticulturae* 246 (2019): 544–549.

149. S. M. H. Molla, S. Rastegar, V. G. Omran, and O. Khademi, "Ameliorative Effect of Melatonin against Storage Chilling Injury in Pomegranate Husk and Arils through Promoting the Antioxidant System," *Scientia Horticulturae* 295 (2022): 110889.

150. J. Jiao, M. Jin, H. Liu, et al., "Application of Melatonin in Kiwifruit (*Actinidia Chinensis*) Alleviated Chilling Injury during Cold Storage," *Scientia Horticulturae* 296 (2022): 110876.

151. W. Guo, C. Zhang, R. Yang, et al., "Endogenous Salicylic Acid Mediates Melatonin-Induced Chilling-And Oxidative-Stress Tolerance in Harvested Kiwifruit," *Postharvest Biology and Technology* 201 (2023): 112341.

152. S. Ali, A. Nawaz, S. Naz, et al., "Exogenous Melatonin Mitigates Chilling Injury in Zucchini Fruit By Enhancing Antioxidant System Activity, Promoting Endogenous Proline and GABA Accumulation, and Preserving Cell Wall Stability," *Postharvest Biology and Technology* 204 (2023): 112445.

153. Y. Luo, R. Wang, X. Lei, Y. Ren, and C. Yuan, "Melatonin Treatment Delays Senescence and Alleviates Chilling Injury in Spaghetti Squash during Low-Temperature Storage," *Scientia Horticulturae* 310 (2023): 111778.

154. A. Mirshekari, B. Madani, E. M. Yahia, J. B. Golding, and S. H. Vand, "Postharvest Melatonin Treatment Reduces Chilling Injury in Sapota Fruit," *Journal of the Science of Food and Agriculture* 100, no. 5 (2020): 1897–1903.

155. Q. Y. Dong, Y. Lai, C. M. Hua, H. P. Liu, and R. Kurtenbach, "Polyamines Conjugated to Plasma Membrane Were Involved in Melatonin-Mediated Resistance of Apple (*Malus Pumila* Mill.) Fruit to Chilling Stress," *Russian Journal of Plant Physiology* 69 (2022): 67.

156. Q. Dong, H. Liu, and R. Kurtenbach, "Polyamines in Plasma Membrane Function in Melatonin-Mediated Tolerance of Apricot Fruit to Chilling Stress," *Czech Journal of Food Sciences* 40, no. 4 (2022): 313–322.

157. D. Wang, Q. Chen, W. Chen, et al., "Melatonin Treatment Maintains Quality and Delays Lignification in Loquat Fruit during Cold Storage," *Scientia Horticulturae* 284 (2021): 110126.

158. M. S. Aghdam, A. Jannatizadeh, M. S. Nojadeh, and A. Ebrahimzadeh, "Exogenous Melatonin Ameliorates Chilling Injury in Cut Anthurium Flowers during Low Temperature Storage," *Postharvest Biology and Technology* 148 (2019): 184–191.

159. S. Cao, K. Bian, L. Shi, H. H. Chung, W. Chen, and Z. Yang, "Role of Melatonin in Cell-Wall Disassembly and Chilling Tolerance in Cold-Stored Peach Fruit," *Journal of Agricultural and Food Chemistry* 66, no. 22 (2018): 5663–5670.

160. Y. Saijo, E. P. Loo, and S. Yasuda, "Pattern Recognition Receptors and Signaling in Plant–Microbe Interactions," *The Plant Journal* 93, no. 4 (2018): 592–613.

161. D. Solairaj, Q. Yang, N. N. Guillaume Legrand, M. N. Routledge, and H. Zhang, "Molecular Explication of Grape Berry-Fungal Infections and Their Potential Application in Recent Postharvest Infection Control Strategies," *Trends in Food Science & Technology* 116 (2021): 903–917.

162. C. Liu, L. Chen, R. Zhao, et al., "Melatonin Induces Disease Resistance to *Botrytis cinerea* in Tomato Fruit By Activating Jasmonic Acid Signaling Pathway," *Journal of Agricultural and Food Chemistry* 67, no. 22 (2019): 6116–6124.

163. S. Li, Y. Xu, Y. Bi, et al., "Melatonin Treatment Inhibits Gray Mold and Induces Disease Resistance in Cherry Tomato Fruit during Postharvest," *Postharvest Biology and Technology* 157 (2019): 110962.

164. S. Li, Y. Cheng, R. Yan, Y. Liu, C. Huan, and X. Zheng, "Preharvest Spray with Melatonin Improves Postharvest Disease Resistance in Cherry Tomato Fruit," *Postharvest Biology and Technology* 193 (2022): 112055.

165. C. Sun, Y. Huang, S. Lian, M. Saleem, B. Li, and C. Wang, "Improving the Biocontrol Efficacy of Meyerozyma Guilliermondii Y-1

with Melatonin against Postharvest Gray Mold in Apple Fruit," *Postharvest Biology and Technology* 171 (2021): 111351.

166. Z. Li, S. Zhang, J. Xue, B. Mu, H. Song, and Y. Liu, "Exogenous Melatonin Treatment Induces Disease Resistance against *Botrytis cinerea* on Postharvest Grapes By Activating Defence Responses," *Foods.* 11, no. 15 (2022): 2231.

167. S. Gao, W. Ma, X. Lyu, X. Cao, and Y. Yao, "Melatonin May Increase Disease Resistance and Flavonoid Biosynthesis through Effects on Dna Methylation and Gene Expression in Grape Berries," *BMC Plant Biology* 20, no. 1 (2020): 231.

168. S. Promyou, Y. Raruang, and Z. Y. Chen, "Melatonin Treatment of Strawberry Fruit during Storage Extends Its Postharvest Quality and Reduces Infection Caused By *Botrytis cinerea*," *Foods.* 12, no. 7 (2023): 1445.

169. M. Wang, Y. Li, C. Li, H. Xu, T. Sun, and Y. Ge, "Melatonin Induces Resistance against *Penicillium expansum* in Apple Fruit through Enhancing Phenylpropanoid Metabolism," *Physiological and Molecular Plant Pathology* 127 (2023): 102082.

170. T. Li, Q. Wu, H. Zhu, et al., "Comparative Transcriptomic and Metabolic Analysis Reveals the Effect of Melatonin on Delaying Anthracnose Incidence Upon Postharvest Banana Fruit Peel," *BMC Plant Biology* 19, no. 1 (2019): 289.

171. S. Fan, Q. Li, S. Feng, et al., "Melatonin Maintains Fruit Quality and Reduces Anthracnose in Postharvest Papaya Via Enhancement of Antioxidants and Inhibition of Pathogen Development," *Antioxidants* 11, no. 5 (2022): 804.

172. G.-Y. Zhu, P.-F. Sha, X.-X. Zhu, et al., "Application of Melatonin for the Control of Food-Borne Bacillus Species in Cherry Tomatoes," *Postharvest Biology and Technology* 181 (2021): 111656.

173. K. Huang, Y. Sui, C. Miao, et al., "Melatonin Enhances the Resistance of Ginger Rhizomes to Postharvest Fungal Decay," *Postharvest Biology and Technology* 182 (2021): 111706.

174. G. Qu, W. Wu, L. Ba, R. Wang, and S. Cao, "Melatonin Enhances Fruit Disease Resistance in Postharvest Blueberries By Modulating the Jasmonic Acid Signaling Pathway and Phenylpropanoid Metabolites," *Frontiers in Chemistry* (2022).

175. A. Jannatizadeh, R. Aminian-Dehkordi, and F. Razavi, "Effect of Exogenous Melatonin Treatment on Aspergillus decay, Aflatoxin B1 Accumulation and Nutritional Quality of Fresh "Akbari" Pistachio Fruit," *Journal of Food Processing and Preservation* 45, no. 6 (2021): e15518.

176. J. Peng, S. Zhu, X. Lin, et al., "Evaluation of Preharvest Melatonin on Soft Rot and Quality of Kiwifruit Based on Principal Component Analysis," *Foods* 12, no. 7 (2023): 1414.

177. Y. Wang, G. Wang, W. Xu, Z. Zhang, X. Sun, and S. Zhang, "Exogenous Melatonin Improves Pear Resistance To *Botryosphaeria Dothidea* By Increasing Autophagic Activity And Sugar/organic Acid Levels." *Phytopathology* 112, no. 6 (2022): 1335–1344.

178. Z. Zhang, T. Wang, G. Liu, et al., "Inhibition of Downy Blight and Enhancement of Resistance in Litchi Fruit By Postharvest Application of Melatonin," *Food Chemistry* 347 (2021): 129009.

179. S. Li, C. Huan, Y. Liu, X. Zheng, and Y. Bi, "Melatonin Induces Improved Protection against *Botrytis cinerea* in Cherry Tomato Fruit By Activating Salicylic Acid Signaling Pathway," *Scientia Horticulturae* 304 (2022): 111299.

180. M. S. Aghdam and J. R. Fard, "Melatonin Treatment Attenuates Postharvest Decay and Maintains Nutritional Quality of Strawberry Fruits (Fragaria×Anannasa Cv. Selva) By Enhancing GABA Shunt Activity," *Food Chemistry* 221 (2017): 1650–1657.

181. L. Zhang, Y. Yu, L. Chang, X. Wang, and S. Zhang, "Melatonin Enhanced the Disease Resistance By Regulating Reactive Oxygen Species Metabolism in Postharvest Jujube Fruit," *Journal of Food Processing and Preservation* 46, no. 3 (2022): e16363.

182. G. Qu, W. Wu, L. Ba, C. Ma, N. Ji, and S. Cao, "Melatonin Enhances the Postharvest Disease Resistance of Blueberries Fruit By Modulating the Jasmonic Acid Signaling Pathway and Phenylpropanoid Metabolites," *Frontiers in Chemistry* 10 (2022): 957581.

183. S. Fan, T. Xiong, Q. Lei, et al., "Melatonin Treatment Improves Postharvest Preservation and Resistance of Guava Fruit (*Psidium guajava* L.)," *Foods* 11, no. 3 (2022): 262.

184. Y. Chen, Y. Zhang, G. Nawaz, et al., "Exogenous Melatonin Attenuates Postharvest Decay By Increasing Antioxidant Activity in Wax Apple (*Syzygium samarangense*)," *Frontiers in Plant Science* 11 (2020): 569779.

185. Y. Lin, L. Fan, X. Xia, et al., "Melatonin Decreases Resistance to Postharvest Green Mold on Citrus Fruit By Scavenging Defense-Related Reactive Oxygen Species," *Postharvest Biology and Technology* 153 (2019): 21–30.

186. T. Chen, D. Ji, Z. Zhang, B. Li, G. Qin, and S. Tian, "Advances and Strategies for Controlling the Quality and Safety of Postharvest Fruit," *Engineering.* 7, no. 8 (2021): 1177–1184.

187. M. S. Aghdam, F. Kakavand, V. Rabiei, F. Zaare-Nahandi, and F. Razavi, "γ-Aminobutyric Acid and Nitric Oxide Treatments Preserve Sensory and Nutritional Quality of Cornelian Cherry Fruits during Postharvest Cold Storage By Delaying Softening and Enhancing Phenols Accumulation," *Scientia Horticulturae* 246 (2019): 812–8817.

188. M. S. Aghdam, R. Mahmoudi, F. Razavi, V. Rabiei, and A. Soleimani, "Hydrogen Sulfide Treatment Confers Chilling Tolerance in Hawthorn Fruit during Cold Storage By Triggering Endogenous H2S Accumulation, Enhancing Antioxidant Enzymes Activity and Promoting Phenols Accumulation," *Scientia Horticulturae* 238 (2018): 264–271.

189. Z. Niazi, F. Razavi, O. Khademi, and M. S. Aghdam, "Exogenous Application of Hydrogen Sulfide and γ-aminobutyric Acid Alleviates Chilling Injury and Preserves Quality of Persimmon Fruit (*Diospyros Kaki*, Cv. Karaj) during Cold Storage," *Scientia Horticulturae* 285 (2021): 110198.

190. K. Wang, S. Cai, Q. Xing, et al., "Melatonin Delays Dark-Induced Leaf Senescence By Inducing miR171b Expression in Tomato," *Journal of Pineal Research* 72, no. 3 (2022): e12792.

191. J.-C. Yu, J.-Z. Lu, X.-Y. Cui, et al., "Melatonin Mediates Reactive Oxygen Species Homeostasis Via SLCV to Regulate Leaf Senescence in Tomato Plants," *Journal of Pineal Research* 73, (2022): e12810.

192. N. Wang, H. Fang, Q. Yang, Z. Liu, H. Feng, and S. Ji, "Exogenous Melatonin Alleviated Leaf Yellowing via Inhibiting Respiration and Ethylene Biosynthesis during Shelf Life in Pakchoi," *Plants* 11, no. 16 (2022): 2102.

193. L. Song, S. Liu, H. Yu, and Z. Yu, "Exogenous Melatonin Ameliorates Yellowing of Postharvest Pak Choi (*Brassica rapa* Subsp. Chinensis) By Modulating Chlorophyll Catabolism and Antioxidant System during Storage at 20°C," *Scientia Horticulturae* 311 (2023): 111808.

194. X. Liu, Y. Li, J. Zhu, and P. Li, "Integrative Analysis of Transcriptome Reveals the Possible Mechanism of Delayed Leaf Senescence in Pak Choi (*Brassica rapa* Subsp. Chinensis) Following Melatonin Treatment," *Food Quality and Safety* 7 (2023): 1–13.

195. X. Liu, R. An, G. Li, S. Luo, H. Hu, and P. Li, "Melatonin Delays Leaf Senescence in Pak Choi (*Brassica rapa* Subsp. Chinensis) By Regulating Biosynthesis of the Second Messenger Cgmp," *Horticultural Plant Journal* 10, no. 1 (2024): 145–155.

196. R. Yan, M. Kebbeh, Y. Cheng, et al., "Exogenous Melatonin Delays Yellowing in Broccoli Based on Hormone, Nitrogen and Sucrose Metabolism Regulation during Postharvest," *Scientia Horticulturae* 314 (2023): 111944.

197. H. Miao, W. Zeng, M. Zhao, J. Wang, and Q. Wang, "Effect of Melatonin Treatment on Visual Quality and Health-Promoting

Properties of Broccoli Florets under Room Temperature," *Food Chemistry* 319 (2020): 126498.

198. J. Lou, C. Wu, H. Wang, et al., "Melatonin Treatment Delays Postharvest Senescence of Broccoli with Regulation of Carotenoid Metabolism," *Food Chemistry* 408 (2023): 135185.

199. H. Hu, S. Luo, R. An, and P. Li, "Endogenous Melatonin Delays Sepal Senescence and Extends the Storage Life of Broccoli Florets By Decreasing Ethylene Biosynthesis," *Postharvest Biology and Technology* 188 (2022): 111894.

200. C. Wu, S. Cao, K. Xie, et al., "Melatonin Delays Yellowing of Broccoli during Storage By Regulating Chlorophyll Catabolism and Maintaining Chloroplast Ultrastructure," *Postharvest Biology and Technology* 172 (2021): 111378.

201. Z. Jiang, J. Lou, S. Cao, et al., "Exogenous Melatonin Delays Programmed Cell Death in Broccoli Via Maintenance of Ros Homeostasis and Reduction of Mitochondrial Dysfunction," *Postharvest Biology and Technology* 210 (2024): 112749.

202. A. Cano, M. Giraldo-Acosta, S. García-Sánchez, J. Hernández-Ruiz, and M. B. Arnao, "Effect of Melatonin in Broccoli Postharvest and Possible Melatonin Ingestion Level," *Plants* 11, no. 15 (2022): 2000.

203. L. Wei, C. Liu, H. Zheng, and L. Zheng, "Melatonin Treatment Affects the Glucoraphanin-Sulforaphane System in Postharvest Fresh-Cut Broccoli (*Brassica oleracea* L.)," *Food Chemistry* 307 (2020): 125562.

204. M. Giraldo-Acosta, D. Ruiz-Cano, A. Cano, J. Hernández-Ruiz, and M. B. Arnao, "Extended Postharvest Effect of Melatonin in Fresh-Cut Broccolini Plants (Bimi®)," *Agronomy* 13, no. 10 (2023): 2459.

205. L. Zhu, H. Hu, S. Luo, Z. Wu, and P. Li, "Melatonin Delaying Senescence of Postharvest Broccoli By Regulating Respiratory Metabolism and Antioxidant Activity," *Transactions of the Chinese Society of Agricultural Engineering* 34, no. 3 (2018): 300–308.

206. J. Xue, K. Wang, Z. Li, et al., "Influences of Postharvest Melatonin Treatment on Preservation Quality and Shelf Life of Fresh-Cut Cauliflower," *Transactions of the Chinese Society of Agricultural Engineering (Transactions of the CSAE)* 37, no. 13 (2021): 273–283.

207. X. L. Tan, Z. Fan, J. Kuang, et al., "Melatonin Delays Leaf Senescence of Chinese Flowering Cabbage By Suppressing ABFs-Mediated Abscisic Acid Biosynthesis and Chlorophyll Degradation," *Journal of Pineal Research* 67, no. 1 (2019): e12570.

208. X. Tan, Z. Fan, Z. Zeng, et al., "Exogenous Melatonin Maintains Leaf Quality of Postharvest Chinese Flowering Cabbage By Modulating Respiratory Metabolism and Energy Status," *Postharvest Biology and Technology* 177 (2021): 111524.

209. X. Tan, Y. Zhao, W. Shan, et al., "Melatonin Delays Leaf Senescence of Postharvest Chinese Flowering Cabbage through Ros Homeostasis," *Food Research International* 138, no. Pt B (2020): 109790.

210. L. Yue, Y. Kang, M. Zhong, et al., "Melatonin Delays Postharvest Senescence through Suppressing the Inhibition of BrERF2/BrERF109 on Flavonoid Biosynthesis in Flowering Chinese Cabbage," *International Journal of Molecular Sciences* 24, no. 3 (2023): 2933.

211. C. Li, X. Shen, Z. Fan, J. Chen, N. Tao, and X. Tan, "Melatonin Retards Leaf Senescence By Modulating Phytohormone Metabolism in Stored Chinese Flowering Cabbage," *Food Quality and Safety* 7 (2023): 1–16.

212. M. Wang, J. Xu, Z. Ding, and J. Xie, "Prolong the Postharvest Shelf Life of Spinach through the Antioxidative Ability of Melatonin," *Food Chemistry: X* 19 (2023): 100769.

213. H. Di, Z. Li, Y. Wang, et al., "Melatonin Treatment Delays Senescence and Maintains the Postharvest Quality of Baby Mustard (*Brassica juncea* var. Gemmifera)," *Frontiers in Plant Science* 12 (2022): 817861.

214. A. Shekari, R. N. Hassani, M. S. Aghdam, M. Rezaee, and A. Jannatizadeh, "The Effects of Melatonin Treatment on Cap Browning and Biochemical Attributes of Agaricus Bisporus during Low Temperature Storage," *Food Chemistry* 348 (2021): 129074.

215. L. Li, H. Kitazawa, X. Zhang, et al., "Melatonin Retards Senescence Via Regulation of the Electron Leakage of Postharvest White Mushroom (*Agaricus Bisporus*)," *Food Chemistry* 340 (2021): 127833.

216. S. Luo, H. Hu, Y. Wang, et al., "The Role of Melatonin in Alleviating the Postharvest Browning of Lotus Seeds through Energy Metabolism and Membrane Lipid Metabolism," *Postharvest Biology and Technology* 167 (2020): 111243.

217. L. Sun, S. Luo, H. Huali, et al., "Melatonin Promotes the Normal Cellular Mitochondrial Function of Lotus Seeds through Stimulating Nitric Oxide Production," *Postharvest Biology and Technology* 185 (2022): 111814.

218. C. Zhang, Y. Xin, Z. Wang, et al., "Melatonin-Induced Myeloblastosis Viral Oncogene Homologs Alleviate Fresh-Cut Lotus Root Browning during Storage By Attenuating Flavonoid Biosynthesis and Reactive Oxygen Species," *Journal of the Science of Food and Agriculture* 103, no. 11 (2023): 5452–5461.

219. Q. Ma, T. Zhang, P. Zhang, and Z. Y. Wang, "Melatonin Attenuates Postharvest Physiological Deterioration of Cassava Storage Roots," *Journal of Pineal Research* 60, no. 4 (2016): 424–434.

220. W. Hu, H. Kong, Y. Guo, et al., "Comparative Physiological and Transcriptomic Analyses Reveal the Actions of Melatonin in the Delay of Postharvest Physiological Deterioration of Cassava," *Frontiers in Plant Science* 7 (2016): 736.

221. C. Li, J. Suo, L. Xuan, et al., "Bamboo Shoot-Lignification Delay By Melatonin during Low Temperature Storage," *Postharvest Biology and Technology* 156 (2019): 110933.

222. B. Yang, Y. Han, W. Wu, X. Fang, H. Chen, and H. Gao, "Impact of Melatonin Application on Lignification in Water Bamboo Shoot during Storage," *Food Chemistry: X* 13 (2022): 100254.

223. B. Yang, Y. Han, H. Gao, et al., "Application of Melatonin Delays Lignification in Postharvest Water Bamboo Shoots in Association with Energy Metabolism," *Postharvest Biology and Technology* 196 (2023): 112149.

224. D. Liu, F. Wang, C. Brennan, et al., "Combined Melatonin and UV-C Treatment Maintains the Quality of Fresh-Cut Bamboo Shoots during Storage By Altering Microbial Diversity and Metabolites," *Postharvest Biology and Technology* 200 (2023): 112327.

225. M. S. Aghdam, Z. Luo, L. Li, A. Jannatizadeh, J. R. Fard, and F. Pirzad, "Melatonin Treatment Maintains Nutraceutical Properties of Pomegranate Fruits during Cold Storage," *Food Chemistry* 303 (2020): 125385.

226. H. Meighani and M. Roozkhosh, "Effect of Melatonin Treatment on the Quality of Minimally-Processed Pomegranate Arils during Cold Storage," *Journal of Food Measurement and Characterization* 18 (2023): 1740–1747.

227. Y. Zhang, D. J. Huber, M. Hu, et al., "Delay of Postharvest Browning in Litchi Fruit By Melatonin Via the Enhancing of Antioxidative Processes and Oxidation Repair," *Journal of Agricultural and Food Chemistry* 66, no. 28 (2018): 7475–7484.

228. T. Wang, M. Hu, D. Yuan, et al., "Melatonin Alleviates Pericarp Browning in Litchi Fruit By Regulating Membrane Lipid and Energy Metabolisms," *Postharvest Biology and Technology* 160 (2020): 111066.

229. Z. Zhang, J. Liu, D. J. Huber, et al., "Transcriptome, Degradome and Physiological Analysis Provide New Insights into the Mechanism of Inhibition of Litchi Fruit Senescence By Melatonin," *Plant Science* 308 (2021): 110926.

230. J. Xie, Z. Qin, J. Pan, et al., "Melatonin Treatment Improves Postharvest Quality and Regulates Reactive Oxygen Species Metabolism in "Feizixiao" Litchi Based on Principal Component Analysis," *Frontiers in Plant Science* 13 (2022): 965345.

231. K. A. Marak, H. Mir, P. Singh, et al., "Exogenous Melatonin Delays Oxidative Browning and Improves Postharvest Quality of Litchi Fruits," *Scientia Horticulturae* 322 (2023): 112408.

232. L. Wang, M. Yang, Y. Dong, et al., "Melatonin Confers Enhanced Polyamine Metabolism and Cell Tolerance in *Vitis vinifera* against Oxidative Damage: Quantitative Proteomic Evidence," *Postharvest Biology and Technology* 184 (2022): 111756.

233. M. Yang, L. Wang, T. Belwal, et al., "Exogenous Melatonin and Abscisic Acid Expedite the Flavonoids Biosynthesis in Grape Berry of *Vitis vinifera* cv. Kyoho," *Molecules.* 25, no. 1 (2020): 12.

234. Y.-D. Sun, D.-L. Guo, S.-D. Yang, et al., "Melatonin Treatment Improves the Shelf-Life and Postharvest Quality of Table Grape (*Vitis Labrusca* L. cv. 'Fengzao')," *Journal of Berry Research* 10, no. 4 (2020): 665–676.

235. Z. Ban, S. Zhang, C. Niu, et al., "Potential Role of Exogenous Melatonin Involved in Postharvest Quality Maintenance Of Vitis Labrusca × Vinifera 'Kyoho'," *Journal of the Science of Food and Agriculture* 103, no. 13 (2023): 6243–6251.

236. L. Wang, Z. Luo, M. Yang, et al., "Role of Exogenous Melatonin in Table Grapes: First Evidence on Contribution to the Phenolics-Oriented Response," *Food Chemistry* 329 (2020): 127155.

237. L. Xu, Q. Yue, F. Bian, H. Sun, H. Zhai, and Y. Yao, "Melatonin Enhances Phenolics Accumulation Partially Via Ethylene Signaling and Resulted in High Antioxidant Capacity in Grape Berries," *Frontiers in Plant Science* 8 (2017): 1426.

238. H. Xia, Y. Shen, H. Deng, et al., "Melatonin Application Improves Berry Coloration, Sucrose Synthesis, and Nutrient Absorption in 'Summer Black' Grape," *Food Chemistry* 356 (2021): 129713.

239. W. Ma, L. Xu, S. Gao, X. Lyu, X. Cao, and Y. Yao, "Melatonin Alters the Secondary Metabolite Profile of Grape Berry Skin By Promoting Vvmyb14-Mediated Ethylene Biosynthesis," *Horticulture Research* 8, no. 1 (2021): 43.

240. M. A. Nasser, M. M. El-Mogy, M. S. F. Samaan, et al., "Postharvest Exogenous Melatonin Treatment of Table Grape Berry Enhances Quality and Maintains Bioactive Compounds during Refrigerated Storage," *Horticulturae* 8, no. 10 (2022): 860.

241. C. Liu, H. Zheng, K. Sheng, W. Liu, and L. Zheng, "Effects of Melatonin Treatment on the Postharvest Quality of Strawberry Fruit," *Postharvest Biology and Technology* 139 (2018): 47–55.

242. L. Pang, Y. Wu, Y. Pan, Z. Ban, L. Li, and X. Li, "Insights into Exogenous Melatonin Associated with Phenylalanine Metabolism in Postharvest Strawberry," *Postharvest Biology and Technology* 168 (2020): 111244.

243. F. Wang, X. Zhang, Q. Yang, and Q. Zhao, "Exogenous Melatonin Delays Postharvest Fruit Senescence and Maintains the Quality of Sweet Cherries," *Food Chemistry* 301 (2019): 125311.

244. S. Miranda, P. Vilches, M. Suazo, et al., "Melatonin Triggers Metabolic and Gene Expression Changes Leading to Improved Quality Traits of Two Sweet Cherry Cultivars During Cold Storage," *Food Chemistry* 319 (2020): 126360.

245. Y. Sharafi, A. Jannatizadeh, J. R. Fard, and M. S. Aghdam, "Melatonin Treatment Delays Senescence and Improves Antioxidant Potential of Sweet Cherry Fruits during Cold Storage," *Scientia Horticulturae* 288 (2021): 110304.

246. L. Pang, L. Chen, Y. Jiang, C. Zhou, F. Liang, and L. Duan, "Role of Exogenous Melatonin in Quality Maintenance of Sweet Cherry: Elaboration in Links between Phenolic and Amino Acid Metabolism," *Food Bioscience* 56 (2023): 103223.

247. F. Shang, R. Liu, W. Wu, et al., "Effects of Melatonin on the Components, Quality and Antioxidant Activities of Blueberry Fruits," *LWT* 147 (2021): 111582.

248. A. Magri and M. Petriccione, "Melatonin Treatment Reduces Qualitative Decay and Improves Antioxidant System in Highbush Blueberry Fruit During Cold Storage," *Journal of the Science of Food and Agriculture* 102, no. 10 (2022): 4229–4237.

249. Y. Cao, Y. Zang, S. Wu, et al., "Melatonin Affects Cuticular Wax Profile in Rabbiteye Blueberry (*Vaccinium ashei*) during Fruit Development," *Food Chemistry* 384 (2022): 132381.

250. G. Qu, L. Ba, R. Wang, et al., "Effects of Melatonin on Blueberry Fruit Quality and Cell Wall Metabolism During Low Temperature Storage," *Food Science and Technology* 42 (2022): 5224.

251. R. Liu, S. Fanzhen, B. Niu, et al., "Melatonin Treatment Delays the Softening of Blueberry Fruit By Modulating Cuticular Wax Metabolism and Reducing Cell Wall Degradation," *Food Research International* 173, no. Pt 2 (2023): 113357.

252. J. Li, Y. Cao, S. Bian, et al., "Melatonin Improves the Storage Quality of Rabbiteye Blueberry (Vaccinium Ashei) By Affecting Cuticular Wax Profile," *Food Chemistry: X* 21 (2024): 101106.

253. H. M. S. Shah, Z. Singh, M. U. Hasan, E. Afrifa-Yamoah, and A. Woodward, "Preharvest Melatonin Application Alleviates Red Drupelet Reversion, Improves Antioxidant Potential and Maintains Postharvest Quality of 'Elvira' Blackberry," *Postharvest Biology and Technology* 203 (2023): 112418.

254. H. M. S. Shah, Z. Singh, M. U. Hasan, J. Kaur, E. Afrifa-Yamoah, and A. Woodward, "Melatonin Application Suppresses Oxidative Stress and Maintains Fruit Quality of Cold Stored 'Esperanza' Raspberries By Regulating Antioxidant System," *Postharvest Biology and Technology* 207 (2024): 112597.

255. J. Cheng, A. Zheng, H. Li, et al., "Effects of Melatonin Treatment on Ethanol Fermenation and Erf Expression in Kiwifruit cv. Bruno during Postharvest," *Scientia Horticulturae* 293 (2022): 110696.

256. X. Dong Liang, Y. Xie, and X. J. Hui Xia, "Melatonin Application Increases Accumulation of Phenol Substances in Kiwifruit during Storage," *Emirates Journal of Food and Agriculture* 31, no. 5 (2019): 361–367.

257. S. Cao, G. Qu, C. Ma, et al., "Effects of Melatonin Treatment on the Physiological Quality and Cell Wall Metabolites in Kiwifruit," *Food Science and Technology* 42 (2022): e85421.

258. Z. Luo, J. Zhang, M. Xiang, J. Zeng, J. Chen, and M. Chen, "Exogenous Melatonin Treatment Affects Ascorbic Acid Metabolism in Postharvest 'Jinyan' Kiwifruit," *Frontiers in Nutrition* 9 (2022): 1081476.

259. Y. Zhang, H. Tang, D. Lei, et al., "Exogenous Melatonin Maintains Postharvest Quality in Kiwiberry Fruit By Regulating Sugar Metabolism during Cold Storage," *LWT* 174 (2023): 114385.

260. D. Wang, M. S. Randhawa, M. Azam, et al., "Exogenous Melatonin Treatment Reduces Postharvest Senescence and Maintains the Quality of Papaya Fruit During Cold Storage," *Frontiers in Plant Science* 13 (2022): 1039373.

261. H. Gao, Z. K. Zhang, H. K. Chai, et al., "Melatonin Treatment Delays Postharvest Senescence and Regulates Reactive Oxygen Species Metabolism in Peach Fruit," *Postharvest Biology and Technology* 118 (2016): 103–110.

262. C. Wu, W. Hao, L. Yan, et al., "Postharvest Melatonin Treatment Enhanced Antioxidant Activity and Promoted GABA Biosynthesis in Yellow-Flesh Peach," *Food Chemistry* 419 (2023): 136088.

263. S. Rastegar, H. Hassanzadeh Khankahdani, and M. Rahimzadeh, "Effects of Melatonin Treatment on the Biochemical Changes and Antioxidant Enzyme Activity of Mango Fruit during Storage," *Scientia Horticulturae* 259 (2020): 108835.

264. S. Liu, H. Huang, D. J. Huber, Y. Pan, X. Shi, and Z. Zhang, "Delay of Ripening and Softening in 'Guifei' Mango Fruit By Postharvest

Application of Melatonin," *Postharvest Biology and Technology* 163 (2020): 111136.

265. J. Dong, M. Kebbeh, R. Yan, C. Huan, T. Jiang, and X. Zheng, "Melatonin Treatment Delays Ripening in Mangoes Associated with Maintaining the Membrane Integrity of Fruit Exocarp during Postharvest," *Plant Physiology and Biochemistry* 169 (2021): 22–228.

266. A. Njie, W. Zhang, X. Dong, C. Lu, X. Pan, and Q. Liu, "Effect of Melatonin on Fruit Quality Via Decay Inhibition and Enhancement of Antioxidative Enzyme Activities and Genes Expression of Two Mango Cultivars during Cold Storage," *Foods* 11, no. 20 (2022): 3209.

267. Z. Hu, J. Wei, W. Zhang, et al., "Attenuation of Prochloraz Phytotoxicity to Postharvest Mango Fruit By Melatonin is Associated With the Regulation of Detoxification Capacity," *Postharvest Biology and Technology* 208 (2024): 112671.

268. R. Zhai, J. Liu, F. Liu, et al., "Melatonin Limited Ethylene Production, Softening and Reduced Physiology Disorder in Pear (*Pyrus Communis* L.) Fruit During Senescence," *Postharvest Biology and Technology* 139 (2018): 38–46.

269. J. Liu, J. Yang, H. Zhang, et al., "Melatonin Inhibits Ethylene Synthesis Via Nitric Oxide Regulation to Delay Postharvest Senescence in Pears," *Journal of Agricultural and Food Chemistry* 67, no. 8 (2019): 2279–2288.

270. S. Wei, H. Jiao, H. Wang, et al., "The Mechanism Analysis of Exogenous Melatonin in Limiting Pear Fruit Aroma Decrease Under Low Temperature Storage," *PeerJ* 10 (2022): e14166.

271. H. Sun, X. Cao, X. Wang, et al., "RBOH-Dependent Hydrogen Peroxide Signaling Mediates Melatonin-Induced Anthocyanin Biosynthesis in Red Pear Fruit," *Plant Science* 313 (2021): 111093.

272. H. Sun, X. Wang, Y. Shang, X. Wang, G. Du, and D. Lü, "Preharvest Application of Melatonin Induces Anthocyanin Accumulation and Related Gene Upregulation in Red Pear (*Pyrus Ussuriensis*)," *Journal of Integrative Agriculture* 20, no. 8 (2021): 2126–2137.

273. H. Zheng, W. Liu, S. Liu, C. Liu, and L. Zheng, "Effects of Melatonin Treatment on the Enzymatic Browning and Nutritional Quality of Fresh-Cut Pear Fruit," *Food Chemistry* 299 (2019): 125116.

274. Q. Tang, C. Li, Y. Ge, et al., "Exogenous Application of Melatonin Maintains Storage Quality of Jujubes By Enhancing Anti-Oxidative Ability and Suppressing the Activity of Cell Wall-Degrading Enzymes," *LWT* 127 (2020): 109431.

275. B. Deng, C. Xia, S. Tian, and H. Shi, "Melatonin Reduces Pesticide Residue, Delays Senescence, and Improves Antioxidant Nutrient Accumulation in Postharvest Jujube Fruit," *Postharvest Biology and Technology* 173 (2021): 111419.

276. L. Wang, Z. Luo, Z. Ban, N. Jiang, M. Yang, and L. Li, "Role of Exogenous Melatonin Involved in Phenolic Metabolism of Zizyphus Jujuba Fruit," *Food Chemistry* 341, no. Pt 2 (2021): 128268.

277. Y. Sun, M. Li, S. Ji, et al., "Effect of Exogenous Melatonin Treatment on Quality and Softening of Jujube Fruit during Storage," *Journal of Food Processing and Preservation* 46, no. 7 (2022): e16662.

278. Y. Li, L. Zhang, L. Zhang, et al., "Exogenous Melatonin Alleviates Browning of Fresh-Cut Sweetpotato By Enhancing Anti-Oxidative Process," *Scientia Horticulturae* 297 (2022): 110937.

279. B. Dong, Q. Yao, D. Zhu, H. Han, H. Tang, and X. Ding, "Exogenous Melatonin Maintains Quality of Postharvest *Rosa roxburghii* Fruit By Modulating Reactive Oxygen Species Metabolism and Energy Status," *Scientia Horticulturae* 304 (2022): 111346.

280. Y. Fan, C. Li, Y. Li, et al., "Postharvest Melatonin Dipping Maintains Quality of Apples By Mediating Sucrose Metabolism," *Plant Physiology and Biochemistry* 174 (2022): 43–50.

281. J. C. Onik, S. C. Wai, A. Li, et al., "Melatonin Treatment Reduces Ethylene Production and Maintains Fruit Quality in Apple during Postharvest Storage," *Food Chemistry* 337 (2021): 127753.

282. Q. Wang, Y. Han, R. Yang, et al., "Melatonin Facilitates the Deposition of Suberin Polyphenolic and Lignin at Wounds of Potato Tubers By Mediating Nitric Oxide and Reactive Oxygen Species," *Postharvest Biology and Technology* 198 (2023): 112270.

283. X. Yang, X. Lin, Q. Wei, M. Chen, J. Chen, and Q. Ma, "Understanding the Influence of 2,4-dichlorophenoxyacetic Acid and Melatonin Treatments on the Sweet and Acidic Flavors and Citric Acid Metabolism of 'Olinda' Orange (*Citrus sinensis* (L.) Osbeck)," *Scientia Horticulturae* 304 (2022): 111287.

284. Q. Ma, X. Lin, Q. Wei, X. Yang, Y. Zhang, and J. Chen, "Melatonin Treatment Delays Postharvest Senescence and Maintains the Organoleptic Quality of 'Newhall' Navel Orange (*Citrus sinensis* (L.) Osbeck) By Inhibiting Respiration and Enhancing Antioxidant Capacity," *Scientia Horticulturae* 286 (2021): 110236.

285. P. Hayati, M. Hosseinifarahi, G. Abdi, M. Radi, and L. Taghipour, "Melatonin Treatment Improves Nutritional Value and Antioxidant Enzyme Activity of *Physalis peruviana* Fruit during Storage," *Journal of Food Measurement and Characterization* 17 (2023): 2782–2791.

286. S. Cai, Z. Zhang, J. Wang, et al., "Effect of Exogenous Melatonin on Postharvest Storage Quality of Passion Fruit through Antioxidant Metabolism," *LWT* 194 (2024): 115835.

287. Y. Wang, M. Guo, W. Zhang, et al., "Exogenous Melatonin Activates the Antioxidant System and Maintains Postharvest Organoleptic Quality in Hami Melon (Cucumis. Melo Var. Inodorus Jacq.)," *Frontiers in Plant Science* 14 (2023): 1274939.

288. D. Wei, J. Yang, Y. Xiang, L. Meng, Y. Pan, and Z. Zhang, "Attenuation of Postharvest Browning in Rambutan Fruit By Melatonin Is Associated With Inhibition of Phenolics Oxidation and Reinforcement of Antioxidative Process," *Frontiers in Nutrition* 9 (2022): 905006.

289. S. Guo, T. Li, C. Wu, G. Fan, H. Wang, and D. Shen, "Melatonin and 1-Methylcyclopropene Treatments on Delay Senescence of Apricots during Postharvest Cold Storage By Enhancing Antioxidant System Activity," *Journal of Food Processing and Preservation* 45, no. 10 (2021): e15863.

290. Y. Zhang, X. Cui, Z. Du, et al., "Melatonin Enhances the Synthesis of Volatile Esters and Lactones in Apricot during Low Temperature Storage," *Scientia Horticulturae* 325 (2024): 112700.

291. R. Yan, Q. Xu, J. Dong, et al., "Effects of Exogenous Melatonin on Ripening and Decay Incidence in Plums (*Prunus salicina* L. cv. Taoxingli) during Storage at Room Temperature," *Scientia Horticulturae* 292 (2022): 110655.

292. R. Yan, S. Li, Y. Cheng, M. Kebbeh, C. Huan, and X. Zheng, "Melatonin Treatment Maintains the Quality of Cherry Tomato By Regulating Endogenous Melatonin and Ascorbate-Glutathione Cycle during Room Temperature," *Journal of Food Biochemistry* 46, no. 10 (2022): e14285.

293. T. Luo, F. Yin, L. Liao, et al., "Postharvest Melatonin Treatment Inhibited Longan (*Dimocarpus Longan* Lour.) Pericarp Browning By Increasing Ros Scavenging Ability and Protecting Cytomembrane Integrity," *Food Science & Nutrition* 9, no. 9 (2021): 4963–4973.

294. L. Shi, Y. Chen, W. Dong, et al., "Melatonin Delayed Senescence By Modulating the Contents of Plant Signalling Molecules in Postharvest Okras," *Frontiers in Plant Science* 15 (2024): 1304913.

295. P. Li, R. Zhang, H. Zhou, et al., "Melatonin Delays Softening of Postharvest Pepper Fruits (*Capsicum annuum* L.) By Regulating Cell Wall Degradation, Membrane Stability and Antioxidant Systems," *Postharvest Biology and Technology* 212 (2024): 112852.

296. D. Zhao, Y. Luan, W. Shi, Y. Tang, X. Huang, and J. Tao, "Melatonin Enhances Stem Strength By Increasing Lignin Content and Secondary Cell Wall Thickness in Herbaceous Peony," *Journal of Experimental Botany* 73, no. 17 (2022): 5974–5991.

297. R. M. Mazrou, S. Hassan, M. Yang, and F. A. S. Hassan, "Melatonin Preserves the Postharvest Quality of Cut Roses through Enhancing the Antioxidant System," *Plants* 11, no. 20 (2022): 2713.

298. F. Zulfiqar, A. Moosa, A. Darras, M. Nafees, A. Ferrante, and K. H. M. Siddique, "Preharvest Melatonin Foliar Treatments Enhance Postharvest Longevity of Cut Tuberose Via Altering Physio-Biochemical Traits," *Frontiers in Plant Science* 14 (2023): 1151722.

299. N. E. H. Lezoul, M. Serrano, M. C. Ruiz-Aracil, et al., "Melatonin As a New Postharvest Treatment for Increasing Cut Carnation (*Dianthus caryophyllus* L.) Vase Life," *Postharvest Biology and Technology* 184 (2022): 111759.

300. C. Zhou, L. Luo, P. Miao, et al., "A Novel Perspective to Investigate How Nanoselenium and Melatonin Lengthen the Cut Carnation Vase Shelf," *Plant Physiology and Biochemistry* 196 (2023): 982–9992.

301. Y. Wang, X. Liu, M. Sun, et al., "Melatonin Enhances Vase Life and Alters Physiological Responses in Peony (*Paeonia lactiflora* Pall.) Cut Flowers," *Postharvest Biology and Technology* 212 (2024): 112896.

302. A. Njie, X. Dong, Q. Liu, C. Lu, X. Pan, and W. Zhang, "Melatonin Treatment Inhibits Mango Fruit (cv. 'Guiqi') Softening By Maintaining Cell Wall and Reactive Oxygen Metabolisms during Cold Storage," *Postharvest Biology and Technology* 205 (2023): 112500.

303. M. Michailidis, G. Tanou, E. Sarrou, et al., "Pre- and Postharvest Melatonin Application Boosted Phenolic Compounds Accumulation and Altered Respiratory Characters in Sweet Cherry Fruit," *Frontiers in Nutrition* 8 (2021): 695061.

304. D. Sircar, H. G. Cardoso, C. Mukherjee, A. Mitra, and B. Arnholdt-Schmitt, "Alternative Oxidase (AOX) and Phenolic Metabolism in Methyl Jasmonate-Treated Hairy Root Cultures of *Daucus Carota* L," *Journal of Plant Physiology* 169, no. 7 (2012): 657–663.

305. J. Liu, R. Yue, M. Si, et al., "Effects of Exogenous Application of Melatonin on Quality and Sugar Metabolism in 'Zaosu' Pear Fruit," *Journal of Plant Growth Regulation* 38, no. 3 (2019): 1161–1169.

306. X. Lin, S. Huang, D. J. Huber, et al., "Melatonin Treatment Affects Wax Composition and Maintains Storage Quality in 'Kongxin' Plum (*Prunus salicina* L. cv) during Postharvest," *Foods* 11, no. 24 (2022): 3972.

307. J. Liu, H. Liu, T. Wu, et al., "Effects of Melatonin Treatment of Postharvest Pear Fruit on Aromatic Volatile Biosynthesis," *Molecules.* 24, no. 23 (2019): 4233.

308. H. Di, C. Zhang, A. Zhou, et al., "Transcriptome Analysis Reveals the Mechanism By Which Exogenous Melatonin Treatment Delays Leaf Senescence of Postharvest Chinese Kale (*Brassica oleracea* Var. Alboglabra)," *International Journal of Molecular Sciences* 25, no. 4 (2024): 2250.

309. H. Zhao, L. Wang, T. Belwal, et al., "Chitosan-Based Melatonin Bilayer Coating for Maintaining Quality of Fresh-Cut Products," *Carbohydrate Polymers* 235 (2020): 115973.

310. Y. Lin, L. Zhan, P. Shao, and P. Sun, "Phase-Change Materials and Exogenous Melatonin Treatment Alleviated Postharvest Senescence of Agaricus Bisporus By Inhibiting Browning and Maintaining Cell Membrane Integrity," *Postharvest Biology and Technology* 192 (2022): 112009.

311. L. Feng, X. Jiang, H. Kitazawa, et al., "Characterization of Bioactive Films Loaded with Melatonin and Regulation of Postharvest ROS Scavenging and Ascorbate-Glutathione Cycle in Agaricus Bisporus," *Postharvest Biology and Technology* 194 (2022): 112107.

312. L. Feng, X. Jiang, J. Han, et al., "Properties of an Active Film Based on Glutenin/Tamarind Gum and Loaded with Binary Microemulsion of Melatonin/Pummelo Essential Oil and Its Preservation for Agaricus Bisporus," *Food Chemistry* 429 (2023): 136901.

313. L. Feng, N. Zhang, J. Wang, et al., "Sustained Release of a Novel Bilayer Packaging Film Loaded with Binary Microemulsion of Melatonin/Pummelo Essential Oil and Its Regulation of Postharvest Energy Metabolism in *Agaricus bisporus*," *Food Control* 161 (2024): 110396.

314. M. Wang, J. Xu, L. Li, H. Shen, Z. Ding, and J. Xie, "Development of Packaging Films Based on UiO-66 MOF Loaded Melatonin with Antioxidation Functions for Spinach Preservation," *Food Chemistry* 440 (2024): 138211.

315. K. Venkatachalam, N. Charoenphun, S. Lekjing, and P. Noonim, "Investigation of Melatonin Incorporated CMC-Gelatin Based Edible Coating on the Alleviation of Chilling Injury Induced Pericarp Browning in Longkong," *Foods* 13, no. 1 (2024): 72.

316. A. D. Al-Qurashi, M. A. Awad, M. I. Elsayed, and M. A. Ali, "Postharvest Melatonin and Chitosan Treatments Retain Quality of 'Williams' Bananas during Ripening," *Journal of Food Science and Technology* 61, no. 1 (2024): 84–96.

317. E. Bal, "Impact of Chitosan-Melatonin Composite Coating on Postharvest Quality of Sweet Cherry," *Applied Fruit Science* 66 (2024): 763–770.

318. S. Mwelase, U. L. Opara, and O. A. Fawole, "Effect of Chitosan-Based Melatonin Composite Coating on the Quality of Minimally Processed Pomegranate Aril-Sacs during Cold Storage," *Journal of Food Processing and Preservation* 46, no. 12 (2022): e17096.

319. M. S. Aghdam, Z. Luo, A. Jannatizadeh, and B. Farmani, "Exogenous Adenosine Triphosphate Application Retards Cap Browning in *Agaricus bisporus* during Low Temperature Storage," *Food Chemistry* 293 (2019): 285–290.

320. J. Choi, K. Tanaka, Y. Cao, et al., "Identification of a Plant Receptor for Extracellular ATP," *Science* 343, no. 6168 (2014): 290–294.

321. S.-H. Cho, K. Tóth, D. Kim, et al., "Activation of the Plant Mevalonate Pathway By Extracellular ATP," *Nature Communications* 13, no. 1 (2022): 450.

322. M. Soleimani Aghdam, M. Sayyari, and Z. Luo, "Exogenous Phytosulfokine α Application Delays Senescence and Promotes Antioxidant Nutrient Accumulation in Strawberry Fruit during Cold Storage By Triggering Endogenous Phytosulfokine α Signaling," *Postharvest Biology and Technology* 175 (2021): 111473.

323. M. S. Aghdam and M. Alikhani-Koupaei, "Exogenous Phytosulfokine α (PSKα) Applying Delays Senescence and Relief Decay in Strawberry Fruits during Cold Storage By Sufficient Intracellular Atp and Nadph Availability," *Food Chemistry* 336 (2021): 127685.

324. M. S. Aghdam, M. Alikhani-Koupaei, and R. Khademian, "Delaying Broccoli Floret Yellowing By Phytosulfokine α Application during Cold Storage," *Frontiers in Nutrition* 8 (2021): 609217.

325. M. S. Aghdam, A. Ebrahimi, J. R. Fard, and M. Sheikh-Assadi, "Phytosulfokine α (Pskα) Delays Senescence in Cut Rose Flowers By Keeping Intracellular Atp and Ros Homeostasis," *Scientia Horticulturae* 331 (2024): 113145.

326. M. S. Aghdam, A. Ebrahimi, and M. Sheikh-Assadi, "Phytosulfokine α (PSKα) Delays Senescence and Reinforces SUMO1/SUMO E3 Ligase SIZ1 Signaling Pathway in Cut Rose Flowers (*Rosa hybrida* cv. Angelina)," *Scientific Reports* 11, no. 1 (2021): 23227.

327. M. S. Aghdam, A. Ebrahimi, M. Sheikh-Assadi, and R. Naderi, "Endogenous Phytosulfokine α (PSKα) Signaling Delays Petals Senescence and Prolongs Vase Life of Cut Rose Flowers (*Rosa hybrida* cv. Angelina)," *Scientia Horticulturae* 289 (2021): 110444.

328. M. S. Aghdam and F. B. Flores, "Employing Phytosulfokine α (PSKα) for Delaying Broccoli Florets Yellowing during Cold Storage," *Food Chemistry* 355 (2021): 129626.

329. M. S. Aghdam, F. B. Flores, and B. Sedaghati, "Exogenous Phytosulfokine α (Pskα) Application Delays Senescence and Relieves Decay in Strawberry Fruit during Cold Storage By Triggering

Extracellular Atp Signaling and Improving ROS Scavenging System Activity," *Scientia Horticulturae* 279 (2021): 109906.

330. M. S. Aghdam and Z. Luo, "Exogenous Application of Phytosulfokine α (PSKα) Delays Senescence in Broccoli Florets during Cold Storage By Ensuring Intracellular ATP Availability and Avoiding Intracellular ROS Accumulation," *Scientia Horticulturae* 276 (2021): 109745.

331. M. S. Aghdam, M. Sayyari, and Z. Luo, "Exogenous Application of Phytosulfokine α (PSKα) Delays Yellowing and Preserves Nutritional Quality of Broccoli Florets during Cold Storage," *Food Chemistry* 333 (2020): 127481.

332. X. Kong, H. Tian, Q. Yu, et al., "PHB3 Maintains Root Stem Cell Niche Identity through ROS-Responsive AP2/ERF Transcription Factors in Arabidopsis," *Cell Reports* 22, no. 5 (2018): 1350–1363.

333. J. Heyman, T. Cools, F. Vandenbussche, et al., "ERF115 Controls Root Quiescent Center Cell Division and Stem Cell Replenishment," *Science* 342, no. 6160 (2013): 860–863.

334. W. Hu, W. Tie, W. Ou, et al., "Crosstalk between Calcium and Melatonin Affects Postharvest Physiological Deterioration and Quality Loss in Cassava," *Postharvest Biology and Technology* 140 (2018): 42–449.

335. G. Liu, B. Li, X. Li, Y. Wei, D. Liu, and H. Shi, "Comparative Physiological Analysis of Methyl Jasmonate in the Delay of Postharvest Physiological Deterioration and Cell Oxidative Damage in Cassava," *Biomolecules* 9, no. 9 (2019): 451.

336. G. Liu, B. Li, Y. Wang, et al., "Novel Role of Ethanol in Delaying Postharvest Physiological Deterioration and Keeping Quality in Cassava," *Food and Bioprocess Technology* 12, no. 10 (2019): 1756–1765.

337. Y. Yin, C. Wang, C. Cheng, Z. Yang, and W. Fang, "Exogenous Methyl Jasmonate Promotes the Biosynthesis of Endogenous Melatonin in Mustard Sprouts," *Plant Physiology and Biochemistry* 203 (2023): 108055.

338. Q. Zhou, Z. Bao, Y. Yu, et al., "IAA Regulated Levels of Endogenous Phytohormones in Relation to Chilling Tolerance in Cold-Stored Peaches after Harvest," *Postharvest Biology and Technology* 205 (2023): 112490.

339. W. Dong, S. Cao, Q. Zhou, et al., "Hydrogen-Rich Water Treatment Increased Several Phytohormones and Prolonged the Shelf Life in Postharvest Okras," *Frontiers in Plant Science* 14 (2023): 1108515.

340. Y. Wang, S. Jin, Z. Liu, et al., "H2 Supplied Via Ammonia Borane Stimulates Lateral Root Branching Via Phytomelatonin Signaling," *Plant Physiology* 194, no. 2 (2024): 884–901.

341. Y. Ma, P. Li, C. B. Watkins, et al., "Chlorine Dioxide and Sodium Diacetate Treatments in Controlled Atmospheres Retard Mold Incidence and Maintain Quality of Fresh Walnuts during Cold Storage," *Postharvest Biology and Technology* 161 (2020): 111063.

342. E. P. Gomes, C. Vanz Borges, G. C. Monteiro, et al., "Preharvest Salicylic Acid Treatments Improve Phenolic Compounds and Biogenic Amines in 'Niagara Rosada' Table Grape," *Postharvest Biology and Technology* 176 (2021): 111505.