褪黑素在果蔬采后保鲜的应用研究进展

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摘要：目的 通过介绍褪黑素对采后果蔬生理、营养品质、能量代谢、风味变化、冷害调控和抗病性的影响，为褪黑素在果蔬采后保鲜的应用提供理论借鉴。**方法** 综述国内外褪黑素在不同品种果蔬采后上的保鲜效果。**结果** 褪黑素可以调控果蔬的成熟与衰老，提高果蔬的抗冷性和抗病性，维持果蔬较高的营养物质，保持果蔬更好的生理品质。**结论** 褪黑素可显著延长采后果蔬的贮藏期，在未来采后果蔬保鲜领域具有广阔的发展空间。

关键词：褪黑素；果蔬；保鲜效果；研究进展
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Application of Melatonin in Postharvest Preservation of Fruits and Vegetables

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ABSTRACT: The work aims to introduce the effects of melatonin on physiological and nutritional quality, energy metabolism, flavor change, chilling injury regulation and disease resistance of postharvest fruits and vegetables, so as to provide theoretical reference for the application of melatonin in postharvest preservation of fruits and vegetables. The effects of melatonin on postharvest preservation of different fruits and vegetables at home and abroad were reviewed. Melatonin could regulate the ripening and senescence of fruits and vegetables, improve the cold resistance and disease resistance, and maintain higher nutrients and better physiological quality. Melatonin can significantly prolong the postharvest storage period of fruits and vegetables, and has broad development space in the field of postharvest preservation of fruits and vegetables in the future.

KEY WORDS: melatonin; fruits and vegetables; preservation effect; research progress

褪黑素（Melatonin, MT）是一种内源性、具有多种调节功能的生物活性分子，可以参与果蔬的生长、分化、成熟、衰老和防御等多种生理活动[1]。褪黑素也是一种天然、高效、安全性高、无污染的新型生物保鲜剂[2]，其已广泛应用于果蔬的采后保鲜，可有效提高果实的抗冷性[3]，延缓果蔬的成熟衰老进程[4-5]，保持鲜切果实较高的营养品质[6]，提高果蔬的抗病性[7-8]。

近年来研究者发现，褪黑素对果蔬采后的保鲜作用主要通过降低果蔬的呼吸速率、降低乙烯生成

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量[9-10]、延缓果实成熟来达到；也有研究者报道，褪黑素作为一种信号分子，具有较强的抗氧化能力，不仅可以诱导内源褪黑素积累，从而调控果蔬的生理、生化和分子机制，还能通过中和自由基、增强酶或非酶抗氧化活性、防止细胞内抗氧化酶失活、抑制活性氧自由基的产生等模式来调控果实的成熟衰老[11-12]。文中主要综述国内外研究者报道的关于褪黑素对果蔬采后成熟衰老、品质劣变、病害防控的调控作用等方面，以期为褪黑素在果蔬采后贮藏保鲜上的进一步研究提供理论指导。

1 褪黑素对采后果蔬成熟衰老的调控

1.1 褪黑素对呼吸及乙烯的影响

果蔬在呼吸过程中伴随着内源乙烯的增加，内源乙烯的积累加快了果蔬的成熟软化进程[13]。近年来，MT 在改善采后果蔬品质、延缓果蔬成熟衰老中发挥着重要作用。Hu 等[14]研究发现，外源褪黑素处理能显著抑制香蕉果实中乙烯合成相关基因 ACS、ACO 表达和淀粉的降解，推迟了香蕉果实呼吸高峰的出现，有效延迟了香蕉果实成熟的进程。Tan 等[5]研究发现，采用褪黑素喷洒处理的大白菜，其对照组的呼吸速率和乙烯释放量显著高于处理组，并且处理组的叶绿素含量显著大于对照组，从而有效延缓了大白菜的衰老黄化进程。研究者还发现，采用褪黑素处理可以显著提升梨果实内一氧化氮合酶的活性与 TDC、T5H 基因的表达量，从而导致梨果的乙烯生物合成量和呼吸速率下降[15]。MT 还可通过调节苹果贮藏期间的呼吸速率和乙烯的生成，降低果实细胞中丙二醛的积累和果实水分的流失，显著延长苹果的贮藏期[16]。此外，外源褪黑素处理还可降低桃果[3]、芒果[17]、白菜[5]的呼吸强度及内源乙烯的生成量，使采后果蔬的呼吸处于一种低而正常的状态，有利于延长果蔬贮藏期。

1.2 褪黑素对能量代谢的影响

采后贮藏的果蔬仍然可以正常进行呼吸和生理机能代谢活动，而果蔬的生理机能代谢活动需 ATP 提供能量[18]，低能量状态会增强果蔬的呼吸速率，消耗大量的有机物，加剧活性氧的积累，并加速膜脂过氧化，导致果蔬生理机能下降[19]，而高能量状态可维持果蔬正常的生理机能代谢活动，延迟采后果蔬的后熟衰老进程。胡苗[19]研究发现，外源褪黑素均能抑制冷藏期间水蜜桃 SDH、CCO、H^+-ATP 酶和 Ca^{2+}-ATP 酶的活力，提高桃果的能荷水平。Wang 等[20]研究结果显示，0.4 mmol/L 褪黑素处理可抑制荔枝果皮 SDH、CCO、H^+-ATP 酶和 Ca^{2+}-ATP 酶的活性，维持荔枝果中较高的脂肪酸、ATP 和 ADP 等含量，使果皮组织细胞处于高能量状态，从而延缓荔枝果实的品质劣变进程。此外，褪黑素处理还能激活三磷酸腺苷酶和烟酰胺腺嘌呤二核苷酸激酶活性，维持大白菜叶片较高的能量状态，延缓大白菜叶片黄化进程[5]。由此可见，能量状态与果蔬的生理活动密切相关，调控采后果蔬的能量状态对延长果蔬的贮藏期尤其重要。

2 褪黑素对采后果蔬品质劣变的调控

2.1 褪黑素对生理和营养的影响

果蔬在采摘后会快速衰老，表现为脱水、表皮皱缩、果肉软化及腐烂等[13]，导致果蔬的品质下降。Liu 等[21]研究发现，采用 0.1 mol/L 外源褪黑素浸泡处理草莓果实，有效降低了草莓的腐烂率和质量损失率，有效减缓了果实中水分的流失，提高了草莓果实的亮度。据 Gao 等[3] 报道可知，外源褪黑素浸泡处理可诱导提高桃果实在贮藏期间的抗氧化酶活性，从而维持 ROS 代谢平衡，促进了桃果实酚类物质的积累。Rastegar 等[22] 研究了褪黑素浸泡处理采后芒果，发现处理后可显著抑制芒果中抗坏血酸、总酚、总黄酮和可滴定酸等含量的下降，稳定果实膜脂结构、增强膜脂功能，提高了芒果贮藏期的营养品质。Xia 等[23]的研究结果表明，褪黑素喷洒处理可上调葡萄浆果 MYBA1 和 MYBA2 基因表达，促进果实中花青素的积累，增加可溶性糖的含量，并提高矿物质营养素 N、K、Cu、Fe、Zn 的含量。研究还发现，经褪黑素浸泡过的黄瓜，其处理组的可滴定酸、抗坏血酸、可溶性蛋白和叶绿素等含量显著高于对照组，有效减少了黄瓜贮藏期间营养物质的流失[24]。此外，褪黑素处理还可诱导双孢菇帽酚类物质和抗坏血酸含量的增加，改善双孢蘑菇帽的营养品质[25]。

2.2 褪黑素对风味变化的影响

果蔬中的有机酸、糖类、酯类化合物、挥发性物质等是形成果蔬风味的重要物质[26]。果蔬的风味与果蔬的品质密切相关，当果蔬的品质发生劣变，果蔬的风味会受到一定的影响，并散发出令人不愉快的气味。杜天浩等[27]研究发现，MT 浸泡处理提高了在盐胁迫的逆境环境下番茄果实的有机酸、糖酸比和挥发性芳香物质等含量，增加了番茄果实的香气成分。王纪忠等[28]发现，MT 有效提高了梨果实货架期的可溶固形物含量，增加了果实中酯类、醛类和酮类物质，保持了梨果特有的风味。朱赛赛等[26]探究不同浓度 MT 对采后蜂糖李果实保鲜效果的影响，结果表明，适宜的 MT 含量会将果实中抗坏血酸、可滴定酸和可溶性糖等含量维持在较高的水平，有利于果实挥发性成分的积累，有效保持了蜂糖李的鲜味。另外，刘建龙[29]研究结果表明，褪黑素处理可上调蔗糖磷酸合酶和蔗糖合酶基因表达，降低酸性转化酶的基因表达，从而诱导增强蔗糖磷酸合酶和蔗糖合酶的活性，维持

较低酸性转化酶活性，有助于减缓梨果实中糖的降解进程。Xia 等[23]报道，褪黑激素会诱导增强蔗糖磷酸合酶的活性，增加葡萄果实的可溶性糖含量，从而促进果实内源 MT 的积累和激活花青素合成的通路。此外，Tan 等[5]研究发现，外源 MT 处理可调节大白菜中葡萄糖-6-磷酸脱氢酶和 6-磷酸葡萄糖酸脱氢酶活性的上升，使白菜叶片的总糖含量保持在较高的水平。由此可知，外源褪黑素处理通过诱导提高果蔬中有机酸、糖酸比、醛类和酮类等物质的含量，从而维持果蔬的风味。

2.3　褪黑素对冷害调控的影响

低温能降低果蔬贮藏环境中氧气与二氧化碳的比例，抑制果蔬中有机物的降解和病原菌的生长，限制采后果蔬中酶的活力，从而延长果蔬采后的贮藏期[9]。由于低温贮藏容易导致果蔬发生冷害，果蔬低温冷害的发生通常表现为冰点以上温度对果蔬的细胞、组织和器官造成伤害，使果蔬的细胞、组织和器官的机能下降，引起果蔬代谢紊乱，对致病菌的抵抗能力下降[30]。发生冷害的果蔬表面较黏滑，跃变型果实不能正常后熟，果蔬表皮出现皱缩凹陷、斑纹，果肉出现点蚀，且花萼变黑、组织水分流失，导致果实的硬度上升，从而出现僵果、木质化加重、局部果肉部分浸水、果蔬组织褐变、果蔬风味丧失、产生异味、腐烂等现象[30-31]。此外，有些果蔬在货架时才表现出冷害症状，导致果蔬快速腐烂变质，失去食用价值。

2.3.1　调节 ROS 代谢平衡

果蔬细胞中 ROS 自由基积累会引起果蔬膜完整性和功能的丧失，膜脂抗氧化能力下降，以及电解质外渗，从而导致果蔬冷害的发生[32]。Shang 等[33]研究结果显示，采用 0.05 mmol/L 褪黑素处理会显著提高蓝莓中抗坏血酸过氧化物酶和谷胱甘肽 S-转移酶的活性，维持较高 ROS 自由基清除能力，有效提高蓝莓果实的抗冷能力。Gao 等[34]还发现，褪黑素处理促进了草菇柠檬酸循环、谷胱甘肽代谢和脯氨酸代谢，激活了脂氧合酶、谷胱甘肽还原酶和 SOD 活性，以此减轻了镉对草菇的损伤，有利于草菇对冷胁迫的抵御。另外，褪黑素还可诱导提高苹果中抗坏血酸过氧化物酶、脂氧合酶和谷胱甘肽硫转移酶等的活性，增强苹果的抗冷性[35]。此外，MT 会触发番茄果实中 ROS 自由基清除系统，以及抑制细胞凋亡的蛋白质积累，从而增强番茄果实的抗冷应激能力[36]。

2.3.2　调节膜脂及酚类代谢

采后果蔬的冷害和衰老与细胞膜系统的完整性和功能紧密相关，膜结构和功能的损伤导致果实细胞中膜脂降解，以及酚类物质被酶氧化转化为醌类物质，从而引起果蔬褐变，且食用时感觉淡而无味[37-38]。研究发现，采用褪黑素处理荔枝果实，其磷脂酶 D、脂肪酶和脂氧合酶的活性显著上升，同时减缓了磷脂酰胆碱（PC）水解成磷脂酸（PA），使荔枝果实中油酸、亚油酸和亚麻酸的含量维持在较高水平，减轻了荔枝冷害及褐变的发生[20]。Gao 等[3]报道了采用褪黑素浸泡桃果，维持了桃果较高的不饱和脂肪酸含量和较低的饱和脂肪酸含量，诱导 G6PDH、SKDH 和 PAL 活性增加，且促进了总酚物质和内源性水杨酸的积累，减轻了桃果冷害的发生。Aghdam 等[39]研究结果显示，褪黑素处理能够提高石榴果实在冷藏过程中 APX、GR、G6PDH 活性，促进酚类、花青素、AA 和谷胱甘肽的积累，增强石榴果实的抗冷能力。此外，褪黑素处理还可增加青椒脯氨酸、亚油酸与亚麻酸的比例[40]，激活番茄果实 GABA 分流通路活性[41]，从而减轻了果蔬的冷害症状。

2.3.3　激活精氨酸代谢通路

果蔬中聚胺、脯氨酸、γ-氨基丁酸和一氧化氮等物质能够在果蔬受冷激胁迫下作出响应，而精氨酸不仅通过 NOS 反应生成一氧化氮，还可通过精氨酸脱羧酶和精氨酸酶合成聚胺和鸟氨酸，鸟氨酸进一步生成腐胺[42-43]。此外，精氨酸又可用于鸟氨酸脱羧酶或脯氨酸氨基转移酶合成聚氨酸[42]。可见，精氨酸的代谢受到多种酶的调控，当果蔬受到冷激胁迫或外界环境刺激时，酶活性的变化会调控精氨酸的代谢途径和方向。Bajwa 等[44]研究发现，褪黑激素通过上调 ZAT10 和 ZAT12 基因的表达，并激活 CBFs 基因表达，促进拟南芥内源性聚胺的积累，提高拟南芥的抗冷性。研究还发现，褪黑激处理上调了 ZAT12 基因的表达，提升了内源性聚胺的积累和 ROS 清除系统的活性，增强了黄瓜幼苗的耐寒性[45]。此外，据 Aghdam 等[42]报道可知，褪黑素诱导了番茄果实 ADC、ODC、P5CS、OAT 和 NOS 基因表达上调，激活了 CBF1 信号触发精氨酸的代谢通路，从而促进了内源性聚氨酸、脯氨酸和一氧化氮的积累，增强了番茄果实的耐寒性。

2.3.4　诱导采后果蔬基因表达

近年来，关于 MT 在果蔬采后保鲜的研究主要集于果蔬的生理层面，也有许多研究者从分子的角度解释了 MT 在一些果蔬上的作用机制。果蔬的生理机能不仅受到外部环境的干扰，还受到内部基因和转录因子的调控。据报道，MT 通过抑制 BrABF1、BrABF4 和 BrABI5 表达，阻止了脱落酸的生成和叶绿素的降解，提高了大白菜叶片对逆境胁迫的抗性[46]。Shang 等[33]研究表明，MT 诱导了抗氧化基因 VcAPX、VcGST 和 VcPAL 的表达量上调，使蓝莓的膜脂过氧化降低，延缓了蓝莓果实冷害的发生。MT 还能诱导上调基因 MeCAT1、MeGPX、MePX3 和 MeGST 的表达量，从而延缓木薯根的衰老[47]。另外，MT 调节基因 SND2、KNAT7、MYB20 和 MYB85 表达量的下

调，减轻了竹笋的木质化[48]，触发了 TDC、T5S、SNAT 和 ASMT 基因的表达，从而提高了内源 MT 的积累，并调控了苯丙烷通路，增加了酚类、花青素及谷胱甘肽等含量，增强了石榴果实的抗冷能力[39]。此外，褪黑素处理诱导了 miR528 表达，降低了 MaPPO1、MaPPO2 和 MaPPO3 潜在靶基因表达，促进了香蕉果实中磷脂和不饱和脂肪酸的积累，减轻了果皮褐变，提高了果实的抗冷胁迫能力[49]。Kong 等[40]研究发现，采用 100 μmol/L 褪黑素处理上调节了 CaSOD、CaPOD、CaCAT 和 CAAPX 基因的转录水平，触发了青椒中的抗氧化保护系统，从而抵抗了氧化损伤，增强了青椒对冷胁迫的抵抗。

3 采后果蔬病害的防控

果蔬采后在贮运和贮藏过程中容易遭受损伤，引起果蔬代谢紊乱，导致果蔬的免疫力下降，从而促进病原菌的生长繁殖。由病原菌引起果蔬采后品质劣变是近年来仍需解决的一个难题。生吉萍等[50]采用 100 mmol/L 褪黑素采前喷施处理诱导番茄果实中几丁质酶、β-1,3-葡聚糖酶等抗病相关酶活力的上升，有效增强了贮藏期间番茄果实的抗病能力。孙子荀等[51]发现，外源褪黑素能有效抑制黑斑病致病菌链格孢菌的菌丝生长，增强采后草莓对黑斑病入侵的抵御。外源褪黑素也能诱导果实内防御酶活性的上升，抑制苹果灰霉病病斑的扩大[52]，并且还可激活苯丙烷代谢的通路，促进果实 IAA 的积累，增强荔枝对霜霉病的抵抗能力[53]。此外，褪黑素诱导提高 PbOPR3 基因表达来调控茉莉酸的通路[54]，激活 SA 信号通路，并诱导 SA 受体蛋白 NPR1 的核定位[55]，调控果蔬细胞 H_2O_2 的积累，调节细胞内活性氧自由基平衡[56]，上调 NO 合成基因表达，促进果实细胞内 NO 的积累[42,56]，并且激活 MaHSP90s 信号分子，增加吲哚乙酸的积累[57]，从而提高采后果蔬的抗病能力。目前关于 MT 调控增强采后果蔬的抑菌机制的研究报道仍较少，还需进一步探究 MT 诱导果蔬抗病的机制。

4 结语

褪黑素不仅可作为一种信号分子，参与调节果蔬采后生理代谢，保持果蔬较好的营养品质，提高采后果蔬总糖含量和能量水平，改善果蔬风味，提高果蔬的抗病性，还可作为一种抗氧化物质诱导增加果蔬的采后抗氧化能力，调节 ROS 代谢平衡，增强果蔬对外界生物或非生物胁迫，提高果蔬对冷激胁迫的应答，延迟果蔬采后成熟衰老。目前，褪黑素对采后果蔬的冷害机制以及冷害影响果蔬的生理生化的研究已比较深入，但褪黑素对采后果蔬的风味变化和抗病性的研究报道还较少，且多数集中于果蔬的生理层面，未来可探究褪黑素对采后果蔬风味及抗病性的影响，为褪黑素在果蔬保鲜方面的应用提供更多理论支撑。

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