采后苹果虎皮病研究进展

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摘要 苹果是典型的呼吸跃变型果实,采后苹果在长期低温贮藏后或从低温贮藏结束转移到货架后易发生虎皮病,降低了果实的贮运价值。虽然国内外学者对苹果虎皮病发生机理进行了全面深入的研究,普遍认为虎皮病的发生与α-法呢烯及其氧化产物的积累存在密切的关系,但苹果虎皮病系统的发生机制至今仍未完全阐明。主要从虎皮病症状、虎皮病发生机制、延缓虎皮病的措施等方面进行了综述,以期为全面阐明虎皮病的发生机制和防治虎皮病的发生提供理论依据。

关键词 苹果;虎皮病;症状;机理;α-法呢烯;防治措施
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Research Progress of Superficial Scald in Postharvest Apple Fruits

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Abstract Apple is a typical climacteric fruit. Superficial scald often develops after long-term low-temperature storage or transfer from low-temperature storage to shelves, which reduces the storage and transportation value of the fruit. Although domestic and foreign scholars have conducted comprehensive and in-depth research on the occurrence mechanism of superficial scald, it is generally believed that the occurrence of superficial scald is closely related to the accumulation of α-farnesene and its oxidation products, but the mechanism of the apple superficial scald system has not yet been fully elucidated. This article mainly reviewed the symptoms of superficial scald, the mechanism of superficial scald and the measures to delay tiger skin disease, in order to provide a theoretical basis for the comprehensive elucidation of the occurrence mechanism of superficial scald and the prevention and treatment of superficial scald.

Key words Apple; Superficial scald; Symptoms; Mechanism; α-farnesene; Prevention and treatment measures

苹果(*Malus domestica*)是世界上广泛种植的特色水果之一,由于其较高的营养价值和商业价值而受到消费的喜爱。低温冷藏对提高苹果果实品质和经济价值有非常重要的作用,但往往在长期冷藏期间伴随着虎皮病、衰老褐变病、苦痘病等各种类型生理病害的发生,严重影响果实的贮运和货架期。虎皮病是苹果冷藏过程中最容易发生的一种生理失调病害。虎皮病的发生严重影响了苹果外观色泽和经济效益。虽然国内外学者对苹果虎皮病系统的发生机制进行了全面深入的研究,普遍认为α-法呢烯及其氧化产物的积累与虎皮病的发生具有密切的关系[1-3]。在苹果长期冷藏期间采用合适的商品化处理对抑制虎皮病的发生、保持良好的果实品质和贮运价值具有重要意义。因此,采后苹果虎皮病发生机理的研究仍然是目前苹果果实采后生理研究中迫切需要解决的重点和难点问题。笔者主要从虎皮病症状、虎皮病发生机制、延缓虎皮病的措施等方面进行了综述,以期为控制苹果虎皮病的发生和全面阐明虎皮病的发生机制提供理论依据,同时对保持苹果良好的品质和商业价值具有重要的科学意义和应用价值。

1 虎皮病症状

虎皮病是苹果和梨在采后长期低温贮藏中易发生的一种生理失调性病害[3-4],其发病症状表现为果皮出现浅褐色至黑色的斑块,呈不规则微凹陷状。但一般在果肉中不会出现虎皮病病斑,也不影响果实的风味;在果皮感病较严重时,其症状类似于烫伤且连成大片,可成片撕下病果皮,甚至造成果肉褐变、发黏和发绵,稍带酒味,加速了果实腐烂变质的过程。组织学研究观察表明苹果果皮发病部位是由4~6层亚表皮细胞坏死所致[5]。因此,苹果采后冷藏中虎皮病的发生严重降低了果实的外观色泽和贮运价值。

2 虎皮病发病机理

2.1 α-法呢烯与苹果虎皮病 伴随苹果虎皮病发生的同时产生E,E-α-法呢烯和Z,E-α-法呢烯2种类型,但是果皮中Z,E-α-法呢烯的含量仅为E,E-α-法呢烯的1/100[6]。研究发现,苹果虎皮病的形成与α-法呢烯的产生存在密切的相关性,并且α-法呢烯受到乙烯的调控[7-8]。在果实呼吸跃变前,α-法呢烯含量较低,随后随着后熟过程中乙烯含量的升高而增加,在出现高峰含量后随之下降[9]。采用乙烯作用抑制剂1-MCP或者乙烯合成抑制剂AVG处理苹果能够降低α-法呢烯及其氧化产物的积累,那么使用乙烯利处理苹果果实则诱导α-法呢烯含量的积累[10]。但有研究表明α-法呢烯的含量与虎皮病指数不一定呈正相关。例如在易发虎皮病的晚采收苹果中α-法呢烯含量明显低于成熟度较低的果实[11]。在虎皮病抗性较强的“Idared”品种果实中的α-法呢烯含量低于易发虎皮病“Law Rome”品种[12],但在抗虎皮病较强的“Belfot”品种中α-法呢烯含量高于易发虎皮病“Granny Smith”品种[13]。

2.2 α-法呢烯氧化产物与苹果虎皮病 α-法呢烯氧化产

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物在不同的苹果品种栽培环境和采后冷藏环境中的积累量与果实虎皮病的发生不一定呈正相关。有研究学者证实了α-法呢烯的氧化产物是诱导虎皮病发生的重要因素[14]。Ding 等[3]研究发现 α-法呢烯氧化产物为共轭三烯醇(conjugated trienols,CTols)[15]。Soria 等[14]研究发现,将共轭三烯醇涂在“Granny Smith”苹果果皮上有效控制了虎皮病的发生;在虎皮病敏感的品种中,在冷藏 4~6 个月时 CTols 的含量达最大值。Marc 等[16]在抗氧化系统受到严重破坏的苹果果皮中发现,α-法呢烯氧化产物在诱导虎皮病发生中并不占主导地位,而是 α-法呢烯氧化过程中产生的自由基或毒性挥发物会增加病症的发生和严重程度。在苹果冷藏期间 α-法呢烯及其氧化产物共轭三烯醇变化规律中发现,虎皮病可能是由于在低温下破坏线粒体电子传递并由此产生超氧化物阴离子形成的一种氧化应激反应。除共轭三烯醇外,苹果贮藏期间三萜类化合物含量如熊果酸和 β-谷甾醇含量的增加与虎皮病的发生有密切的关系[17]。在苹果皮冷藏 30 d 后,α-法呢烯氧化产物如甲酯、甾醇和其他化合物的不同含量与叶绿体完整性和氧化应激反应有关[18]。此外,α-法呢烯及其氧化产物可以作为信号系统,多酚类化合物和细胞的程序性死亡可能是虎皮病发生的原因[19]。

2.3 酚类物质与苹果虎皮病 苹果果皮中含有丰富的根皮苷、儿茶素、绿原酸、表儿茶素、类黄酮、花色素苷等酚类物质[20]。酚类物质不仅作为抗氧化剂与苹果虎皮病发生密切相关,而且它可以作为酶促褐变的底物,生成褐色物质使虎皮病症状表现出来。苹果褐变主要由多酚氧化酶(PPO)所导致的酶促褐变,果皮组织中的酚类物质在 PPO 催化氧化下生成醌类物质,然后醌类物质经聚合反应生成褐色物质使得果皮褐变症状表现出来。Song 等[21]在苹果加工产品中发现,果皮中 PPO 可催化氧化表儿茶素、原花色素、儿茶素等酚类物质而导致褐变的发生。研究表明,同一品种采收时和贮藏期间 PPO 活力越高,虎皮病发病率就越高[22]。Du 等[23]研究表明,易发生虎皮病的品种“Cortland”和“Delicious”中 PPO 的活性高于抗性品种“Empire”。在低温冷藏前经 20 ℃ 下短期无氧处理“Granny Smith”果实,发现果皮中 PPO 的活性有所下降,并且虎皮病指数降低[24]。这些研究表明,采后苹果冷藏期间果皮中 PPO 活性与虎皮病的发生有着密切的相关性。

酚类物质的种类及含量与采后苹果冷藏期间虎皮病的发生存在着密切的关系。一些简单的酚类物质和类黄酮含量在采后苹果虎皮病发生进程中呈现出降低的规律。苹果经 UV 光照射后,苯丙素类物质含量明显增加而且果皮虎皮病症状减轻[17]。在探讨“Rall”和“Delicious”果实中酚类种类与虎皮病的相关性研究中表明,果皮中花色素苷的含量与虎皮病呈负相关,而果皮中类黄酮的含量与虎皮病的发生并不相关,可能由于花色素苷具有较强的抗氧性而减轻了虎皮病的发生[25]。Rudell 等[17]研究发现,槲皮素-3-芸香糖苷在苹果虎皮病发生过程中含量增加,可能与虎皮病的发生密切相关。Busatto 等[19]利用靶向的代谢组学技术研究代谢化合物与苹果虎皮病的相关性中发现,苹果果皮中绿原酸、根皮苷、表儿茶素、儿茶素、黄酮醇化合物的含量相对较高,并且虎皮病较严重的果皮中总酚含量比果肉高很多,其中绿原酸的含量与虎皮病的发生呈正相关;利用 LC-MS 技术发现 α-法呢烯及其氧化产物 6-甲基-5-庚烯-2-酮与苹果虎皮病的发生存在密切的关系。Farneti 等[26]利用 LC-MS 结合非靶向的代谢组学技术研究了挥发性化合物可能参与苹果虎皮病发生,表明 6-甲基-5-庚烯-2-酮(MHO)与苹果虎皮病的发生有密切的关系。Leisso 等[18]分析表明,DPA 处理的“Granny Smith”苹果果皮中酚类物质的含量与对照存在显著差异,DPA 处理表现得更为明显;对照果实中的表儿茶素、黄烷醇和儿茶素的含量仍较高,而这些化合物在 DPA 处理的果实中含量较低;在“Granny Smith”贮藏 120 和 180 d 时,虎皮病发病症状出现,对照和 DPA 处理果实中苯丙素衍生的化合物中绿原酸含量增加,表儿茶素和儿茶素在苹果贮藏 180 d 时含量降低,但它们在对照果实中含量高于 DPA 处理;对照组“Granny Smith”果实中根皮苷含量在冷藏 180 d 时出现了少量的增加,而 DPA 处理则明显诱导了根皮苷含量的增加。在易发生虎皮病的品种“Red Delicious”和“Cortland”中研究表明,虎皮病的发生与根皮苷含量呈负相关,与绿原酸含量呈正相关[20]。这些研究表明,苹果虎皮病的发生与酚类的种类和含量有很大的关系。

3 延缓虎皮病发生的措施

3.1 物理防治

3.1.1 品种。不同苹果品种对虎皮病的敏感程度有较大的差异。大量研究表明,“Empire”“Pink Lady”和“Gala”很少发生虎皮病,而“Cortland”“Starking”“Granny Smith”和“Red Delicious”[20,27-28]则易发生虎皮病。因此,培育虎皮病抗性较强的品种,可以有效减少采后苹果虎皮病发生所导致的商业损失。

3.1.2 热处理。热处理技术对抑制苹果冷藏期间虎皮病的发生有显著作用。一般来说,在适宜的时间内采用 30~50 ℃ 处理苹果果实,从而延缓果实的后熟进程和抑制微生物的活动,实际上是提高苹果冷藏效果的一种有效的物理辅助手段。该方法因具备无化学药物残留、杀病虫害和病原菌以及保鲜的优点,已广泛应用于苹果、香蕉、番茄、柑橘等果实的低温贮藏试验中并且效果显著。苹果经 46 ℃ 的高温热处理 12 h 或者 42 ℃ 的高温处理 1 d,然后将其置于 0 ℃ 库中冷藏 90 d,结果表明,热处理的果实虎皮病发病情况显著低于对照组,尤其是与虎皮病发生相关的 α-法呢烯和共轭三烯醇的含量受到明显的抑制[29]。“澳洲青苹”经 38 ℃ 高温处理后其虎皮病的发病症状明显减轻,α-法呢烯的合成量明显低于对照组;可能是苹果经热处理后,果皮蜡质结构和厚度发生较大的改变,进而降低了 α-法呢烯的氧化和共轭三烯醇的合成,抑制了虎皮病的发生[30]。但在苹果冷藏中一旦热处理温度控制不当就会对果实造成更大的伤害作用。

3.1.3 气调贮藏。气调贮藏对抑制采后苹果虎皮病的发生有明显效果。Asif 等[31]在研究不同薄膜包装材料对红富士

苹果冷藏效果的试验中发现,薄膜包装材料内含有低浓度的 O_2 和 CO_2,能有效抑制虎皮病的发生,特别是超低 O_2 浓度其效果更加明显,苹果一般在 0~1 ℃、0.5%~3.0% CO_2 和 1.0%~2.5% O_2 气调贮藏中效果最佳。苑克俊等[32]对低 O_2 气调贮藏对新红星苹果冷藏中虎皮病的发生情况进行了观察,发现虎皮病指数在新红星苹果贮藏 123 d 时为 1.02%,可见低 O_2 气调贮藏在一定程度上降低了 α-法呢烯和共轭三烯醇的合成。随后利用低 O_2 并结合自发气调贮藏玫瑰红苹果,其虎皮病的发病情况较对照更轻[33]。

3.2 化学防治

3.2.1 DPA 处理。虎皮病的发生与苹果采后处理存在密切的关系,采用合适的采后处理能有效控制虎皮病的发生,从而保持果实良好的品质和经济价值。一般来说,化学处理可以有效抑制苹果虎皮病的发生,但是化学处理的同时会带来毒性物质进而危害人们的身体健康。苹果市场中经常使用二苯胺(Diphenylamine,DPA)来防治虎皮病的发生。从大量有关 DPA 处理对苹果果实生理品质的影响中发现,DPA 不仅通过阻断 α-法呢烯氧化产物共轭三烯醇(CTols)和 6-甲基-5-庚烯-2-酮(MHO)的合成来控制虎皮病的发生,而且也影响其他代谢过程如降低乙烯的产生,降低过氧化物酶(POD)和脂氧合酶(LOX)的酶活力,增加磷酸戊糖途径和改变香气物质代谢等[34]。Du 等[35]研究表明,DPA 处理能够有效抑制"Cortland"和"Red Delicious"虎皮病的发生。虽然 DPA 在控制采后苹果虎皮病的发生中有良好效果,但同时对消费者的身体带来了化学伤害作用,目前很多国家已明确禁止在苹果冷藏保鲜中使用 DPA。

3.2.2 1-MCP 处理。1-甲基环丙烯(1-Methylcyclopropene,1-MCP)具有无毒、无味、用量小的优点,能抑制苹果后熟进程中乙烯的合成,从而有效控制虎皮病的发生,现已替代 DPA 广泛在苹果冷藏保鲜中应用[36]。实际上,1-MCP 处理抑制果实的后熟和乙烯的合成,对 α-法呢烯的合成和氧化形成抑制作用,从而控制了虎皮病的发生[10]。Larrigaudière 等[37]研究表明,1-MCP 处理能够有效抑制"Red Delicious"虎皮病的发生。商业上经常使用 1-MCP 处理来控制苹果和梨虎皮病的发生[38-39]。

4 展望

综上所述,虎皮病发生机制是一个复杂的系统,与很多因素息息相关。α-法呢烯及氧化产物的积累、酚类种类和含量以及 PPO、POD、漆酶都可能参与虎皮病的发病机制,甚至在虎皮病的发生中起着至关重要的作用。Gong 等[20]研究发现,DPA 和 1-MCP 处理明显抑制"Red Delicious"和"Cortland"果实虎皮病的发生,并且显著降低了漆酶的活性。DPA 和 1-MCP 处理对苹果果皮中漆酶基因表达规律与乙烯的调控存在密切的关系。在这种情况下,α-法呢烯的生物合成、共轭三烯醇的积累与虎皮病的形成有密切关系,而且在底物表儿茶素存在的条件下,与漆酶催化氧化反应产生的褐色物质也可能与虎皮病的发生有关。然而,漆酶介导褐色产物的形成与 α-法呢烯氧化积累共轭三烯醇的相互作用需进一步研究。从漆酶的角度,在低氧条件下,以易发虎皮病"Granny Smith"为材料,结合不同的冷藏方式,加强漆酶在苹果虎皮病发生过程中的生物学作用研究,在今后仍然需要进一步地研究漆酶动力学性质以及在苹果组织中的定位,这有利于开发新的虎皮病抑制剂以替代 DPA。

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