

Molecular Mechanism Research Progress of Melatonin-Mediated Abiotic/Biotic Stress Response in Plant

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Abstract

Melatonin is a derivative of tryptophan and it is widely found in plants. Plant melatonin is an evolutionarily conserved molecule, involved in regulating multiple physiological processes including flowering, photosynthesis, senescence, rooting, seed germination, vegetative growth, and responses to various abiotic and/or biotic stresses. The present review covers the latest advances on the mechanistic roles of phyto-melatonin and signaling transduction pathway. Meanwhile, we propose the possible research direction of plant melatonin-mediated stress responses in future. This will provide references for studying on molecular mechanism of plant melatonin mediated abiotic and biotic stress responses.

Keywords

Melatonin, Abiotic/Biotic Stress, Stress Response, Signaling Transduction Mechanism

褪黑素调控植物生物与非生物胁迫应答的分子机制研究进展

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摘要

褪黑素是一种色氨酸衍生物,广泛存在于植物体内。植物中褪黑素不仅能够调节开花、光合作用、凋亡、根的形态建成、种子萌发等生长发育过程,还参与调控植物对各种生物与非生物胁迫应答过程。本文重点综述了褪黑素调控植物各种生物与非生物胁迫应答的生理和分子机制及其信号转导途径的研究进展。同时,对褪黑素调控植物胁迫应答研究中存在的主要问题及今后研究的重点进行讨论和展望,以期为进一步揭示褪黑素信号在植物生物与非生物胁迫应答中的调控机制提供参考。

关键词

褪黑素,生物与非生物胁迫,胁迫应答,信号转导机制

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1. 引言

自1995年褪黑素(N-乙酰-5-甲氧基色胺)在植物中首次被发现以来,一直受到国内外植物科研工作者的广泛关注。学者们研究表明,褪黑素几乎广泛存在于所有的高等植物中,其含量从0.1 pg·g⁻¹ FW至230 μg·g⁻¹ DW均有报道[1] [2]。植物中褪黑素合成途径包括四步(见图1)。褪黑素由色氨酸经过色氨酸脱羧酶(TDH)、色氨酸羟化酶(TPH)、色胺5-羟化酶(T5H)、血清素5-乙酰转移酶(SNAT)、N-乙酰血清素-O-甲基转移酶(ASMT)和咖啡酸O-甲基转移酶(COMT)催化生成[3]。褪黑素不仅能够调节植物的开花、光合作用、凋亡、生长节律、根的形态建成、种子萌发等生长发育过程,还参与调控植物的各种生物与非生物胁迫应答[4] [5]。本文综述了近几年褪黑素调控植物各种生物与非生物胁迫应答的生理及分子机制,并对褪黑素信号转导途径进行归纳总结,以期为进一步解析褪黑素信号在植物生物与非生物胁迫应答中的调控机制提供参考。

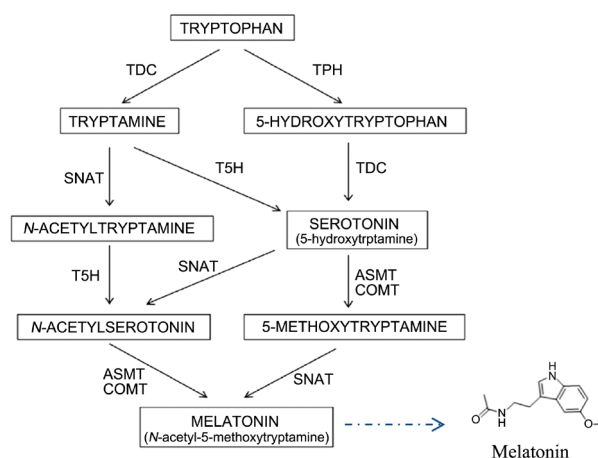


Figure 1. The multiple pathways of melatonin biosynthesis in plants

图1. 植物中褪黑素合成途径[41]

2. 褪黑素在植物生物与非生物胁迫应答中具有重要作用

2.1. 褪黑素作为一种抗氧化剂提高植物的生物与非生物胁迫抗性

许多研究发现,在响应各种生物与非生物胁迫过程中,植物体内的内源褪黑素含量发生改变,其功能是内源褪黑素作为一种次级信使参与调控植物的多种胁迫应答[4]。在低温胁迫下内源褪黑素含量增加,抑制其合成基因 *SNAT* 的表达,其突变体植株表现为冷敏感表型[6]。与之相似, Lee 和 Back [7] 也指出,过表达水稻褪黑素合成基因 *OsSNAT1* 提高了水稻的镉胁迫抗性。这些研究均表明,褪黑素作为一种信号分子在植物的胁迫应答中发挥关键作用。植物遭遇环境胁迫后,其体内产生大量的活性氧(ROS)/活性氮(RNS),从而导致植物细胞内发生氧化损伤[8]。褪黑素作为一种抗氧化剂能够有效地清除各种生物与非生物胁迫诱导地大量积累的 ROS/RNS [9]。许多研究表明,在重金属、高温、 NaHCO_3 和高盐等胁迫条件下,外源褪黑素显著降低了植物体内 ROS 含量和丙二醛的积累[10] [11] [12] [13]。而且,外源褪黑素处理可以提高 AsA-GSH 循环、SOD、POD、CAT、APX 等多种抗氧化酶活性及相关基因的表达,降低由于环境胁迫产生的过量的 ROS 和细胞膜损伤,从而增强植物的胁迫抗性[14] [15] [16] [17] [18]。这说明外源褪黑素能够抑制多种胁迫条件下植物体内 ROS 的过量积累,提高抗氧化防御体系活性,降低膜质过氧化水平,保护脂膜的完整性,从而提高植物的胁迫抗性。

2.2. 褪黑素能够提高植物的光合效率

褪黑素除了作为抗氧化剂外,还能够缓解各种环境胁迫对植物光合作用的抑制作用。在盐胁迫下,外施褪黑素能够有效地提高番茄的光合效率,其机制是褪黑素通过平衡 PSII 的供体侧、受体侧和反应中心的电子传递来缓解盐胁迫对番茄 PSII 造成的伤害,从而提高番茄的耐盐性[19]。Ding 等[20]研究发现,低温导致最大光化学效率(Fv/Fm)下降,而外源施用褪黑素可以有效地提高 Fv/Fm 和非光化学猝灭(NPQ),从而缓解低温对西红柿幼苗 PSII 造成的损伤。相似地研究报道指出,褪黑素能够增加光合碳还原的电子流[Je(PCR)]和光呼吸电子流[Je(PCO)],降低 O_2 依赖的可交替电子流(Ja),表明褪黑素能够通过调控光合电子流平衡来提高植物的抗性[21] [22] [23] [24]。非生物胁迫降低叶绿素含量,而外源褪黑素处理能够显著提高植物的叶绿素含量[18] [25] [26]。对低温胁迫下小麦叶绿素缺乏突变体 ANK32B 的研究发现,叶面积喷施 1 mM 褪黑素能够有效地提高 ANK32B 的光合效率,但是与野生型相比, Pn 和 Fv/Fm 增加量较少[27]。Li 等[16]研究发现,外源褪黑素能够有效提高低温胁迫下干旱预处理的大麦 Rubisco 活性,然而大麦的 ABA 缺乏突变体 Az34 中则表现为不显著差异变化,这说明褪黑素可能通过 ABA 依赖的方式调控植物的光合响应。Ahammed 等[28]研究显示,沉默褪黑素合成基因 COMT1 加剧了高温胁迫对番茄幼苗光合碳同化效率的抑制,这一研究证实了褪黑素作为一种保护物质能够提高胁迫条件植物的光合碳同化效率。

2.3. 褪黑素重新调整初生和次生代谢平衡来调控植物的胁迫应答

在胁迫条件下,外源褪黑素处理能够提高植物的多种渗透保护物质积累,如可溶性糖、脯氨酸、多胺等[4] [14] [26] [29],这些渗透保护物质一方面可以维持或降低植物细胞内的渗透势,防止水分外渗透造成的细胞膜损伤;另一方面作为抗氧化剂能够清除环境胁迫产生的过量的 ROS,从而减轻环境胁迫对植物造成的氧化损伤[30]。转录组研究发现,外源褪黑素处理狗牙根诱导 2361 个上调基因和 1572 个下调基因,进一步分析表明氮代谢、碳水化合物代谢和渗透保护物质代谢相关的基因显著富集。另外,代谢组研究显示外源褪黑素提高植物的抗性还可以通过诱导更高的氨基酸、有机酸、可溶性糖(葡萄糖、果糖、蔗糖、海藻糖、麦芽糖)和脯氨酸积累[14]。不饱和脂肪酸的积累有利于维持细胞膜的流动性从而增强植物的抗性[31]。Gao 等[32]研究表明,0.1 mM 外源褪黑素增加桃子中不饱和脂肪酸和饱和脂肪酸的比率和

酚类物质的积累,从而缓解了低温伤害作用。褪黑素还能够调节植物次生代谢合成来调控植物的衰老。Liang 等[33]研究发现,外源褪黑素通过增加类黄酮类物质积累提高猕猴桃叶片的衰老。这些研究表明褪黑素作为一种调节剂能够调节植物的初生和次生代谢平衡,从而调控植物的抗性。

3. 褪黑素信号转导研究进展

3.1. 褪黑素-ROS-RNS 信号在植物生物与非生物胁迫应答中发挥关键作用

褪黑素作为一种重要的植物激素,其合成和代谢途径已经被阐明[3],近年来其信号转导途径成为研究热点话题。在多种胁迫环境下褪黑素具有改变植物细胞内 Ca^{2+} 浓度和调节细胞膜透性的作用[34]。目前,学者们认为,褪黑素-ROS-RNS 信号作为次级信使在植物低温等逆境应答中发挥关键作用。褪黑素信号调控植物生物与非生物胁迫应答的信号网络见图 2。Gong 等[35]研究发现, H_2O_2 信号作为褪黑素的下游信号调控植物的非生物胁迫抗性。褪黑素通过抑制巯基亚硝基化酶活性,刺激 NADPH 氧化酶(RBOH)活性诱导 H_2O_2 产生,而 H_2O_2 的积累与植物的低温抗性增强正相关。抑制 RBOH 活性或者化学药剂清除 H_2O_2 阻碍了胁迫相关基因如 *CDPK1*、*MAPK1*、*ERF4*、*ERD15* 等表达,减弱了褪黑素诱导的防御作用。LEE 和 BACK [36]研究指出, H_2O_2/NO - 褪黑素 - MAPK 信号在植物免疫应答中的重要作用。其中, H_2O_2 和 NO 信号在褪黑素调控的防御响应是必需的。褪黑素通过激活 MAPKKK3 和 OXII (oxidative signal-inducible1)激酶活性,进一步诱导 MAPK 信号级联响应。NO 作为褪黑素的下游信号调控植物胁迫应答已有许多报道[37] [38]。在 Fe 缺乏胁迫下外源褪黑素诱导 NO 的释放,而在多胺缺乏突变体 *adc2-1* 中 NO 的释放量并未发生显著改变,说明褪黑素通过调控多胺诱导的 NO 产生来调节植物的 Fe 缺乏胁迫[29]。与之相似, Kaur 等[39]报道, NO 和褪黑素相互作用调控 GSH 水平和 GR 活性,维持较低的 H_2O_2 积累,从而调控植物的盐胁迫抗性。

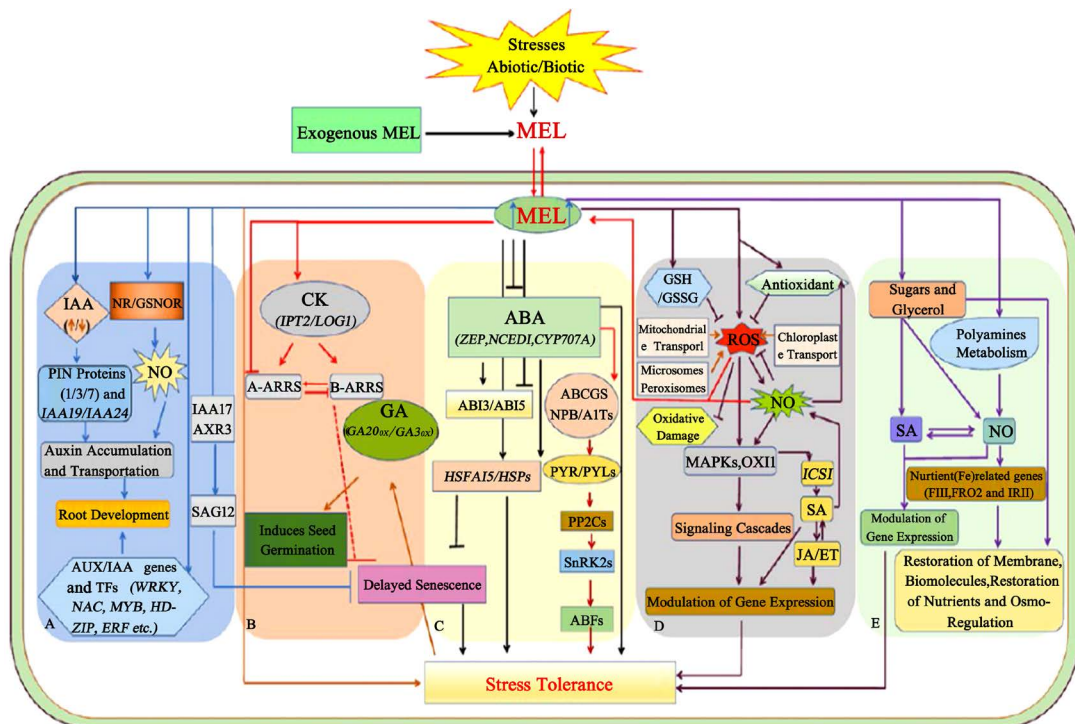


Figure 2. The signaling transduction mechanism of melatonin-regulated response to stress in plants
图 2. 植物褪黑素信号转导模式图[5]

3.2. 褪黑素与多种激素存在对话机制

ABA 作为重要的胁迫信号参与调控植物的多种胁迫应答。褪黑素能够通过调控 ABA 信号途径来调节植物的胁迫响应。低温胁迫下转录组研究发现, 外源褪黑素诱导 ABA 受体 *PYL5* 和 *PP2C* 的表达[14]。Fu 等[40]研究发现, 低温胁迫下, 叶面积喷施褪黑素能够提高垂穗披碱草叶片中内源 ABA 含量, 然而外源 ABA 和 ABA 合成抑制剂处理并未改变内源褪黑素水平, 这表明褪黑素可能作为 ABA 的上游信号调控植物的低温胁迫应答[41]。细胞分裂素(CKs)在褪黑素调节的热胁迫应答中也发挥重要作用, 表现为上调 CKs 合成基因和其信号转录因子 *type B ARRs* 的表达[42]。其次, 褪黑素也诱导其他激素如生长素(IAA)、赤霉素(GA)、水杨酸(SA)、茉莉酸(JA)、和乙烯(ETH)信号途径中基因的表达, 进而调控植物的生长发育与胁迫抗性[5]。SA 和 ETH 信号参与褪黑素诱导的生物胁迫免疫, 其机制在于诱导防御相关基因 *PRI*、*PR5* 和 *PDF1.2* 的表达[43]。褪黑素与 GA4 相互作用调控植物的盐胁迫抗性, 主要是通过诱导 GA 合成基因 *GA20ox* 和 *GA3ox* 表达[44]。ABA 和 JA 处理诱导水稻褪黑素合成基因 *ASMT* 表达, 这也意味着褪黑素具有调控植物的多种胁迫应答的作用[45]。近年来研究发现, 褪黑素以浓度依赖的方式与 IAA 信号互作调控植物的生长发育。低浓度(50 μM)褪黑素增强 IAA 信号转导基因 *IAA19* 和 *IAA24* 以及 IAA 转运基因 *PIN1*、*PIN3* 和 *PIN7* 表达, 高浓度(600 μM)褪黑素则抑制 IAA 的合成和转运。进一步研究发现 NO 作为褪黑素的下游信号参与调控 IAA 的合成、转运和信号转导[46]。以上研究均表明, 其他植物激素也参与褪黑素调控植物的生物与生物胁迫应答。然而, 褪黑素与其他激素互作调控植物胁迫应答的机制仍需进一步挖掘。

3.3. 褪黑素在转录水平和转录后水平调控植物的生物与非生物胁迫应答

褪黑素与多种转录因子构成互作网络调控植物的胁迫应答。转录组分析表明, 褪黑素还能够诱导 *WRKY*、*MYB*、*NAC* 和 *HSF* 等转录因子表达, 从而调控植物的生长发育及胁迫应答[14]。Bajwa 等[47]报道, 在低温胁迫下褪黑素诱导低温应答关键转录因子 *CBF/DREBs* 和下游低温响应基因 *COR15a* 以及其他转录因子相关的基因 *CAMTA1*、*ZAT10* 和 *ZAT12* 表达。另外, *ZAT6* 激活的 CBF 信号转导途径在褪黑素调节的植物低温胁迫应答中也具有关键作用, 表现为低温胁迫下外源褪黑素处理上调了 *AtZAT6* 和 *AtCBFs* 的表达, 而过表达 *AtZAT6* 增加了褪黑素诱导的抗低温能力, 敲除 *AtZAT6* 则减弱了褪黑素的作用[48]。褪黑素通过抑制 *miR159-5p*、*miR858*、*miR8029-3p* 和 *m0048-3p* 表达正向调控植物的低温抗性, 这些 miRNAs 的靶基因 *CDPK*、*BHLH*、*WRKY*、*MYB* 和 *DREB* 上调表达[49]。MKK4/5/7/9-MPK3/6 信号途径在褪黑素激活的植物防御中发挥重要作用[50]。蛋白质组学研究发现, 褪黑素处理或过表达其合成基因 *ASMT* 能够增加 *HSPs* 表达和蛋白丰度, 降低聚合蛋白积累[51]。相似地研究表明, 褪黑素处理通过抑制吞噬相关基因 *ATGs* 表达, 降低蛋白的降解[52]。这些研究表明, 褪黑素能够在转录水平和转录后水平调控植物的生物与非生物胁迫应答。

4. 展望

目前, 虽然关于褪黑素调控植物生物与非生物胁迫应答的研究已取得很大的进展, 然而对于植物是如何感知褪黑素信号, 并将其逐级放大传递到下游进一步在生理代谢水平上调控植物的胁迫应答尚未有定论。最近研究发现的褪黑素受体 *CAND2/PMTR1* 为学者们进一步探究褪黑素的信号转导奠定了基础[53]。因此, 在今后的研究中, 褪黑素信号是如何与各种生物与非生物胁迫信号感受器作用, 通过哪些途径进一步放大褪黑素与胁迫信号的相互作用将会是一个非常重要的研究领域。

1) 运用多种组学如蛋白修饰组学、代谢组学、转录组学结合 CRISPR 敲除及 pull down、免疫共沉淀等蛋白互作方法将有助于我们进一步探究褪黑素受体信号及其合成基因的重要调控元件, 这将会加快我们揭示褪黑素调控植物代谢通路的分子机制。

2) 褪黑素作为一种重要的次级信号, 有关外援褪黑素是通过怎样的一系列信号转导途径影响其它激素含量及信号发生改变, 进而诱导下游的一系列生理生化代谢响应的作用机理还不明确。因此, 探索褪黑素受体信号与其它植物激素信号之间相互作用机制将对于我们进一步解析褪黑素信号调控植物的胁迫应答机理提供重要线索。

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