Overview of Melatonin’s Impact on Postharvest Physiology and Quality of Fruits

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Abstract: Fruits are important horticultural commodities because they provide nutrients that help human health. Fruits are mostly consumed as fresh products; however, there are challenges in retaining the freshness, such as the rapid ripening process that triggers fruit deterioration and reduces fruit quality and nutrient content. The postharvest quality of horticultural crops is affected by pre- and postharvest treatment. Most farmers use chemical compounds and fungicides to prevent postharvest damage; however, this results in health hazards and environmental pollution. Melatonin can be used for maintaining and improving postharvest horticultural crops such as fruits. Melatonin is a new bioactive compound that is a potent free radical scavenger and antioxidant. It has been studied as an alternative to harmful chemicals used commercially in the postharvest management of fresh products. For human health, melatonin plays a regulatory role in circadian and seasonal rhythms, sleep, retinal functions, and the immune system. In plants, melatonin regulates many biological processes, particularly when plants have experienced abiotic stress, germination, aging, and growth. The effect of exogenous melatonin on fruit ripening has focused primarily on the relationship between melatonin and ethylene plant hormones. Many studies in recent years have discussed melatonin’s role in plants, particularly in delaying plant aging as an alternative way of increasing fruit shelf life. This review provides a comprehensive overview of melatonin biosynthesis in plants, factors that affect the content of melatonin in fruit, melatonin mechanisms in fruit ripening, the impact of melatonin on postharvest fruit quality, the effect of melatonin on postharvest quality, and the change in metabolite content of horticultural products, particularly fruits.

Keywords: metabolite; horticulture; antioxidant

1. Introduction

Melatonin is a biomolecule that has pleiotropic effects on living organisms ranging from the smallest microbes (bacteria) to humans, animals, and plants, but most of it is related to the regulation of circadian rhythms and biological cycles in animals and plants [1,2]. Melatonin (N-acetyl-5-methoxy tryptamine) was discovered in plants in 1995 and is structurally similar to indole amine compounds such as tryptophan, auxin, and serotonin [1]. In plants, melatonin functions as a biological signal involved in several plant processes, such as photosynthesis, development, defense, germination, efflorescence, germination, flowering, leaf senescence, membrane integrity, root development, osmoregulation, and plant protection against biotic and abiotic stresses [3,4]. For postharvest purposes, melatonin improves the postharvest quality of horticultural crops [5].
Fruit is a popular horticultural product owing to its good taste and high nutritional content, such as polyphenolic compounds, organic acids, and vitamins [6]. Fruit is mainly consumed as a fresh product. However, several problems were found in fruits, such as perishability and rapid aging during postharvest storage, causing decreased nutritional content and taste quality, and reduced consumer interest [7]. Moreover, undesirable changes occurred during fruit ripening, such as softening, shrinkage, ethylene production, and fruit decay [8–10]. Several methods have been studied to prevent postharvest losses of perishable products, such as preventing the ethylene effect at the receptor level using 1-methylcyclopropene as an ethylene inhibitor [11–14], mutation techniques in ethylene receptor genes [15–18], modified atmospheres, and applying chemical compounds, such as fungicides, waxing, and nitric oxide [19]. However, applying chemical compounds results in health hazards and environmental pollution; in particular, pesticide residues on fresh fruits and vegetables will be a potential hazard for consumers. Recently, melatonin has been studied as an alternative to harmful chemicals used commercially in the postharvest management of fresh products such as fruits [1].

The postharvest quality of horticultural crops is affected by pre- and postharvest treatment. Unfavorable conditions during growth and storage will be a major problem in reducing and losing postharvest quality. Melatonin is a potential nontoxic chemical compound that can be used for pre- or postharvest treatment. In the field, melatonin increases pathogen/disease resistance, such as Marssonina apple blotch fungal disease against Diplodocarpum mali [20], inhibits mycelial growth of Phytophthora infestans in potato [21], increases resistance against Podosphaera xanthii and Phytophthora capsici in cucurbits and watermelon [22], and increases plant growth and reduces plant stresses, such as salinity, cold, heat, drought, and heavy metal [1,23]. Preventing unfavorable conditions during growth and storage will improve the yield, yield quality, and postharvest characteristics of fresh products.

The effect of melatonin on postharvest quality is still being studied in depth because the different effects depend on the species. Several studies have reported that melatonin regulates fruit ripening by regulating ethylene biosynthesis and its roles in harvested products and provide evidence that melatonin is involved in fruit maturation. However, the effect of melatonin on regulating ethylene biosynthesis that affects fruit ripening differs depending on the fruit species. In some species, melatonin improves postharvest quality [24], such as by promoting fruit ripening and improving the fruit quality of tomatoes and grapes [25,26], or by delaying fruit senescence and increasing the chilling tolerance of peaches [27]; however, in some species, it reduces postharvest decay and maintains nutritional quality, such as in strawberries [28]. Previous studies have shown that using melatonin is important in the postharvest handling of several horticultural crop commodities and in improving postharvest quality. This review provides a comprehensive overview of the effect of melatonin on postharvest quality and the change in the metabolite content of horticultural products, particularly fruits.

2. Melatonin Biosynthesis in Plants

Compared to animals, the biosynthetic process of melatonin in plants is more complex. Melatonin biosynthesis typically occurs in chloroplasts but can also in mitochondria [1]. Six enzymes are involved in melatonin biosynthesis: L-tryptophan decarboxylase (TDC), tryptamine 5-hydroxylase (T5H), serotonin N-acetyltransferase (SNAT), acetyl serotonin O-methyltransferase (ASMT), caffeic acid 3-O-methyltransferase (COMT), and putative tryptophan hydroxylase (TPH) that has not yet been identified [29].

Figure 1 shows the melatonin biosynthesis. The first step in melatonin biosynthesis process is the conversion of tryptophan, which is the key compound for melatonin biosynthesis, to serotonin through two different pathways, namely the hydroxylation and decarboxylation processes. Decarboxylation occurs more commonly in plants compared to hydroxylation. The first pathway is the decarboxylation of tryptophan to tryptamine with the help of TDC, then tryptamine is hydroxylated at the 5th position of the indole
ring to form 5-hydroxytryptamine (serotonin) with the help of tryptamine-5-hydroxylase (T5H); conversely, the second pathway involves the hydroxylation of tryptophan to 5-hydroxytryptophan with the help of TPH, followed by the decarboxylation process of 5-hydroxytryptophan to form serotonin with the help of TDC [29].

![Biosynthetic pathway of melatonin](image)

**Figure 1.** Biosynthetic pathway of melatonin. Solid lines and dotted lines indicate common and alternative pathways of melatonin biosynthesis, respectively. TDC, L-tryptophan decarboxylase; T5H, tryptamine 5-hydroxylase; TPH, tryptophan hydroxylase; SNAT, serotonin N-acetyltransferase; ASMT, acetylserotonin O-methyltransferase; COMT, caffeic acid 3-O-methyltransferase.

The second step in the melatonin biosynthesis process is the process of converting serotonin into melatonin through two different pathways; namely SNATs catalyze serotonin into N-acetyl-serotonin, and then, N-acetyl-serotonin is converted into melatonin with the help of ASMTs. The second pathway is the process of converting serotonin into 5-methoxy tryptamine with the help of ASMTs or COMT, followed by the process of converting 5-methoxy tryptamine into melatonin catalyzed by SNATs or COMT [29,30].

### 3. Factors That Affect the Melatonin Content in Fruits

#### 3.1. Genetic Makeup

Many studies have broadly examined the presence of melatonin in plants, including various vegetables, cereals, fruits, seeds, and medicinal plants [31,32]. The melatonin content of fruits varies depending on the type and variety of the fruit. Several studies have reported endogenous melatonin in different plant families, such as Rosaceae, Vitaceae, and Arecaceae. As shown in Table 1, the concentration of endogenous melatonin varies among species in the same family or in different families, and also according to the quantification method.

<table>
<thead>
<tr>
<th>Family</th>
<th>Species</th>
<th>Concentration (ng/g)</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td>Actinidiaceae</td>
<td><em>Actinidia chinensis</em></td>
<td>0.02</td>
<td>[3]</td>
</tr>
<tr>
<td>Anacardiaceae</td>
<td><em>Mangifera indica</em></td>
<td>0.70</td>
<td>[33]</td>
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<td></td>
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<td>0.17</td>
<td>[34]</td>
</tr>
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<td>Family</td>
<td>Species</td>
<td>Melatonin Levels</td>
<td>Ref.</td>
</tr>
<tr>
<td>-------------------</td>
<td>----------------------------------------------</td>
<td>------------------</td>
<td>------</td>
</tr>
<tr>
<td>Arecaee</td>
<td>Phoenix dactylifera</td>
<td>0.17</td>
<td>[34]</td>
</tr>
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<td>Bromeliaceae</td>
<td>Ananas comosus (L.) Meri.</td>
<td>0.04</td>
<td>[3]</td>
</tr>
<tr>
<td></td>
<td>Ananas comosus (L.) Meri.</td>
<td>0.28</td>
<td>[35]</td>
</tr>
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<td>Ananas comosus (L.) Meri.</td>
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<td>Ananas comosus (L.) Meri.</td>
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<td>[37]</td>
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<tr>
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<td>[38]</td>
</tr>
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<td>Carica papaya</td>
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</tr>
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<td>Cucurbitaceae</td>
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<td>[3]</td>
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<td>Cucumis sativus L.</td>
<td>0.59</td>
<td>[35]</td>
</tr>
<tr>
<td></td>
<td>Cucumis sativa</td>
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<td>[38]</td>
</tr>
<tr>
<td>Juglandaceae</td>
<td>Juglans regia L.</td>
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<td>[39]</td>
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<tr>
<td>Lythraceae</td>
<td>Punica granatum L.</td>
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<td>[35]</td>
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<tr>
<td>Musaceae</td>
<td>Musa paradisiaca L.</td>
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<td>[40]</td>
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<td>Musa sapientum L.</td>
<td>0.01</td>
<td>[36]</td>
</tr>
<tr>
<td></td>
<td>Musa ensete</td>
<td>0.66</td>
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<td>Prunus cerasus L.</td>
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<td>0.01–124.7</td>
<td>[35]</td>
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<tr>
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<td>[41]</td>
</tr>
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<td>[43]</td>
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<tr>
<td></td>
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<td>0.14</td>
<td>[35]</td>
</tr>
<tr>
<td></td>
<td>Fragaria ananassa Duch.</td>
<td>0.01</td>
<td>[3]</td>
</tr>
<tr>
<td></td>
<td>Fragaria ananassa Duch.</td>
<td>5.50–11.26</td>
<td>[44]</td>
</tr>
<tr>
<td></td>
<td>Fragaria magana</td>
<td>0.01</td>
<td>[38]</td>
</tr>
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<td>Rutaceae</td>
<td>Citrus sinensis Osbeck.</td>
<td>0.15</td>
<td>[33]</td>
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<tr>
<td>Solanaceae</td>
<td>Solanum lycopersicum</td>
<td>0.5</td>
<td>[40]</td>
</tr>
<tr>
<td></td>
<td>Solanum lycopersicum</td>
<td>0.3</td>
<td>[35]</td>
</tr>
<tr>
<td></td>
<td>Solanum lycopersicum</td>
<td>7.5–250</td>
<td>[45]</td>
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<tr>
<td></td>
<td>Solanum lycopersicum</td>
<td>0.03</td>
<td>[38]</td>
</tr>
<tr>
<td></td>
<td>Solanum lycopersicum</td>
<td>1.2–3.4</td>
<td>[46]</td>
</tr>
<tr>
<td></td>
<td>Solanum lycopersicum</td>
<td>4.1–114.5</td>
<td>[44]</td>
</tr>
<tr>
<td>Vitaceae</td>
<td>Vitis vinifera L.</td>
<td>0.97</td>
<td>[47]</td>
</tr>
<tr>
<td></td>
<td>Vitis vinifera L.</td>
<td>1.2–1.50</td>
<td>[48]</td>
</tr>
</tbody>
</table>

3.2. Environment

Another factor that influences the content of melatonin in fruit is the growth environment. Based on the research by Burkhardt et al. [41] on Montmorency tart cherries, no significant difference was noted when planted in different locations. However, this statement was refuted by the research of Arnao and Hernandez-Ruiz [49], who showed that environmental conditions affected melatonin levels, which were observed in several studies of indoor and outdoor tomato cultivation in different environmental conditions.

Melatonin concentration can also be affected by external factors such as stress. Abiotic stresses can stimulate melatonin synthesis in plants. Melatonin can help ease the negative consequences, particularly oxidative stress in plants. Melatonin can efficiently cancel the deleterious effects of toxic oxygen derivatives because of its ability to neutralize them and increase plant resilience against stress [32]. Moreover, melatonin accumulates in plant tissues as a protective molecule in response to different environmental conditions. Ultraviolet (UV)-B radiation increased endogenous melatonin up to 7-fold in Glycyrhiza uralensis compared with the control [50]. The application of zinc salts, hydrogen peroxide,
and sodium chloride in barley and lupin plants resulted in increased endogenous melatonin [36,51]. Salt stress increased endogenous melatonin up to 2- and 6-fold in the roots and cotyledons of sunflower seedlings, respectively [52].

3.3. Fruit Ripening Stages of Development

Fruit ripening is another factor that affects the melatonin content of the fruit. According to research by Murch et al. [53] on berries, the melatonin concentration in all berries decreases with fruit ripening, Vitalini et al. [54] observed that as the fruit ripens, the melatonin content in grape skins decreases but increases in the seeds and fruit flesh. Another study found that cherries with the highest maturity level had the highest melatonin content [42].

4. Melatonin Mechanism in Fruit Ripening

Ripening is a normal process during fruit maturation. Several biochemical and physiological changes occur, such as those involving flavor, color, aroma, and texture, and there are also increases in ethylene production and respiration [16,55]. Ethylene is an important plant hormone for fruit ripening, triggering climacteric fruit ripening [56]. Several studies have reported that melatonin affects ethylene biosynthesis pathways, but it differs among species. Melatonin may induce or inhibit ethylene production during different processes in plants. In tomatoes, melatonin increased ethylene production by upregulating the expression of 1-aminocyclopropane carboxylic acid synthase 4 (ACS4) [26]. However, in pears, melatonin reduces ethylene production [57]. In bananas, melatonin can be used to ripen bananas of different varieties, and it can be used for biological control of postharvest fruit ripening and quality [58].

The effect of exogenous melatonin on the fruit ripening stage is related to the relationship between melatonin and plant ethylene hormones. Sun et al. [26] found that exogenous melatonin increased ethylene biosynthesis before and after the climacteric peak by increasing the expression of 1-aminocyclopropane-1-carboxylic acid (ACC) synthetase along with the ethylene receptor gene. Proteins that are involved in ripening, cell walls, carbohydrates, flavonoids, and fatty acid biosynthesis are affected by melatonin. Proteins are involved in anthocyanin biosynthesis during fruit ripening, showing that exogenous melatonin regulates fruit ripening and fruit senescence [59]. Strawberries treated with 0.1–1.0 mM melatonin within 5 min and then stored later at 4 °C and 90% humidity showed a decrease in spoilage and weight [60]. The aging parameters include color, firmness, total dissolved solid content, titratable acidity, hydrogen peroxide, and malondialdehyde (MDA). In contrast to the increased phenolic and flavonoid content, a higher antioxidant capacity was produced. This exogenous melatonin treatment also increased the expression of endogenous melatonin geosynthetic genes.

Melatonin promotes abscisic acid biosynthesis on various ethylene signaling elements and increases various primary and secondary metabolic steps to accelerate fruit ripening by promoting ethylene and anthocyanin biosynthesis. The effect of melatonin on aging happens in reverse, delaying melatonin through a redox network involving reactive oxygen species (ROS) and reactive nitrogen species (especially NO), lowering ROS levels, and upregulating various antioxidant enzymes and metabolites that delay aging. Furthermore, several aging-related genes are derived from melatonin to improve fruit quality and extend the shelf life. Melatonin treatment has different effects on ethylene biosynthesis. At one time, it can induce 1-aminocyclopropane-1-carboxylic acid oxidase (ACO) and 1-aminocyclopropane-1-carboxylic (ACC) synthase (ACS) to promote fruit ripening. However, melatonin also downregulates the same enzymes at other times to reduce ethylene formation and promote longer shelf life through delayed aging. In this process, ripening is genetically regulated and characterized by the action of ethylene, whereas aging is an oxidative process involving damage and disruption. These two processes are different but inseparable [24,49].
5. The Effects of Melatonin on Postharvest Damages

Plants need external agents such as melatonin to grow properly from pre- to postharvest. During postharvest, plants are susceptible to pest and disease attacks, which will result in a decrease in plant quality. Melatonin protects the plants from pests and diseases. It was reported that the increase in disease resistance might be due to the effects of increasing endogenous melatonin, inducing salicylic acid (SA) signaling pathways associated with ROS burst and pathogenesis-related proteins (PRs), activating phenylpropanoid pathways, and increasing the content of lignin, phenolic compounds, and flavonoids in plants. Therefore, applying postharvest melatonin is highly recommended because it can be a natural and economical elicitor in controlling postharvest spoilage; for example, in tomatoes [59] and strawberries [60] as a valuable approach to increasing fruit quality, and in bananas [58] and pears [57].

Melatonin treatment increases disease resistance to *Pseudomonas syringae* pv. on *Arabidopsis* [61] and against *Marssonina* blotch (*Diplocarpon mali*) on apples [33], against the leaf pathogen *Podosphaera xanthii* (powdery mildew), and the soil-borne oomycete *Phytophthora capsici* in watermelon and other Cucurbita [22]. This result was associated with increased NO production, which then arranged gene transcription related to SA, activated cell wall invertase-dependent pathogen defense pathways, maintained intracellular hydrogen peroxide (H2O2) concentrations, and mediated defense signaling.

Another study also mentioned that melatonin is involved in several plants’ responses to biotic and abiotic stress. For instance, Lee et al. [62] reported that knockout of serotonin N-acetyltransferase (SNAT), a rate-limiting enzyme in the melatonin biosynthetic pathway in *Arabidopsis*, results in decreased melatonin and SA, which are associated with greater susceptibility to pathogens. Recently, several studies have indicated that the effect of melatonin treatment on increasing endogenous melatonin levels is associated with the increased biosynthetic expression of melatonin genes, thereby contributing to the quality care of fresh strawberries or the inhibition of browning in longan fruit [60,63].

The presence of melatonin inhibits the development of pathogens such as gray mold during postharvest. The effect of melatonin on plants makes them resistant to decay and disease. Endogenous melatonin given to plants receives a burst of ROS, which has relevance for the upregulation of several genes involved in melatonin biosynthesis. This ROS burst is induced by chemical elicitors and triggers the activation of a H2O2-fueled defense response, which is highly correlated with lower susceptibility to *Trichothecium roseum* in muskmelons [64], *Penicillium expansum* in apples [65], or *Colletotrichum musae* infection in bananas [66]. In addition, SA, as an important endogenous immune signal, triggers resistance that can be obtained through the systematic induction of a response to the disease resistance in fruits [67].

Several studies showed that melatonin treatment increased ROS in cherries due to the formation of O2, whereas the H2O2 content increased significantly with melatonin treatment. Furthermore, melatonin treatment significantly increased endogenous SA content and the levels of PRs such as CHI and GLU. Moreover, NO is considered an important regulatory molecule in the response of plants to pathogen infection in synergy with ROS [68]. NO interacts with H2O2 in resistance responses, for example, in tomatoes against *Rhizopus nigrans* [69], in peaches against *Monilinia fructicola* [70], and in oranges against *Colletotrichum gloeosporioides* during postharvest [71]. However, not all plants immediately respond to melatonin postharvest. Likewise, the effect of melatonin application in regulating fruit development or ripening differs by dose or fruit type or cultivar [72]. Thus, the effect of melatonin treatment on regulating ROS signaling to activate the SA signaling pathway may be involved in the disease resistance induced in tomato fruit during postharvest.

Moreover, melatonin has other effects as observed in Fuji apples in cold storage, which showed that melatonin can reduce ethylene production compared to the control treatment. Respiration rates immediately decreased in cold storage. The rate of CO2 production gradually decreased from 21 to 35 days of storage, followed by a steady rate of
CO₂ production toward the end of storage. The respiration rate pattern of the control and melatonin treatments was similar, except that at the end of storage, if melatonin was not given, ethylene production increased rapidly compared to the melatonin treatment, so it suppressed ethylene production to a relatively lower level than the fruit control. The physical impact of receiving melatonin treatment on the study of Fuji apples showed that after 56 days of fruit storage, the fruit retained its skin appearance as it did during harvest season compared with the control fruit that had black necrotic spots on the skin. The underlying metabolic changes between control and melatonin-treated fruit at 56 days of storage were investigated by UPLC-Q-TOF MS-based metabolic profiles. The results showed that 40 metabolites, including amino acids, sugars, organic acids, and phenols were expressed differently in the melatonin-treated samples compared with controls. Most importantly, the results showed that applying exogenous melatonin increased internal melatonin levels in apples. Several other metabolites such as phloretin, (+)-catechin, isoquercitrin, and procyanidins were also influenced by melatonin treatment, which might positively affect the cold storage of apples [73].

6. Melatonin Effects on Fruits

Many studies have proven that melatonin can effectively influence changes in fruit metabolite content, such as increasing and maintaining ascorbic acid, phenol, and flavonoids [63]. The application of melatonin changes the physiological index during ripening and postharvest fruit storage, such as increased phenol, flavonoid, amino acid, fatty acid, and anthocyanin [74–76].

Subsequently, melatonin has also been reported as an inducer of nonenzymatic antioxidant accumulation, including phenolics, ascorbic acid, flavonoids, and anthocyanins [77–80]. Melatonin can increase the total phenol and flavonoid content by regulating the cinnamic acid-4-hydroxylase (C4H) and phenylalanine ammonia lyase (PAL) activities in the phenylpropanoid metabolic pathway, which regulates flavonoid synthesis and other metabolites [78]. Melatonin can increase C4H activity during initial storage but decrease it during final storage [78]. This also occurs in PAL activities, where melatonin causes a significant increase in activity during final storage [78].

In general, during the storage of ascorbic acid, the content decreases due to the change of L-ascorbic acid to dehydroascorbic acid due to the ascorbic acid oxidase process [81]. However, current research indicates that melatonin treatment can change the ascorbic acid content in fruit, resulting in a higher level of resistance to oxidative stress during fruit ripening [19, 27,82]. Table 2 shows the different responses that may occur when applying melatonin to fruit due to differences in species, stages of fruit maturity, and treatment concentrations.
Table 2. Several studies on the effect of exogenous melatonin on the postharvest treatment of fruits.

<table>
<thead>
<tr>
<th>Family</th>
<th>Species</th>
<th>Optimum Concentration (µM)</th>
<th>Effects</th>
<th>Application</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Actinidiaceae</td>
<td>Actinidia deliciosa</td>
<td>100</td>
<td>Delayed the decline of fruit hardness, reduced the loss of soluble protein, and lowered the accumulation of malondialdehyde; improved total phenolic, total flavonoid and flavanol content, and the antioxidant capacity; and delayed fruit softening.</td>
<td>Soaked for 30 min</td>
<td>[83]</td>
</tr>
<tr>
<td>Anacardiacae</td>
<td>Mangifera indica L.</td>
<td>1000</td>
<td>Maintained firmness, improved ascorbic acid and phenolic compound content, and antioxidant capacity; controlled the activity of polyphenol oxidase; and increased the activity of the catalase (CAT) and peroxidase enzymes during storage.</td>
<td>Immersed for 10 min</td>
<td>[19]</td>
</tr>
<tr>
<td>Anacardiacae</td>
<td>Mangifera indica L.</td>
<td>100</td>
<td>Reduced respiration rate and ethylene production; increased firmness, titratable acidity, and ascorbic acid content; lowered weight loss, total soluble solids, pH, total soluble solid and acidity ratio; maintained a higher concentration of total phenolics and total flavonoids; increased the activities of antioxidant enzymes superoxide dismutase and CAT; and improved membrane stability.</td>
<td>Dipped for 120 min</td>
<td>[84]</td>
</tr>
<tr>
<td>Anacardiacae</td>
<td>Mangifera indica</td>
<td>1000</td>
<td>Improved postharvest quality; maintained firmness; improved bioactive compounds; increased phenolic content; and increased the activity of CAT and peroxidase (POD).</td>
<td>Immersed for 10 min</td>
<td>[19]</td>
</tr>
<tr>
<td>Caricaceae</td>
<td>Carica papaya</td>
<td>400</td>
<td>Delayed fruit softening; reduced anthracnose incidence; enhanced antioxidant activity; and decreased fruit oxidative injury; induced total phenol, total flavonoid, and ascorbic acid accumulation; increased CAT, ascorbate peroxidase, NADH oxidase, glutathione reductase, polyphenol oxidase, superoxide dismutase, and peroxidase activity; enhanced the activity of defense-related enzymes, such as chitinase, 4-coumaric acid-CoA-ligase, and phenylalanine ammonia lyase; repressed lipid metabolism.</td>
<td>Immersed for 2 h</td>
<td>[85]</td>
</tr>
<tr>
<td>Cucurbitaceae</td>
<td>Momordica charantia L.</td>
<td>120</td>
<td>Increased chlorophyll, total soluble solids (TSS), soluble sugar, soluble protein, and ascorbic acid (AsA); promoted the synthesis of total phenols and flavonoids.</td>
<td>Immersed for 10 min</td>
<td>[86]</td>
</tr>
<tr>
<td>Family</td>
<td>Species</td>
<td>Concentration</td>
<td>Description</td>
<td>Treatment</td>
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<td>-----------</td>
</tr>
<tr>
<td>Ericaceae</td>
<td><em>Vaccinium spp</em></td>
<td>50</td>
<td>Maintained the contents of AsA, anthocyanin, and total phenol; reduced the accumulation of reactive oxygen species and membrane lipid peroxidation; and promoted the activities of ascorbate peroxidase (APX), glutathione S-transferase, and phenylalanine ammonia lyase (PAL).</td>
<td>Sprayed</td>
<td>[87]</td>
</tr>
<tr>
<td>Musaceae</td>
<td><em>Musa paradisiaca</em> L.</td>
<td>200–500</td>
<td>Inhibited the ripening process.</td>
<td>Soaked for 2 h</td>
<td>[88]</td>
</tr>
<tr>
<td>Myrtaceae</td>
<td><em>Psidium guajava</em> L.</td>
<td>600</td>
<td>Maintained postharvest quality, delayed fruit softening, and reduced the incidence of anthracnose; enhanced the antioxidant capacity and reduced the oxidative damage; enhanced the activities of CAT, superoxide dismutase, ascorbate peroxidase, and glutathione reductase; and maintained total flavonoids and AsA.</td>
<td>Soaked for 2 h</td>
<td>[78]</td>
</tr>
<tr>
<td></td>
<td><em>Malus domestica</em> Borkh</td>
<td>1000</td>
<td>Reduced ethylene production and weight loss; maintained skin structure; increased the activity of three enzymes, including POD, superoxide dismutase (SOD), and CAT.</td>
<td>Sprayed</td>
<td>[89]</td>
</tr>
<tr>
<td></td>
<td><em>Malus domestica</em> Borkh</td>
<td>200</td>
<td>Inhibited gray mold diseases.</td>
<td>Immersed</td>
<td>[90]</td>
</tr>
<tr>
<td></td>
<td><em>Prunus persica</em></td>
<td>100</td>
<td>Reduced weight loss, decay incidence, and respiration rate; maintained firmness, TSS, and AsA contents; enhanced the activities of superoxide dismutase, CAT, peroxidase, and ascorbate peroxidase; decreased the activity of lipoxygenase, levels of superoxide anion and hydrogen peroxide, and malondialdehyde content.</td>
<td>Dipped for 10 min</td>
<td>[27]</td>
</tr>
<tr>
<td>Rosaceae</td>
<td><em>Prunus persica</em></td>
<td>100</td>
<td>Reduced chilling injury; increased extractable juice rate and TSS; enhanced expression of <em>PpADC</em>, <em>PpODC</em>, and <em>PpGAD</em>; increased polyamines and γ-aminobutyric acid (GABA) contents.</td>
<td>Immersed for 2 h</td>
<td>[73]</td>
</tr>
<tr>
<td></td>
<td><em>Prunus persica</em></td>
<td>1000</td>
<td>Melatonin-treated nectarines exhibited higher total antioxidant activity than controls, which was correlated primarily to the increase in the levels of total phenolics and to a decrease in the loss to AsA and flavonoids contents. These results demonstrated that melatonin treatment could be a good practice for extending postharvest life of nectarine fruits, maintaining the appearance and nutrient value, and reducing the loss of health-promoting compounds.</td>
<td>Immersed for 30 min</td>
<td>[91]</td>
</tr>
<tr>
<td></td>
<td><em>Prunus salicina</em></td>
<td>1000</td>
<td>Reduced weight loss and maintaining greater firmness; increased AsA content, total phenolic content, and antioxidant; reduced decay rate.</td>
<td>Immersed</td>
<td>[77]</td>
</tr>
<tr>
<td>Plant Family</td>
<td>Species</td>
<td>Conc.</td>
<td>Effect</td>
<td>Immersion Time</td>
<td></td>
</tr>
<tr>
<td>-------------</td>
<td>---------</td>
<td>-------</td>
<td>--------</td>
<td>----------------</td>
<td></td>
</tr>
<tr>
<td><em>Prunus salicina</em></td>
<td></td>
<td>100</td>
<td>Enhanced S-adenosylmethionine decarboxylase and TGase activities.</td>
<td>Immersed for 100 min [92]</td>
<td></td>
</tr>
<tr>
<td><em>Fragaria × ananassa, Duch.</em></td>
<td></td>
<td>100 or 1000</td>
<td>Reduced decay and weight loss of fruit; delayed senescence; reduced the accumulation of hydrogen peroxide (H₂O₂) and malondialdehyde (MDA); increased the total phenolics and flavonoid contents resulting in the higher antioxidant capacity, extending the postharvest life, and improving the fruit quality; enhanced the expression of melatonin biosynthetic genes including <em>FaTDC, FaT5H, FaSNAT</em>, and <em>FaASMT</em>; and increased the content of endogenous melatonin.</td>
<td>Immersed for 5 min [60]</td>
<td></td>
</tr>
<tr>
<td><em>Fragaria × ananassa, Duch.</em></td>
<td></td>
<td>100</td>
<td>Increased the accumulation of H₂O₂; increased the activity of SOD; reduced the activity of CAT and APX; and decreased the fruit decay.</td>
<td>Immersed for 2 h [93]</td>
<td></td>
</tr>
<tr>
<td><em>Prunus avium L.</em></td>
<td></td>
<td>100</td>
<td>Reduced flesh browning and decay incidence; increased phenols, flavonoids, anthocyanins accumulation, and antioxidant potential; maintained the membrane integrity.</td>
<td>Dipped for 5 min [94]</td>
<td></td>
</tr>
<tr>
<td><em>Eriobotrya japonica Lindl.</em></td>
<td></td>
<td>50</td>
<td>Inhibited weight loss and firmness; increased sugar, acid, and phytochemical content; decreased MDA content; improved antioxidant capacity; and reduced lignin content.</td>
<td>Immersed for 30 min [95]</td>
<td></td>
</tr>
<tr>
<td><em>Pyrus communis L.</em></td>
<td></td>
<td>100</td>
<td>Delayed the ethylene production; increased fruit firmness; increased antioxidant; and delayed the senescene process.</td>
<td>Immersed for 12 h [57]</td>
<td></td>
</tr>
</tbody>
</table>

**Rutaceae**

<table>
<thead>
<tr>
<th>Species</th>
<th>Conc.</th>
<th>Effect</th>
<th>Immersion Time</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Citrus sinensis (L.) Osbeck</em></td>
<td>200</td>
<td>Decreased respiration and weight loss rates; increase fruit firmness, TSS, soluble sugar content, titratable acidity, and citrus color index; impeded the accumulation of hydrogen peroxide and malondialdehyde; inhibited reactive oxygen species (ROS) burst and oxidative damage; increased the activity and expressions of CAT, superoxide dismutase, ascorbate peroxidase, and glutathione reductase; and delayed postharvest senescence.</td>
<td>Dipped for 5 min [96]</td>
</tr>
</tbody>
</table>

**Rhamnaceae**

<table>
<thead>
<tr>
<th>Species</th>
<th>Conc.</th>
<th>Effect</th>
<th>Immersion Method</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Ziziphus jujuba Mill.</em></td>
<td>100</td>
<td>Enhanced degradation of pesticides, such as chlorothalonil, malathion, and glyphosate; delayed fruit senescence by reduced weight loss, decay incidence, and firmness.</td>
<td>Sprayed [97]</td>
</tr>
</tbody>
</table>

**Sapindaceae**

<table>
<thead>
<tr>
<th>Species</th>
<th>Conc.</th>
<th>Effect</th>
<th>Immersion Time</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Litchi chinensis Sonn.</em></td>
<td>400</td>
<td>Delayed the development of pericarp browning, inhibited lipid degradation, and maintained membrane integrity and energy status.</td>
<td>Immersed for 5 min [75]</td>
</tr>
<tr>
<td><em>Litchi chinensis Sonn.</em></td>
<td>400</td>
<td>Inhibited pericarp browning; reduced discoloration during storage; decreased membrane relative leakage rate.</td>
<td>Immersed for 5 min [98]</td>
</tr>
<tr>
<td>Solanaceae</td>
<td>Solanum lycopersicum</td>
<td>100</td>
<td>Increased the content of total flavonoids, total phenolics, and lignin; inhibited gray mold development, induced a ROS burst, increased endogenous melatonin and salicylic acid (SA); enhanced activities of chitinase (CHI) and β-1,3-glucanase (GLU); increased the activities of PAL, 4-coumarate-coenzyme A ligase (4CL), and POD; and increased total phenols, flavonoids, and lignin in tomato.</td>
</tr>
<tr>
<td>--------------------</td>
<td>----------------------</td>
<td>------</td>
<td>--------------------------------------------------------------------------------</td>
</tr>
<tr>
<td>Solanum lycopersicum</td>
<td>50</td>
<td></td>
<td>Increased lycopene and water loss; enhanced fruit softening; increased water-soluble pectin and decreased protopectin; increased ethylene production, accelerated the climacteric phase, enhanced fruit ripening, and improved quality of tomatoes.</td>
</tr>
</tbody>
</table>
In papayas, applying melatonin can increase flavonoid and phenolic total content and ascorbic acid during fruit ripening to increase the accumulation of metabolite content [85]. In guava, melatonin treatment resulted in increased ascorbic acid content accumulation. Melatonin has the effect of increasing the respiration rate of fruit during final storage, so this impacts the secondary metabolite content accumulation of guava.

Melatonin application on strawberries can reduce malondialdehyde (MDA) and H$_2$O$_2$ concentrations while increasing phenolic and flavonoid total content, thereby contributing to the fruit’s potential for high antioxidant content [60]. However, melatonin treatment on strawberries resulted in lower ascorbic acid content. The response differed from that of melatonin treatment in peaches, which showed that it maintained its ascorbic acid content [27,60]. This may be due to differences in species, fruit conditions, and melatonin concentrations.

Melatonin treatment of cold-stored fruits with adequate supplies of intercellular NADPH can result in higher metabolite content. In addition to melatonin treatment in pomegranates, these conditions activate the ROS prevention system and increase phenylpropanoid metabolic pathway activity, resulting in a higher accumulation of phenols and anthocyanins [28]. PAL activity increased in cherry tomatoes due to melatonin application; this response positively impacted fruit phenolic and flavonoid total and lignin content during storage [99]. In addition, changes in metabolite content have also increased in several other fruits that have been studied, such as plums [77], mangoes [19,84], and kiwis [83].

7. Conclusions

The primary function of melatonin in fruit is its ability to induce parthenocarpy. It also promotes ripening and aging of fruits by upregulating and downregulating many gene elements related to ethylene, anthocyanins, flavonoids, cell wall enzymes, senescence, carbohydrate metabolism. Melatonin has the potential to serve as a natural postharvest alternative for enhancing postharvest quality, reducing the incidence of spoilage, and increasing the antioxidant potential of fruits by either increasing or maintaining bioactive compounds.

**Author Contributions:** Conceptualization, S.M. and E.S. (Erni Suminar); methodology, S.M., A.H.A., C.A.S., E.S. (Erik Setiawan) and A.S.B.; validation, S.M.; investigation, A.H.A., C.A.S., E.S (Erik Setiawan), and A.S.B.; resources, S.M., A.H.A., C.A.S., E.S (Erik Setiawan), and A.S.B.; writing—original draft preparation, S.M., A.H.A., C.A.S., E.S. (Erik Setiawan) and A.S.B.; writing—review and editing, S.M. and E.S. (Erni Suminar); visualization, S.M.; supervision, S.M.; project administration, S.M.; funding acquisition, S.M. All authors have read and agreed to the published version of the manuscript.

**Funding:** This research received no external funding.

**Data Availability Statement:** The data are included in the article.

**Acknowledgments:** We thank all of the members of our laboratory for helpful discussions throughout the work. We also thank Universitas Padjadjaran, Indonesia, for supporting the APC.

**Conflicts of Interest:** The authors declare no conflict of interest.

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