Regulatory Role of Melatonin in Flowering, Fruit Setting, and Ripening

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Abstract

Role of melatonin in vertebrates and plant growth and metabolism is well evident now. Melatonin is a non-toxic biological substance (N-acetyl-5-methoxytryptamine), synthesized naturally in the pineal gland of animals, whereas tissues (leaves, fruits, stems, roots, and seeds) of various plant parts. It plays a crucial role in the plant immune response along with other important chemicals like nitric oxide and various hormones like salicylic acid and jasmonic acid. Plant releases melatonin in response to both abiotic (elevated soil salinity, variations in temperature, drought, toxins, etc.) and biotic (fungal infection) stress conditions. In fruit and vegetable crops, melatonin is widely involved in physiological and biological processes at both pre-harvest and postharvest stage. These

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include plant growth, flowering, germination of pollen, enhance fruit production, rhizogenesis, senescence, and postharvest preservation. Apart from this, it plays an important role in improving cell–water relationship, photosynthesis, primary and secondary metabolism, CO_2 uptake, etc. It is also reported that melatonin is associated with majority of other plant hormones. Melatonin triggers the production of pathogenesis-related proteins, which bolster the plant's defence against pathogens, and antioxidant enzymes, which help neutralize harmful reactive oxygen species produced during stress. This chapter highlights the regulatory role of melatonin in the context of its pre-harvest (flower development, flowering, and fruit setting) as well as postharvest influence (fruit development and fruit ripening) on fruit and vegetables.

Keywords

Melatonin · Biological substance · Flowering · Fruit setting · Parthenocarpy · Fruit ripening

4.1 Introduction

In the living kingdom, melatonin is a widely distributed biomolecule having pleiotropic effects. Melatonin (N-acetyl-5-methoxytryptamine) is an indoleamine that shows structural similarity with other indoleamine compounds such as auxin, tryptophan, serotonin, and others. Melatonin is a pervasive biomolecule with a wide range of effects throughout the living kingdom, and it belongs to the group of indoleamine compounds. Its chemical name is N-acetyl-5-methoxytryptamine and shares a structural similarity with other important indoleamine compounds, such as tryptophan, auxin, and serotonin (a neurotransmitter and hormone in animals) (Sharif et al. 2022). Other than its structural similarity with other indole amine compounds, melatonin and auxin share a common precursor, tryptophan, and have a similar biosynthetic pathway (Gao et al. 2022). It is produced through the catalysis of tryptamine-5 hydroxylase, N-acetyl-5 hydroxytryptamine-methyltransferase tryptophan decarboxylase, and 5-hydroxy tryptamine-N-acetyltransferase, which results in the catabolization to 2-hydroxymelatonin (Nawaz et al. 2020). It usually occurs in the mitochondria and chloroplast of the leaves and roots of plants and is then transmitted to the flowers, meristem, and fruits (Wang et al. 2016; Nawaz et al. 2020). Melatonin has a profound impact on various physiological systems in both animals and plants such as sleep, circadian rhythms, the immune system, and body temperature (Manzoor et al. 2023). Additionally, it plays a very important role in various cellular processes as an antioxidant and has outstanding free radical scavenger activities both in vitro and in vivo (Sun et al. 2021; Ze et al. 2021; Ahammed and Li 2022). The role of melatonin as a plant growth regulator (PGR) in seed germination, root development, blooming, fruit setting, and ripening has been extensively studied in plants (Gao et al. 2022). Additionally, postharvest fruit's quality and shelf life can both be enhanced by melatonin (Ze et al. 2021).

Its capacity to provide resistance to many biotic and abiotic stressors, including microbial infections (fungi, bacteria, and viruses) (Zhang et al. 2017), cold (Jayarajan and Sharma 2021; Li et al. 2021), salinity, drought, and high temperatures (Moustafa-Farag et al. 2020) has been noticed. Melatonin has been shown in recent research to be effective in lowering the accumulation of heavy metals and pesticide residues in foods (Yan et al. 2019; Gao et al. 2022). These qualities make melatonin a compelling contender to increase the development of horticulture crops and ensuring food safety (Nawaz et al. 2020).

This chapter highlights the regulatory role of melatonin in context to its pre-harvest (development of flower, flowering, and fruit setting) as well as postharvest influence (fruit development and fruit ripening) on fruit and vegetables.

4.2 Regulatory Role of Melatonin in Flowering

4.2.1 Influence of Melatonin on Flowering of Crops

Melatonin accumulation in flowers serves a protective role, shielding the various reproductive tissues from several abiotic stresses like more light intensity and low temperatures and this protection is especially crucial during the vulnerable stages of a plant's life cycle (Park et al. 2013; Tiwari et al. 2021). The timing of harvest and the yield are greatly impacted by flowering. Flowering has a big impact on when to harvest and how much of a yield forms (Gao et al. 2022). When fruit trees are in the late spring flowering stage, they frequently encounter cold spells. In order to prevent blossoms on fruit trees from being damaged by freezing during these cold spells, flowering time should be postponed (Gao et al. 2022). Melatonin levels in apple trees always dropped when the trees started to blossom, according to Zhang et al. (2019). Prior to the germination of the mixed bud, 'Fuji' apple trees were treated with various conc. of melatonin, i.e., 0, 20, 200, and 1000 μM. Melatonin treatments at 20 and 200 μM delayed flowering in apple by 2 days in compared to the control, while high conc., i.e., 1000-μM, postponed flowering by 3 days (Mou et al. 2022). Melatonin exogenously applied at 20 and 200 μM enhanced flowering rates by 63.8 and 72.7%, respectively, over the control (57.4% blooming rate). Transgenic *Oryza sativa* plants were able to prolong blooming by 1 week when endogenous melatonin levels were high (Mou et al. 2022). Previous reports on the potential role of melatonin in regulation of flowering used the short-day plant *Chenopodium rubrum*. These studies revealed that flower induction was reduced by an average of 40–50% when high amounts of melatonin were used between 2 h before and 2 h after the start of the inductive dark phase (Kolar et al. 2003; Park 2011). CGP-52608 (1-[3-allyl-4-oxothiazolidine-2-ylidene]-4-methyl-thiosemicarbazone) was discovered to be a potent melatonin antagonist that effectively prevents flower induction. Melatonin application, however, had no impact on the flowering stage, indicating that it controlled a mechanism taking place before the flowers changed. In a parallel experiment, melatonin concentrations of 100 or 500 μM affected anthesis, leaf and rosette counts, and flowering in the long-day plant (LDP) *Arabidopsis thaliana.*

Similar research in the long-day plant *Arabidopsis thaliana* revealed that flowering was somewhat postponed in plants when they were treated with various conc. of melatonin, i.e., 100 or 500 μM, which had an effect on anthesis, number of leaves, and rosettes (Arnao and Hernandez-Ruiz 2020). Devil's trumpet (*Datura metel*), a highly addictive plant, produced the most melatonin as its flower buds grew, which is utilized in natural medicine all over the world. This finding suggests melatonin had a protective effect on reproductive tissue (Murch et al. 2009; Arnao and Hernandez-Ruiz 2020).

4.2.2 Role of Melatonin on the Yield Potential of Crops by Influencing Flowering

The melatonin accumulation in flowers provides protection to the reproductive organs from different abiotic stresses, like more light intensity and cold stress, at the most crucial and vulnerable stages of a plant's life cycle (Murch et al. 2009; Aghdam et al. 2019; Sun et al. 2021). A field-grown rice plant's melatonin levels were measured at the plant's pre-flowering, flowering, and post-flowering stages of reproduction. The panicle (flower) was discovered to have a sixfold higher rate of melatonin production than the flag leaves. Melatonin may be implicated in floral development as this induction coincided with the induction of melatonin biosynthesis enzymes (Park et al. 2013). According to the studies, in Arabidopsis, which lacks ascorbic acid, melatonin may help regulate time of flowering in a manner comparable to that of ascorbic acid. The scientists speculate that melatonin may regulate time of flowering in a same manner to how ascorbic acid does in the ascorbic acid-deficient plant Arabidopsis. An ascorbic acid-rich mutant had delayed flowering, whereas the Arabidopsis mutant had an early flowering phenotype (Fig. 4.1). Levels of ascorbic acid and probable hormonal and changes in metabolites have been linked, even if the results do not conclusively correlate flowering to the antioxidant status of tissues (Kotchoni et al. 2009). Additionally, phenotypes of melatonin-rich transgenic plants overexpressing sheep serotonin N-acetyltransferase (SNAT) exhibited a biomass increase of twice and an endogenous melatonin content that was three times higher than that of wild-type plants in rice plants grown in field conditions. Flowering took a week longer in the transgenic strains. The grain yield of the transgenic lines with high melatonin levels was on average 33% lower. This opens up new opportunities to use melatonin to boost crop yields by regulating flowering time and extending the harvest season (Gao et al. 2022).

In *Arabidopsis thaliana,* the ambient temperature, photoperiod, gibberellic acid, age pathways, vernalization, and autonomous are among the at least 6 distinct signalling flowering pathways. A MADS box-containing transcription factors (TFs) that bind to the promoters of flowering locus T (FT) and suppressor of overexpression of ConstanS1 (SOC1) to inhibit floral transition are encoded by the crucial autonomous pathway gene flowering locus C (FLC). Both squamosa promoter-binding protein-like (SPL) and FLC, which act as GA signalling antagonists, encode for proteins connected to the DELLA proteins (Fig. 4.2).

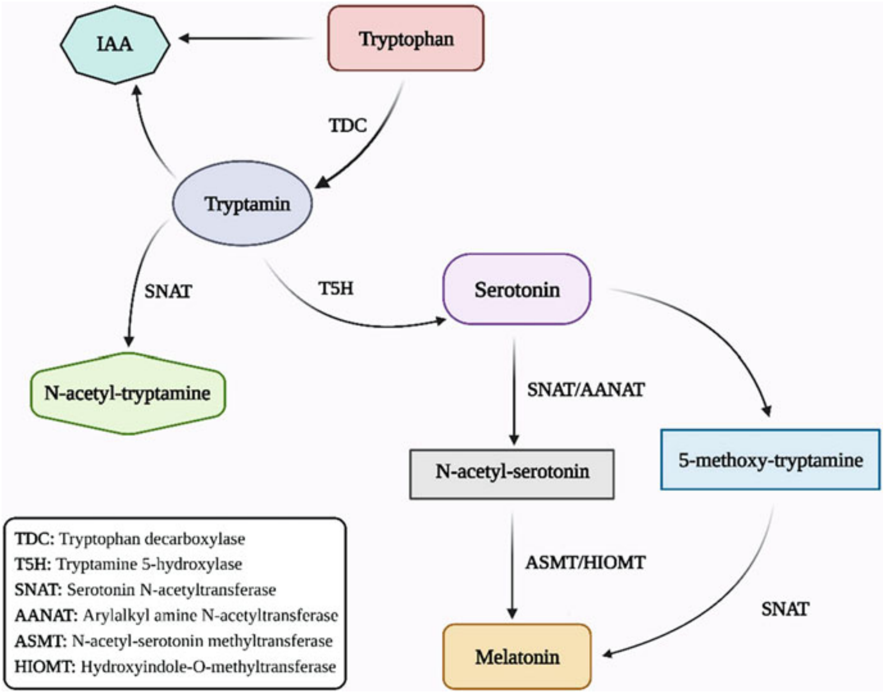

Fig. 4.1 Schematic pathway of melatonin expression

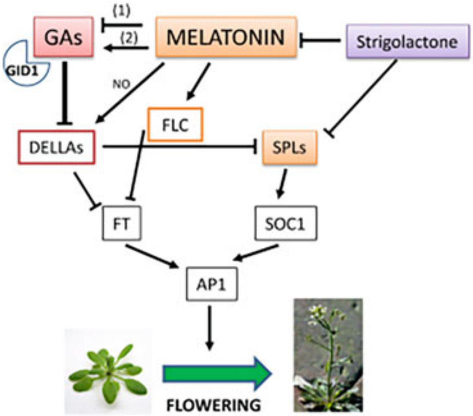

Fig. 4.2 Melatonin role in flowering. Melatonin slows down Arabidopsis flowering through controlling the expression of FLC, GA, and DELLA. Strigolactone works by impairing the production, signalling, and SPLs of melatonin, resulting in early flowering. *FLC* flowering locus C (core repressor of vernalization), *SOC1* suppressor of overexpression of Constans 1, *GID1* GA receptor, *SPL* Squamosa promoter-binding protein-like, *FT* flowering locus T, *DELLAs* transcriptional repressors of GA responses, *API1* Apetala1

Researchers have described the relationships between phytomelatonin and other phytohormones (Khan et al. 2022). According to the scientists, strigolactones (SLs) function upstream of melatonin to postpone flowering because they activate FLC when the amount of melatonin in plant tissues exceeds a particular threshold. It is interesting to note that NO, whose synthesis is melatonin-stimulated, raises DELLA protein levels and prevents the transition of flower in Arabidopsis (Sun et al. 2021). Shi et al. (2016) initially identified the direct relationship between floral transition and melatonin and hypothesized that NO may have a role in the melatonin-stimulated stabilization of DELLA proteins, which results in a definite late flowering.

4.3 Regulatory Role of Melatonin in Fruit Setting

4.3.1 Melatonin Influences Fruit Setting

The crucial role of melatonin in fruit set and development has been the subject of numerous investigations (Arnao and Hernandez-Ruiz 2020). Around 10–15 days after anthesis in the developing ovule, when the early stages of seed development were taking place, melatonin levels in *Datura metel* fruits significantly increased over the course of fruit growth (Park 2011). Veraison, which is marked by softening of berries and a quick rise in weight of seed, is when wine grapes produce the most melatonin. According to these results, the rise in melatonin levels during a specific stage of fruit development may act as a transitional signal for seed growth (Murch et al. 2010). The greatest contents of melatonin were identified during II stage of fruit development of cherry *(Prunus avium*), growth of embryo, and lignification of endocarp, which has also been connected to reactive oxygen species generation in “watery” seeds, suggesting that rapid biosynthesis of melatonin increased by oxidative stress (Arnao and Hernandez-Ruiz 2020). More concentration of melatonin has been found in the flowers, as well as immature and mature red fruits and seeds of two pepper (*Capsicum annuum*) cultivars. The amount of melatonin in both fruit and seeds considerably enhanced as the fruit and, consequently, seeds developed. The authors find that the higher levels of melatonin found in both cultivars’ reproductive organs, mature fruits, and seedlings at the cotyledon stage are evidence that these organs are being protected from adverse environmental conditions due to the higher levels of melatonin (Korkmaz et al. 2014). Micro-Tom tomato fruits have been found to contain melatonin throughout the fruit’s growth, with the fruit’s highest concentration occurring in the final stages, when the fruits take on a pink-red tint (Arnao and Hernandez-Ruiz 2020). The fact that seeds of tomato were containing maximum concentration of melatonin is interesting because it shows that melatonin in seeds may have a protective function, as was previously suggested. The highest values were seen during uninucleate development in *Hypericum perforatum.* According to Murch and Saxena (2002), isolated anthers had a better regeneration capability when melatonin levels were high. The expression of melatonin biosynthesis genes is perfectly synchronized with melatonin production in the growth of red Fuji apple fruits (*Malus domestica*). Malondialdehyde, a byproduct of lipid peroxidation, and the amount of melatonin in fruits showed an inverse association. Two significant melatonin peaks emerged during fruit development, which coincided with the fruits' rapid growth and an increase in respiration and ROS (Lei et al. 2013). In a study of tomato fruits, serotonin content, a precursor to melatonin, increased during fruit development in all fruit tissues (mesocarp, exocarp, placenta, columella, seed and jelly), reaching a maximum in the completely ripe stage (Arnao and Hernandez-Ruiz 2020). In comparison to leaves, stems, or flower heads, mature hemp (Cannabis sativa) plant seeds contain 4–10 times more melatonin (Allegrone et al. 2019). In any event, it is still not apparent if melatonin peaks are a sign of fruit growth or a defence mechanism to keep fruits and seeds' proper redox status while they are developing.

4.3.2 Melatonin Influences Fruit Development and Parthenocarpy

The development of fruit without fertilization of ovule is known as parthenocarpy and can occur naturally or artificially. Auxin and gibberellins, two plant hormones, can cause parthenocarpy in a variety of horticulture species (Srivastava and Handa 2005). Melatonin stimulates parthenocarpy in the Starkrimson pear (*Pyrus communis*) by boosting GA_3 and GA_4 production, resulting in development of fruits that resemble those produced by hand pollination through fruit cell proliferation and enlargement of mesocarp (Liu et al. 2018a). Exogenous melatonin treatment caused the seeds of the fruit to develop abnormally and abortion during fruit setting. According to the research, the fruit shape index dramatically increased, the transverse diameter of the fruit dropped, and the longitudinal diameter definitely increased, all effects that are identical to those of GA treatment (Arnao and Hernandez-Ruiz 2020). The outcome of this research revealed that the ovaries' GA_3 and GA_4 levels enhanced, the fruit shape index raised noticeably, the transverse diameter of the fruit reduced, and the longitudinal diameter obviously widen, all effects that were identical to those of GA application. Melatonin significantly raised the level of active GAs by upregulating GA20ox (which creates active GAs) and downregulating GA2ox (which produces inactive GAs). Comparatively, the IAA content decreased after pollination compared to the control, and neither the IAA content nor the number of seed cell layers in the ovary increased following melatonin application. These findings conflict with those obtained using eggplant parthenocarpy induced by IAA (Arnao and Hernandez-Ruiz 2020). Melatonin application had little effect on auxin-signalling-related genes, demonstrating that IAA is not a significant contributor to pear parthenocarpy. Genes associated with photosystems I and II, carbohydrates, and chlorophyll showed increased expression following melatonin application. The number of genes connected to the cell cycle and growth of cell was altered by treatment of melatonin, according to transcriptome data. Plant cyclins and expansins perform crucial functions in plant development and cell division (Choi et al. 2006).

4.4 Regulatory Role of Melatonin in Fruit Ripening and Senescence

4.4.1 Postharvest Losses in Fruit and Vegetables Due to Improper Ripening and Senescence

The postharvest losses occur approximately 20–40% in various fruits and vegetables (Prasad et al. 2018a), which takes place at several stages of postharvest handling, i.e., fruit characteristics (Saroj and Prasad 2023; Prasad et al. 2020), harvesting (Prasad et al. 2019), transportation, storage (Prasad et al. 2016), marketing (Prasad et al. 2018a, 2022a), and ripening/senescence management (Prasad et al. 2020). Hence, it is crucial to use postharvest management techniques that are both effective and efficient when managing fresh horticultural produce (Prasad et al. 2022a, b). These include proper harvesting method (Prasad et al. 2019), pre-cooling, sorting, grading, packaging, and storage (Prasad and Sharma 2018; Prasad et al. 2022b). Many postharvest techniques have been proposed to mitigate chilling injury, physiological disorders (Prasad and Sharma 2016), minimizing decay (Prasad et al. 2016), thereby control ripening which ultimately enhances shelf life of the produce (Prasad and Sharma 2018; Prasad et al. 2018b). Melatonin is an emerging postharvest molecule in this context (Jayarajan and Sharma 2021).

4.4.2 Regulatory Role of Melatonin in Fruit Ripening

Numerous researches have revealed that exogenous melatonin increased the amount of natural melatonin in fruits after harvesting. The level of endogenous melatonin in banana fruit was increased by exogenous melatonin, and similar results were shown in litchi (*Litchi chinensis*), sweet cherries and tomato (Wang et al. 2020). This effect is brought about by melatonin activating the shikimic acid pathway, which causes a buildup of aromatic amino acids and, in turn, increases the synthesis of melatonin (Aghdam et al. 2019; Wang et al. 2020). Fruit firmness was retained in pear, banana, and mango after exogenous melatonin application because the activities of enzymes involved in starch and cell wall degradation were blocked (Ze et al. 2021). Fruit colour was also considerably delayed in mango, kiwifruit, and banana. After melatonin treatment, the qualitative characteristics of various fruits, such as soluble sugars, carotenes, weight loss, respiration rate, organic acids, volatile aroma, and titratable acidity can be maintained to a large extent (Ze et al. 2021).

The fundamental factor controlling fruit ripening is ethylene production, but ethylene and antioxidants such as organic acids and phenolic substances also limit senescence. According to the literature, melatonin may have some influence over the speed at which fruit ripens, although the exact mechanism by which it does this is yet unknown. Melatonin when applied externally, positively regulated production of ethylene and signalling, which in turn stimulated the ripening of tomato after harvest and brought about biochemical changes such as volatiles biosynthesis, production of lycopene and carotenoid and cell wall breakdown (Jayarajan and Sharma 2021)

Table 4.1 Effect of melatonin treatment on fruit ripening

Fruit	Melatonin concentration	Effect	References
Tomato	50 μM	Upregulating the expression of the gene for colour development, ethylene production improved postharvest shelf life and encouraged ripening	Jayarajan and Sharma (2021)
‘Moldova’ grape	100 μM	Enhanced ripening via controlling abscisic acid signalling	Jayarajan and Sharma (2021)
Banana	200, 500 μM	Postponed the ripening after harvest. By controlling the expression of the MaACO1 and MaACS1 genes, endogenous amount of melatonin was increased, which in turn decreased the generation of ethylene	Hu et al. (2017)
Strawberry	100 μM	Enhanced activities of antioxidants enzymes, phenolics, total antioxidant	Aghdam and Fard (2017) and Liu et al. (2018b)
Peach	0.1 mM, 10 min	Delayed ripening	Gao et al. (2016)
Jujubes	100 μM	Application of melatonin slowed down colour variations and encouraged the synthesis of phenolic chemicals	Wang et al. (2021)

Musa acuminata 1-aminocyclopropane-1-carboxylic acid oxidase 1, *MaACS1 Musa acuminata* 1-aminocyclopropane-1-carboxylic acid synthase 1

(Table 4.1). Exogenous melatonin lowered the production of ROS in a variety of fruits and hence delayed fruit ripening by boosting the enzymatic activity and gene expression of antioxidant enzymes (Onik et al. 2020; Wang et al. 2020). At a dosage of 100 μM, melatonin significantly enhanced the contents of ABA, H_2O_2, and production of ethylene and accelerated the ripening of ‘Moldova’ fruit (Table 4.1). It is interesting to note that exogenous melatonin also increased endogenous melatonin levels, which decreased the synthesis of ethylene through controlling the expression of MaACS1 and MaACO1 genes and postponed abrupt changes in qualitative characteristics (Jayarajan and Sharma 2021). Hu et al. (2017) revealed how melatonin affected the quality and ripening of various banana types with various ripening times. They discovered that exogenous melatonin treatment considerably slowed postharvest ripening in all varieties at concentrations of 200 or 500 μM. Prunus domestica plums were submerged in a different concentrations of melatonin solutions at 1 °C for 40 days and observed that the 0.1- and 1-mM solutions of melatonin worked best for halting weight loss and preserving better firmness. Arnao and Hernandez-Ruiz (2020) examined that, melatonin-treated plums had higher ascorbic acid concentration, antioxidant activity and total phenolic content, than the control. Additionally, strawberries (Aghdam and Fard 2017; Liu et al. 2018b), grapes (Meng et al. 2015), peaches (Gao et al. 2016), and jujubes (Wang et al. 2021) have all benefited from melatonin treatment in terms of postharvest quality and life.

4.4.3 Regulatory Role of Melatonin in Fruit Senescence

By blocking biosynthesis of ethylene through nitric oxide regulation, inhibiting biosynthesis of ABA, chlorophyll degradation, increasing ascorbic acid, total phenol content, controlling membrane lipid, energy metabolism, melatonin showed good performance in postponing senescence of fruit and vegetable (Wang et al. 2020; Wu et al. 2021). Broccoli heads treated with melatonin (100 L/L) displayed increased antioxidant activity, greater vitamin C and total carotenoids protection, and higher antioxidant activity. According to Jayarajan and Sharma (2021), it also prevented broccoli from yellowing by 4 days compared to the control, which is a major obstacle to broccoli marketing. Similar to this, melatonin-treated pears showed decreased production of ethylene, improved firmness, reduced senescence, over the course of storage compared to control fruits. In three different cultivars on pear, i.e., “Starkimson,” “Abbe Fetel,” and “Red Anjou,” the treatment blocked the expression of the genes PcACS1 and PcACO1 which are responsible for ethylene biosynthesis as well as gene which is responsible for the cell wall degradation (PcPG). Aside from that, the treated pear fruits had a high AOX capacity and showed no signs of water core or core browning (Zhai et al. 2018).

4.5 Conclusion

Melatonin may actively influence the growth of flowers and fruits, as well as fruit set, ripening, and senescence. It has been suggested that stresses like light and temperature can prevent flowering. The direct link between the stimulation of melatonin producing enzymes and melatonin peak(s), however, raises the possibility that it plays a very important role in flower development. The most important function of melatonin during fruit set is its capacity to trigger parthenocarpy. Ripening of fruit is accelerated and their senescence is postponed by melatonin. The potential use of melatonin to delay flowering needs additional research in terms of future prospects. More information on the interactions between melatonin and phytohormones is critical with regard to the fruit set.

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