Melatonin as Plant Immune Booster: Pros and Cons

Kinjal Mondal[1]* and Ayush G Jain[2]
[1]Department of Molecular Biology and Biotechnology, Maharana Pratap University of Agriculture and Technology, Udaipur-313001 (Raj.), India
[2]Department of Environmental Biotechnology, Gujarat Biotechnology University, Gandhinagar- 382355 (Guj.), India
*Corresponding Author: kinjal.mondal1234@gmail.com

Melatonin (N-acetyl-5-methoxytryptamine) is ubiquitously spread across all kingdoms of life and is prominently regarded as a sleep regulator in humans. In plants, melatonin has principally been considered as an antioxidant, controlling the pool of reactive oxygen and nitrogen species. It has been extensively studied for its function in a variety of physiological processes, including growth, roots, photosynthesis, fruit maturity, and protection against abiotic and biotic stresses (Arnao and Hernández-Ruiz, 2019). Melatonin biosynthetic genes present in *Rhodospirillum rubrum*, a purple non-sulphur photosynthetic bacteria that evolved into mitochondria in eukaryotes and cyanobacteria that became chloroplasts, are thought to have been progressively transferred to other organisms over time (Kanwar *et al.*, 2018). In animals, melatonin is synthesized from serotonin, which is produced from tryptophan in two steps involving tryptophan 5-hydroxylase (Trp5H) and aromatic L-amino acid decarboxylase (AADC), where tryptophan hydroxylase acts as the rate-limiting enzyme. In contrast to animals, plants contain two organelles for the production of phytomelatonin, namely mitochondria and chloroplasts. Due to their respective roles in respiration and photosynthesis, mitochondria and chloroplasts are continually exposed to incessantly produced reactive oxygen species (ROS) under steady-state circumstances (Kanwar *et al.*, 2018). In light of this, the capacity of plants to synthesise phytomelatonin in two organelles stimulates the intense curiosity of plant scientists to comprehend how phytomelatonin and ROS interact throughout various activities in subcellular compartments. It has a significant role in regulating the gene expression of plant hormones, including those involved in the metabolism of indole-3-acetic acid, cytokinin, ethylene, gibberellin, and auxin carrier proteins. The pleiotropic role of melatonin in controlling the transcripts of many genes supports its critical role as a multi-regulatory chemical that designs many aspects of plant development. Most of the plant species in which the presence of melatonin has been reported belong to the families Rosaceae, Vitaceae, Poaceae, Apiaceae, and Brassicaceae (Murch and Erland, 2021).

Melatonin biosynthesis in plants

The integrity of melatonin biosynthesis in plants is merely influenced by the genotype, environmental factors (photoperiod, temperature), and stage of development. Evidence suggesting that melatonin in plants is produced from the aromatic amino acid tryptophan (Murch and Erland, 2021). Empirically, tryptophan is first converted to tryptamine through a decarboxylation reaction catalyzed by tryptophan decarboxylase (TDC). Tryptamine is then hydroxylated to serotonin (5HT; 5-hydroxytryptamine) by tryptamine-5-hydroxylase. While TDC is highly regulated in most plant species, the conversion of tryptamine to 5HT appears to occur rapidly and with little feedback or regulation, aside from competition for tryptamine, which also serves as a precursor for many secondary metabolic pathways. Biosynthesis of melatonin from 5HT occurs through two major intermediates, *i.e.,* (1) N-acetylserotonin (NAS), in a reaction catalyzed by serotonin N-acetyltransferase (SNAT), and/or (2) 5-methoxytryptamine (5-MT), in a reaction catalyzed by a caffeic acid-O-methyltransferase (COMT; **Figure 1**). SNAT can use tryptamine as a substrate for NAS production, skipping the need for production of 5HT, and can also catalyze the acetylation of 5- MT to form melatonin. Recently, a novel deacetylase enzyme, NAS-deacetylase (ASDAC), has been characterized that catalyzes the reverse reactions converting NAS to 5HT, or melatonin to 5-MT allowing for the possibility of interconversion between 5HT and melatonin (Lee *et al.,* 2018). The final step in this pathway includes methylation of NAS to melatonin catalyzed by the enzyme either NAS methyl transferase (ASMT), or COMT.

Melatonin biosynthesis has been shown to occur in both the chloroplast (Zheng *et al.*, 2017) and the mitochondria (Wang *et al.*, 2017) with some possible cytosolic involvement. Melatonin is metabolized to produce a number of important bioactive molecules in plants that can generally be grouped as: (a) products of oxidation reactions, (b) products of catabolism and (c) conjugates and derivatives (**Figure 1**). Nitroso-melatonin, N-acetyl-N-formyl-5-methoxykynuramine (AFMK) and N-acetyl-5-methoxykynuramine (AMK) are products of oxidation reactions as are several of the 5- MT derivatives. AFMK and AMK were the first melatonin metabolites described in plants and function as antioxidants with the capacity to quench reactive oxygen (ROS) and reactive nitrogen species (Schaefer and Hardeland, 2009). The levels of AFMK have also been found to vary in coordination with melatonin making it unlikely that melatonin is the primary precursor. With so many potential roles and interactions, further investigation of the functions of these metabolites and isomers is warranted. These future investigations should include not just quantification of these compounds but also aim to understand the roles of these metabolites in plant metabolism.

Melatonin boosts plant's innate immunity

A handful studies in the late 1990s related to plant melatonin research, has blossomed into a vibrant and active area of investigation. Melatonin has been found to play critical roles in mediating plant responses and development at every stage of the plant life cycle from pollen and embryo development through seed germination, vegetative growth and stress response (Murch and Erland, 2021). In-field

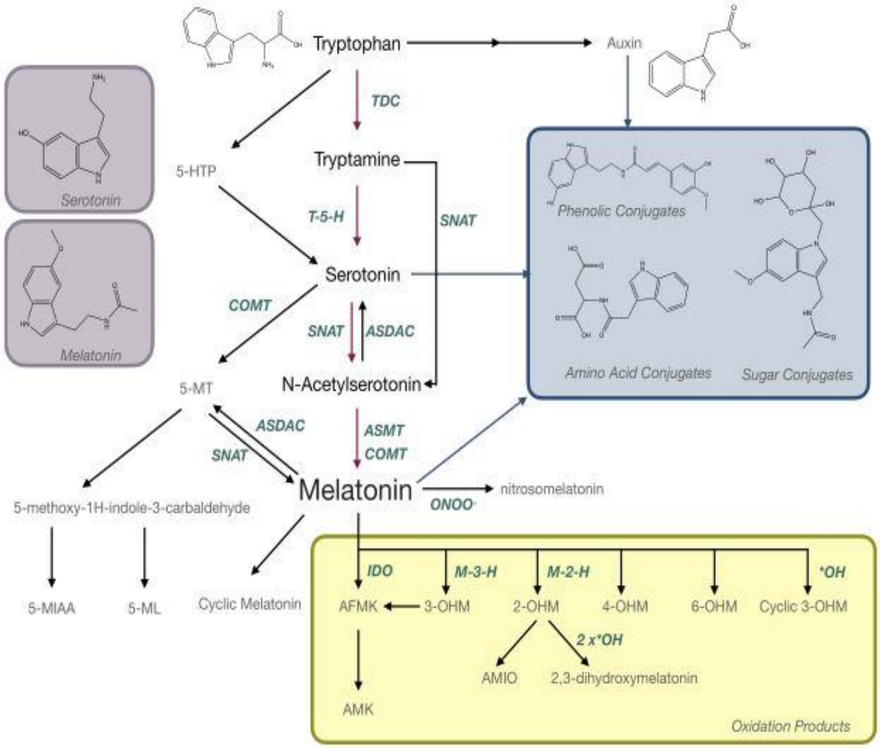

Figure 1. Biosynthesis and metabolism of melatonin in plants

investigations have significantly supported the possible role of melatonin on flower development, enhancing male to female ratio in vegetables (cucurbits), improvement of fruit setting, fruit development, parthenocarpy, fruit drop (especially in citrus, mango, guava, etc.), breaking seed and tuber dormancy, fruit quality (size, colour, nutraceutical value), seed development, fruit ripening and senescence (to improve postharvest life/shelf life of fruits, vegetables, and cut flowers). Root treatment of melatonin may help to improve the success ratio and initial root development and growth of crops which require nursery transplanting (rice, tomato, chilies, cabbage, cauliflower, eggplant etc). Recently, scientists have anticipated melatonin to have auxin like properties and its involvement with auxin remarkably promotes grafting and vascular connection establishment (Melnyk *et al.*, 2015). Keeping in mind the physiological, biochemical, and genetic and epigenetic actions of melatonin in multiple organisms, it seems melatonin may prove to be an important molecule to influence especially field crops, and may prove helpful in increasing crops yields and the nutraceutical value helping to address the food security issues around the world.

Melatonin for abiotic stress management

Several studies have revealed melatonin to regulate physiological functions of plants. Melatonin is now known to alter many plant characteristics including germination, seedling growth, alteration of flowering time, grain yields, and senescence (Byeon and Back, 2014). Melatonin as potential immune booster for plant system significantly involve in stress mitigation (Turk *et al.*, 2014). Exogenous application of melatonin (0.1µM) significantly alleviated the growth inhibition caused by elevated salinity; this enabled the plants to maintain their photosynthetic capacity (Arnao and Hernandez-Ruiz, 2019). Melatonin has also been found to be involved in the biosynthesis and catabolism of gibberellic (GA) and abscisic acids (ABA), respectively; it was shown to up-regulate ABA catabolism genes and down-regulate ABA biosynthesis genes resulting to a rapid reduction in ABA. At the same time, it positively up-regulated GA biosynthesis genes during the early stage of germination, which leads to better germination and better plant growth during the initial stages. Melatonin application enhanced tolerance to salt and drought stress in soybean, and upregulated the expression of genes that were inhibited by salt stress (Wei *et al.*, 2015). Recently, melatonin has been reported to provide protection against butafenacil (a singlet oxygen-generating herbicide), in the study in question, melatonin-rich transgenic rice plants exhibited lower levels of malondialdehyde and hydrogen peroxide. These plants also exhibited elevated superoxide dismutase and catalase activities compared to control plants (Park *et al.*, 2013).

Melatonin for diseases and pest control

In addition to many other positive functions in plants, exogenous application of melatonin (0.05–0.5 mM) improved resistance against one of the most severe diseases, Marssonina apple blotch (fungal diseases caused by *Diplocarpon mali*); this involved modulating the activities of antioxidant enzymes and plant defense related enzymes. In a recent study, the application of 10 µM melatonin on to *Arabidopsis* induced pathogenesis-related genes which further supports the idea that melatonin may be a defense signalling molecule in plants against pathogens (Lee *et al.*, 2018). Certainly, the possibility that melatonin may help in controlling plant diseases (fungal, bacterial, viral, viroides) should not be overlooked and requires further investigation. Moreover, melatonin (an indoleamine) is believed to have a role against insect attack, and could prove to be a potential means to control or reduce insect feeding on commercial crops, as insects cause huge losses (billions of dollars) and substantially reduce crops yields.

Conclusion

The abundance of information on melatonin indicates that it is a crucial signalling molecule and that it is essential for supporting the immune system of plants against both biotic and abiotic stress factors. Melatonin works as a key regulator of gene expression and interacts with other phytohormones in a variety of plant biological processes, both under favourable and unfavourable environmental conditions. The melatonin generated by the body, nevertheless, is occasionally insufficient to handle challenging situations. As a result, exogenous melatonin and other methods are used to raise endogenous melatonin levels in order to maintain plant immunity and normal development capability. Underpinning this information regarding the plant immune resiliency is believed undeniably to open new paradigms of phytomelatonin potential to architect the plant growth under capricious environments, especially for sustainable agriculture.

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