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REVIEW

Melatonin as an Endogenous Plant Regulatory Signal: Debates and Perspectives

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Abstract Melatonin (*N*-acetyl-5-methoxytryptamine) exists in plants, although it is commonly known as a neurohormone in animals. Indeed, the melatonin level is very high in some medicinal plants and changes developmental stage specifically, indicating that it plays specific physiological roles. Plant melatonin may play unique roles in plants as well as similar functions in animals. Furthermore, exogenously applied melatonin affects developmental processes during both vegetative and reproductive growth. In this study, current knowledge regarding plant melatonin is reviewed and its implications and problems are discussed.

Keywords Melatonin (*N*-acetyl-5-methoxytryptamine) · IAA · Plant development · Oxidative stress

Introduction

Melatonin (*N*-acetyl-5-methoxytryptamine) has long been known as an animal hormone that is involved in daily cycles. In mammals, the blood level of melatonin is high at night, regardless of whether the animal is active or not (Challet 2007). Although melatonin was initially identified as the nocturnal signal, it has been found to have diverse effects in animal systems (Boutin et al. 2005). In addition to the use of melatonin to cure sleep disease (Ferguson et al. 2010), many efforts have been made to control pain (Ambriz-Tututi et al. 2009) and treat cancer with melatonin (Srinivasan et al. 2008). Melatonin also shows antioxidative activities (Rodriguez et al. 2004) and plays regulatory roles in metabolism (Korkmaz et al. 2009).

However, the distribution of melatonin is not limited to animals. Indeed, melatonin is found in diatoms, fungi, algae, ferns, and higher plants (Hardeland and Poeggeler 2003), indicating that it was selected as a regulatory substance during the early stages of the evolution of life. Although the physiological roles of melatonin in organisms other than animals are still uncertain, there is evidence indicating that it plays physiological roles in plants (Table 1). Specifically, melatonin may carry out similar functions in plants as observed in animals, namely, acting as a daily rhythm regulator and antioxidative agent. Conversely, plant melatonin may act as a growth-regulatory signal like auxin or as a regulator of reproductive development (Kim et al. 2007).

Distribution and Contents of Melatonin in Plants

Since melatonin was first identified in vascular plants (Dubbels et al. 1995), its distribution has been established in more than 20 families of angiosperms including both monocot and dicot plants (Murch and Saxena 2002a; Paredes et al. 2009; Posmyk and Janas 2009); however, melatonin has not yet been identified in gymposperms. Further, exceptionally high contents of melatonin have been reported in some medicinal plants (Chen et al. 2003). However, high levels may not be important per se because the content of melatonin varies among plant organs depending on the given physiological and environmental conditions. In lupin and barley, melatonin was detected in both the shoots and roots and altered by light conditions (Hernández-Ruiz and Arnao 2008a). In addition, the melatonin level in tomato changed following developmental progress, indicating a probable

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Table 1 Effects of exogenously applied melatonin or changes in melatonin contents implicating the physiological roles of melatonin in plants

Physiology	Effects or characteristic changes of melatonin
Vegetative development	Increase of germination rate
	Stimulation of coleoptile elongation
	Promotion of lateral leaflet generation
	Inhibition of root elongation
	Adventitious and lateral root formation in regeneration system
Reproductive development	Influence on flowering
	Stage-specific accumulation during fruit development
	High accumulation in maturating seeds
Senescence	Preservation of chlorophyll during senescence
	Attenuation of apoptosis
Stress resistance	Protective effects against oxidative stress
	Resistance against cold stress
	Tolerance to photodamage and UV-B

physiological function (Okazaki and Ezura 2009). Nocturnal increases of melatonin were detected in *Chenopodium rubrum* (Kolář et al. 1997; Wolf et al. 2001). Many species of plants also accumulated melatonin in seeds, suggesting that it plays a role in protection of the embryo (Manchester et al. 2000). Current trends in analytical studies of melatonin are to trace changes in melatonin in a specific organ under a specific condition to verify physiological functions.

Biosynthesis

Melatonin is secreted from the pineal gland, after which it circulates in the animal system. Regulation of the level of melatonin in blood is achieved mainly by modulation of its biosynthesis. Tryptophan, which is the starting material for melatonin biosynthesis, is converted to 5-hydroxytryptophan in animals (Fig. 1), after which it is decarboxylated to serotonin and further modified to melatonin via two steps. The reaction step converting 5-hydroxytryptamine to *N*-acetylserotonin catalyzed by serotonin-*N*-acetyltransferase (AANAT) has long been thought of as the rate-limiting step (Boutin et al. 2005). However, new evidence indicates that the next step in which *N*-acetylserotonin is converted to melatonin catalyzed by hydroxyindole-*O*-methyltransferase (HIOMT) may be the rate-limiting step (Ribelayga et al. 2000; Ceinos et al. 2004; Johnston et al. 2004; Liu and Borjigin 2005).

It has been suggested that plant melatonin is synthesized *in planta*, as other hormones, and that this likely occurs via similar biosynthetic pathways as in animals (Fig. 1). Murch et al. (2000) fed radio-labeled tryptophan to regenerated plantlets of St. John's wort (*Hypericum perforatum*), which plant had been known to have melatonin in high amount. The radioactivity was recovered from isolated melatonin, as well as in IAA and serotonin, indicating that tryptophan is the starting material of melatonin synthesis in plants. Another experiment using water hyacinth (*Eichhornia crassipes*) revealed increased melatonin levels after feeding of tryptophan (Tan et al. 2007a). Feeding tryptophan to the leaf sections of *Viola* plants had no effect on the level of melatonin. However, feeding tryptamine, the next substance produced from tryptophan (Fig. 1), increased the level of melatonin, which supports the hypothesized melatonin biosynthetic pathway from tryptophan (Kim et al. 2011). In rice, senescence-induced serotonin accumulation was

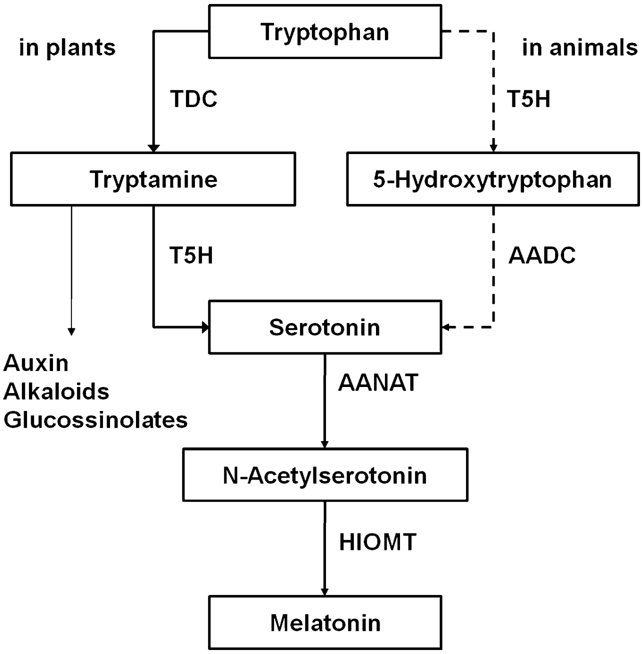

Fig. 1 Proposed biosynthetic pathway of melatonin biosynthesis. Tryptophan decarboxylase (TDC) appears to be rate-limiting in plants, while hydroxyindole-*O*-methyltransferase (HIOMT) is rate-limiting in animals. *T5H* tryptophan-5-hydroxylase, *AADC* aromatic-L-amino-acid decarboxylase, *AANAT* serotonin-*N*-acetyltransferase

correlated with the expression of tryptophan decarboxylase (TDC), and a transgenic rice line with suppressed TDC expression by RNAi produced less serotonin (Kang et al. 2009). Recently, the AANAT gene was cloned in rice and its activity was confirmed (Kang et al. 2011), demonstrating that the hypothesized biosynthetic pathway of melatonin is functional in rice. This group suggested that the step catalyzed by TDC would be the rate-limiting step (Kang et al. 2008), which differs from the animal pathway. In animals, decarboxylation is catalyzed by aromatic-L-amino-acid decarboxylase (AADC) after tryptophan is hydroxylated at C5 (Boutin et al. 2005). Evidence collected from other plants to date is still fragmented and incomplete. Additionally, it is unclear whether the postulated biosynthetic pathway in plants is ubiquitous or not.

The regulation of biosynthesis is even more unclear. It has been reported that UV-B increased the melatonin level in the roots of *Glycyrrhiza uralensis* (Afreen et al. 2006). Furthermore, in water hyacinth, the melatonin level was higher under sunlight than that under artificial light (Tan et al. 2007a). In contrast, the daily cycle of melatonin in *C. rubrum* showed that the level of melatonin was high in the dark (Kolář et al. 1997). Overall, more studies are needed to understand the diverse modes of melatonin regulation.

Uptake and Transport

Because melatonin circulates in animal without any hindrance through any route and can be easily taken up by cells regardless of developmental barriers (Reiter, 2001), it has also been assumed that similar uptake of melatonin occurs in plants. Recently, there has been evidence of melatonin uptake in plants. Specifically, melatonin (5 μM) applied to the growth medium for water hyacinth for 5 days was detected in the leaf extract during HPLC analysis (Tan et al. 2007a). When the cotyledon of lupin was imbibed with various concentrations (1 nM–1 μM) of melatonin, accumulation of melatonin increased in a concentration-dependent manner (Hernández-Ruiz and Arnao 2008b). The concentration-dependent uptake of melatonin was also observed in sections of barley leaves (Arnao and Hernández-Ruiz 2009b). Furthermore, the concentrations of melatonin applied to barley leaf sections were higher (0.1 μM–1 mM) than those used in previous studies and the saturation of uptake was not observed (Arnao and Hernández-Ruiz 2009b; Yoon and Park, unpublished data). Although the structurally related plant hormone auxin is transported by saturable uptake carriers (Bennett et al. 1996), current data do not predict any saturable carrier of melatonin.

There have been no detailed studies of the transport of melatonin in plants to date. However, the absorbed melatonin in the root system is likely transported to other organs because melatonin exogenously applied to the growth medium was detected in leaves in water hyacinths (Tan et al. 2007a) and barley (Yoon and Park, unpublished data).

Roles for Vegetative Development

Root Development

Melatonin and natural auxin IAA share tryptophan as the biosynthetic starting material and have similar structural moieties. Both molecules are based on indole with a side chain at the C3 position. One of the well-known actions of auxin is to stimulate root formation. Therefore, the initial attempt to investigate the correlation between root development and melatonin adopted inhibitors for auxin action and transport as well as inhibitors of melatonin biosynthesis and serotonin transport (Murch et al. 2001). PCIB (*p*-chlorophenoxyisobutyric acid; an auxin action inhibitor) reduced the melatonin contents in the presence of auxin. Under the same conditions, the generation rate of adventitious roots decreased, suggesting correlations between melatonin and root generation rate. However, the lack of data on the effect of melatonin on root generation in the presence of IAA and PCIB left the main question unsolved. The group also tested the effect of biosynthetic inhibitor of melatonin. Auxin transport inhibitor TIBA (2,3,5-triiodobenzoic acid) reduced the melatonin level, but its effects on root generation were inhibitory or stimulatory depending on the concentrations applied. CPA (*p*-chlorophenylalanine), which blocks conversion from serotonin to melatonin, reduced both the melatonin contents and root generation rate, strongly suggesting the involvement of melatonin in root formation. Additional evidence indicating the involvement of melatonin in root formation was obtained in a study of the etiolated hypocotyls of *Lupinus albus* (Arnao and Hernández-Ruiz 2007). Exogenously applied melatonin stimulated adventitious root generation in amounts proportional to concentrations from 0.001 to 10 μM. In the same concentration range of melatonin, lateral root induction was optimal at 1 μM.

Auxin inhibits the elongation of preexisting roots in contrast that it stimulates root formation. Exogenously applied melatonin inhibited root growth in mustard in a manner similar to auxin (Chen et al. 2009). IAA concentrations in the same sample increased following applied melatonin concentrations and were saturated above 0.1 μM, indicating that the observed melatonin effect was due to increased auxin levels. However, it is still unclear whether melatonin induces auxin biosynthesis or if melatonin itself can be metabolized and converted to IAA. In animal systems, 5-methoxyindole-3-acetic acid, which is a weak auxin (Katekar 1979), is a catabolic product of melatonin (Hardeland et al. 1993), although 5-methoxyindole-3-acetic acid did not stimulate the elongation of lupin coleoptiles (Hernández-Ruiz and Arnao 2008b). Therefore, it might be possible that melatonin degraded to a certain molecule that can be converted to active auxin. Otherwise, application of melatonin might block the biosynthetic pathway of melatonin, resulting in redirection of the tryptophan to auxin biosynthesis because melatonin and auxin share the starting materials and some intermediates. Accordingly, the influence of melatonin on auxin biosynthesis warrants further study.

Shoot Development

Comparative studies have revealed that IAA and melatonin stimulated elongation in lupin hypocotyls (Hernández-Ruiz et al. 2004). Specifically, the dose–response curves of melatonin and IAA for the elongation of hypocotyls that were isolated, derooted, or decapitated were investigated. Melatonin showed relatively weak elongation-promoting effects in isolated or decapitated hypocotyls, but strong stimulatory effects in derooted hypocotyls to an extent similar to that obtained with IAA. Melatonin-induced expansion was also observed in lupin cotyledons (Hernández-Ruiz and Arnao 2008b). In some monocot species, melatonin stimulated the growth of coleoptiles and induced cell wall acidification similar to auxin (Hernández-Ruiz et al. 2005). Because coexistence of melatonin and IAA was verified in both lupin hypocotyls and cotyledons and in the coleoptiles of monocot plants, co-participation of the two substances in the regulation of cell growth was suggested (Hernández-Ruiz et al. 2005). However, experimental evidence indicating whether melatonin acts directly or indirectly through effects on auxin biosynthesis are not yet available.

Genetic manipulation of 2,3-dioxygenase revealed a new insight into the role of melatonin in plant development (Okazaki et al. 2010). When the gene of 2,3-oxyganase isolated from rice was overexpressed in tomato, the melatonin level decreased, showing reduced numbers of lateral leaflets. Considering that exogenously applied melatonin increased the numbers of lateral roots (Arnao and Hernández-Ruiz 2007), it could be suggested that melatonin is involved in lateral development in plants.

Roles for Reproductive Development

Flowering

Because melatonin is involved in the daily cycle in animals, melatonin could also be involved in circadian cycle-related physiology in plants. One of the sensitive plant responses to the cycle is flowering, which is tightly regulated by photoperiodism. When melatonin was applied to a shot-day plant, *C. rubrum*, at levels higher than 100 μM it reduced flowering (Kolář et al. 2003). Interestingly, the effects of melatonin only appeared when it was applied before the start of night or in the first half of the dark period. It was also reported that melatonin contents fluctuated with daily cycle and were highest in the dark period in *C. rubrum* (Kolář et al. 1997), although the duration of increased melatonin was not affected by the changes in photoperiod (Wolf et al. 2001). There are still only a few data available regarding daily rhythm and melatonin in plants. The role of melatonin in the daily cycle should be studied further.

Flower and Fruit Development

Analytical studies during flower development in St. John's wort revealed that the contents of serotonin and melatonin changed developmental stage specifically (Murch and Saxena 2002b). When the flower development was divided into six stages, serotonin and melatonin revealed peak values at stage 2 and stage 3, respectively, showing characteristics different from auxin content variations. Stage-specific increases in serotonin and melatonin strongly suggested that they play physiological roles in reproductive development. Increases of melatonin in a specific stage may act as a trigger signal for certain developmental procedures. Because the transition from the tetrad to uninucleate microspore occurs between phase 2 and 3, decreased serotonin and increased melatonin was interpreted as the signal for the phase transition (Murch and Saxena 2002b).

In *Datura metel*, contents of both serotonin and melatonin were highest in the flower bud and decreased sharply following the floral development (Murch et al. 2009). These authors suggested that melatonin played a protective role in developing flower buds rather than acting as a triggering signal for development, because cold treatment increased the level of melatonin.

During the course of fruit development in *D. metel*, melatonin showed a very sharp peak at 10–15 days after anthesis in the developing ovule, where early stages of seed development were in the progress (Murch et al. 2009). The melatonin level in wine grapes reached its maxima during véraison, which is characterized by softening accompanied by a rapid increase in seed weight (Murch et al. 2010). These findings suggest that the spike of melatonin level in a certain stage may act as a transition signal for seed growth during fruit development.

Roles in Stress Resistance

Oxidative Stress Resistance

During cell metabolism, diverse reactive oxygen species (ROS) are generated, mainly from the electron transport system (Rodriguez et al. 2004). The superoxide radical is the most abundant ROS and dismutated to hydrogen peroxide, which can be easily converted to the most damaging hydroxyl radical. The ROS could be directly scavenged by an antioxidant defense system or removed by enzymes.

Melatonin is a powerful antioxidant and more effective than previously identified substances, such as vitamins C, E, and K (Terrón et al. 2001; Poeggeler et al. 2002). Indeed, it has been estimated that melatonin could scavenge up to ten reactive oxygen species (Tan et al. 2007b).

In plants, melatonin appears to play protective roles against ozone damage (Dubbels et al. 1995), photooxidation of the photosynthetic system (Paredes et al. 2009), and UV damage (Tan et al. 2007a). All of these effects are expected to appear through a receptor-independent free radical scavenging mechanism (Tan et al. 2007b).

However, receptor-independent antioxidative action does not fit with the concept of a regulatory signal. Rather, it is a chemical reaction that might have been adopted before receptor-mediated signaling mechanisms had evolved. Animals have receptor-mediated antioxidative mechanisms of melatonin, which regulates the activities of antioxidative enzymes and their gene expression (Rodriguez et al. 2004).

Exogenously administrated melatonin amplified the activity of glutathione peroxidase (Barlow-Walden et al. 1995; Pablos et al. 1995) and superoxide dismutase (Liu and Ng 2000; Ozturk et al. 2000) in animals. Melatonin also increased the transcript levels of superoxide dismutases in hamsters (Antolin et al. 1996). Melatonin-regulated gene expression of antioxidative enzymes in plants is still unknown, although it has been reported that exogenously applied $ZnSO_4$ and H_2O_2 increased melatonin level in barley roots (Arnao and Hernández-Ruiz 2009a). Gene expression, related to antioxydative enzymes and others, by melatonin in plants is certainly worth being investigated.

Other Protective Effects

When melatonin was applied to senescing barley leaves, senescence was clearly delayed when the chlorophyll contents were used as the indicator (Arnao and Hernández-Ruiz 2009b). The delaying effect was even higher than that of cytokinin, which is a known anti-senescence hormone (Thomas and Howarth 2000).

Melatonin also exerted protective effects against cold stress-induced apoptosis in a carrot suspension culture (Lei et al. 2004). A similar protective effect was also observed in the cryopreserved callus of *Rhodiola crenulata* (Zhao et al. 2011). The mechanism of the enhanced resistance against the cold stress might be related to antioxidative activities.

Receptor and Signal Transduction

Melatonin is recognized by multiple membrane receptors in animals (Dobocovich and Markowska 2005). The signal of melatonin is perceived and transduced via two high-affinity G protein-coupled receptors, the MT_1 and MT_2. In plants, no proteins showing similarity with animal melatonin receptors have been identified to date. Plants might use different types of melatonin receptors that are still unidentified. Alternatively, melatonin might act via a receptor-independent mechanism as suggested in neurons (Jan et al. 2011).

Because melatonin exerts auxin-like effects on root initiation and coleoptile elongation, the possibility that melatonin itself may act as an auxin has been considered (Kolář and Macháčková 2005). Melatonin has an indole ring with a side chain at the C3 position and an unsaturated bond close to C3 similar to IAA (Fig. 2). The general structural requirements for auxin activity are an unsaturated ring, acidic side chain, and certain spatial configurations between the ring and the side chain (Taiz and Zeiger 2006). Kolář and Macháčková (2005) also pointed out that the distance between the end of indole ring and the carbonyl of melatonin is about 0.52 nm, which is reminiscent of the charge separation theory for auxin activity (Porter and Thimann 1965). Although it was assumed that the carbonyl of melatonin may simulate the electronegative charge group, no evidence or detailed mechanism has been provided to date. Strictly speaking, melatonin does not fulfill the structural requirements for auxin activity, e.g., its side chain is not acidic. Based on currently available evidence, melatonin is unlikely to act directly as an auxin, although it may be metabolized to IAA or affect auxin contents.

Concluding Remarks

Plant melatonin may play roles in daily rhythm regulation and defense against oxidative stress as observed in animals.

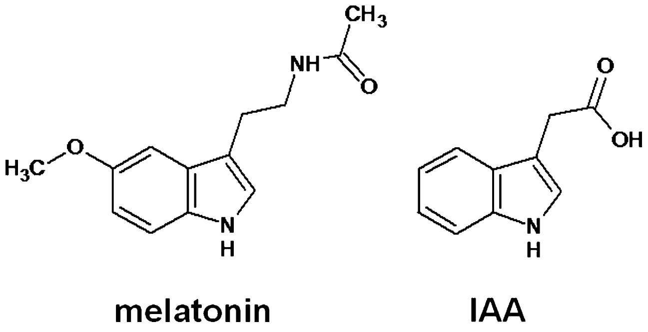

Fig. 2 Chemical structures of melatonin and indole-3-acetic acid (IAA)

However, there may be unique functions of plant melatonin in the regulation of both vegetative and reproductive development. The effects of melatonin on vegetative growth resemble the activities of auxin, e.g., stimulation of root initiation and coleoptile elongation. These effects of melatonin may appear indirectly by influencing the auxin levels. During reproductive development, melatonin may act as a transition signal to indicate the time point for seed growth. Considering the ubiquitous distribution of melatonin in angiosperms, melatonin may play other important roles in plants.

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