Melatonin in plants: what we know and what we don’t

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Abstract

Melatonin is an endogenous micromolecular compound of indoleamine with multiple physiological functions in various organisms. In plants, melatonin is involved in growth and development, as well as in responses to biotic and abiotic stresses. Furthermore, melatonin functions in phytohormone-mediated signal transduction pathways. There are multiple melatonin biosynthesis pathways, and the melatonin content in plants is greatly affected by intrinsic genetic characteristics and external environmental factors. Although melatonin biosynthesis has been extensively studied in model plants, it remains uncharacterized in most plants. This article focuses on current knowledge on the biosynthesis, regulation and application of melatonin, particularly for fruit quality and preservation. In addition, it highlights the links between melatonin and other hormones, as well as future research directions.

Keywords: Melatonin; biosynthesis; regulators; crosstalk; application.

Introduction

Melatonin (MT, N-acetyl-5-methoxytryptamine) is an indole tryptamine that was initially isolated from the bovine pineal gland and was subsequently structurally characterized (Lerner et al., 1958, 1959). In animals, MT has been associated with the regulation of physiological functions such as improving sleep, delaying aging, alleviating allergic symptoms, and regulating the immune system. Due to its important roles in human health, MT is now widely used as a key ingredient in medicines and health-care products that regulate the circadian clock and sleep (Slominski et al., 2018; Rui and Ronell, 2019).

MT is currently the only conserved broad-spectrum physiological regulator that is naturally present in most biological organisms (Arnao and Hernández-Ruiz, 2019). It has been identified in a unicellular alga (Balzer and Hardeland, 1991) and subsequently in higher plants, including tomato and tobacco (Van Tassell et al., 1993; Van Tassell, 1995). Since its identification in plants, there has been an explosion of research into MT in plant species, particularly in the past decade (Arnao and Hernández-Ruiz, 2014, 2018; Fan et al., 2018; Zhang et al., 2015). MT is reported to participate in the regulation of plant growth and development, circadian rhythms and photoperiodic responses, antioxidation and stress resistance (Arnao and Hernández-Ruiz, 2015; Tan et al., 2015).

The MT content in a plant is species-dependent and relates to the growth stage and environmental conditions. Moreover, extraction and detection processes may lead to differences in the MT quantified among plant samples (Murch et al., 2004; Afreen et al., 2006; Reiter et al., 2007). In contrast to animals, which can escape from stresses, plants are sessile and therefore have to adopt different strategies to cope with adverse environmental conditions. For instance, high levels of MT, which function as an antioxidant to reduce damage, are present in Mediterranean and alpine plants exposed to strong UV radiation (Hardeland et al., 2007). The antioxidant capacity of MT is caused by its great ability to scavenge free radicals. Furthermore, MT can increase the activity of other free radical scavenging enzymes, such as superoxide dismutase (Russel et al., 2015).

MT is also extremely important for fruit quality and preservation; in particular, it can promote fruit ripening and delay fruit senescence.
MT functions by regulating genes involved in secondary metabolism, ethylene (ET) signaling, flavonoids and cell wall modification, as well as senescence-related genes and those involved in carbohydrate metabolism and the ascorbate–glutathione (ASC–GSH) cycle (Arnao and Hernández-Ruiz, 2020). The ET-transducing genes (EIL1/3, ERF2), and the biosynthesis genes (ACS and ACO), can be up- or downregulated by MT (Sun et al., 2015; Liu et al., 2019a).

Increasingly, studies have demonstrated that MT can act as a hormone and functionally synergize with other plant hormones (Shi et al., 2016a, 2016b; Hwang and Back, 2018; Zhai et al., 2018; Zhang et al., 2019). Its specific regulation mechanisms in plants have also been gradually characterized. In this review, we summarize the current state of knowledge concerning the biosynthesis, regulation, and application of MT, and suggest future research directions and goals.

What We Know About MT in Plants
The MT biosynthesis pathways in plants
The pathway for MT biosynthesis has been well defined in vertebrates (Figure 1A), including mammals, birds, and amphibians. The site of synthesis is mainly in pineal gland, while the cerebellum, retina, accessory lacrimal gland, salivary gland, intestinal eosinophils and red blood cells also play a role (Reiter, 1991; Falcón et al., 2009).

In the first step of MT biosynthesis in animals, tryptophan ingested from food acts as a substrate that is then catalyzed by tryptophan hydroxylase (TPH) to produce 5-hydroxytryptophan. This is then catalyzed by tryptophan decarboxylase (TDC) to produce serotonin (Figure 1A). The subsequent steps are conserved among plants.

The biosynthesis of MT in plants has been less well studied than in animals and is far more complex (Park and Back, 2012; Back et al., 2016). In plants, MT synthesis begins with tryptophan and the intermediate steps involve six enzymes and at least four different routes (Figure 1B; Tan et al., 2015). In contrast to generation in animals, generation of serotonin in plants requires TDC and tryptamine 5-hydroxylase (TSH) in a specific order, and the biosynthesis pathway from tryptophan to serotonin starts in the chloroplast and ends in the endoplasmic reticulum (ER) (Van Tassel et al., 2001). Notably, plants also probably contain TPH-like genes, and 5-hydroxytryptophan is present in seeds of *Griffonia simplicifolia*. Moreover, a similar enzyme to TPH probably catalyzes the conversion of tryptophan to 5-hydroxytryptophan in rice roots, but in rice, serotonin is probably produced in the cytoplasm (Back et al., 2016).

TDC catalyzes the conversion of tryptophan to tryptamine with high specificity and is the first rate-limiting enzyme in the MT biosynthesis pathway. The rice genome (MSU-RGAP) contains three TDC genes (OsTDC1, OsTDC2, OsTDC3), which belong to the family of aromatic l-amino acid decarboxylases (Kang et al., 2007a). Rice lines that overexpress OsTDC1 or OsTDC2 are phenotypically similar to wild type under normal growth conditions, except that the content of serotonin in leaves and seeds is higher.
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than that in the corresponding wild-type organs (Kang et al., 2007b). Moreover, studies in senescing rice indicated that OsTDC1 plays a leading role during serotonin synthesis. Serotonin is also believed to delay senescence by reducing reactive oxygen species (ROS) in rice leaves (Kang et al., 2008). However, the overexpression of OsTDC1 leads to retarded growth, decreased fertility and serotonin accumulation (Kanjanaaphachoot et al., 2012; Byeon et al., 2014a). The expression of PepTDC1 (LOC107877290) is induced in pepper fruits inoculated with fungus or treated with ET and is highly expressed in unripe green fruit but not in ripe red fruit. By contrast, PepTDC2 (LOC107842494) is expressed constitutively at a low level in all tissues of pepper (Park et al., 2009). The study of TDC in mulberry, sweet cherry fruits, and herbaceous peony demonstrated that the efficient production of MT depends on gene expression (Zhao et al., 2015; Wang et al., 2016; Zhao et al., 2018). This suggests that genetic manipulation of TDC gene expression is one potential way to increase the MT content in specific plant tissues.

TSH was initially identified as a soluble enzyme with high activity in rice roots. The activity of TSH is inhibited by MT synthesis intermediates such as tryptamine and tryptophan (Kang et al., 2007b). Subsequently, it was shown that the P450 monooxygenase CYP71P1, which catalyzes the conversion of tryptamine to serotonin, possesses TSH activity. Although the expression of CYP71P1 was induced by blast fungus infection of rice (Fujiiwara et al., 2010), the phenotypes of TSH overexpression and antisense lines were inconsistent with those for the altered expression of other genes involved in MT synthesis (Park et al., 2013b). Mutants of rice that lack TSH activity can synthesize tryptamine and N-acetyltryptamine during senescence, and moreover, the content of N-acetyltryptamine inhibits MT synthesis (Park and Back, 2012). To date, few studies have been performed on the role of TSH in plant MT synthesis, presumably because its activity is unstable and does not correlate with MT content.

The next two steps in MT production are mainly catalyzed by serotonin N-acetyltransferase (SNAT) and N-acetylserotonin methyltransferase (ASMT)/caffeic acid O-methyltransferase (COMT), and the intermediate products are synthesized in either the chloroplasts or cytoplasm (Arnao and Hernández-Ruiz, 2015). Cyanobacterial SNAT, which is unlike that from animals, is localized to the chloroplast stroma in Arabidopsis and the gymnosperm, loblolly pine (Park et al., 2014; Lee et al., 2015). The overexpression of OaSNAT in the chloroplasts and cytoplasm of rice led to increased enzyme activity but low MT production, which may be due to the multifactorial regulation of MT (Byeon et al., 2015b). Unlike other enzymes in the MT biosynthesis pathway, SNAT is relatively conserved among different plant species (Byeon et al., 2016). The SNAT enzyme from Arabidopsis is more active in catalyzing the conversion of 5-methoxytryptamine to MT (Lee et al., 2014b).

ASMT and COMT are functionally similar members of the O-methyltransferase family that are localized to the cytoplasm (Byeon et al., 2014b). In Arabidopsis, the activity of COMT in the step from N-acetyl-5-hydroxytryptamine to MT is much higher than that of ASMT, as the MT content of comt knockout mutants is significantly lower than that of the wild type (Byeon et al., 2014b; Lee et al., 2014b). The COMT enzyme in rice was reported to show in vivo catalytic activity, as COMT overexpression caused an increase in the MT content, whereas COMT-silenced lines exhibited a reduction in the MT level (Byeon et al., 2015a). COMT can catalyze the conversion of serotonin to 5-methoxytryptamine and can also replace ASMT in the biosynthesis of MT from N-acetyl-5-hydroxytryptamine (Byeon and Back, 2016).

Figure 2 shows a phylogenetic analysis of the ASMT gene family. Although rice ASMT has OMT catalytic activity, its homologs are absent in many species, suggesting that other types of ASMT are associated with MT synthesis and may be present in some species (Kang et al., 2011; Park et al., 2013a). Eight members of the Arabidopsis OMT gene family were expressed in Escherichia coli, and the COMT gene was demonstrated to possess ASMT activity and to play a major role in MT biosynthesis (Byeon et al., 2014a).

The tomato genome encodes at least 14 SLASMT genes, with three possibly being pseudogenes; moreover, chromosome mapping of the loci showed that this gene family presumably evolved rsa tandem duplication events (Liu et al., 2017). Systematic analysis of the CaASMT gene family of pepper was also performed based on the whole-genome sequence, and at least 16 members were identified, which could be divided into three groups. Among the 16 genes, 13 were unevenly distributed on eight of the 12 chromosomes, and CaASMT16 was localized on Chr00. RNA sequencing and quantitative real-time polymerase chain reaction analysis showed that CaASMT07, CaASMT10, CaASMT11, and CaASMT14 were upregulated markedly by heat stress, and CaASMT01 and CaASMT12 were expressed constitutively at all of the stages analyzed, whereas CaASMT06 was expressed at early stages (Pan et al., 2019).

The multipathway and multisite synthesis of MT is important to ensure the stability of the MT content, which enables plants to cope with various stresses.

Regulation of MT biosynthesis

Due to the importance of MT in plants, it is necessary for its biosynthesis to be appropriately regulated. The MT content varies among different plant species, tissues, developmental stages, and growth conditions. The MT concentration was demonstrated to be dependent on the degree of fruit maturation in tomato and grape (Murch et al., 2010). Cherry fruit is rich in MT, and contents are particularly high during embryonic development and endocarp lignification; moreover, the MT content varies greatly among different varieties (González-Gómez et al., 2009; Zhao et al., 2013). The MT content is highest at the tips of mulberry leaves and is higher in juvenile leaves than in older leaves (Pothinuch and Tongchitpakdee, 2011). A high concentration of MT was detected in pepper at the seedling stage, but then decreased gradually. In addition, differences in MT content in roots, leaves, fruits and seeds of pepper showed that the level of MT is differentially regulated in different tissues (Korkmaz et al., 2014). Higher levels of MT are often observed in seeds, where it can alleviate damage caused by oxidative stress at later stages (Manchester et al., 2000; Iriti et al., 2006).

The accumulation of MT in plants is also light-sensitive and exhibits circadian rhythms, similar to accumulation in animals. However, the accumulation of MT differs among plant species. The levels of MT in tomato and Chenopodium rubrum increase under shade conditions, but some peppers show increasing MT levels during the light period (Kolár et al., 1999; Dongen et al., 2001; Riga et al., 2014). This suggests that the regulation of MT by light among different species is varied and complex, and its specific mode of action remains unknown.

Many stress factors can induce the accumulation of MT in plants, which can then alleviate potential damage. Cold treatment significantly induces the accumulation of endogenous MT in Arabidopsis (Shi et al., 2014). In field-grown tomato, the content of MT in leaves is approximately 10-fold higher than that of greenhouse-grown seedlings, which might be due to adverse environmental field conditions (Arnao and Hernández-Ruiz, 2013). In Glycyrrhiza uralensis,
intense UV-B radiation could induce MT, which is thought to act as a scavenger of free radicals and have a photoprotective function (Afreen et al., 2006). Salinity stress causes an increase in the content of 5-hydroxytryptamine and MT in the roots and cotyledons of sunflower, and significantly increases activities of the MT synthesis enzyme hydroxyindole-O-methyltransferase (Mukherjee et al., 2014). The final key enzyme of MT synthesis, ASMT, is significantly induced during leaf senescence and various stress conditions. High temperature and darkness also enhance the enzymatic activity of SNAT and ASMT and increase the synthesis of MT (Byeon et al., 2014b).

Crosstalk between MT and other phytohormones
The interactions between MT and other hormones have been studied under normal growth and stress conditions (Figure 3). Plant stress responses can be regulated by interactions between MT and abscisic acid (ABA) signaling. Treatment of Elymus nutans with MT at low temperature led to a significant increase in the content of ABA. However, treatment with exogenous ABA or ABA synthesis inhibitors did not affect endogenous MT levels, which suggests that MT may act upstream from ABA to regulate plant responses to low-temperature stresses (Fu et al., 2017). MT also regulates plant growth and development by interacting with auxin signaling in a concentration-dependent manner. In tomato, a low concentration of MT enhanced the expression of the auxin signaling genes IAA19, IAA24, PIN1, PIN3, and PIN7, whereas a high concentration inhibited auxin synthesis and transport via NO signaling (Wen et al., 2016). Tolerance to salinity stress in cucumber can be conferred by MT during seed germination, mainly via the regulation of gibberellin
acid (GA) biosynthesis and catabolism (especially GA₄), as well as ABA. Specifically, MT application leads to the upregulation of ABA catabolism genes and GA biosynthesis genes (GA₂₀ox and GA₃ox) during the early stage of seed germination, with ABA biosynthesis genes significantly downregulated (Zhang et al., 2014). Studies in Chinese flowering cabbage suggest that MT-mediated inhibition of leaf senescence involves suppression of ABFs (ABA responsive element binding factors)-mediated ABA biosynthesis and chlorophyll degradation (Tan et al., 2019). The application of MT can delay floral transition in Arabidopsis, which suggests that MT can mediate the activation of FLOWERING LOCUS C by DELLA proteins in flowering (Shi et al., 2016b). A direct link between MT and strigolactones has also been demonstrated in floral bud differentiation in Arabidopsis (Zhang et al., 2019). In addition to MT, the hormones salicylic acid (SA) and ET increase a plant’s ability to induce pathogenesis-related genes, and the dependency of SA and ET responses on MT-induced defense signaling has been demonstrated in Arabidopsis and tobacco (Lee et al., 2014a).

The physiological roles of MT in plants

One of the best-known functions of MT is its ability to scavenge free radicals generated by oxidative stress (Tan et al., 2007; Byeon et al., 2015c). Furthermore, MT not only regulates flowering, fruit ripening, photosynthesis, senescence, apoptosis, growth rhythms, root morphogenesis, seed germination, and other growth development processes, but also participates in the regulation of biotic and abiotic stress responses (Kanwar et al., 2018; Arnao and Hernández-Ruiz, 2019). As an essential growth regulator for life, MT is closely related to the growth and development along with responses to stress signals of plants.

In plants, MT can regulate development by manipulating metabolism. For instance, MT enhances the senescence of kiwifruit leaves by increasing the accumulation of flavonoids (Liang et al., 2018). MT can also induce the release of ET during tomato fruit ripening, thereby promoting fruit ripening and improving fruit quality (Sun et al., 2015). In banana, the application of exogenous MT markedly reduced the incidence of anthracnose and slow postharvest fruit senescence (Hu et al., 2017; Li et al., 2019). Treatment with MT and NO inhibits the increase in polygalacturonase and cellulose in pear fruits and inhibits the expression of ET biosynthesis genes and lowers respiration and ET production, thereby delaying fruit senescence (Liu et al., 2019a). Treatment of pear fruits with MT increases the content of soluble sugars during fruit maturation and increases fruit weight compared with control fruit (Liu et al., 2019b). The same study showed the potential of MT to maintain the commercial value of postharvest fruit and to delay senescence by inhibiting ET production and the reactive oxygen burst during the cold storage of pears (Zhai et al., 2018). In litchi fruit, MT treatment not only delays discoloration by inhibiting methylenedioxyamphetamine (MDA) and ROS generation, but also markedly delays the decrease

Figure 3. MT modulates plant growth and development, stress-signaling pathways and crosstalk with phytohormones. These signal transduction processes of MT are closely related to the process of plant life. They are relatively independent and closely connected by influence each other. MT, melatonin; ABA, abscisic acid; GA, gibberellic acid; IAA, indole acetic acid; SA, salicylic acid; CTK, cytokinin; MeJA, methyl jasmonate; ETH, ethylene; SL, strigolactone.
in the content of total phenolics, flavonoids and anthocyanins and enhances the activities of antioxidant enzymes (Zhang et al., 2018).

Furthermore, MT treatment is an effective method to reduce weight loss and retain greater firmness of plum fruits (Bal, 2019). In MT-treated strawberry, reduced decay and weight loss were observed (Aghdam and Fard, 2017; Liu et al., 2018; El-Mogy et al., 2019). The MT protective role against situations of stress was demonstrated during low-temperature storage in cut anthurium flowers (Aghdam et al., 2019). The studies on fruit of peach and broccoli showed that MT treatment reduced chilling injury during storage for postharvest (Gao et al., 2018; Cao et al., 2018; Wu et al., 2021). Therefore, MT treatment can preserve fruits after harvest and may be useful to extend the postharvest life of plum while maintaining acceptable fruit quality.

**What We Do Not Know About MT in Plants**

**Where is MT synthesized in plants?**

The specific sites of MT synthesis in plants remain unclear. It was proposed that the primary biosynthesis sites of the early MT biosynthesis stages are mitochondria and chloroplasts, because these two organelles are major sources of free radicals. Moreover, MT not only functions as an antioxidant and scavenger of free radicals, but also limits the generation of free radicals (Hattori et al., 1999; Sun et al., 2015). The localization of some MT biosynthesis enzymes also confirms these postulated sites of biosynthesis (Van Tassell and O’Neill, 2001; Byeon and Back, 2014). However, no further convincing evidence concerning synthesis sites exists, such as the tissue localization of key biosynthesis genes or their precise subcellular localization. Furthermore, it remains unclear whether MT functions similarly in different tissues in response to the environment.

**Key regulators of MT in plants**

At least four different pathways for MT biosynthesis have been identified in plants (Back et al., 2016); however, it is unclear whether these pathways function in parallel, or whether one pathway is dominant. It is probable that different biosynthesis routes are adopted under certain conditions, indicating that the biosynthesis pathway of MT in plants is more complex than previously thought and remains to be studied further. Moreover, many of the key regulators within these MT pathways are still poorly understood.

**Key regulators of MT biosynthesis**

Environmental factors such as light and temperature regulate the key developmental stages of plants, such as seed development, flowering, and senescence. Because MT is also related to these processes, it is tempting to speculate that environmental factors may directly regulate MT biosynthesis in plants, similar to in animals. The level of endogenous MT was shown to vary with a circadian rhythm in the short-day plant *Chenopodium rubrum* (Kolár et al., 1997, 1999). However, the key regulators that control MT biosynthesis in response to environmental factors remain to be identified.

Because MT plays important roles under different stress conditions, factors must exist that regulate MT biosynthesis in response to specific stress conditions. Notably, HsfA1a confers Cd tolerance by inducing *COMT1* transcription and inducing the accumulation of MT and upregulating *HSP* expression (Cai et al., 2017). MT enhances plant heat tolerance by increasing the expression of *HSP* and *HSP* (Shi et al., 2015c). In cassava, the *APETALA2/EThYLENE RESPONSE FACTOR* gene family members *MeRAV1* and *MeRAV2* enhance disease resistance by positively regulating MT biosynthesis (Wei et al., 2017). However, additional transcription factors that stimulate MT biosynthesis in response to stresses remain to be characterized.

**Key regulators downstream from MT**

The stress-response factors that function downstream from MT in plants are currently under investigation. In *Arabidopsis*, AtZAT6-activated C-repeat-binding factor (CBF) is required for MT-mediated cold-stress resistance (Shi et al., 2016a). SALT OVERLY SENSITIVE (SOS)1/2/3, which are induced by MT, can activate the SOS pathway (Chen et al., 2017). The PYR/PYL-PP2C-SnRK2-ABFABA pathway, which is involved in drought resistance, is also modulated by MT (Fujita et al., 2013). In *Arabidopsis*, MT-induced CBFs and dehydration-responsive element binding 1 factors are essential for disease resistance (Shi et al., 2016a). In addition, the enhancement of plant autoimmunity by mitogen-activated protein kinase is mediated by MT (Lee and Back, 2016). The protective effects of MT are often associated with enhanced antioxidant enzyme activity, as well as the upregulation of the ion-channel genes *NHX1* and *AKT1* and genes involved in sugar and glycolysis metabolism (Li et al., 2012; Liang et al., 2015; Wei et al., 2015). Transcriptome analysis showed that MT can induce the expression of genes that encode transcription factors such as WRKY, MYB, NAC, and HSF, and these regulate plant growth and development, as well as responses to stresses (Shi et al., 2015a). However, in contrast to stress-response factors, key growth regulators downstream of MT remain to be identified.

**Regulators that link MT with other phytohormones**

Although there is growing evidence for crosstalk between MT and other phytohormones, the precise position of MT within the phytohormone network is yet to be studied. Future studies should focus on genes encoding the key components of different phytohormone signaling pathways and whether these are regulators of MT biosynthesis or are regulated by MT.

**Combined mechanism of MT with other effective factors**

**Combination of MT and environmental factors**

Knowledge concerning how MT regulates the plant response to photoperiod is lacking. MT is present in the roots of the medicinal plant *Glycyrrhiza uralensis*, and the MT content varies with different wavelengths of light, in proportion to the UV-B radiation intensity (Afreen et al., 2006). It is well known that changes in plant circadian rhythms are closely related to light, and this is an especially important feature for plants due to their varying sensitivities to light. Moreover, different light qualities differentially affect plant growth and development, which might be intrinsically connected with MT. This is much more complex than the regulation mechanisms involving MT in animals and needs to be thoroughly investigated.

**The combinatorial function of MT with other phytohormones**

Miscellaneous phytohormones are involved in nearly all aspects of physiology during growth and development. The effects of application of cytokinins, GAs, ABA, auxin, brassinosteroids, and jasmonic acid to plants have been studied extensively. By contrast, the effects of MT application and their underlying mechanisms remain underresearched. Tryptophan is a common precursor for the biosynthesis of MT and indole acetic acid (IAA), which may result in these
compounds having similar regulatory functions during plant growth and development (Edgerton et al., 1994; Arnao and Hernández-Ruiz, 2006; Shi et al., 2015b). The relationships between MT and many other hormones have been directly or indirectly studied, but few signaling models have been proposed. Future studies should investigate the mechanisms of how MT and other plant hormones coordinate plant growth, development, and stress responses.

Conclusions and Future Perspectives

Melatonin is essential for plant quality and storage, and due to the diverse and valuable physiological functions of MT in plants, research on plants has attracted increasingly more attention. This review summarizes recent progress in understanding the biosynthesis of plant MT and its biological functions, and elaborates what is known about its interactions with phytohormones. Compared with well-known hormones, many problems remain to be solved in the field of MT research.

The accumulation of plant MT is affected by genetic factors and the external environment. Current research into the molecular regulation of MT mainly focuses on the model plants Arabidopsis and rice. Few studies exist for other plants, and the rate-limiting enzymes in plant MT synthesis have not been precisely established. The synthesis and metabolic pathways of plant MT remain unclear, and its metabolic processes are complex, and may involve the degradation of enzymes, pseudo-enzymes and free radicals. Under severe stress conditions, freedom basis interaction may be the main pathway for MT degradation, but these metabolic processes in plants still need to be demonstrated. The MT metabolic enzyme M2H is highly active; thus, its metabolism might be more efficient than its synthesis (Byeon et al., 2015d).

No conclusive information exists concerning how plants perceive MT signals, or the downstream signal transduction that regulates the response of plants to stress at the physiological and metabolic levels. It was reported that CAND/PMTR can act as an MT receptor for signal transduction, which lays the foundation for the further study of MT signaling (Wei et al., 2018). Study of the interactions between MT signaling and other hormones will elucidate the molecular mechanisms of MT signaling and how MT functions as a plant regulator.

Author contributions

Yang Zhang contributed to the conception of the study with constructive discussions. Zixin Zhang and Yang Zhang wrote and revised the manuscript. Both authors read and approved the final manuscript.

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Conflict of Interest

The authors declare no conflict of interest.

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