

· 专题论坛 ·

## 褪黑素参与植物抗逆功能研究进展

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**摘要** 褪黑素(*N*-乙酰基-5-甲氧基色胺)是一种生命必需的小分子吲哚胺类物质, 广泛存在于动植物体内, 对动植物的生长发育起至关重要的作用。随着植物褪黑素研究的逐渐深入, 褪黑素在植物体内的合成途径及作用也更加明确。研究表明, 褪黑素在提高植物抵抗非生物和生物胁迫能力等方面具有调控作用。该文对近年来有关植物褪黑素参与非生物和生物胁迫的研究进展进行总结, 旨在为阐明褪黑素影响植物抵御逆境胁迫的调控机理提供参考。

**关键词** 褪黑素, 生物合成, 生长发育, 非生物和生物胁迫

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褪黑素(melatonin, MT)又称褪黑激素、松果体素等, 是一种生命必需的小分子吲哚胺类物质。20世纪初, 人们发现有一种物质可以使蛙皮肤中的黑色素褪变成白色。Lerner等(1958)从牛松果体内分离提取出该物质并鉴定其化学结构, 证明该物质是色氨酸衍生物, 分子式为 $C_{13}H_{16}N_2O_2$ , 化学名称为*N*-乙酰基-5-甲氧基色胺(*N*-acetyl-5-methoxytryptamine) (图1)。

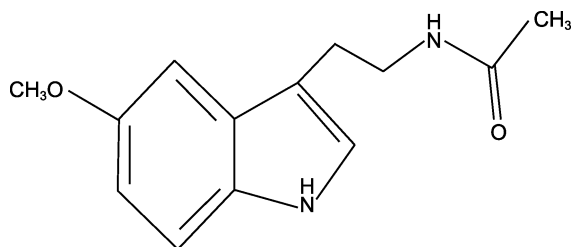


图1 褪黑素的化学结构

Figure 1 The chemical structure of melatonin

长期以来, 人们普遍认为褪黑素作为一种神经内分泌激素仅在动物体内广泛存在。随着研究的深入, 发现褪黑素是一种分布广泛的小分子活性物质, 存在于细菌、微生物、真菌、藻类以及动物和植物绝大多数有机体中(Tan et al., 2003)。1993年, Van Tassel

和O'Neill采用放射免疫分析法(radioimmunoassay, RIA)和气相色谱-质谱联用(gas chromatography-mass spectrometry, GC-MS)方法在高等植物牵牛花(*Pharbitis nil*)和番茄(*Lycopersicon esculentum*)果实中检测到褪黑素(van Tassel et al., 2001)。Dubbels等(1995)采用RIA和高效液相色谱-质谱联用(high performance liquid chromatography-mass spectrometry, HPLC-MS)方法测定了烟草(*Nicotiana tabacum*)、香蕉(*Musa nana*)和甜菜(*Beta vulgaris*)等多种植物中褪黑素的含量, 其中烟草老叶中含量最高( $862 \mu\text{g}\cdot\text{g}^{-1}$ )。同年, Hattori等(1995)利用RIA和HPLC方法对粮食作物、蔬菜和果树中的褪黑素进行了检测。Chen等(2003)测定了108种药用植物中的褪黑素含量, 其中钩藤(*Uncaria rhynchophylla*)、紫花地丁(*Viola philippica*)和石崖茶叶(*Babreum coscluea*) 3种中草药中褪黑素的含量分别高达2.46、2.37和 $2.12 \mu\text{g}\cdot\text{g}^{-1}$  (表1)。

### 1 褪黑素在植物体中的生物合成

动物体内褪黑素的合成和分泌途径研究较多, 其主要由动物大脑中的松果体细胞将摄入的色氨酸, 在4种酶的参与下经4步连续酶促反应转化成褪黑素

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表1 部分植物中褪黑素含量

Table 1 Melatonin content in some plants

科	种	器官	褪黑素含量	参考文献
禾本科(Poaceae)	水稻( <i>Oryza sativa</i> )	种子	96.5 ng·g <sup>-1</sup> DW	王金英等, 2009
			27.6–47.8 ng·g <sup>-1</sup> DW	Setyaningsih et al., 2015
	玉米( <i>Zea mays</i> )	种子	16 ng·g <sup>-1</sup> DW	王金英等, 2009
	甜玉米( <i>Z. mays</i> )	种子	1.37 ng·g <sup>-1</sup> FW	Hattori et al., 1995
	燕麦( <i>Avena sativa</i> )	种子	1.80 ng·g <sup>-1</sup> FW	Hattori et al., 1995
菊科(Asteraceae)	大麦( <i>Hordeum vulgare</i> )	种子	378.1 pg·g <sup>-1</sup> FW	Hattori et al., 1995
十字花科(Brassicaceae)	茼蒿( <i>Glebionis coronarium</i> )	叶	416.80 pg·g <sup>-1</sup> FW	Hattori et al., 1995
十字花科(Brassicaceae)	萝卜( <i>Raphanus sativus</i> )	根	657.20 pg·g <sup>-1</sup> FW	Hattori et al., 1995
十字花科(Brassicaceae)	白菜( <i>Brassica rapa</i> var. <i>glabra</i> )	叶	112.50 pg·g <sup>-1</sup> FW	Hattori et al., 1995
十字花科(Brassicaceae)	甘蓝( <i>B. oleracea</i> )	叶	107.40 pg·g <sup>-1</sup> FW	Hattori et al., 1995
藜科(Chenopodiaceae)	甜菜( <i>Beta vulgaris</i> )	根	2 pg·g <sup>-1</sup> FW	Dubbels et al., 1995
葫芦科(Cucurbitaceae)	黄瓜( <i>Cucumis sativus</i> )	种子	11 ng·g <sup>-1</sup> FW	Posmyk et al., 2009
		果实	24.6 pg·g <sup>-1</sup> FW	Hattori et al., 1995
		果实	86 pg·g <sup>-1</sup> FW	Dubbels et al., 1995
百合科(Liliaceae)	洋葱( <i>Allium cepa</i> )	球茎	31.50 pg·g <sup>-1</sup> FW	Hattori et al., 1995
茄科(Solanaceae)	番茄( <i>Lycopersicon esculentum</i> )	叶	14.5 ng·g <sup>-1</sup> FW	胡永静等, 2019
		茎	2.80 ng·g <sup>-1</sup> FW	胡永静等, 2019
		果实	2.50 ng·g <sup>-1</sup> FW	Okazaki and Ezura, 2009
			32.20 pg·g <sup>-1</sup> FW	Hattori et al., 1995
		果实	1.12–5.06 ng·g <sup>-1</sup> FW	Dubbels et al., 1995
伞形科(Umbelliferae)	芹菜( <i>Apium graveolens</i> )	种子	7 ng·g <sup>-1</sup> DW	Manchester et al., 2000
凤梨科(Bromeliaceae)	菠萝( <i>Ananas comosus</i> )	果实	36.2 pg·g <sup>-1</sup> FW	Hattori et al., 1995
胡桃科(Juglandaceae)	核桃( <i>Juglans regia</i> )	种子	3.5 ng·g <sup>-1</sup> DW	Reiter et al., 2005
芭蕉科(Musaceae)	香蕉( <i>Musa nana</i> )	果实	8.9 pg·g <sup>-1</sup> FW	Sae-Teaw et al., 2013
			4.66 ng·g <sup>-1</sup> FW	Dubbels et al., 1995
石榴科(Punicaceae)	石榴( <i>Punica granatum</i> )	种子	0.54–5.5 ng·g <sup>-1</sup> FW	Mena et al., 2012
鼠李科(Rhamnaceae)	大枣( <i>Ziziphus jujuba</i> )	果实	146 ng·g <sup>-1</sup> DW	Chen et al., 2003
蔷薇科(Rosaceae)	甜樱桃( <i>Cerasus avium</i> )	叶	4.8–21.2 μg·g <sup>-1</sup> FW	李玲等, 2019
			2.48 μg·g <sup>-1</sup> FW	Wang et al., 2020
茄科(Solanaceae)	苹果( <i>Malus pumila</i> )	果实	47.6 pg·g <sup>-1</sup> FW	Hattori et al., 1995
茄科(Solanaceae)	枸杞( <i>Lycium chinense</i> )	叶	12.4 μg·g <sup>-1</sup> FW	赵建芬等, 2015
葡萄科(Vitaceae)	赤霞珠葡萄( <i>Vitis vinifera</i> cv. 'Cabernet Sauvignon')	果皮	800 pg·g <sup>-1</sup>	Steger et al., 2010
			420 pg·g <sup>-1</sup>	Iriti et al., 2006
葡萄科(Vitaceae)	霞多丽葡萄( <i>V. vinifera</i> cv. 'Chardonnay')	果皮	600 pg·g <sup>-1</sup>	Steger et al., 2010
五加科(Araliaceae)	三七( <i>Panax notoginseng</i> )		169 ng·g <sup>-1</sup> DW	Chen et al., 2003
菊科(Asteraceae)	青蒿( <i>Artemisia carvifolia</i> )		84 ng·g <sup>-1</sup> DW	Chen et al., 2003
十字花科(Brassicaceae)	板蓝根( <i>Isatis indigotica</i> )		79 ng·g <sup>-1</sup> DW	Chen et al., 2003
忍冬科(Caprifoliaceae)	金银花( <i>Lonicera japonica</i> )		140 ng·g <sup>-1</sup> DW	Chen et al., 2003
豆科(Fabaceae)	黄芪( <i>Astragalus mongholicus</i> )		178 ng·g <sup>-1</sup> DW	Chen et al., 2003
豆科(Fabaceae)	甘草( <i>Glycyrrhiza uralensis</i> )		112 ng·g <sup>-1</sup> DW	Chen et al., 2003
唇形科(Labiatae)	藿香( <i>Agastache rugosa</i> )		302 ng·g <sup>-1</sup> DW	Chen et al., 2003
唇形科(Labiatae)	丹参( <i>Salvia miltiorrhiza</i> )		187 ng·g <sup>-1</sup> DW	Chen et al., 2003
唇形科(Labiatae)	夏枯草( <i>Prunella vulgaris</i> )		34 ng·g <sup>-1</sup> DW	Chen et al., 2003
百合科(Liliaceae)	芦荟( <i>Aloe vera</i> )	叶	46.60 ng·g <sup>-1</sup> FW	赵建芬等, 2015
			516 ng·g <sup>-1</sup> DW	Chen et al., 2003
木兰科(Magnoliaceae)	五味子( <i>Schisandra chinensis</i> )		86 ng·g <sup>-1</sup> DW	Chen et al., 2003
木樨科(Oleaceae)	连翘( <i>Forsythia suspensa</i> )		45 ng·g <sup>-1</sup> DW	Chen et al., 2003

表 1 (续)  
Table 1 (continued)

科	种	器官	褪黑素含量	参考文献
蓼科(Polygonaceae)	大黄( <i>Rheum palmatum</i> )		1.08 $\mu\text{g}\cdot\text{g}^{-1}$ DW	Chen et al., 2003
马齿苋科(Portulacaceae)	马齿苋( <i>Portulaca oleracea</i> )		686.17 $\text{ng}\cdot\text{g}^{-1}$ DW	瞿星洪和可燕, 2021
毛茛科(Ranunculaceae)	黄连( <i>Coptis chinensis</i> )		1.01 $\mu\text{g}\cdot\text{g}^{-1}$ DW	Chen et al., 2003
	芍药( <i>Paeonia lactiflora</i> )		0.61–1.45 $\text{ng}\cdot\text{g}^{-1}$ FW	石文波等, 2021
茜草科(Rubiaceae)	钩藤( <i>Uncaria rhynchophylla</i> )		2.46 $\mu\text{g}\cdot\text{g}^{-1}$ DW	Chen et al., 2003
玄参科(Scrophulariaceae)	地黄( <i>Rehmannia glutinosa</i> )		97 $\text{ng}\cdot\text{g}^{-1}$ DW	Chen et al., 2003
山茶科(Theaceae)	石崖茶叶( <i>Babreum coscluea</i> )		2.12 $\mu\text{g}\cdot\text{g}^{-1}$ DW	Chen et al., 2003
伞形科(Umbelliferae)	当归( <i>Angelica sinensis</i> )		698 $\text{ng}\cdot\text{g}^{-1}$ DW	Chen et al., 2003
堇菜科(Violaceae)	紫花地丁( <i>Viola philippica</i> )		2.37 $\mu\text{g}\cdot\text{g}^{-1}$ DW	Chen et al., 2003

FW: 鲜重; DW: 干重      FW: Fresh weight; DW: Dry weight

(Fernández-Mar et al., 2012)。植物中褪黑素的合成规律及作用研究起步较晚, 研究者采用<sup>14</sup>C标记的色氨酸体外供给贯叶连翘(*Hypericum perforatum*), 发现植物中褪黑素的合成途径与动物相似, 前体物质均为色氨酸(Murch, 2000, 2001)。

植物体内的褪黑素由色氨酸经过4步连续的酶促反应转化而成, 至少需要6种酶参与, 即色氨酸羟化酶(tryptophan hydroxylase, TPH)、色氨酸脱羧酶(tryptophan decarboxylase, TDC)、色胺-5-羟化酶(tryptamine 5-hydroxylase, T5H)、5-羟色胺-*N*-乙酰基转移酶(serotonin *N*-acetyltransferase, SNAT)、*N*-乙酰基-5-羟色胺-甲基转移酶(*N*-acetylserotonin methyltransferase, ASMT)以及咖啡酸-*O*-甲基转移酶(caffeic acid *O*-methyltransferase, COMT) (Back et al., 2016)。其中TDC、ASMT和COMT是植物褪黑素合成过程中的限速酶(Zhao et al., 2018)。

截至目前, 在植物中已经发现5条褪黑素生物合成途径, 其中4条途径中都含有1种重要的中间产物5-羟色胺。此外, 色胺还可经过SNAT的乙酰化转化为*N*-乙酰色胺, 再经T5H的羟基化合成*N*-乙酰-5-羟色胺, 随后*N*-乙酰-5-羟色胺在ASMT或COMT的催化作用下生成褪黑素(Arnao and Hernández-Ruiz, 2018) (图2)。*N*-乙酰-5-羟色胺可在*N*-乙酰羟色胺脱乙酰酶(*N*-acetylserotonin deacetylase, ASDAC)的作用下乙酰化形成5-羟色胺(Lee et al., 2018)。色胺是植物生长素(auxin, IAA)的前体, 其也可形成吲哚乙酸, 与5-羟色胺的合成形成竞争关系, 因此, 吲哚乙酸与褪黑素和5-羟色胺的合成直接相关(Reiter et al., 2001)。

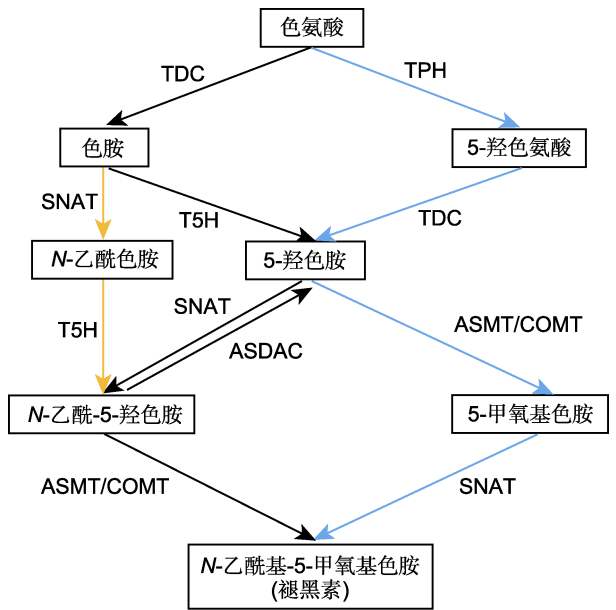


图2 褪黑素在植物中的生物合成途径(Tan et al., 2015; Back et al., 2016)

图中黑色箭头表示褪黑素合成的经典途径, 蓝色和橙色箭头表示褪黑素合成的其它途径。TDC: 色氨酸脱羧酶; TPH: 色氨酸羟化酶; T5H: 色胺-5-羟化酶; SNAT: 5-羟色胺-*N*-乙酰基转移酶; ASMT: *N*-乙酰基-5-羟色胺-甲基转移酶; COMT: 咖啡酸-*O*-甲基转移酶; ASDAC: *N*-乙酰羟色胺脱乙酰酶

Figure 2 Biosynthesis pathways of melatonin in plant (Tan et al., 2015; Back et al., 2016)

The black arrows in the figure indicate the classical pathway of melatonin synthesis, and the blue and orange arrows indicate other pathways of melatonin synthesis. TDC: Tryptophan decarboxylase; TPH: Tryptophan hydroxylase; T5H: Tryptamine 5-hydroxylase; SNAT: Serotonin *N*-acetyltransferase; ASMT: *N*-acetylserotonin methyltransferase; COMT: Caffeic acid *O*-methyltransferase; ASDAC: *N*-acetylserotonin deacetylase

## 2 褪黑素在植物生长发育中的作用

褪黑素在植物中有多种功能,如对种子萌发起促进作用。外源褪黑素处理可提高黄瓜(*Cucumis sativus*)和棉花(*Gossypium hirsutum*)种子萌发率,低浓度褪黑素促进种子萌发而高浓度抑制萌发(Posmyk et al., 2009; Xiao et al., 2019)。在培养基中添加 $1.0\text{ mg}\cdot\text{L}^{-1}$ 褪黑素可提高葡萄(*Vitis vinifera*)愈伤组织和体细胞胚的诱导率(雅蓉等, 2020);添加 $0.6\text{ mg}\cdot\text{L}^{-1}$ 褪黑素可提高霞多丽葡萄种子的萌发率以及初生子叶胚诱导产生体细胞胚的诱导率(张莹等, 2021)。褪黑素参与调控植物根部发育。Chen等(2009)用 $0.1\text{ mmol}\cdot\text{L}^{-1}$ 褪黑素处理芥菜(*Brassica juncea*)幼苗,发现低浓度褪黑素对幼苗根部生长具有促进作用。外源褪黑素可显著促进拟南芥(*Arabidopsis thaliana*)幼苗侧根和不定根的生长(Pelagio-Flores et al., 2012)。

褪黑素还可调节植物的碳氮代谢、调控果实发育、影响果实成熟以及改善果实品质并提高产量(Erdal, 2019)。外源褪黑素能够上调乙烯合成关键酶1-氨基环丙烷-1-羧酸合酶(1-aminocyclopropane-1-carboxylate synthase)合成基因ACS、1-氨基环丙烷-1-羧酸氧化酶(1-aminocyclopropane-1-carboxylate oxidase)合成基因ACO和乙烯响应转录因子ERFs (ethylene response factors)的表达,促进果实转色和成熟(Sun et al., 2015; 许丽丽等, 2017)。向番茄叶面喷施 $20\text{ mg}\cdot\text{L}^{-1}$ 褪黑素既能提高果实中可溶性总糖、维生素C和番茄红素的含量,又能提高番茄产量(Ibrahim et al., 2020)。 $120\text{ }\mu\text{mol}\cdot\text{L}^{-1}$ 褪黑素处理可显著提高苦瓜(*Momordica charantia*)中可溶性固形物、可溶性糖、可溶性蛋白质和维生素C的含量,促进苦瓜中酚类和黄酮类化合物的合成(Lin et al., 2020)。在桃(*Amygdalus persica*)果实膨大期对其叶片喷施褪黑素可增加桃果实单果重及纵横径,提高果实中维生素C、蔗糖、果糖和山梨醇的含量,降低果实硬度(吴彩芳等, 2021)。

## 3 植物褪黑素的抗氧化作用

20世纪90年代, Tan等(1993)报道褪黑素具有抗氧化作用。研究表明,褪黑素是一种高效的内源性自由基清除剂,可以有效清除羟自由基( $\cdot\text{OH}$ )、硝基自由基( $\cdot\text{ONOO}^-$ )、脂质过氧化自由基( $\text{LOO}^\cdot$ )、超氧阴离子

自由基( $\text{O}_2^\cdot$ )、过氧化氢( $\text{H}_2\text{O}_2$ )和一氧化氮自由基( $\text{NO}^\cdot$ )等(Zhang and Zhang, 2015)。其抗氧化能力是维生素E的2倍,谷胱甘肽(glutathione, GSH)的4倍,甘露醇的14倍(Pieri et al., 1995)。

褪黑素很可能是植物抵御氧化胁迫的第一道防线,褪黑素可提高植物的抗氧化能力,降低逆境引发的氧化胁迫对植物生长发育的影响(Zhang et al., 2013)。Bawa等(2020)发现,外源褪黑素处理可增强低温胁迫下大豆(*Glycine max*)幼苗超氧化物歧化酶(superoxide dismutase, SOD)、过氧化物酶(oxidase, POD)、过氧化氢酶(catalase, CAT)和抗坏血酸过氧化物酶(ascorbate peroxidase, APX)的活性,显著增加矿质元素P、K、Ca、Mg的浓度和渗透调节物质脯氨酸(proline, Pro)、可溶性糖及可溶性蛋白的含量,减少丙二醛(malondialdehyde, MDA)的积累,提高大豆幼苗的耐低温能力。用褪黑素处理高温胁迫下的植物可显著提高其SOD、POD、CAT、APX和谷胱甘肽还原酶(glutathione reductase, GR)等抗氧化酶活性,增加非酶抗氧化物质如抗坏血酸(ascorbic acid, AsA)、GSH、酚类和类黄酮的含量,增强植物耐热性(Liang et al., 2018b; Jia et al., 2019; 夏惠等, 2019)。用外源褪黑素处理干旱胁迫下的植物可增强抗氧化酶和AsA-GSH循环中相关酶APX、GR、谷胱甘肽过氧化物酶(glutathione peroxidase, GPX)、谷胱甘肽S-转移酶(glutathione S-transferase, GST)、脱氢抗坏血酸还原酶(dehydroascorbate reductase, DHAR)及单脱氢抗坏血酸还原酶(monodehydroascorbate reductase, MDHAR)的活性,增加抗氧化物质AsA和GSH的含量,减少 $\text{H}_2\text{O}_2$ 、 $\text{O}_2^\cdot$ 和MDA的积累,缓解干旱胁迫造成的氧化损伤,增强植物的耐旱性(Cui et al., 2017; Khan et al., 2019; Liu et al., 2021a)。外源褪黑素通过提高抗氧化酶(POD、SOD、CAT和APX)的活性以及非酶抗氧化物质(AsA和GSH)、酚类物质(总酚、总黄酮和总黄烷醇)和渗透调节物质(Pro、可溶性糖和可溶性蛋白)的含量,抑制活性氧的产生,减轻脂质过氧化,从而缓解盐溶液对玉米(*Zea mays*) (Chen et al., 2018; Ahmad et al., 2021)、油菜(*B. napus*) (Zeng et al., 2018)和猕猴桃(*Actinidia chinensis*) (高帆等, 2018)幼苗造成的损害。此外,褪黑素处理可以上调SOD、POD、CAT、GR、APX、GPX和GST等基因的表达,增强植物体

内抗氧化酶活性并清除活性氧自由基,从而使植物免受氧化损伤,提高其对逆境的抵抗能力(Martinez et al., 2018; Zhao et al., 2019; Shang et al., 2021)。

## 4 褪黑素在植物抵抗非生物胁迫中的作用

### 4.1 抗低温胁迫

作为主要的非生物胁迫之一,低温胁迫影响植物细胞膜的流动性和酶活力,抑制光合作用和营养物质的转运,造成植物体受损伤,导致作物减产。外源褪黑素能减缓低温胁迫下玉米幼苗中矿质元素K、P、S、Mg、Fe、Cu、Mn和Zn的浓度降低,增加Ca和B的浓度,同时增强抗氧化酶活性,进而提高植物的耐寒性(Turk and Erdal, 2015)。100  $\mu\text{mol}\cdot\text{L}^{-1}$ 外源褪黑素处理可显著提高番茄幼苗叶片中光系统I (photosystem I, PSI)和光系统II (photosystem II, PSII)光合电子传递速率,保护类囊体膜免受低温胁迫损伤(Yang et al., 2018);外源褪黑素还能增强石榴(*Punica granatum*)果实中抗氧化酶活性,降低多酚氧化酶(polyphenol oxidase, PPO)活性及MDA含量,促进多酚类物质的积累,保持细胞膜的完整性,增强抗寒能力(周洲, 2019)。

拟南芥转录因子CBFs (C-repeat binding factors)在低温信号途径中发挥重要调控作用。30  $\mu\text{mol}\cdot\text{L}^{-1}$ 褪黑素处理使低温下拟南芥的株高、主根长度以及幼苗鲜重等显著增加,同时,冷响应相关基因如CBFs、DREBs (dehydration responsive element binding factors)、ZAT10 (zinc finger transcription factor 10)、ZAT12和COR15a (cold regulated gene 15a)的表达量也明显增加,刺激相关抗冷化合物的合成,有助于植物抵御冷胁迫(Bajwa et al., 2014; 刘静妍等, 2017)。低温胁迫下拟南芥体内褪黑素合成量增加,同时ZAT6基因表达量也增加,ZAT6通过结合CBFs启动子中的TACAAT元件增强CBFs的表达,从而提高拟南芥抗寒能力(Shi and Chan, 2014)。Ding等(2017)研究发现,外源褪黑素通过调节冷响应基因CBF、ICE (inducer of CBF expression)和 $\delta 1$ -吡咯啉-5-羧酸合成酶( $\delta 1$ -pyrroline-5-carboxylase synthase)基因P5CS以及卡尔文循环中参与光合碳同化的关键酶SBPase (sedoheptulose 1,7-bisphosphatase)的表

达提高植物的耐寒性。RNA-seq分析显示,褪黑素通过下调一些miRNAs (miR159-5p、miR858、miR8029-3p和novel-m0048-3p)的表达水平,上调低温胁迫下参与相关信号转导的靶基因,如钙依赖蛋白激酶(calcium-dependent protein kinases)基因CDPKs、bHLH、DREB、WRKY和MYB的表达水平,从而提高西瓜(*Citrullus lanatus*)的耐寒性(Li et al., 2016)。用褪黑素处理低温胁迫下的西瓜可显著上调其bZIP、bHLH、WRKY、MYB、HSPs和脂肪氧化酶(lipoxygenase)基因LOX的转录水平,同时上调ERF转录因子基因(cI021070、cI022648和cI017389)和茉莉酸(jasmonic acid, JA)途径中的TIFY7基因的表达,下调脱落酸(abscisic acid, ABA)受体基因PYL8的表达(Li et al., 2017b)。Fu等(2017)发现外源褪黑素可能经ABA依赖途径增加ABA含量,以ABA不依赖途径上调冷应答基因CBF9、CBF14和COR14a的表达,促进冷保护化合物的合成,保护垂穗披碱草(*Elymus nutans*)免受冷损伤。

Lei等(2004)研究发现,用褪黑素处理低温胁迫下的胡萝卜(*Daucus carota*)悬浮细胞,可保持细胞膜结构的稳定性,抑制细胞程序性凋亡产生的DNA有序降解;同时,在褪黑素处理的细胞中检测到腐胺和亚精胺含量显著增加,因此褪黑素对细胞的保护作用可能与多胺的合成有关。随后,张贵友等(2005)发现外源褪黑素处理可提高烟草细胞精胺脱羧酶活性,调节多胺合成,提高烟草抵御冷害的能力。Ding等(2017)研究表明,低温胁迫下褪黑素处理过的植株中腐胺、亚精胺和精胺的含量显著增高,褪黑素通过激活多胺合成酶基因的表达,使细胞内多胺的含量增加,从而保护生物膜和生物大分子。

### 4.2 抗高温胁迫

高温胁迫是影响作物产量和地理分布的重要环境因子之一。高温胁迫下植物体内的活性氧含量剧烈增加,从而造成损伤且影响植物的生长发育。植物中热休克蛋白(heat shock proteins, HSPs)可再折叠损伤的蛋白质,阻止聚合物的形成,在一定程度上有助于植物抵御高温胁迫(Fragkostefanakis et al., 2015)。外源施用褪黑素显著上调热应激反应主要调节因子A1类热休克因子(class A1 heat shock factors)基因HSA1s的表达,继而激活热响应基因HSA32 (heat

*stress associated 32*)、*HSFA2*、*HSP90*和*HSP101*, 提高拟南芥植株的耐热性(Shi et al., 2015b)。周永海等(2020)研究发现, 用外源褪黑素处理甜瓜(*C. melo*)幼苗可强烈诱导*HSP70*、*HSP90*和*HSP101*的表达, 从而促进HSPs的产生, 保护植株免受热胁迫损伤。用 $100\ \mu\text{mol}\cdot\text{L}^{-1}$ 褪黑素处理番茄幼苗可诱导*HSP90*、*HSFA2*、*P5CS*和呼吸爆发氧化酶(respiratory burst oxidase homolog)基因*Rboh*的表达, 上调多胺合成基因*ADC*、*SAMDC*、*SPMS*和*SPDS*的表达, 促进多胺的合成, 有助于清除过量活性氧, 进而提高植物对高温胁迫的抵抗能力(Jahan et al., 2019)。Manafi等(2022)研究表明, 褪黑素通过诱导*HSFA2a*、*HSFB1a*和*HSP90*基因的表达来保护暴露在 $40^{\circ}\text{C}$ 下的草莓(*Fragaria \times ananassa*)植株免受高温损伤。褪黑素通过提高HSPs (*HSP20*、*HSP21*、*HSP70*和*HSP90*)基因的表达量, 降低不溶性和泛素化蛋白的含量, 诱导自噬途径相关基因*ATG6* (*autophagy-related genes 6*)、*ATG8a*、*ATG12*和*ATG18c*的表达, 促进自噬体的形成, 减少聚合蛋白的积累和泛素化, 从而增强植物对热胁迫的耐受性(Xu et al., 2016)。Qi等(2018)研究发现, 对番茄植株浇灌 $20\ \mu\text{mol}\cdot\text{L}^{-1}$ 褪黑素可有效缓解高温诱导的花粉失活和花粉萌发被抑制, 褪黑素通过增强HSPs (*HSP21*和*HSP70*)和ATGs (*ATG6*、*ATG8c*、*ATG12*和*ATG18h*)基因的表达降解变性蛋白, 从而保护细胞器, 表明褪黑素具有保护热胁迫下花粉活性的作用。

此外, 褪黑素通过调节类胡萝卜素合成的2个关键基因*PDS* (*phytoene desaturase*)与*ZDS* (*zeta-carotene desaturase*)以及10种热休克蛋白HSPs基因的表达, 促进类胡萝卜素的生物合成, 从而提高猕猴桃幼苗的耐热性(Xia et al., 2021)。多年生黑麦草(*Lolium perenne*)经外源施用褪黑素, 其内源褪黑素和细胞分裂素(cytokinin, CTK)含量增加, 而ABA含量降低; 褪黑素通过上调CTK生物合成基因*IPT2* (*isopentenyl transferases 2*)和信号应答转录因子B型RRs (type-B response regulators)的表达, 下调ABA生物合成基因*NCED1* (*nine-cis-epoxycarotenoid dioxygenase 1*)和信号转导基因*ABI3* (*ABA insensitive 3*)和*ABI5*的表达, 缓解热胁迫诱导的叶片衰老(Zhang et al., 2017)。赵娜等(2012)发现, 向黄瓜幼苗叶面喷施褪黑素, 可显著增加硝态氮含量, 降

低氨态氮含量, 从而减轻氨态氮积累对黄瓜幼苗造成的毒害, 提高黄瓜幼苗抵御高温胁迫的能力。

### 4.3 抗干旱胁迫

干旱是世界范围内严重威胁农业生产的主要逆境之一, 全球农作物产量损失的一半以上由干旱引发(车永梅等, 2021)。干旱使植物体内水分代谢失衡, 光合作用减弱, 营养物质的合成与转运受阻, 植物生长发育缓慢, 严重时可能造成不可逆转的损伤甚至死亡。外源褪黑素可促进植物根系的生长和茎的增粗(Liang et al., 2019), 增加叶片长度、宽度和气孔的数量(Khan et al., 2019), 增厚植物表皮细胞, 保护叶绿体基粒片层和叶片结构的完整性(Cui et al., 2017), 维持细胞膨压和持水能力, 还可减少光合色素的降解(Huang et al., 2019), 促进PSII电子传递, 增强光合作用, 提高植物对光能的利用效率, 增强植物幼苗抗旱能力, 使其恢复正常生长发育(Fleta-Soriano et al., 2017)。

丝裂原活化蛋白激酶(mitogen-activated protein kinases, MAPKs)级联通路在植物抵抗非生物和生物胁迫的信号转导中起重要作用。NAC、WRKY、MYB和DREB等转录因子是逆境胁迫下植物MAPK信号通路的主要组成部分(董燕梅等, 2020)。干旱胁迫下, 褪黑素通过上调MAPKs (*Asmap1*和*Aspk11*)和WRKY1、DREB2和MYB基因的表达, 调节下游逆境响应基因的表达, 增强植物对干旱胁迫的抵抗力(Gao et al., 2018)。外源褪黑素可调节IAA信号相关基因和油菜素类固醇生物合成基因的转录水平, 激活苯丙烷生物合成和谷胱甘肽代谢途径, 通过上调CNGC (*cyclic nucleotide-gated channel*)、CaM/CML (*calmodulin/calmodulin-like protein*)和CDPK家族基因的表达激活钙信号, 进而调节珙桐(*Davidia involucreata*)对干旱的响应(Liu et al., 2021b)。在干旱胁迫下, 异源过表达褪黑素生物合成关键基因COMT可增加植株体内褪黑素含量, 上调RAB18、RD29A、KIN1、DREB2、WRKY33、MYB和LEA基因的表达, 提高植物的抗旱性(Yang et al., 2019; 孙莎莎等, 2019)。褪黑素和NO相互作用诱导WRKY27和MYB174等转录因子的表达, 增强大豆对干旱胁迫的耐受性(Imran et al., 2021)。

褪黑素可上调碳同化途径中关键基因的转录水平, 如Rubisco (*ribulose biphosphate carboxylase*

oxygenase)、PGK (phosphoglycerate kinase)、RPK (phosphoribulokinase)、GAPDH (glyceraldehyde-3-phosphate dehydrogenase)、FBA (fructose-bisphosphate aldolase)、FBP (fructose-1,6-bisphosphatase)、TIM (triosephosphate isomerase)和RPI (ribose 5-phosphate isomerase), 也可上调氮代谢和氮素吸收相关基因NR (nitrate reductase)、NiR (nitrite reductase)、GS (glutamine synthetase)、GOGAT (glutamate synthase)、AMT (ammonium transporters)和NRT (nitrate transporters)的表达, 这表明外源褪黑素可改善干旱胁迫下植物对营养物质的吸收和运输, 从而增强其耐旱性(Liang et al., 2018a, 2019)。在干旱条件下, 褪黑素介导的JUB1、DREB2A和SAG12 (senescence-associated gene 12)基因表达有利于延缓植物叶片衰老(Wang et al., 2013; Ma et al., 2018)。褪黑素通过调节蜡质生物合成基因KCS1 (ketoacyl-CoA synthase 1)、CER3 (eceriferum3)、TTS1 (triterpenoid synthase 1)和LTP1 (lipid transfer protein 1)的表达, 促进蜡质在植物叶表面沉积, 从而减少水分流失, 增强植物的耐旱性。

此外, 褪黑素处理能下调ABA合成基因NCED3、上调细胞色素P450单氧化酶基因(cytochrome P450 monooxygenases, CYP707A1–4) CYP707A1和CYP707A2的表达, 从而降低干旱胁迫下植物体ABA含量(Li et al., 2015)。Ma等(2018)研究发现, 褪黑素通过上调CTK合成基因IPT和信号转导基因A型和B型RRs、HKs (histidine kinases)和HPs (histidine phosphotransfer)的表达, 下调叶绿素分解代谢基因PPH (pheophytinase)和Chl-PRX (chl-degrading peroxidase)的表达, 进而缓解干旱诱导的植物叶片衰老。

#### 4.4 抗盐碱胁迫

在盐碱胁迫下, 植株同时遭受高pH值、渗透和离子胁迫, 植物体内积累有机溶质的能力增强, 细胞内离子平衡遭到破坏, 进一步损害膜系统(郭淑华等, 2018)。光合作用是自然界最重要的物质和能量代谢过程, 盐碱胁迫造成植物光合作用效率下降。外源褪黑素处理可提高盐胁迫下黄瓜幼苗净光合速率和PSII最大光化学量子产量( $F_v/F_m$ ), 减缓总叶绿素含量的下降(Wang et al., 2016); 减轻盐胁迫下玉米幼苗叶中PSII反应中心蛋白(D1)含量的下降, 增加PSII的S蛋

白亚基(PsbS)含量(Chen et al., 2018); 促进水稻(*Oryza sativa*)幼苗叶片叶黄素循环并增大叶黄素循环库, 以耗散多余光能, 增强关键光合酶的活性(Yan et al., 2021b); 抑制西瓜幼苗的气孔关闭, 促进PSII光能吸收和电子传递(Li et al., 2017a); 提高甜瓜幼苗叶片叶绿素含量, 增强盐胁迫下植物的光合作用(Castañares and Bouzo, 2019)。

褪黑素在维持离子稳态及提高植物对盐碱胁迫的耐受性中起关键作用。外源褪黑素处理能降低盐碱胁迫下番茄叶片中的 $\text{Na}^+$ 含量, 增加 $\text{K}^+$ 含量(Liu et al., 2015); 抑制水稻根系对 $\text{Na}^+$ 的吸收, 促进对 $\text{K}^+$ 和 $\text{Ca}^{2+}$ 的吸收和向上转运(Wei et al., 2021); 提高燕麦(*Avena sativa*)和水稻根系质膜和液泡膜的 $\text{H}^+$ 泵活性, 促进 $\text{Na}^+$ 流出和 $\text{K}^+$ 流入, 维持 $\text{K}^+/\text{Na}^+$ 稳态(Gao et al., 2019; Yan et al., 2021a); 上调苹果(*Malus pumila*)液泡 $\text{Na}^+/\text{H}^+$ 逆向转运蛋白NHX ( $\text{Na}^+/\text{H}^+$  exchanger)、高亲和力钾转运蛋白HKT (high-affinity  $\text{K}^+$  transporter)和钾离子通道蛋白AKT ( $\text{K}^+$  transporter)的基因表达水平, 将 $\text{Na}^+$ 转运至液泡, 降低胞质中 $\text{Na}^+$ 含量, 减轻过量 $\text{Na}^+$ 对胞质中代谢酶活性的抑制作用, 从而提高植物的耐盐性(Li et al., 2012, 2019)。

外源褪黑素处理可上调脂质过氧化物酶基因LOX和POX、叶绿素生物合成酶基因ChlG (chlorophyll biosynthesis gene)、MAPK (Asmap1和Aspk11)以及转录因子WRKY1、WRKY3、MYB和NAC的表达(Gao et al., 2019); 增强抗氧化酶基因、烟酰胺腺嘌呤二核苷酸磷酸(nicotinamide adenine dinucleotide phosphate, NADPH)氧化酶基因、MAPK基因(MAPK3、MAPK4和MAPK6)以及盐过度敏感(salt overly sensitive, SOS)基因(SOS1、SOS2和SOS3)的表达, 进而调节下游抗性基因的表达, 增强植物对盐胁迫的抗性(Zhang et al., 2020)。用 $10\text{--}500\ \mu\text{mol}\cdot\text{L}^{-1}$ 褪黑素处理水稻可以提高SOS1、CLC1 (chloride channels 1)和CLC2的转录水平, 降低根和叶中 $\text{Na}^+$ 和 $\text{Cl}^-$ 的含量(Li et al., 2017c)。在盐胁迫下, 异源过表达COMT可增加植株体内褪黑素含量, 上调胁迫响应基因MAPK1、CDPK1、DREB1、WRKY33、MYB和RD29A的表达, 诱导SOS途径相关基因SOS1、NHX1、NHX2和HKT1的表达, 维持 $\text{Na}^+/\text{K}^+$ 平衡, 减轻离子损伤, 提高植株对盐胁迫的耐受性(Zhang et al., 2019; Sun et al., 2020); 过表达SNAT的转基因



拟南芥通过诱导自噬相关基因ATGs (ATG2、ATG5和ATG18a)及NHX1和SOS1的表达,增强植物的耐盐性(Zhao et al., 2019)。褪黑素作为信号分子诱导转录因子MYB108A的表达,进一步调控ACS1的表达,促进乙烯合成,增强葡萄耐盐性(Xu et al., 2019)。

此外,Zhang等(2014)发现外源褪黑素可上调ABA分解代谢基因CYP707A1和CYP707A2、下调ABA生物合成基因NECD2的表达,进而降低ABA含量,同时诱导GA生物合成基因GA20ox和GA3ox的表达,以增加GA<sub>4</sub>的含量,从而缓解盐胁迫对黄瓜种子萌发的抑制作用。褪黑素通过调节ABA信号通路基因GhABF2、GhDPBF2、GhGID1C和GhGID1B的表达增强棉花种子的耐盐性(Chen et al., 2021)。

#### 4.5 抗重金属胁迫

在重金属离子胁迫下,植物细胞酶活性受到抑制,蛋白质结构遭到破坏,从而出现生长缓慢、植株矮小、产量降低及根系伸长受抑制等现象,严重时会导致植物死亡。外源褪黑素处理可增强重金属镉(Cd)胁迫下植株抗氧化酶活性及增加抗氧化物质含量,减轻氧化损伤,提高植物生物量(茎长、根长和干鲜重)(Sami et al., 2020);促进叶绿素和植物螯合肽(phytochelatins, PC)的生物合成,增强植株对Cd的抵抗能力(Amjadi et al., 2021)。

Cd胁迫可诱导HSA1a和HSPs基因的表达,增加褪黑素的生物合成量,促进GSH和PC的生物合成并与Cd<sup>2+</sup>螯合转运至液泡,减轻Cd对植物的毒害作用(汪骢跃等, 2014; Cai et al., 2017)。外源褪黑素通过上调黄色条纹蛋白(yellow stripe 1-like, YSL)、重金属三磷酸腺苷酶(heavy metal ATPases, HMA)和三磷酸腺苷结合盒(ATP-binding cassette, ABC)转运蛋白基因的表达(Xu et al., 2020)和下调相关基因HMA3、HMA4和IRT2 (iron-regulated transporter)的表达水平,减轻Cd胁迫对植株造成的损伤(Lv et al., 2019)。过表达SNAT的转基因拟南芥通过上调ABC、PCR2和HMA4的转录水平,增强植物对Cd胁迫的耐受性(Gu et al., 2017)。褪黑素缓解Cd胁迫与NO有关,NO作为褪黑素下游信号分子参与调控IRT1和IRT2的表达,减少白菜型油菜(B. campestris)幼苗对Cd的吸收和积累,从而提高植物对Cd的耐受性(Wang et al., 2021)。外源施用褪黑素可上调花青素合成酶

(anthocyanidin synthase)基因ANS和查尔酮合成酶(catechin synthase)基因CHS的转录水平,促进花青素的合成,减轻砷(As)对茶(Camellia sinensis)树的毒害(Li et al., 2021)。褪黑素和水杨酸(salicylic acid, SA)可协同作用,减少Cd吸收,增加光合色素含量,加速AsA-GSH循环以及调节乙二醛酶系统,进而增强植株对Cd胁迫的耐受性(Amjadi et al., 2021)。

#### 4.6 抗电离和紫外辐射胁迫

紫外和电离辐射等氧化胁迫会引起植物形态结构发生变化并影响其生长和代谢,长期强紫外辐射引发植物DNA损伤和细胞膜脂过氧化,产生过量自由基,造成有丝分裂异常,最终影响植物的生长发育及生理生化过程(贺芳芳等, 2020)。外源褪黑素处理可减轻UV-B辐射下拟南芥线粒体中的氧化负荷,降低脂质过氧化水平并提高PSII光能转化效率(Haskirli et al., 2021)。Wei等(2019)发现外源褪黑素能增加UV-B辐射下湖北海棠(Malus hupehensis)内源褪黑素的含量,显著改善光合参数、叶绿素荧光参数、气孔开度和叶绿素水平并减轻叶膜损伤,增加酚类物质(如绿原酸、根皮苷和槲皮素-3-半乳糖苷)的含量,提高抗氧化酶相关基因APX、CAT和POD及酚类化合物代谢相关基因CHS、ANS、F3H (flavanone 3-hydroxylase)、LAR (leucoanthocyanidin reductase)和FLS (flavonol synthase)的表达水平。在烟草中异源过表达褪黑素合成酶基因SNAT和COMT可减缓UV-B辐射引起的氧化胁迫损伤(Zhang et al., 2012)。此外,褪黑素还可降低UV-B辐射诱导的植物原生质体DNA损伤,促进DNA损伤的修复,对植物原生质体具有明显的保护作用(张来军等, 2015)。

### 5 褪黑素在植物抵抗生物胁迫中的作用

褪黑素在植物抵御生物胁迫中也发挥重要作用。PPO是植保素合成、酚类物质氧化成醌以及木质素积累等途径的关键酶,可以加快细胞壁木质化,从而减少病原菌侵染对植物造成的损伤。而苯丙氨酸解氨酶(phenylalanine ammonia-lyase, PAL)为苯丙烷代谢途径的首个关键酶,在植物抗病性酚类物质的合成中不可或缺。用外源褪黑素处理接种灰葡萄孢菌(Botrytis cinerea)的苹果果实,可显著提高果实内POD、CAT、



SOD、PPO和PAL的活性, 诱导苹果对灰霉病的抗性, 有效降低灰霉病的发病率和病斑面积(曹晶晶等, 2017)。根施 $0.1 \text{ mmol} \cdot \text{L}^{-1}$ 褪黑素可显著提高POD、PAL、几丁质酶和 $\beta$ -1,3-葡聚糖酶的活性, 增强苹果对褐斑病菌(*Diplocarpon mali*)的抗性(Yin et al., 2013)。褪黑素能够抑制荔枝(*Litchi chinensis*)果实感染霜疫霉菌(*Peronophythora litchii*)病斑的扩展, 通过调节苯丙烷代谢途径、戊糖磷酸途径以及能量代谢诱导荔枝对病原真菌产生抗性(Zhang et al., 2021)。用外源褪黑素处理接种黄曲霉菌(*Aspergillus flavus*)的新鲜开心果(*Pistacia vera*)后, 黄曲霉孢子萌发和芽管伸长受到抑制, 有效减缓了黄曲霉菌造成的果实腐烂, 并降低了黄曲霉素的积累(Jannatizadeh et al., 2021)。

此外, Shi等(2015a)发现, 对感染丁香假单胞菌番茄致病变种(*Pseudomonas syringe* pv. *tomato* DC3000, PstDC3000)的拟南芥外施褪黑素后, 可诱导多种病程相关蛋白(pathogenesis-related proteins, PRs)基因和一系列由NO、SA和JA途径激活的防御基因的表达, 进而抑制病原菌的增殖和扩散, 增强拟南芥对PstDC3000的抗性。拟南芥褪黑素生物合成相关酶敲除突变株*snat*中褪黑素合成量下降至野生型的50%, 对病原菌PstDC3000的敏感性增强, 同时防御基因PR1、ICS1 (*isochorismate synthase 1*)和PDF1.2 (*plant defensin 1.2*)的表达量降低; 进一步用外源褪黑素处理过表达水杨酸羟化酶(salicylate hydroxylase)基因*nahG*的转基因拟南芥植株, 结果无法诱导防御基因的表达, 但恢复了突变株*snat*诱导防御基因的表达, 这表明褪黑素诱导防御基因的表达依赖SA途径(Lee et al., 2015)。外源褪黑素通过上调SA信号通路的关键调控基因NPR1的表达, 提高JA诱导的植物防御素标记基因PDF1.2的转录水平, 以及诱导病程相关蛋白PR1b、PR8a和PR9的表达, 进而降低水稻白叶枯病的发病率(Xian et al., 2020)。孙子荀等(2020)用 $0.5 \text{ mmol} \cdot \text{L}^{-1}$ 褪黑素喷施接种致病菌株格孢菌(*Alternaria alternate*)的草莓叶片和匍匐茎, 有效抑制了病菌菌丝生长, 延缓其发病进程, 还通过激活转录因子WRKY1的表达, 调控相关抗病基因PR1A-like、PR10、PPO和PAL的表达, 增强草莓对病原菌的防御能力。外源褪黑素处理感染PstDC3000的拟南芥通过诱导MAPK级联反应中MAPK3和

MAPK6以及防御相关基因PR1和ICS1的表达, 增强对病原体的抗性(Lee and Back, 2017)。

## 6 研究展望

近年来, 动植物领域对于褪黑素的研究越来越多, 其在动植物中的生理功能已逐渐被认知。褪黑素在植物抗逆中发挥重要作用。众多研究表明, 适宜浓度的褪黑素可有效缓解非生物胁迫引起的氧化应激反应, 保护植物免受逆境损伤。有关褪黑素的研究众多, 且已发现褪黑素的生物合成途径及多种生理功能, 但仍有许多未知领域需要探索与阐明。

首先, 植物中褪黑素含量测定方法较多, 在多种植物中均检测到褪黑素。但对于提高褪黑素含量的作物育种研究甚少, 如何利用现有的生物技术以及褪黑素研究成果, 培育出高褪黑素含量的作物品种将是未来的主要研究方向。

其次, 褪黑素在植物中的信号感知、信号转导受体以及在植物体内的运输方式尚不明晰。利用现有生物学技术(如“组学”和CRISPR/Cas9)鉴定出参与信号转导的受体或相关蛋白也是值得深入研究的课题。

最后, 褪黑素在参与植物应对非生物胁迫时能提高抗氧化酶活性、增加代谢物含量、增强光合效率并诱导一些抗逆基因的表达, 其参与抗逆反应的具体信号通路、中间产物和代谢物的代谢通路仍不够明确完善。同时, 褪黑素可与植物激素相互作用调节植物生长发育, 缓解植物逆境损伤, 促进植物逆境响应等, 但具体分子调控网络仍需进一步挖掘。

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## Research Progress of Melatonin in Plant Stress Resistance

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**Abstract** Melatonin (*N*-acetyl-5-methoxytryptamine) is a small molecule indoleamine that is essential for life. Melatonin is widely present in animals and plants, and plays a vital role in the growth and development. With the study of plant melatonin, its synthesis pathway and roles in plants have become clear. Studies have shown that melatonin has the regulatory effects in improving plant resistance to abiotic and biotic stresses. This review summarizes the research progress of melatonin in plant abiotic and biotic stresses in recent years; it provides reference for in-depth analysis of influence of melatonin on the regulation mechanism of plant resistance to stresses.

**Key words** melatonin, biosynthesis, growth and development, abiotic and biotic stresses

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