

DOI: 10.16861/j.cnki.zggc.2024.0403

马铃薯褐变机制及控制技术研究进展

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摘要: 鲜切马铃薯加工和贮藏过程中的酶促褐变严重影响产品质量和市场价值, 针对这一问题开展了很多控制褐变的相关研究。对鲜切马铃薯褐变发生机制、国内外鲜切马铃薯褐变控制技术进行综述, 其中物理控制技术包括超声、低温、高压、高氧和气调包装等处理; 化学制剂控制褐变技术涉及无机物、有机物、植物提取物和纳米材料; 基因工程技术包括反义基因、人工 microRNA (amiRNA)、基因过表达、基因编辑 (CRISPR/Cas9) 和 RNAi 技术等。总结褐变控制在褐变研究中的最新进展, 并提出相应的建议和展望, 以为后续鲜切马铃薯褐变抑制的深入研究提供参考。

关键词: 马铃薯; 酶促褐变; 控制技术

中图分类号: S532

文献标志码: A

文章编号: 1673-2871(2024)11-010-09

Research progress of mechanisms and control strategies for potato browning

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Abstract: Enzymatic browning during processing and storage of fresh-cut potatoes seriously affects product quality and market value. Many studies have been conducted on browning control to address this issue. This review examines the mechanisms of browning in fresh-cut potatoes and the control techniques for browning both domestically and internationally. Physical control techniques include ultrasound, low temperature, high pressure, high oxygen, and modified atmosphere packaging. Chemical agent control methods involve the application of inorganic and organic compounds, plant extracts, and nanomaterials. Genetic engineering approaches encompass antisense gene technology, artificial microRNA (amiRNA) technology, gene overexpression, gene editing (CRISPR/Cas9), and RNA interference (RNAi) technology. This paper summarizes the latest advancements in technologies for controlling browning in fresh-cut potatoes and offers recommendations and perspectives to guide further in-depth research on browning inhibition of fresh cut potatoes in the future.

Key words: Potato; Enzymatic browning; Control strategy

马铃薯 (*Solanum tuberosum* L.) 富含优质蛋白质、淀粉、膳食纤维和其他多种营养物质^[1], 是继玉米、小麦和水稻后的第四大粮食作物。鲜切马铃薯方便加工且富含营养, 在人们日常饮食中占比较大^[2]。然而, 在马铃薯鲜切过程中, 由机械损伤引起的酶促褐变会影响产品质量和市场价值^[3]。褐变是鲜切蔬菜和水果常见的变色现象, 分为酶促褐变和非酶促褐变, 酶促褐变与酚类物质和多酚氧化酶

(PPO) 相关, 非酶促褐变包括焦糖化反应、美拉德反应、抗坏血酸氧化分解以及酚类氧化缩合现象^[4], 发生在马铃薯加工过程中的主要是酶促褐变和美拉德反应。在正常植物组织中, 根据酚-酶区域分布理论, 酚类物质和多酚氧化酶分别主要存在于液泡和细胞质中^[5]。一旦鲜切处理破坏细胞完整性, PPO 就会与酚类底物接触, 暴露于空气中, 发生氧、底物和酶三种元素共存的酶氧化反应。在此过程中酚

收稿日期: 2024-06-23; 修回日期: 2024-08-20

基金项目: 贵州省自然科学基金(黔科合基础(2022)一般 297); 贵州省科技计划项目(黔科合基础-(2024)青年 069); 国家现代农业产业技术体系专项(CARS-09-ES24); 贵州省育种科研基础平台创新能力建设(黔科合服企(2022)014); 贵州喀斯特山区重要作物生物育种平台建设(黔科合中引地(2023)033)

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类底物被催化成醌类,醌类物质快速聚合,通过非酶反应与蛋白质或糖的氨基或巯基反应生成深棕色色素,对鲜切马铃薯产品的外观和消费者感官产生不利影响^[6]。加工马铃薯市场需求大,目前50%~60%新鲜马铃薯通过加工成为高附加值产品,如切丁、脱水、罐装、冷冻炸薯条、冷冻、烘焙、烹饪(即时)和土豆泥等^[7-8]。加工即食马铃薯经削皮、蒸煮,灭菌及真空包装等过程^[9],这就需要即食马铃薯制备时间短且保质期要长,以确保马铃薯的新鲜。而高温灭菌会导致马铃薯块茎中大量的还原糖和氨基酸发生被称为美拉德反应的非酶褐变反应,这对加工马铃薯外观产生负面影响^[10]。控制美拉德反应水平在理想感官发展中起着重要作用,如一些食物的颜色和味道,包括面包、饼干、烤肉、咖啡、坚果、啤酒等^[11-12]。然而,在即食马铃薯加工中,美拉德反应的发生会导致颜色变化,降低即食马铃薯的商业可接受性^[13]。此外,在美拉德反应的中间阶段形成有毒物质,如丙烯酰胺(AM)和5-羟甲基糠醛(HMF)^[10]。因此,马铃薯即食产品需要降低中间化合物如丙烯酰胺的含量。高温和长时间油炸会形成黑素,这是一种棕色甚至是黑色的大分子物质,导致丙烯酰胺浓度降低^[14]。还可以通过降低还原糖的浓度,尽可能降低美拉德反应的速度来延迟中间化合物生成,从而避免这些有害化合物的形成^[15]。目前对鲜切马铃薯褐变的研究主要集中在抗褐变的方法,如加热、包装和使用抗褐变剂等,以及鲜切马铃薯在褐变过程中代谢变化等方面^[16]。因此,笔者对马铃薯褐变机制、现有控制褐变的方法进行总结,并对未来发展方向进行展望,以期为鲜切马铃薯褐变抑制的深入研究提供借鉴。

1 马铃薯褐变机制

众所周知,鲜切马铃薯的褐变主要是由酶促褐变引起的,酚类化合物底物在酶的作用下产生醌,然后醌转化为色素^[17]。其中涉及多酚氧化酶(PPO)、过氧化物酶(POD)和苯丙氨酸解氨酶(PAL)3个关键酶^[18-20]。

PPO是酶促褐变黑色素形成途径中的关键酶,不仅催化单酚羟基化生成二酚,还催化二酚氧化生成醌^[21]。PPO广泛存在于植物界中,与膜系统关系密切,在胁迫作用下因膜的破坏而活化,导致活性增强^[22]。在植物组织中,酚类底物位于液泡中,而PPO位于细胞质、质膜、质体和线粒体中^[23-24]。酚-酶区域分布阻止了酚类底物与PPO的接触,避免正常

组织发生褐变。马铃薯采后,在产品的加工和贮存过程中,易发生机械损伤(剥削、切割、冷损伤等应激损伤),破坏膜结构的完整性,降解细胞膜,引起脂质过氧化,破坏酚-酶的区域分布。在有氧条件下,酶催化酚类底物形成邻醌化合物,这些化合物聚合成棕色色素,导致酶促褐变^[25-26]。因此,较高的细胞膜完整性可以有效地防止酶促褐变。

POD是另一种重要的氧化酶,在褐变过程中形成自由基^[27]。POD广泛存在于各种动物、植物和微生物中,以H₂O₂为电子受体直接氧化酚类或胺类化合物,具有消除过氧化氢和酚类及胺类毒性的双重作用。POD与植物在逆境条件下酶促防御系统相关,与超氧化物歧化酶(SOD)、过氧化氢酶(CAT)协同作用,清除体内过剩的自由基,从而提高植物的抗逆性^[28]。除了POD外,PAL是苯丙烷代谢途径中的一种限速酶,也是一种重要的伤口诱导酶,参与酶促褐变。PAL通过L-苯丙氨酸途径催化酚类成分的褐变,催化苯丙氨酸脱氨形成肉桂酸和各种酚类物质^[26]。因此,PPO、POD和PAL活性的调控是许多抗褐变策略的关键靶点。

此外,细胞膜的重要成分磷脂在细胞生命活动中对维持细胞结构和信号转导具有重要功能^[29]。磷脂酶D(PLD)和脂氧合酶(LOX)是膜脂代谢的关键酶^[30]。PLD是膜脂降解途径中的第一个酶,也是磷脂水解的关键酶^[31]。在水果和蔬菜机械损伤时,PLD被激活降解细胞膜脂质,导致磷脂酸和游离脂肪酸的积累,并为LOX提供反应底物^[32]。LOX是脂肪酸代谢途径的关键酶,将膜脂中的不饱和脂肪酸氧化为丙二醛(MDA)和自由基,对膜系统产生毒性作用,破坏细胞膜完整性,促进褐变^[33]。MDA是膜脂过氧化的产物之一,可以改变细胞的结构和功能,MDA的浓度常被用于衡量细胞内膜脂过氧化的程度^[34]。在低温胁迫下,膜脂代谢紊乱引起的PLD和LOX活性的增强可诱导梨表面发生褐变^[35]。活性氧(ROS)在褐变调节中起重要作用,可以催化多不饱和脂肪酸转化为MDA^[36]。在过氧化氢存在下,POD可以催化酚类和黄酮类化合物聚合成褐变色素^[37]。

2 马铃薯褐变控制技术

针对鲜切马铃薯褐变控制技术的研究较多,主要包括物理、化学和基因工程技术等。

2.1 物理控制技术

使用超声^[38]、低温^[39]、高压^[40]、高氧^[41]和气调包装等

物理处理方法,对控制马铃薯褐变均具有一定的效果。

2.1.1 超声处理 超声处理(US)是一种非热的、生态友好的褐变控制方法,在食品加工和保存过程中,通过液体系统中的空化现象来保证质量和杀灭病原微生物^[42]。空化作用通常会改变分压,不仅使微生物细胞受到压力,而且使植物组织和细胞交替压缩和扩张。超声处理的空化过程类似于海绵的反复挤压和释放,被称为“海绵效应”。海绵效应使超声波促进液体流动,打开植物内部孔隙和空间^[43]。超声空化现象是由于超声微泡的形成、生长和破裂,直接增强了组织和细胞受到的局部压力和化学能^[44-45]。最近的研究表明,US(20 kHz, 10 min)抑制了鲜切生菜和莲藕的微生物生长,降低了质量损失率、硬度、可溶性固体总量、色差和水的流动性,并保持了细胞壁的完整性^[46-47]。Zhu等^[48]研究了超声耦合马齿苋提取物对鲜切马铃薯在4℃保存8 d期间抗褐变的影响,当超声波工作时间为10 min时,联合施用较低的马齿苋提取物(浓度0.02%, w/w),比单独施用(浓度0.05%, w)具有更好的抗褐变效果,联合应用不仅显著抑制了PPO和POD等关键酶活性,而且有效地缓解了对细胞膜的损伤,保持了其完整性和通透性,同时还提高了贮藏期间的抗氧化能力。

2.1.2 低温处理 低温贮藏是保持鲜切马铃薯品质的重要方法,低温能延缓果蔬采摘后成熟,同时也能抑制病原菌生长。低温贮藏能减缓细胞呼吸速率,保持鲜切产品的新鲜度,也可以延缓组织软化并改变其色泽变化速度,还能让微生物生长缓慢,避免褐变现象发生。在合适温度区间内,贮藏温度越低,保鲜效果越好,但如果超过此温度范围,就容易产生冻害^[49]。马铃薯在4℃低温贮藏中,还原糖含量表现为缓慢升高到快速升高;将部分马铃薯放回20℃复温贮藏,还原糖含量下降,并且低于结束4℃贮藏时马铃薯还原糖的含量。将两种不同贮藏环境的马铃薯在相同条件下油炸,发现经复温处理的马铃薯不易发生褐变,且品质更佳^[50]。

2.1.3 高压处理 高压处理(high pressure, HP)是通过冷巴氏杀菌过程延长水果产品保质期的非热替代方法^[51]。该技术的主要优点在于其能够维持色素、挥发物、维生素和其他能促进健康的化合物不受影响^[52-53]。然而,由于PPO耐压,不能完全避免褐变反应,因此需要将HP与其他技术相结合,如在具有渗透性的薄膜中包装^[54]。在贮存过程中,通过在HP之前应用渗透脱水(osmotic dehydration, OD)对

氧气的有限获取和通过应用HP使PPO部分失活,可以防止褐变。这种策略可以帮助产品暴露于空气后保持产品的颜色^[53]。黄欢等^[55]研究了超高压(HPP, 100~600 MPa, 10 min)对鲜切马铃薯色泽、硬度、咀嚼度、细胞壁相关酶活性及多糖组成的影响,结果表明,HPP在压力 ≥ 500 MPa下对鲜切马铃薯的褐变抑制效果较好,300 MPa时褐变严重且程度高于对照。

2.1.4 高氧技术 在果蔬的保存过程中通过高于60%氧浓度连续处理,能促进抗氧化能力和总酚含量的增加^[56]。60%~100%的氧连续处理也能显著抑制果实腐烂、呼吸和乙烯产生速率,并能灭活病原菌^[57]。这是由于氧化还原生物系统和膜的完整性导致高氧诱导的抗氧化能力增加^[58]。此外,作为一种非生物胁迫,高氧处理不可避免地调节活性氧(ROS)和氧化还原生物系统^[59]。然而,短时间高氧预处理对鲜切马铃薯褐变影响的报道较少。Liu等^[41]通过研究4℃鲜切马铃薯片中PPO、POD和PAL活性、总酚含量、膜渗透性、MDA含量和抗氧化能力,评价短时间高氧预处理对抗褐变的影响,结果表明,80%的氧预处理不仅能抑制PPO活性,而且能显著提高抗氧化能力,在贮存时间内PAL、POD活性和总苯酚的底物生成略有增加。同时,在高氧预处理条件下,MDA的积累明显受到抑制,细胞完整性保持较好。总的来说,短时间高氧预处理是一种简单、安全、低成本、方便的抗褐变方法,有助于鲜切马铃薯加工。

2.1.5 气调包装 气调包装是通过控制果蔬包装内气体的成分及含量,降低果蔬呼吸作用,以实现减少果蔬营养成分流失和延长货架期的目的。韦雪等^[60]研究表明,气调参数30% CO₂能抑制鲜切马铃薯氧化酶的活性,有效抑制马铃薯褐变且保持较好的硬度、脆性。Ayon-Reyna等^[61]研究表明,通过气调结合异抗坏血酸和N-乙酰半胱氨酸可降低鲜切菠萝褐变指数。Shen等^[62]将鲜切马铃薯加压处理后,在4℃条件下保存在体积分数为4% O₂+2% CO₂+94% N₂环境中,能很好地保持鲜切马铃薯的硬度和颜色。赵欣等^[63]在4℃条件下,通过体积分数比40% CO₂+50% O₂+10% N₂混合气体包装鲜切马铃薯片,能有效抑制PPO和POD活性、微生物的增长与MDA的积累,鲜切马铃薯片在16 d内保持较好的感官品质。

2.2 化学制剂控制褐变技术

2.2.1 无机物控制褐变技术 以化合物为基础控

制酶促褐变的方法主要是添加 PPO 抑制剂,水果和蔬菜剥皮或鲜切后,在含有化学合成 PPO 抑制剂的水溶液中浸渍处理或在可食用涂料配方中加入抗褐变剂^[64]。广泛用于抑制酶促褐变的添加剂包括亚硫酸盐和抗坏血酸。用于食品添加剂的不同亚硫酸盐有亚硫酸钠、焦亚硫酸钠和亚硫酸氢钠。这些盐溶解产生 SO_3^- 和 HSO_3^- ,能不可逆抑制 PPO 活性,减少邻醌类物质生成,从而逆转酶促反应,并在亚硫酸盐和邻醌类之间形成加成产物,防止进一步反应生成棕色色素^[65]。但由于存在健康风险,在食品中使用亚硫酸盐存在争议^[66]。抗坏血酸抑制褐变是通过由 PPO 形成的邻醌被还原为前体邻二酚,随后再次被氧化。这种氧化还原循环一直持续到所有的抗坏血酸消耗后,但棕色色素仍然形成。因此,抗坏血酸可以延缓褐变,但不抑制酶活性^[67]。柠檬酸是一种非特异性的酶失活剂,可通过降低 PPO 的 pH 而使酶失活^[68]。环糊精的疏水核心可以与包括酚类底物在内的几种分子形成络合物,从而防止其氧化成醌,形成棕色色素^[69]。螯合剂 EDTA 和草酸也可通过将铜离子捕获在酶的活性部位,从而抑制酶的活性^[70-71]。硫醇是具有巯基官能团(-SH)的化合物,如谷胱甘肽(GSH)、L-半胱氨酸(CYS)和 N-乙酰半胱氨酸(NAC),是一种很好的酶促褐变抑制剂。Cerit 等^[72]研究比较了焦亚硫酸钠和硫醇化合物谷胱甘肽(GSH)、L-半胱氨酸(CYS)和 N-乙酰半胱氨酸(NAC)对马铃薯鲜切 1、24 和 48 h 后酶促褐变、抗氧化酶活性、总酚酸和抗坏血酸含量的影响,结果表明,含 2.0% NAC、1.0% CYS 和 2.0% CYS 的溶液可抑制酶促褐变,显著提高鲜切马铃薯的残留硫醇和抗坏血酸含量及抗氧化酶活性,而 GSH 对褐变无明显的抑制作用。

2.2.2 有机物控制褐变技术 氨基酸在鲜切产品的酶促褐变中起重要作用。氨基酸可通过与醌类反应和影响 PPO 活性参与酶促褐变。氨基酸与醌类化合物结合,能加速褐变,或作为螯合剂形成无色加合物,减少褐变^[73]。PPO 是马铃薯褐变中起核心作用的酶,是一种低聚金属酶,其活性位点包含两个铜离子,每个铜离子与 3 个组氨酸残基配位^[66]。PPO 催化酚类底物被分子氧氧化,得到高活性的有色邻醌,其可进行不可逆的非酶自聚合或与其他酚类、氨基酸或蛋白质反应产生棕色色素^[74]。PPO 主要存在细胞器的细胞膜上,如线粒体、过氧化物酶体和叶绿体类囊体。酶促反应发生在细胞破裂时,酶与液泡中的酚类化合物接触,作为植物

致病防御系统的一部分^[75]。氨基酸和蛋白质可能与醌类发生反应,促进褐变过程,或作为螯合剂,抑制褐变^[76]。L-半胱氨酸标记明显抑制了生菜的 PPO 活性^[77]。L-半胱氨酸作为非竞争性抑制剂抑制 PPO 活性,降低了黄梨的褐变^[78]。精氨酸通过抑制酚类化合物的合成来抑制鲜切蛇皮果的褐变^[79]。精氨酸和赖氨酸的共同作用显著抑制了鲜切苹果的褐变^[80]。10 g·L⁻¹的谷氨酸处理显著抑制了茄子的褐变^[81]。10 g·L⁻¹谷氨酸和 10 g·L⁻¹甜菜碱的组合可显著抑制双孢蘑菇的褐变^[82]。

此外,甘氨酸、苯丙氨酸、蛋氨酸、缬氨酸、谷氨酸和 L-半胱氨酸也可以抑制鲜切马铃薯的褐变^[73]。最近的研究表明,90 mmol·L⁻¹脯氨酸处理显著降低了鲜切马铃薯的褐变^[83]。50 g·L⁻¹氯化钠处理显著抑制鲜切马铃薯的褐变,并诱导内源性谷氨酸合成^[84]。10 g·L⁻¹天冬氨酸处理通过降低 pH 和螯合铜离子(Cu^{2+})来抑制 PPO 活性,从而抑制鲜切马铃薯的褐变^[18]。15 g·L⁻¹异亮氨酸处理通过螯合 Cu^{2+} ,并与 PPO 的氨基酸残基形成相互作用力,抑制 PPO 活性,从而抑制了鲜切马铃薯褐变^[85]。高浓度的甘氨酸、缬氨酸、蛋氨酸和苯丙氨酸通过形成彩色的儿茶酚-氨基酸加合物诱导褐变,而低浓度则抑制马铃薯褐变^[73]。15 g·L⁻¹的谷氨酸处理 4 min,可以抑制总酚的积累,并降低 pH 和螯合 Cu^{2+} 来调节 16 个游离氨基酸的含量,抑制 PPO 活性^[86]。

2.2.3 植物提取物控制褐变技术 目前,许多植物提取物已被证明可以有效抑制 PPO 活性,缓解酶促褐变^[87-88]。绿茶提取物对新鲜苹果片具有较强的抗褐变作用,这是由于提取物中儿茶素对 PPO 活性具有竞争性的抑制作用^[91]。杧果皮提取物(0.04 g·mL⁻¹)由于原儿茶酚、杧果苷的存在,可以竞争性地抑制马铃薯 PPO 活性^[89]。洋葱和大蒜提取物的抗褐变活性主要是由于硫化物对 PPO 活性的抑制作用^[90-91]。Sukhonthad 等^[92]研究了全脂和商业脱脂米糠提取物(RBE 和 CDRBE)对马铃薯和苹果酶促褐变的抑制能力,与 CDRBE 相比,RBE 对马铃薯和苹果中 PPO 活性和褐变的抑制作用更为有效;采用 HPLC 鉴定了 RBE 和 CDRBE 中的 5 种酚类化合物(原儿茶酸、香草酸、对香豆酸、阿魏酸和芥子酸);然后利用一个模型系统评估了他们在抑制中的重要作用,发现 RBE 中的阿魏酸和 CDRBE 中的对香豆酸在马铃薯和苹果的酶促褐变抑制中具有活性,其中对香豆酸对马铃薯和苹果 PPO 的抑制作用最强;几乎所有酚类化合物对马铃

薯和苹果 PPO 的抑制作用均强于 $100 \mu\text{g} \cdot \text{mL}^{-1}$ 的柠檬酸。Liu 等^[93]研究表明,马齿苋水提取物(0.5%, w)对新鲜切割马铃薯的切片褐变程度、PPO、POD 和 PAL 活性表现出有效的抑制作用,其自由基清除能力在多酚(如香兰素、3-香豆酸、13s-羟基十八二烯酸、阿魏酸)和生物碱(如甜菜碱、2-脱氧肌昔、三烯碱、*N*-methylhernagine)的褐变抑制中起主要作用。Zhang 等^[94]研究了沙棘叶提取物(以花茶素、金丝桃素、没食子酸、木麻黄素和异鼠李素为沙棘叶提取物的主要成分)对鲜切马铃薯褐变的影响,结果表明,与沙棘果实提取物相比,沙棘叶提取物对鲜切马铃薯的褐变有显著的抑制作用。进一步研究表明,沙棘叶提取物对 PPO 活性具有竞争性抑制作用,IC₅₀ 浓度值为 $0.7 \text{ mg} \cdot \text{mL}^{-1}$ 。分子对接结果表明,没食子酸能稳定地结合在 PPO 的活性位点上,而异鼠李素对 PPO 的亲合力较低。以上结果表明,沙棘叶提取物通过降低过氧化物酶和苯丙氨酸解氨酶活性,降低酚类物质含量,提高抗氧化能力,从而抑制了鲜切马铃薯的褐变。

2.2.4 纳米材料控制褐变技术 纳米技术是通过研究和开发长度为 1~100 nm 的纳米材料来延长食品保质期的一项新兴技术^[95]。纳米颗粒可以显著地改变特定材料的物理和化学性质,如提高机械强度、热稳定性、电导率等^[96]。早期对银纳米颗粒(101~109 nm)的研究表明,其对蔬菜汁的保存效果良好^[97]。应用 Ag-PVP 涂层有利于延长鲜切芦笋保质期,2 °C 和 10 °C 环境下分别可以延长 25 和 20 d,而未应用 Ag-PVP 涂层的对照组在 2 °C 和 10 °C 环境下分别可保存 15 和 10 d^[98]。另外一种与 MAP 结合的纤维素切片纳米颗粒混合材料,将甜瓜的保质期延长了 5 d^[99]。

氧化锌纳米颗粒也具有抑制微生物生长的潜力。Li 等^[100]开发了一种新型聚氯乙烯薄膜,与氧化锌纳米颗粒混合用于保存鲜切苹果。结果表明,与对照(聚氯乙烯薄膜包装)相比,氧化锌纳米包装使鲜切富士苹果的衰变率显著降低了 21.9%,保质期延长了 6 d。Meng 等^[101]报道了氧化锌纳米颗粒涂层结合超声可将鲜切猕猴桃的保存寿命延长 4 d。此外, TiO₂ 纳米颗粒涂层定向聚丙烯(OPP)包装膜能使大肠杆菌从 6.4 下降到 4.9 log CFU·g⁻¹,而未涂层 OPP 薄膜袋中的样品从 6.4 下降到 6.1 log CFU·g⁻¹^[102]。Rabea 等^[103]通过化学方式合成了 CuO 和 MgO 金属氧化物纳米颗粒,研究其对马铃薯褐腐病的影响,结果表明,在质量浓度为 $3 \text{ mg} \cdot \text{mL}^{-1}$ 时, CuO-NPs 和

MgO-NPs 对马铃薯的生长有强烈的抑制作用,抑制圈(ZOI)分别为 19.3 和 17.0 mm; CuO-NPs 和 MgO-NPs 的最低抑菌质量浓度(MIC)和最低杀菌质量浓度(MBC)分别为 0.50、0.60 和 0.60、0.75 mg·mL⁻¹。

2.3 基因工程褐变控制技术

PPO 是鲜切马铃薯块茎酶促褐变的关键酶。Bachem 等^[104]利用反义基因技术降低 *StPPO* 的表达量,可以减轻马铃薯的褐变发生。Coetzer 等^[105]将番茄 *PPO* 反义基因转化马铃薯,可以有效抑制马铃薯多酚氧化酶的活性,从而降低褐变程度。进一步的研究表明,在马铃薯中发现了 12 个 *PPO* 基因,即 *StPPO1*、*StPPO2*(*StPOT32*)、*StPPO3*(*StPOT33*)、*StPPO4*~*StPPO12*^[106]。然而,通过人工 microRNA (amiRNA) 技术发现 4 种 *StPPOs* (即 *StPPO1* 到 *StPPO4*) 在块茎中高表达,其蛋白含量和酶活性负责马铃薯块茎的酶促褐变^[107]。陈明俊^[108]利用 CRISPR/Cas9 技术编辑 *StPOT32* 基因获得突变株,较野生型 PPO 活性和褐变强度降低,更晚发生褐变且褐变程度更低。方圆等^[109]利用 RNAi 和 Gene-Deletor 技术对 *StPOT32* 基因构建干扰载体,转基因马铃薯块茎较野生型对照 PPO 活性和褐变指数均大幅降低。除 *PPO* 基因外,天冬氨酸蛋白酶抑制剂基因(*StASPI*)的过表达也抑制了鲜切马铃薯的酶促褐变^[110]。Li 等^[111]过表达 *StSN2* 通过提高抗氧化酶活性,降低酚类和可溶性醌含量,同时改变了重要的激酶和其他蛋白磷酸化水平,从而抑制了鲜切马铃薯的酶促褐变。Shi 等^[112]通过 CRISPR/Cas9 构建 *StPHB3* 突变体,结果表明,突变体马铃薯块茎中 *StPHB3* 的转录水平有所提高。*StPHB3* 突变提高抗褐变活性,MDA 含量降低,PPO 和 POD 活性受到抑制,酚底物含量增加,有色醌产物形成减少,最终缓解鲜切马铃薯褐变。此外,还发现 *StPHB3* 定位于叶绿体,并与 *StPOT32* 相互作用,而 *StPHB3* 的突变导致了 PPO 含量的降低,表明 PPO 的激活受到 *StPHB3* 的调控。

3 展望

笔者介绍了马铃薯褐变发生的机制,综述了近年来鲜切马铃薯褐变控制技术的最新研究进展,其中物理控制技术包括超声、低温、高压、高氧和气调包装等处理;化学制剂控制褐变技术涉及无机物、有机物、植物提取物和纳米材料;基因工程技术包括反义基因、人工 microRNA (amiRNA)、基因过表

达、基因编辑(CRISPR/Cas9)和RNAi技术等。每一种控制褐变的技术都有其优点和局限性,加工过程中发生的褐变问题仍然需要进一步研究,如何在不影响感官和营养品质的情况下,延长鲜切产品的保质期,未来的研究应着眼于通过这些新技术的复合处理来实现,这与王海艳等^[7]的观点相一致。同时还应加强这些新技术在有效性、成本效益比和操作方便性等方面的研究。目前很多新技术的应用仍处于实验室早期阶段,这需要在今后的工作中以试点规模和工业规模进行广泛的试验。以食品安全为导向的技术被认为优于以便利性为导向的技术,因此,有关部门须对纳米材料等新技术进行潜在毒性和综合风险方面的评估。

此外,还可以通过遗传育种来改良马铃薯抗褐变能力。近年来,笔者也对一些马铃薯材料褐变抗性进行了鉴定^[113-114],筛选出的高抗褐变材料已用于新种质创制,易褐变材料结合已报道的褐变相关基因更好地了解马铃薯褐变分子机制奠定了基础,也为未来的遗传改良工作提供借鉴与指导。马铃薯褐变研究的不断深入和突破,将为改善马铃薯品质和提高市场价值提供重要的科学依据和技术支持。

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