

# Melatonin: plant growth regulator and/or biostimulator during stress?

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**Melatonin regulates the growth of roots, shoots, and explants, to activate seed germination and rhizogenesis and to delay induced leaf senescence. The antioxidant properties of melatonin would seem to explain, at least partially, its ability to fortify plants subjected to abiotic stress. In this Review we examine recent data on the gene-regulation capacity of melatonin that point to many interesting features, such as the upregulation of anti-stress genes and recent aspects of the auxin-independent effects of melatonin as a plant growth regulator. This, together with the recent data on endogenous melatonin biosynthesis induction by environmental factors, makes melatonin an interesting candidate for use as a natural biostimulating treatment for field crops.**

## Melatonin in plants: discovery and roles

Melatonin (*N*-acetyl-5-methoxytryptamine) was discovered in 1958 in the bovine pineal gland [1]. It is one of the best-studied biological molecules and its role has been explored in mammals, birds, amphibians, reptiles, and fish. Melatonin has many physiological roles in animals [2–5], influencing circadian rhythms, mood, sleep, body temperature, locomotor activity, food intake, retina physiology, sexual behavior, seasonal reproduction, and the immune system [6]. Melatonin acts as a signal of darkness, providing information to the brain and peripheral organs and serving as an endogenous synchronizer for physiological rhythms (e.g., sleep–wake cycles, seasonal reproduction, and endocrine release cycles). Alterations in rhythmic melatonin production have been associated with many disorders [2,7,8] such as Alzheimer's and Parkinson's syndrome [9], glaucoma, multiple sclerosis, depression, insomnia, chronic fatigue syndrome, schizophrenia, anxiety, metabolic syndrome, osteoporosis, and some types of cancer [10,11].

Thirty years after the discovery of melatonin in mammals, the detection of melatonin in the unicellular dinoflagellate *Lingulodinium polyedrum* (synonym *Gonyaulax polyedra*) completely altered the way in which this methoxyindole was regarded [12]. In 1993 melatonin was detected in Japanese morning glory (*Pharbitis nil*), although these results were not published extensively until 1995 [13]. The almost simultaneous publication of two

papers on edible plants in 1995 unequivocally demonstrated the existence of melatonin in higher plants [14,15]. Since that time, successive studies have quantified the presence of melatonin in many plants [16], and it is now accepted that melatonin is present in all kingdoms, from prokaryotes to eukaryotes, from animals to plants [17–21]. The term 'phytomelatonin' was suggested in 2004 [22]. However, the presence of melatonin in lichens has not yet been investigated, and there is still only limited information about melatonin in fungi, bacteria, and non-vascular plants.

In the past 2–3 years there has been much progress in unraveling the role of melatonin in plants, and the number of publications has undergone an exponential increase, underlining the growing interest in this topic. Melatonin functions as a chronoregulator in mammals and birds: its role in photoperiodic regulation had been demonstrated based on the duration and timing of the melatonin signal [3,5,23]. Initial investigations in plants explored whether melatonin played a similar chronoregulatory role in plants. Melatonin levels have been reported to oscillate in some species, such as goosefoot (*Chenopodium rubrum*) [24], water hyacinth (*Eichhornia crassipes*) [25], grape vine (*Vitis vinifera*) [26], sweet cherry (*Prunus avium*) [27], and the green macroalga *Ulva* sp. [28]. This rhythmic behavior, which is dependent on light–dark cycles, could be a regulatory element in photoperiodism such as flowering. Although the influence of light and other environmental factors on endogenous levels of melatonin has been demonstrated (discussed below), there are no conclusive data on its true role in the circadian rhythms of plants [29].

Various studies have suggested specific physiological actions for melatonin in plants, where it can act as a growth regulator [30,31], governing the growth of roots, shoots and explants [32–34], activate rhizogenesis [35], and delay-induced leaf senescence [36]. The natural antioxidant capacity of melatonin might explain some of its physiological actions: for example, its ability to fortify plants subjected to abiotic stresses such as drought, cold, heat, salinity, chemical pollutants, herbicides, and UV irradiation makes melatonin an interesting candidate for use as a natural biostimulating substance for treating field crops [16,37,38]. We review here recent studies on the gene-regulation capacity of melatonin and on the relationship between melatonin and chemical or environmental factors ([29,30,39–41] for further reviews), and discuss the potential for melatonin to be used as both a plant growth regulator and as a biostimulator in stress situations.

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### Melatonin as a plant growth regulator

A range of different functions of melatonin have been investigated in higher plants, some more thoroughly than others, but in all cases the data are scarce (Table 1). Among the studies that have tried to identify a specific role for melatonin in plants, its role as a possible growth regulator has been widely discussed. Melatonin acts as a growth promoter in etiolated lupin (*Lupinus albus*), acting in a similar way as auxin, indolyl-3-acetic acid (IAA), and induces active growth of hypocotyls at micromolar concentrations while having an inhibitory effect at high concentrations. The growth-promoting effect of melatonin is 63% that of IAA, which is a considerable auxinic effect [33]. In a similar study, using several monocots, oat (*Avena sativa*), wheat (*Triticum aestivum*), barley (*Hordeum vulgare*), and canary grass (*Phalaris canariensis*), the growth-promoting activity of melatonin ranged from 10% that of IAA in oat coleoptiles to 55% in barley coleoptiles. Furthermore, similarly to IAA, melatonin showed a concentration-dependent growth-inhibitory effect on the roots, ranging from 56% that of IAA in canary grass to 86% in wheat root [34]. The endogenous level of IAA and melatonin showed similar values, between 25 and 150 ng/g fresh weight; however, in the cases of barley and oat the coleoptile melatonin levels were significantly higher than those of IAA, suggesting possible co-action in some tissues [34]. These promoting and inhibitory effects of melatonin, depending on the concentration, have also been described in red cabbage (*Brassica oleracea rubrum*) [42]. In mustard (*Brassica juncea*) roots, 0.1  $\mu$ M melatonin has been shown to have a stimulatory effect on root growth, whereas 100  $\mu$ M has an inhibitory effect. Furthermore, endogenous free IAA levels increase at low melatonin concentrations. The authors suggested that the stimulation of root growth by low concentrations of melatonin was triggered by melatonin-stimulated IAA biosynthesis, although the specific relationship between IAA and melatonin is unclear [43].

Experiments with transgenic rice (*Oryza sativa*) seedlings overexpressing sheep serotonin *N*-acetyltransferase

(SNAT; the penultimate enzyme of the melatonin biosynthetic pathway; Box 1) showed enhanced (twofold) seminal root growth, which correlated with the production of 10-fold higher levels of melatonin in their shoots relative to wild type seedlings, pointing to a direct relationship between the endogenous melatonin level and root growth-rate [44]. The growth-promoting effect has also been observed in lupin cotyledons, which expanded in the presence of exogenous melatonin [45].

Another well-known physiological action of auxin is its capacity to induce changes in the organogenic pattern of plants. The role of melatonin in the induction of rhizogenesis was first demonstrated in 2007 [35]. Melatonin induced root primordials from pericycle cells in lupin, resulting in the generation of adventitious or lateral roots. This rhizogenic effect has recently been confirmed in cucumber (*Cucumis sativus*) [46], four cherry rootstocks (*Prunus cerasus*; *P. cerasus*  $\times$  *P. canescens*; *P. avium*  $\times$  *P. mahaleb*; *P. avium*  $\times$  *P. cerasus*) [47,48], rice [44], and pomegranate (*Punica granatum*) [49].

In an analysis of the auxin-inducible gene expression marker DR5:GUS in roots of *Arabidopsis* (*A. thaliana*), transgenic lines treated with either IAA, the synthetic auxin 1-*N*-naphthaleneacetic acid (NAA), or melatonin, only IAA and NAA resulted in increased GUS activity throughout the primary and lateral root meristems. By contrast, DR5:GUS seedlings treated with three different melatonin concentrations did not show any increase in GUS expression, but did show a staining pattern similar to that obtained in control seedlings [50], which supports data showing that the early response activation of auxin signaling by IAA is not mimicked by melatonin [51]. Curiously, this inability of melatonin to induce auxin-responsive gene expression does not mean that it cannot activate the promotion of lateral roots. Whole-transcriptome sequencing (RNA-seq) analysis of a collection of cucumber roots with and without melatonin treatment generated 16 866 670 sequence reads aligned with 17 920 genes, which has provided abundant data for the analysis of lateral root formation. The expression of 121 genes was significantly

**Table 1. Functions of phytomelatonin in higher plants**

	Physiological action of melatonin	Refs
Vegetative development	Activates the growth of diverse seedlings	[33,34,42,45]
	Activates or inhibits the growth of primary roots	[34,43,44]
	Promotes lateral and adventitious rooting in several species	[35,44,46–49,52]
	Modifies the development pattern of stems and leaves (branching)	[54,55]
	Delays chlorophylls lost during leaf-induced senescence	[36,46,56,58,59]
	Enhances photosynthesis, CO <sub>2</sub> uptake and biomass	[28,46,48,56,60,81]
	Promotes rhizogenesis and caulogenesis in explant cultures	[31,32,53]
	Cryopreserves callus or shoot tips for long-term storage	[73–75]
	Functions as a chronoregulator	[24–28]
Reproductive development	Affects different stages of floration in several species	[81,88–91]
	Levels are altered during fruit development and seed formation in several species	[27,62,90,92–95]
Stress environment	Affects growth of plants subjected to stress situations, e.g., low and high temperatures, drought, UV irradiation, chemical stressors, and herbicides	[46,55,56,58,63,64,70,71,76,77,79–82,96,97]
	Provokes an increase in the proline level in stressed plants	[48]
	Increases the germination rate of stressed seeds	[42,46,65,72,98]
	Improves resistance to the fungal pathogen <i>Diplocarpon mali</i> in inoculated apple ( <i>Malus prunifolia</i> ) trees, mitigating premature defoliation and pathogen expansion	[99]

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