果皮蜡质与果实贮藏关系的研究进展

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摘要：目的 概述果皮蜡质的成分、性质、形态结构，以及调控与转运途径等，以探讨果皮蜡质与果实耐藏性的关系及其作用机理，展望如何延长果实的贮藏期。**方法** 通过分析文献，理清果皮蜡质与果实耐藏性关系的研究范畴和热点，从果皮天然蜡质的成分、性质、形态结构，果皮蜡质与果实耐藏性的关系及其作用机理，果皮蜡质的合成、调控与转运途径等方面入手，对相关研究成果进行整理与综述，并对蜡质研究在果实采后贮藏中的应用前景进行展望。**结论** 果实表面的蜡质层是保护果实的天然屏障，具有防止果实水分散失、维持表面清洁、避免病菌侵害等作用，对果实耐藏性具有重要的影响。
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Research Advances on the Relationship between Epicuticular Wax and Fruit Storability

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ABSTRACT: The work aims to summarize the components, property, morpho-ultrastructure and biosynthetic and transport pathway of fruit epicuticular wax, so as to discuss the mechanism and relationship between the epicuticular wax and fruit storability, and predict how to prolong the storage period of fruits. Literature analysis was carried out to clarify the research scope and hot spots of the relationship between the epicuticular wax and fruit storability. The related research results were sorted out and summarized from the components, property and morpho-ultrastructure of fruit epicuticular wax, the relationship between fruit epicuticular wax and postharvest shelf-life of fruit, as well as the function, biosynthetic and transport pathway of fruit epicuticular wax. The application prospect of epicuticular wax research in postharvest storage of fruits was also prospected. The epicuticular wax on the outer surface of fruit is a natural defensive barrier to fruits, playing important roles in preventing the water loss of fruit, keeping fruit surface clean, protecting fruit from invasions of pathogens, and consequently enhances storability of fruits.
KEY WORDS: fruit; epicuticular wax; wax synthesis; storage

新鲜果实含水量高达 75%～95%，这是维持果实正常生理代谢和新鲜品质的必要条件。果实失水主要由果皮蒸腾作用引起，少量通过气孔直接散失[1]。在果实未采收之前，水可由植株的生理作用而获得，但

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采收后果实失去的水不能再从果树上得到补充，其结果必然导致果实质量减少、果皮皱缩、代谢失调、耐藏性下降等。通常果实的外果皮覆盖着极为细密的一层膜，称为角质层（cuticle）。角质层由最外层的上表皮蜡质膜层和角质膜层构成，疏水的蜡质层可起到防止体内水分丧失的作用[2]。可见，果实表面的蜡质层是保护果实的天然屏障，当果实表面蜡质层合成不足、覆盖不够或者采后处理不当时，则果实失水速度加快，果实的耐藏性随之下降。近年来，关于采后果实蜡质的生理生化特性及其对果实耐贮性的关系也有一些研究报道，表皮蜡质被证实在果实采后贮藏品质变化中起着一定的作用[3—5]。由此可见，从蜡质的生理生化特性、细胞水平、分子机制等方面研究蜡质的形成与果实采后耐藏性和保鲜的关系十分重要，对提高果实的耐藏性和抗病性具有非常重要的科学意义和应用价值。

1 果实表皮蜡质

1.1 成分

果实表皮蜡质成分复杂。Morice 等[6]（2010）利用 GC-MS 技术比较了'Granny Smith'、 'Dougherty'和'Sturmer'等苹果品种的蜡质成分，表明蜡质是由长链脂肪酸、烷烃、初级醇、萜类化合物等物质组成的混合物。不同的果实种类，其蜡质成分存在很大的差异，Xiao 等[7]（2017）发现，脂肪酸和烷烃是梨表皮蜡质的主要成分，但在草莓和树莓中难以检测到相同的组分[8]，柑橘果实中蜡质的主要成分为类黄酮[9]，而葡萄果实的蜡质成分则主要为萜类化合物和醛类化合物[10]。

1.2 性质

果皮蜡质是一类复杂有机物质混合物的总称，具有不溶于水而易溶于有机溶剂的性质，因此常采用正己烷、氯仿等有机溶剂来提取果实表皮的蜡质。以氯仿作为溶剂，适当加热能将辣椒果实表皮蜡质完全提取。如果以正己烷为溶剂，则果实表皮蜡质还有少量呈不规则小粒状残存；采用常温法，则 2 种溶剂都不能将辣椒果实表皮蜡质完全提取。此外，采用局部加热并利用活性剂的吸附作用，便可将果实蜡质提取完全[11]。Isaacson 等[12]（2009）对番茄蜡质突变体 cd1，cd2 和 cd3 的表皮蜡质的生化特性进行了研究，结果表明烷烃可能是蜡质组分中保水性能最好的成分，而萜类含量的增加则会降低蜡质的保水性。有光泽番茄突变体的果皮比野生型番茄表现出更强的水分渗透性，这可能跟番茄果实表皮蜡质中长链烷烃的比例较低有关[13]。

1.3 形态结构

不同果实组织、种类的蜡质结构存在很大的差异。Han 等[14]（2006）研究发现，香梨果实在贮藏前期表皮蜡质层致密而平滑，而在贮藏后期果皮蜡质出现了较多的裂纹。Riedel 等[15]（2007）发现，葡萄、李以及部分苹果品种的果实表皮蜡质呈白霜状或淡蓝色。Sivakumar 等[16]（2008）发现，'Mauritius'和'McLean's Red'等 2 种荔枝果实表皮蜡质层表面粗糙、盘绕，更加紧凑、皱褶。Wu 等[17]（2018）研究发现，'Kucheamute'和'Hongxiangsu'果实表皮蜡质呈垂直多边形小棒状。通过对 13 000 种植物蜡质结构进行系统的观察和分类，将蜡质分为蜂窝状、垂直状、网状、柱状、线状等 26 种微观形态结构[18]。

2 果皮蜡质与果实耐藏性的关系

2.1 果皮蜡质层的厚度、结构、形态等对果实贮藏性具有重要影响

一般来说，耐藏性好的品种，其果实蜡质层厚、表皮细胞排列整齐致密，不耐藏的果实则蜡质层较薄，蜡质排列疏松，在贮藏期间易失水、皱皮或褐变。Morice 等[6]（2010）比较了不同苹果品种果实表皮蜡质的结构，大部分苹果品种表皮蜡质层呈均匀分布，且无断层结构，表明这些苹果品种不易失水，耐贮藏，但金冠品种果实的表皮蜡质层疏松，易出现断层，形成了堆积结构，表明金冠苹果果实易失水皱缩，且不耐贮藏。由此可见，通过改善果实蜡质层的组织结构或性能，可提高果实的贮藏性。例如，采用 1-MCP 处理苹果，通过蜡质的变化影响内部乙烯的释放，1-MCP 处理后果实蜡质具有更多的酚类物质和较强的清除自由基能力[19]。

2.2 果皮蜡质在提高果实耐藏性中的作用

2.2.1 果皮蜡质防止水分散失

蜡质由长链烷烃、脂肪酸、醛类等疏水物质构成，在果实表皮形成了一层限制水分散失的蜡被膜。Parsons 等[20]（2012）比较了蜡质和角质对防止水分散失的相关性，发现角质含量对水分散失作用不大，而蜡质在防止水分散失中起着重要作用。套袋使梨果实表皮细胞长度增加，角质膜发育不良，角质膜变薄，蜡质含量低，果实易发生裂纹，从而导致果实的抗病性降低，水分散失速率较快[21]。苹果蜡质总量随着果实的成熟呈持续上升的趋势，采后果实在不同的贮藏条件下，其蜡质总量和成分存在一定差异[22]。中型或大型番茄在发育过程中，果实蜡质层积累缓慢，导致果实防止失水能力降低[23]。蜡质成分在果实后熟时不断变化，进而影响果实的失水速率[24]。

2.2.2　蜡质与果实软化的关系

果实蜡质在延缓果实软化过程中起着一定的作用。蓝莓果实表皮蜡质能显著降低多种细胞壁降解酶的活性，从而抑制果实细胞壁物质的快速分解，保持果实较好的色泽和硬度。当果皮蜡质被破坏时，则会加速果实的软化衰老进程[25—26]。李宏建等[27]（2013）发现，采后苹果硬度和失水率变化小的品种具有浓厚且均匀致密的蜡质层，对果实的软化具有一定的抑制作用。

2.2.3　蜡质与抗病的关系

果实蜡质的厚度、结构和组成成分是影响果实抗病性的主要因素。Konarska 等[28]（2012）研究发现，蜡质层的厚度和结构跟苹果果实的感病性有关，较厚的蜡质层能够阻止微生物侵染苹果果实，并延缓果实的贮藏期。Fan 等[29]（2018）报道，苹果果实表皮蜡质层厚度和密度与果实贮藏过程中发生褐变有关。Gabler 等[30]（2003）研究发现，葡萄表皮蜡质厚度和含量与对葡萄孢属（B. cinerea）的抗病性呈正相关。研究发现，与野生型番茄相比，突变体番茄果实蜡质结构缺失，导致其质量降低，病原体侵染果实的能力明显加强[12]。研究发现，梨果实和苹果果实表皮蜡质布满网状裂纹，成为病原菌的入侵通道[31—32]。蜡质组分跟果实的抗病性存在密切的关系，如苹果和梨果实蜡质组分中含有抗真菌成分，这些蜡质组分可抑制 A. alternata 分生孢子的生长和萌发[33]。苹果虎皮病发病程度与果实表皮蜡质组分中长度为 C29—C32 的长链脂肪酸和聚亚甲基有较大的相关性[34]。果实中 C12—C18 饱和、不饱和脂肪酸的蜡质组分能抑制酸橙枯萎病的发生，苹果叶片中的酸性蜡质组分具有抗霉菌的能力[35]。

3　果实表皮蜡质的合成与调控

3.1　果实表皮蜡质的合成途径

蜡质的合成途径主要包括超长链脂肪酸（very long chain fatty acids, VLCFAs）的合成和蜡质合成等 2 步[36—38]。首先是 VLCFAs 的合成，C16 和 C18 饱和脂肪酸在质体内从头合成，然后在长链酰基辅酶 A 合酶（long-chain acyl-CoA systhase, LACS）的作用下将 C16 和 C18 饱和脂肪酸酯化为相应的酰基辅酶 A，再进入内质网，在脂肪酸延伸酶（fatty acid elongase, FAE）复合体的作用下，经过多步循环反应，最终延伸为 20~34 个碳原子的 VLCFAs。VLCFAs 通过脱羰途径合成长链烷烃、醛、仲醇和酮等蜡质成分，偶数碳原子的伯醇和蜡酯等蜡质分子则通过酰基还原途径合成。

3.2　果实表皮蜡质的调控

随着分子生物学和遗传学的快速发展，调控果实蜡质合成的相关基因被大量克隆（见表 1），为阐明果实蜡质成分的生理生化作用和分子机制打下了良好的基础。例如，苹果果实 *MdWIN1* 转录因子能诱导果皮表面蜡质总量的合成，可调控蜡质合成，同 *MdWIN1* 能诱导蜡质合成相关的基因（如 *MdCER1*、*MdKCS1* 和 *MdCER2*）的表达[39—41]。*MdCER1* 可能参与苹果果实表皮蜡质的合成[42]。*CsWIN1* 诱导柑橘果实角质和表皮蜡质的沉积[43]。*PaLACS2* 参与甜樱桃果实长链脂肪酸的合成[44]。蜡质基因在果实基因组中也有冗余存在，例如甜樱桃的蜡质基因 *PaKCS1*、*PaCER3*、*PaKCR1*[44]。随着果实蜡质合成基因功能被相继证实，通过克隆蜡质突变基因或过表达蜡质相关转录因子可以改良果皮的蜡质特性。从基因表达水平调控和改善果皮表面蜡质的成分、含量及结构方面，可以提高果实的耐藏性和抗病性。这为果实新品种的培育提供理论依据，也为采后果实的保鲜技术研究提供新的思路。

表 1　果实中已克隆的部分蜡质基因

Tab.1 Several cloned wax genes in fruit

Genes	Gene function
CER1	Aldehyde decarbonylase, convention of long chain aldehydes to alkanes[42—43]
CER2	Coenzyme A-dependent acyltransferase[45]
CER3	May encode a regulatory protein[46]
CER6	Elongate C24 very-long-chain fatty acids[47]
KCS1	Encodes a condensing enzyme (fatty acid elongase)[44]
WIN1	Activate wax deposition[39]
WAX2	Encode a transmembrane protein, associated with cuticle membrane and wax synthesis[48]
ECR	Involve in the synthesis of very long chain fatty acids[49]
KCR	Enhance fatty acid elongase activity[44]
LACS2	Encode acyl coenzyme A synthetase[44,50]

3.3　果实蜡质层的转运

目前疏水的蜡质在果实表皮细胞内质网中合成，如何将蜡质分子在内质网中转运到胞外亲水的细胞壁上的机制尚未阐明。Kunst 和 Samuels 认为有 2 种转运方式：蜡质分子在高尔基体介导向外分泌的作用，直接将蜡质分子转移至果实细胞膜上，然后再转移至胞外亲水的细胞壁上；蜡质借助非特异性脂类蛋白（nonspecific lipid proteins，ns LTP）和 ABC（ATP binding cassette）转运器蛋白的作用，将蜡质分子从质膜转运到质体外[51]。研究表明，非特异性

脂转运蛋白底物种类分布广泛，可以转运多种长链脂肪酸、脂肪醛等蜡质分子[52—54]。*SlCER5* 编码的 ABC 转运器蛋白定位在细胞质膜上，能够将蜡质分子从质膜内转运质外体中，证实了 ABC 转运蛋白参与蜡质分子的运输[55]。由此可见，蜡质分子在质体内向外运输需要 ns LTP 蛋白和 ABC 转运蛋白的协同参与，从质体内穿过细胞壁基质才可运输到果实表皮细胞中。

4 结语

蜡质层是果实抵御非生物逆境的最外保护层。近年来，学者们利用多种分子生物技术手段对果实的蜡质组分、性质、形态结构、作用以及合成途径等方面进行了深入探讨，但有关果皮蜡质与果实耐藏性的关系报道较少。从采后果实耐藏性和采后处理与保鲜的角度，笔者认为应加强以下 3 个方面的研究。

1）加强果实表皮蜡质层的成分、数量与形态结构方面的研究，为培育耐藏水果新品种打下基础。国内外对果实蜡质成分进行了相关的研究，果实裂果、抗病性和耐藏性均与果实蜡质层的特性存在密切的关系。对于采后果皮蜡质的积累规律和微观结构的观察缺乏系统的探究，在采后果实处理与保鲜研究中，可以考虑如何改善果实蜡质层的成分和数量，从而培养抗病性和耐贮性好的新品种。

2）加强采收后果皮蜡质层的变化规律及其影响因素的研究，为水果采后处理和保鲜技术提供理论参考。目前国内外对果实在发育期间的蜡质层变化规律研究较多，但针对采收后及在贮藏过程中的果表面蜡质层研究很少。对果实在贮藏过程中蜡质层的变化规律和影响因素（如湿度、温度、包装方式、气体成分、包装方式等）进行详细研究，有利于合理改善采后处理技术，以达到提高果实贮藏保鲜质量的目的，延长货架期，获得更好的经济效益。水果采后处理中添加的保鲜剂或防腐剂与果皮蜡质层直接接触，蜡质层结构和成分对它们的作用具有哪些方面的影响，也是值得研究的课题。由此，深入研究采后果实蜡质层的变化规律和影响因素，对改善果实的采后处理技术和贮运保鲜技术具有重要意义。

3）对果实表皮蜡质合成调控机制的研究。目前在苹果和柑橘果实中报道了一些参与蜡质的基因，与蜡质复杂的成分和突变体数量相比，仅仅研究这些蜡质基因的调控是不够的。随着现代分子技术手段的发展和蜡质相关基因克隆的不断深入，运用瞬时表达和转基因技术对参与果实蜡质合成关键基因的功能研究，可进一步揭示这些基因对果实表皮蜡质合成的调控机制。

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