Melatonin (N-acetyl-5-methoxytryptamine) synthesized by plants is known as phytomelatonin. It was first detected by several independent research groups in 1995 (Dubbels et al., 1995; Hattori et al., 1995; Kolar et al., 1995; Van Tassel et al., 1995). The biosynthesis of melatonin in animals and plants begins from tryptophan via several similar consecutive enzymatic steps. The first phytomelatonin receptor, PMTR1, was identified in Arabidopsis in 2018 (Wei et al., 2018). Recently, several independent research groups have discovered that PMTR1 and its homologous proteins are required for perceiving phytomelatonin signaling in stomatal closure, seed germination and seedling growth, flowering, leaf senescence, and in responding to various biotic and abiotic stresses in Arabidopsis, tobacco, alfalfa, maize, and cassava (Bai et al., 2022; Chen et al., 2022). Phytomelatonin is therefore comparable to the more well-known plant hormones and regulates nearly all aspects of plant life history (Box 1).

Metabolism of phytomelatonin

Melatonin is an ancient molecule that is present in nearly all organisms; its structure has not changed in 2.5–3.5 billion years of evolution (Tan et al., 2014). The biosynthesis of melatonin and phytomelatonin begins from tryptophan and shares some similar consecutive enzymatic steps in animals and plants (Arnao et al., 2022; G. Liu et al., 2022; Y. Liu et al., 2022). Plants contain at least six enzymes for phytomelatonin biosynthesis, namely (1) tryptophan decarboxylase (TDC) localized in the cytoplasm, (2) tryptamine 5-hydroxylase (TSH) localized in the endoplasmic reticulum, (3) serotonin N-acetyltransferase (SNAT) localized in the chloroplasts, (4) acetylserotonin O-methyltransferase (ASMT) and (5) caffeic acid 3-O-methyltransferase (COMT), which are both expressed in the cytoplasm, and (6) a putative and unidentified tryptophan hydroxylase (TPH) (Arnao et al., 2022; G. Liu et al., 2022; Y. Liu et al., 2022).

The biosynthesis of phytomelatonin is largely influenced by internal and environmental cues. For example, endogenous phytomelatonin shows circadian rhythms in Arabidopsis, Chenopodium, rice, Paonia lactiflora, morning glory, apple, and Hypericum perforatum (Chen et al., 2022). Additionally, light, temperature, water status, salt stress, and pathogen invasion can also affect the biosynthesis of endogenous phytomelatonin and expression of related genes (Mou et al., 2022). Several transcription factors can directly bind to the promoters of genes related to phytomelatonin biosynthesis, including heat-shock factor A1a (HsfA1a) in tomato (Cai et al., 2017), RAV1 and RAV2 in the apetala2/ethylene response factor family in cassava (Y. Wei et al., 2018), and ELONGATED HYPOCOTYL 5 (HY5) in Arabidopsis (L. Wang et al., 2022).

In animals, melatonin can be converted into a series of compounds, including cyclic 3-hydroxymelatonin (3-OHM), 2-hydroxymelatonin (2-OHM), and Nα-acetyl-Nβ-formyl-5-methoxyamine (AFMK). Interestingly, some enzymes that can degrade melatonin in vertebrates have also been shown to degrade phytomelatonin (G. Liu et al., 2022; Y. Liu et al., 2022). For example, melatonin 3-hydroxylase (M3H) and melatonin 2-hydroxylase (M2H) responsible for the biosynthesis of 3-OHM and 2-OHM have been identified in rice plants. In addition, AFMK has also been identified in Eichhornia crassipes, and concentrations of phytomelatonin are significantly decreased in transgenic tobacco plants expressing rice indoleamine 2, 3-dioxygenase (IDO) (G. Liu et al., 2022; Y. Liu et al., 2022).

Phytomelatonin signaling in plant growth and development

Signaling pathways and functions are a central research area for phytohormones. The identification of phytomelatonin receptor1 (PMTR1) in 2018 was a turning point in this research field (J. Wei et al., 2018; Arnao and Hernández-Ruiz, 2019; Li et al., 2022). PMTR1 is a putative GPCR-like protein that regulates stomatal closure via either production of reactive oxygen species (ROS) and Ca2+ transient influx mediated by GPA1 (G protein α-subunit 1) and NADPH oxidase, or mitogen-activated protein kinase (MAPK) cascades (Chen et al., 2022). Several independent groups have further confirmed that PMTR1...
and its homologous proteins are associated with perceiving phytomelatonin signaling in seedling growth, flowering, stomatal closure, immunity, and salt and drought tolerance in Arabidopsis, tobacco, and alfalfa (Chen et al., 2022). More recently, MePMTR1 and ZmPMTR1 have been identified in cassava and maize, respectively (Bai et al., 2022; L.-F. Wang et al., 2022). MePMTR1 and ZmPMTR1 are membrane proteins that show a high affinity for melatonin binding and are required for melatonin-mediated drought resistance and alleviation of darkness-induced leaf senescence and stomatal closure. It is interesting to note that the protein phosphatase MePP2C1 can interact with MePMTR1 and dephosphorylate it at the S11 residue, thereby repressing its binding to melatonin (Bai et al., 2022).

Flowering is a critical stage in plant life history (Mou et al., 2022). Several well-known pathways determine the optimum time to flower, including the photoperiod, vernalization, autonomous, age, and gibberellin (GA) pathways (Chen et al., 2022; Mou et al., 2022). Exogenous melatonin delays flowering time in both long- and short-day plants (Chen et al., 2022; Mou et al., 2022). Genetic analyses have shown that the Arabidopsis mutants comt1 and snat1 that have lower endogenous phytomelatonin concentrations display earlier flowering times than wild-type Col-0 plants (Zhang et al., 2019). Phytomelatonin delays flowering through interactions with other hormones (e.g., GA and strigolactone), ROS signaling, and the central components of floral-gene regulation networks (Chen et al., 2022). CRISPR/cas9-edited plants and overexpressing
lines of PMTR1 show earlier and later flowering, respectively, than Arabidopsis wild-type Col-0 (Yin et al., 2022), indicating the phytomelatonin-mediated delay of flowering time is likely to be dependent on the PMTR1 receptor.

As an essential part of a balanced diet, fruit plays an important role in human nutrition and health. From the perspective of the plant, fruits provide the appropriate environment for the formation and maturation of seeds (Corpas et al., 2022). Endogenous phytomelatonin concentrations vary during the development, growth, and ripening of fruits. For example, in sweet cherry, the phytomelatonin content reaches a maximum at early stages of fruit set and development, and then decreases at the start of ripening (Tijero et al., 2019). External application of melatonin retards senescence and extends the postharvest life of fruits during storage via regulation of ROS, reactive nitrogen species (RNS), and ethylene (Arnao and Hernández-Ruiz, 2020a, 2021; Aghdam et al., 2022; Corpas et al., 2022; K. Wang et al., 2022).

Seed formation, growth, maturation, and germination are crucial developmental stages in the life cycle of seed plants. Several studies have found that melatonin can promote seed germination under stress conditions, especially in old or damaged seeds, improving germination rate probably through fit hormonal balance (K. Wang et al., 2022). In contrast, Ly et al. (2021) and Yin et al. (2022) have shown that high concentrations of melatonin inhibit Arabidopsis seed germination and seedling growth, possibly due to disorder in ABA, GA, and auxin balance. It is interesting that PMTR1-knockout mutants contain higher ABA concentrations in developing seeds, but accumulate lower ABA contents in dry and imbibed seeds than the wild-type Col-0 (Yin et al., 2022), indicating that PMTR1 is involved in phytomelatonin-mediated seed development, dormancy, germination, and seedling growth via crosstalk with ABA signaling. Transgenic Arabidopsis plants overexpressing AtPMTR1 produce smaller seeds and germinate more slowly than Col-0 plants (Yin et al., 2022). The application of melatonin can induce seedless fruits of pear via regulation of GA pathways (Liu et al., 2018). However, an increase in production of wheat and soybean is observed under abiotic stress conditions when the seeds have been coated with melatonin (Cui et al., 2017; Wei et al., 2015).

Phytomelatonin functions in nutrient homeostasis and stress resistance

Annual food production needs to be doubled by 2050 to match predicted population growth (Huang et al., 2022); however, at the same time changes in global climate and their impact on current agricultural systems are severely limiting crop growth and yield, and threatening food security. Long-term intensification of agricultural practices and inadequate nutrient inputs have changed the properties of soils, causing mineral nutrient deficiencies and ion toxicities (Sun et al., 2022). Under conditions of nutrient deficiency (e.g. K, Fe, P, S, and N), phytomelatonin is a very important signal molecule in uptake, transport, homeostasis, and use efficiency via regulating the expression of related genes and/or directly regulating activities of transporters, plasma membrane H+–ATPase, and the ROS–Ca2+ hub, and through crosstalk with other phytohormones (Huang et al., 2022). In addition, phytomelatonin is also required for plant resistance to salinity, osmotic stress, hazardous metals (e.g. Cd, Al, Ni, Pb), drought stress, and high-light stress via receptor-dependent or -independent systems in the regulation of ROS, RNS, and H₂ signaling and in crosstalk with other plant hormones (e.g. auxin, cytokinin, ABA, ethylene, brassinosteroids, jasmonates, salicylic acid, and strigolactones; Arnao and Hernández-Ruiz, 2020b; Sun et al., 2022; Y. Wang et al., 2022).

Phytomelatonin has been suggested to be a central molecule in plant resistance to bacterial, fungal, and viral diseases via crosstalk with ROS, RNS, and phytohormones (e.g. salicylic acid, jasmonates, ABA) and via regulation of expression of genes associated with pathogen responses, disease resistance, and immunity (Zeng et al., 2022). In Panax notoginseng, fo- liar application of melatonin decreases the incidence of leaf diseases such as grey mould, round spot, and black spot, with phytomelatonin-induced stomatal closure playing a prominent role in preventing bacterial invasion in Arabidopsis and P. notoginseng via PMTR1-mediated activation of the GPA1- and MAPK-signaling pathways, respectively (Yang et al., 2021). It is worth noting that pmtr1 and gud1 mutants are also insensitive to flg22-induced stomatal closure in Arabidopsis, indicating that PMTR1 is required for FLS1- and BAK1-mediated flg22 signaling in stomata-mediated defence (Yang et al., 2021).

Phytomelatonin regulates primary and secondary metabolism

Using light energy, photosynthesis converts carbon dioxide and water into organic compounds and oxygen, in a process that is essential for all living organisms on our planet. In plants, ROS are by-products of O₂ during the photosynthetic and oxidative phosphorylation processes in chloroplasts, where phytomelatonin is mainly synthesized. The biosynthesis of phytomelatonin can be induced by light, and shows daily rhythms and peaks during daytime (Li et al., 2020; Chen et al., 2022; G. Liu et al., 2022; Y. Liu et al., 2022), which may play an important role in scavenging ROS when it is overproduced. As well as directly protecting chloroplasts from excess ROS stress, phytomelatonin also acts as a signaling molecule in regulating chlorophyll and protein synthesis and degradation, photosynthetic rates, and the metabolism of sugars, lipids, and secondary metabolites through modulating the transcription of related genes and crosstalk with hormone signals (Arnao et al., 2021, 2022; Lee et al., 2022; Yang et al., 2022).
Secondary metabolites are essential for plant defence and hence crop yield. Application of exogenous melatonin can regulate the levels of phenolic compounds, glucosinolates, and terpenoids (Arnao et al., 2022). In this special issue, Zhao et al. (2022) show that applied melatonin and endogenous phytomelatonin enhance stem strength in herbaceous peony and tobacco plants by increasing lignin content and the S/G lignin compositional ratio. Phytomelatonin might have dual roles in the biosynthesis of flavonoids; for example, exogenous melatonin can induce flavonoid biosynthesis under stress, after harvest, and in conditions of leaf senescence and endogenous phytomelatonin plays a negative role in the biosynthesis of flavonoids under normal growth conditions (Chen et al., 2022). For instance, melatonin increases luteolin biosynthesis and up-regulates the expression of related genes in salt-stressed pigeon pea plants (Song et al., 2022), which might be associated with maintenance of antioxidant capacity under stress conditions (Chen et al., 2022). However, exogenous melatonin and endogenous phytomelatonin have a comparable negative effect on the biosynthesis of anthocyanins in Arabidopsis, rice, and alfalfa (Chen et al., 2022).

Conclusions and future directions

During the past two decades, at least 1000 articles have been published about the physiological functions of phytomelatonin. The number of such studies is expected to increase in the coming years (Arnao et al., 2022), indicating that phytomelatonin is now a very active research area in plant science.

Plant hormones are chemical compounds present in very low concentrations that act at or near the site of synthesis, or in distant tissues to regulate all aspects of plant growth, development, and environmental responses (Santer, et al., 2009). Biosynthesis pathways of phytomelatonin have been well characterized in many plant species (Arnao et al., 2022; G. Liu et al., 2022; Y. Liu et al., 2022). The identification of the phytomelatonin receptor PMTR1 in Arabidopsis and its homologous proteins in alfalfa, tobacco, maize, and cassava should lead to exciting models of the perception and functioning of this new phytohormone (Bai et al., 2022; Chen et al., 2022). Phytomelatonin is distributed in almost all tissues (e.g. roots, stems, leaves, flowers, fruits, and seeds) and is involved in nearly all physiological processes (Box 1), and several phytomelatonin-mediated functions are dependent on PMTR1, including seed development and germination, shoot growth, flowering, fruit development and ripening, stomatal closure, and biotic and abiotic stresses (Chen et al., 2022).

Although phytomelatonin is becoming well established as a new plant hormone (Arnao and Hernández-Ruiz, 2019; Chen et al., 2022; Li et al., 2022; J. Wei et al., 2018), there are many issues that remain to be resolved.

(1) Phytomelatonin transport. Phytomelatonin is structurally similar to auxin, which need various types of transporters for distribution to the respective basal parts after being synthesized in the apices of shoots and roots. In animals, the glucose transporter GLUT1 and the oligopeptide transporters PEPT1/2 have been proposed to transport melatonin across plasma and mitochondrial membranes. Local and long-distance transport of phytomelatonin may have an essential role in many aspects of plant growth and development, and in stress responses. Identification of phytomelatonin transporters in future studies should help uncover the mysteries of this new phytohormone.

(2) Phytomelatonin receptors and signaling transduction pathways. Although several studies have found that PMTR1 plays important roles in perceiving phytomelatonin in plant growth and development, and in stress resistance, examination of the underlying signal-transduction pathways is still a nascent field. For example, do plants contain other phytomelatonin receptors? How does PMTR1 regulate the G protein and MAPK cascades? Are there any transcription factors involved in the phytomelatonin-mediated expression of large numbers of genes?

(3) The use of phytomelatonin in agriculture. Exogenous melatonin affects a broad range of physiological processes and has been shown to have significant potential in agricultural practices; for example, in improving photosynthesis and crop production, in delaying flowering time and extending the postharvest life of fruit, in regulating seed development and germination, and in increasing contents of valuable secondary metabolites. In addition, the application of natural phytomelatonin-rich plant extracts as alternative growth regulators for crops is an interesting area of study (Hernández-Ruiz et al., 2021). The cultivation of crops with modified endogenous phytomelatonin concentrations or signaling components via the use of current plant molecular and genetic methods might also be in the subject of future studies.

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Author contributions

CQ and MBA conceived this work; QC wrote and revised the manuscript with suggestions from MBA.

Conflict of interest

The authors declare that they have no conflicts of interest in relation to this work.
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