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## 采后果实表皮蜡质结构、功能及其调控——综述与展望

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#### 摘要

表皮蜡质在植物果实生长和贮藏中发挥着重要作用。蜡质是覆盖在果实表皮细胞最外层不溶于水的物质, 主要包括超长链脂肪酸(VLCFAs)及其衍生物(酯、初级醇、次级醇、醛、酮等)和三萜。这种复杂的脂类化合物在大多数植物表皮细胞中合成并转运至细胞表面。蜡质不仅有利于果实免受微生物侵染, 还能减少果实的机械损伤, 从而保持果实的商品价值。迄今为止, 关于果实蜡质的研究多集中于采前果实蜡质的变化、功能和调控, 而忽略了果实采后贮藏过程中蜡质变化及生物学功能。本文对果实表皮蜡质组成、结构及其代谢调控进行综述。重点阐述影响蜡质组成的采后因素, 如贮藏温度、相对湿度(RH)、气体环境、外源激素等, 以及蜡质对果实采后品质的影响, 包括水分散失、果实软化、生理失调、抗病性等。这些总结可能有助于更好地了解采后果实表皮蜡质变化及其在果实品质保持中的作用。

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## 1. 引言

植物角质层是植物响应其生存环境而长期自然进化的结果。它是保护植物免受生物或非生物胁迫的天然屏障[1–2]。角质层有覆盖在植物器官或组织表面的疏水性物质组成, 主要分为角质和蜡质。角质构成角质层的基本骨架, 内蜡镶嵌在角质骨架中, 而外蜡分布在角质骨架外[3]。蜡质在果实品质保持方面也发挥着重要作用[4–5]。近年来, 越

来越多的研究集中在果实蜡质生物学功能的进一步挖掘。蜡质可以防止果实失水、营养流失、机械损伤和果实开裂[6–8]。蜡质的存在还可以阻止病原菌侵染、害虫入侵以及外界环境因素(如干旱和紫外线)带来的伤害[9–10]。果实表皮蜡质是减少水分散失和抵御微生物侵袭的主要屏障, 可有效延缓贮藏货架期间果实皱缩和品质下降[11]。采后果实蜡质的生理生化特性及其与果实耐贮性关系的研究日益受到重视[2,5,12]。因此, 我们总结了采后果实

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蜡质结构和功能及其调控的最新研究进展。这些研究可能为果实采后保鲜提供新的思路和策略，从而有利于减少水果采后损失。

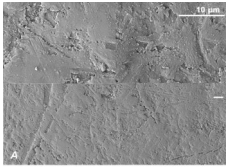
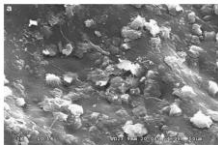
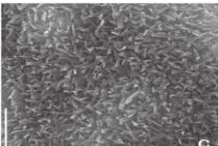
## 2. 蜡质形态结构和组分

### 2.1. 形态结构

蜡质分为内蜡和外蜡[13]。内蜡通常为无定形态，而外蜡由细胞内分泌到植物表面，通过自组装形成不同的蜡质晶体。通过扫描电子显微镜（SEM）可以观察到植物蜡质晶体的形态、大小和分布的多样性。Koch和Ensikat[14]报道植物外蜡形态主要为片状（plate）和板状（plate-

let）两种。而果实的外蜡形态主要包括无定形状（amorphous film）、片状/板状（plates/platelet）、棒状/小杆状（rods/rodlet）和管状（tube）。除此之外，还有小部分呈现薄层状（lamellae）和颗粒状/卵状（granules/ovate）（表1 [15–32]）。不同物种间果实的蜡质形态不同，即使是同一物种的不同品种间外蜡形态也有所差异。例如，大部分枸杞品种（*Lycium barbarum* L.）外蜡以薄层状结构存在，但在某些特定品种中也存在小棒状和片状[15]。不同品种梨果实蜡质晶形包括无定形状、小杆状、板状和卵状等[16]。Lanza和Di Serio [17]发现油橄榄果皮蜡质形态主要为颗粒状、板状和片状，还有少量小杆状。Chu等[18]研究发现蓝莓果实外蜡结构主要为管状，长度在2~5 μm之间。

表1 果皮外蜡主要的形态类型

Morphological types	Species	Family	References	
Amorphous films  Reproduced from Ref. [19]	<i>Lycopersicon esculentum</i>	Solanaceae	[20]	
	<i>Mangifera indica</i>	Anacardiaceae	[21]	
	<i>Olea europaea</i> cv. Carboncella	Oleaceae	[17]	
	<i>Vaccinium corymbosum</i> Bluecrop	Ericaceae	[22]	
	<i>Pyrus sinkiangensis</i> Yü. Kuerle	Rosaceae	[23]	
	<i>Pyrus bretschneideri</i> Rehd. Xuehua	Rosaceae	[23]	
	<i>Pyrus bretschneideri</i> Kuerle × Xuehua	Rosaceae	[23]	
	<i>Malus domestica</i> Borkh., Florina and Prima	Rosaceae	[19]	
	<i>Prunus avium</i> cv. Hongdeng	Rosaceae	[24]	
	<i>Olea europaea</i> cv. Ascolana tenera	Oleaceae	[17]	
	Plates/platelets  Reproduced from Ref. [25]	<i>V. vitis-idaea</i>	Ericaceae	[26]
		<i>Empetrum nigrum</i>	Empetraceae	[26]
		<i>Malus domestica</i> Borkh.	Rosaceae	[27]
		<i>Lycium barbarum</i> (goji)	Solanaceae	[15]
<i>Citrus sinensis</i>		Rutaceae	[25,28]	
<i>Citrus unshiu</i>		Rutaceae	[28–29]	
<i>F. crassifolia</i> Swingle cv. Suichuan		Rutaceae	[30]	
<i>Olea europaea</i> cv. Cucco, Gentile di Chieti, Dritta, Kalamata, Castiglione, Intosso and Cassanese		Oleaceae	[17]	
<i>Pyrus sinkiangensis</i> Yü. Kuerle		Rosaceae	[23]	
<i>Prunus laurocerasus</i>		Rosaceae	[31]	
<i>Vaccinium myrtillus</i>		Ericaceae	[26]	
<i>V. vitis-idaea</i>		Ericaceae	[26]	
<i>Lycium barbarum</i> (goji)		Solanaceae	[15]	
Z44 and Z168				
Rods/rodlets  Reproduced from Ref. [22]	<i>Olea europaea</i> cv. Cassanese	Oleaceae	[17]	
	<i>Vaccinium corymbosum</i> Bluecrop	Ericaceae	[22]	
	<i>Pyrus bretschneideri</i> Rehd. Xuehua	Rosaceae	[23]	
	<i>V. uliginosum</i>	Ericaceae	[26]	
	<i>Vaccinium myrtillus</i>	Ericaceae	[26]	
	<i>Lycium barbarum</i> (goji) Ningnongqi-9	Solanaceae	[15]	

Morphological types	Species	Family	References
Tubes 	<i>Vaccinium corymbosum</i> cv. Misty, O'Neal and Sharpblue	Ericaceae	[18]
Reproduced from Ref. [18]	<i>Vaccinium corymbosum</i> cv. Brigitta, Darrow and Legacy	Ericaceae	[18]
Lamellae 	<i>Vaccinium ashei</i> cv. Britewell, Premier and Powderblue	Ericaceae	[18,32]
Reproduced from Ref. [15]	<i>Lycium barbarum</i> (goji)	Solanaceae	[15]
Reticulum 	<i>Lycium barbarum</i> (goji) Ningqi-1 and Ningqi-5	Solanaceae	[15]
Reproduced from Ref. [15]	<i>Lycium barbarum</i> (goji) Ningnongqi-9 and 16-23-7-8	Solanaceae	[15]
Granules/ovate crystals 	<i>Pyrus sinkiangensis</i> Qiubai, Kuerle, Clapp Favorite and Jinfeng	Rosaceae	[16]
Reproduced from Ref. [16]			

## 2.2. 化学组分

角质层蜡质主要由超长链脂肪酸 (VLCFAs) 及其衍生物 (碳链长度一般介于 C20~C34 之间) 组成, 包括烷烃、醇、酯、醛、酮等[33]。此外, 某些特殊的三萜环状化合物往往也是蓝莓和欧洲越橘等水果的主要蜡质成分 [18,34]。蜡质中还少量存在一些甾醇和酚类化合物。表 2 列出了文献报道的常见果实表皮蜡质组成和含量 [2,4,18,23,26-29,34-51]。不同物种果实蜡质的组成和含量不同, 同一物种不同品种或栽培品种之间也存在差异。例如, 不同苹果品种的总蜡含量在 366~2186  $\mu\text{g}\cdot\text{cm}^{-2}$  之间 [27,35-38]。这种差异可能是由于苹果的基因型和生长环境不同所致。

### 2.2.1. VLCFAs 及其衍生物

脂肪酸是蜡质合成的重要前体物质。与三萜化合物的特异性存在不同, 脂肪酸几乎存在于所有果实蜡质中。大多数脂肪酸以无支链碳链的饱和脂肪酸形式存在, 其中, 碳原子数以偶数为主 (被称为“偶数碳链优势”, even-

over-odd), 通常从 C16 到 C34 不等。例如, 笃斯越橘 [26]、葡萄 [41] 和枣 [43] 中的蜡质脂肪酸富含碳链为 C16~C32 的饱和脂肪酸。十六烷酸 (C16:0) 和十八烷酸 (C18:0) 是柑橘 [2]、苹果 [37] 和番茄 [31] 等多种常见水果蜡质的主要脂肪酸。此外, 在蓝莓 [32]、杨梅 (*Myrica pensylvanica*) [52] 等浆果中还存在一定量的偶数碳链不饱和脂肪酸, 如油酸 (C18:1) 和亚油酸 (C18:2) 等。三十二烷酸 (C32:1) 和三十烷酸 (C30:1) 分别是柠檬 (*Citrus limon*) 和柑橘 (*Citrus sinensis*) 果蜡含量最高的不饱和脂肪酸 [25,44]。

烷烃是最常见的果蜡组分之一, 存在奇数碳原子优势。甜橙 (*Citrus sinensis* L.) 果蜡的主要烷烃碳链长度在 C22~C32 之间, 其中, C29 烷和 C31 烷的比例最高 [53]。桃果实蜡质中烷烃含量仅次于三萜含量, 占蜡质总量的 19%, 其中, 二十五烷 (C25) 为含量最高的烷烃 [46]。烷烃也是柠檬蜡质的主要组分, 占总蜡的 50%, 但在甜樱桃 [34] 中只占到总蜡的 0.89%~1.05%。

表2 常见果实表皮蜡质组成及含量

Species	Wax amount ( $\mu\text{g}\cdot\text{cm}^{-2}$ )	Wax composition	References
Apple	366.00–2186.00	Alkanes, alcohols, fatty acids, terpenes, esters, and aldehydes	[27,35–38]
Bilberry	108.50	Triterpenoids, alkanes, fatty acids, aldehydes, primary alcohols, and ketones	[26]
Bog Bilberry	331.30	Fatty acids, ketones, aldehydes, triterpenoids, primary alcohols, and alkanes	[26]
Lingonberry	871.10	Triterpenoids, fatty acids, alkanes, primary alcohols, and aldehydes	[26]
Crowberry	921.80	Alkanes, fatty acids, triterpenoids, aldehydes, primary alcohols, and ketones	[26]
Cranberry	340.00	Triterpenoids, aldehydes, alkanes, fatty acids, alcohols, and sterols	[39]
Blueberry	48.00–332.00	Triterpenoids, $\beta$ -diketones, aldehydes, primary alcohols, fatty acids, and alkanes	[18,40]
Citrus	3.80–8.20	Triterpenoids, aldehydes, fatty acids, alkanes, and alcohols	[2,28–29]
Grape	61.60–71.60	Fatty acids, alkanes, phenols, alcohols, ketones, and aldehydes	[4,41]
Guava	37.38	Fatty acids, triterpenoids, primary alcohols, alkanes, aldehydes, secondary alcohols, and ketones	[42]
Jujube	172.00–368.00	Fatty acids, primary alcohols, alkanes, triterpenoids, Amines, aldehydes, phenols, esters, and ketones	[43]
Lemon	1.36	Alkanes, aldehydes, alcohols, and fatty acids	[44]
Olive	No data	Esters, alkanes, alcohols, aldehydes, fatty acids, and triterpenoids	[45]
Peach	518.00	Triterpenoids, alkanes, fatty acids, alcohols, and sterols	[46]
Persimmon	337.00–770.00	Triterpenoids, alkanes, and alcohols	[47–48]
Pear	653.00–1431.00	Alkanes, primary alcohols, aldehydes, fatty acids, terpenoids, and esters	[23,49]
Sweet cherry	20.09–59.77	Triterpenoids, alkanes, fatty acids, sterols, and alcohols	[34,50]
Tomato	14.60–17.90	Alkanes, triterpenoids, sterols, fatty acids, and alcohols	[51]

根据羟基官能团在碳链骨架中的位置不同,醇类又分为初级醇和次级醇。初级醇中的羟基取代基位于碳氢链的末端位置。蓝莓果蜡中含有32%~40%的初级醇,其中,C28醇占总醇含量的81%~87% [18]。在甜樱桃[34]、苹果[37]、柑橘[2]等多种植物果实中均发现初级醇的存在。次级醇的羟基官能团位于碳链中间位置。苹果果蜡中的次级醇从C26到C30不等,具奇数碳链优势,直链的C8到C11位均可能含有羟基官能团[54]。

酮类化合物往往伴随着次级醇而出现,酮类是笃斯越橘蜡质中占比第二高的组分(22.5%),但是在欧洲越橘和红梅中的含量却只占到3.6%和0.03% [26]。 $\beta$ -二酮类是酮类化合物的重要组成部分,其主要特征是在C1和C3位分别存在一个羰基官能团,碳原子数在C27~C33之间。三十一烷-10,12-二酮只存在于高丛蓝莓蜡质中,而三十烷-12,14-二酮特异性存在于兔眼蓝莓中[18]。但是蓝莓果蜡中存在的 $\beta$ -二酮是否具有分类学意义,尚待在其不同的蓝莓品种中进一步确定。

果蜡中的酯类物质主要为烷基酯、酮酸酯、芳香酯、交内酯(脂肪酸聚酯)、甘油酯。在鲜食葡萄表皮蜡质中发现少量脂肪酸甲酯的存在[41]。在苹果果蜡中还检测到包括棕榈酸乙酯、亚油酸乙酯、油酸乙酯、亚油酸乙酯和棕榈酸己酯在内的其他烷基酯[37]。交内酯是由两个或多个羟基脂肪酸分子通过酯化反应形成的一类聚酯。甘油酯

通常以单甘酯、甘油二酯或甘油三酯的形式存在,在蓝莓蜡质中少量存在[32]。

蜡质中的醛类大多数是以偶数碳链为主。欧洲越橘蜡质中含有10%的醛类,以二十八烷醛为主要醛类,其次为二十六烷醛和三十烷醛[55]。醛类物质在柑橘[28]果皮蜡质中含量最高,在苹果[38]和红豆越橘[26]蜡质中含量较低,这表明醛类在不同果实蜡质中含量分布存在差异。

### 2.2.2. 三萜

三萜化合物通常基于碳骨架结构进行分类,具有特征的五环结构。目前报道的基本三萜骨架结构已超过两百余种,但是只有为数不多的几种存在于植物表皮蜡质中。其中绝大多数为五环三萜类。在表皮蜡质中存在较多的三萜碳骨架结构型有羽扇豆烷型(lupane)、齐墩果烷型(oleanane)和熊果烷型(ursane)三种(图1)。其中,齐墩果烷型和熊果烷型是蓝莓(*Vaccinium corymbosum*和*Vaccinium ashei*) [18]和番茄(*Solanum lycopersicum* L.) [51]蜡质三萜的主要类型,而在葡萄[41]、橄榄[45]等果实表皮蜡质三萜中齐墩果烷型占主导地位。熊果酸、齐墩果酸和 $\alpha/\beta$ -香树脂醇是苹果[56]和甜橙[2]果蜡的主要三萜组分。此外,果蜡中还存在少量的三萜衍生物,如烷基醚、烷基酯和酰基类。例如,亚洲梨的果蜡中检测到少量羽扇豆醇乙酸酯和3-(acetyloxy)-(3 $\beta$ )-urs-12-en-28-al [23]。

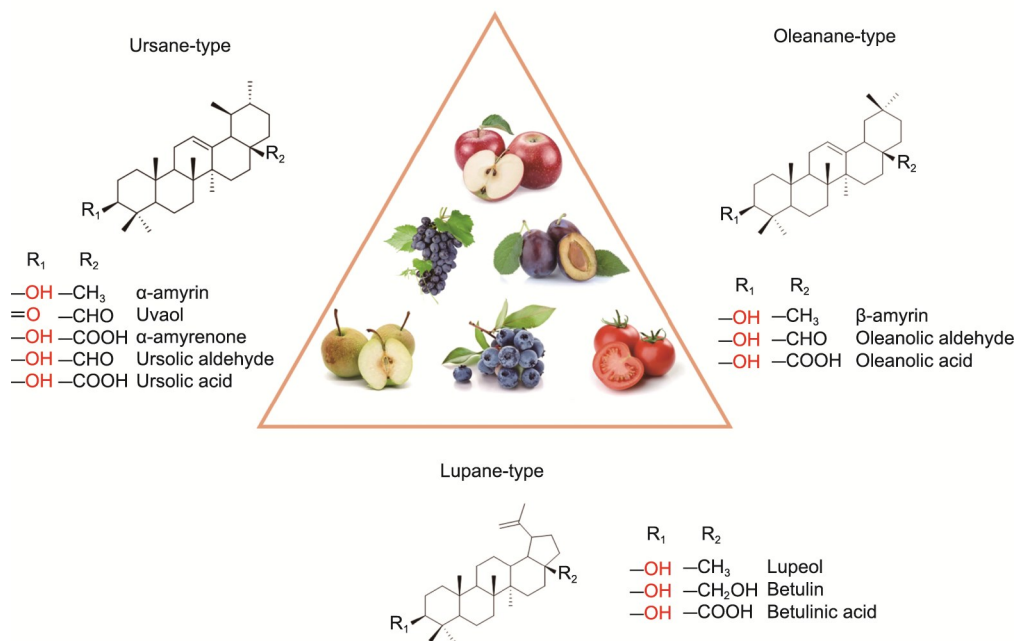


图1. 果实蜡质中常见的三萜类型。这里展示三萜类化合物可根据其结构分为三萜酸、醇、醛和酮，它们在结构上来源于齐墩果烷、乌苏烷和羽扇豆烷。

### 2.2.3. 其他

除了上述存在于水果表皮蜡质中的几类主要成分外，甾醇和类黄酮等物质也有报道。从蔓越莓、番茄和甜樱桃的表皮蜡质中鉴定到包括β-谷甾醇和豆甾醇在内的甾醇化合物。这些结构与五环三萜非常相似，它们可以主动或被动运输到植物表皮层的不同部位。植物甾醇可以积累在细胞质膜上，这使得植物组织中的甾醇富集[57]。在特殊情况下，蜡质以外的其他化学成分也可能出现在植物表面。这类物质包括二萜类化合物和天然生育酚（α-生育酚、γ-生育酚和ε-生育酚）等[49]。

## 3. 蜡质代谢通路及其调控

### 3.1. 蜡质代谢通路

根据蜡质组分差异，其生物合成途径可以划分为两类：VLCFAs及其衍生物途径以及三萜环状化合物途径。前者比较常见，主要形成长链脂肪族化合物，如脂肪酸、醇、酯、烷烃、醛、酮等。后者可以形成不同碳骨架结构的三萜类化合物及其衍生物，如三萜醇、三萜酮和三萜酸。关于表皮蜡质生物合成和转运途径的总结如图2所示。蜡质合成的场所位于表皮细胞的细胞质中。

VLCFAs及其衍生物途径在拟南芥和番茄等模式植物中研究得比较清楚。首先，在质体中脂肪酸从头合成形成C16和C18酰基载体蛋白（C16/C18 acyl-ACP），此过程脂

肪酸合成酶复合体（FAS）发挥重要作用。然后脂肪酰基-ACP硫酯酶（FAT）将C16/C18 acyl-ACP转化为游离的C16和C18脂肪酸。C16和C18脂肪酸被转运到内质网，被长链酰基辅酶A合成酶（LACS）酯化形成C16和C18酰基辅酶A，然后通过脂肪酸延长酶复合物（FAE）合成VLCFAs（碳链长度主要在C20~C34之间）。VLCFAs随后通过酰基还原途径和脱羧途径形成各种VLCFAs的衍生物。其中，通过酰基还原途径形成初级醇和酯，通过脱羧途径形成醛、烷烃、次级醇和酮。三萜途径主要来源于异戊烯焦磷酸（IPP, C5），它是乙酰辅酶A为起始底物，通过甲羟戊酸（MVA）途径在细胞质中产生的[58]。随后在香叶基焦磷酸合成酶（GPS）、法尼基焦磷酸合成酶（FPS）、角鲨烯合成酶（SQS）和角鲨烯环氧化酶（SQE）共同作用下生成2,3-氧化鲨烯（C30）。2,3-氧化鲨烯是三萜合成的重要前体，经氧化鲨烯环化酶（OSCs）、细胞色素P450（细胞色素p450s）和糖基转移酶（UGTs）对其进行环化、羟基化、糖基化等结构修饰，合成不同的三萜[3,59]。这些蜡质组分在ATP结合转运蛋白（ABC转运蛋白）和脂质转移蛋白（LTP）的共同作用下，通过高尔基体网络转运并分泌到外表皮。整个过程需要几十种酶和上百个基因共同参与[33]。

### 3.2. 果实蜡质代谢通路中的结构基因

果实蜡质代谢需要一些重要基因共同参与。表3中列举了常见的与果实蜡质生物合成和转运调控相关的结构基

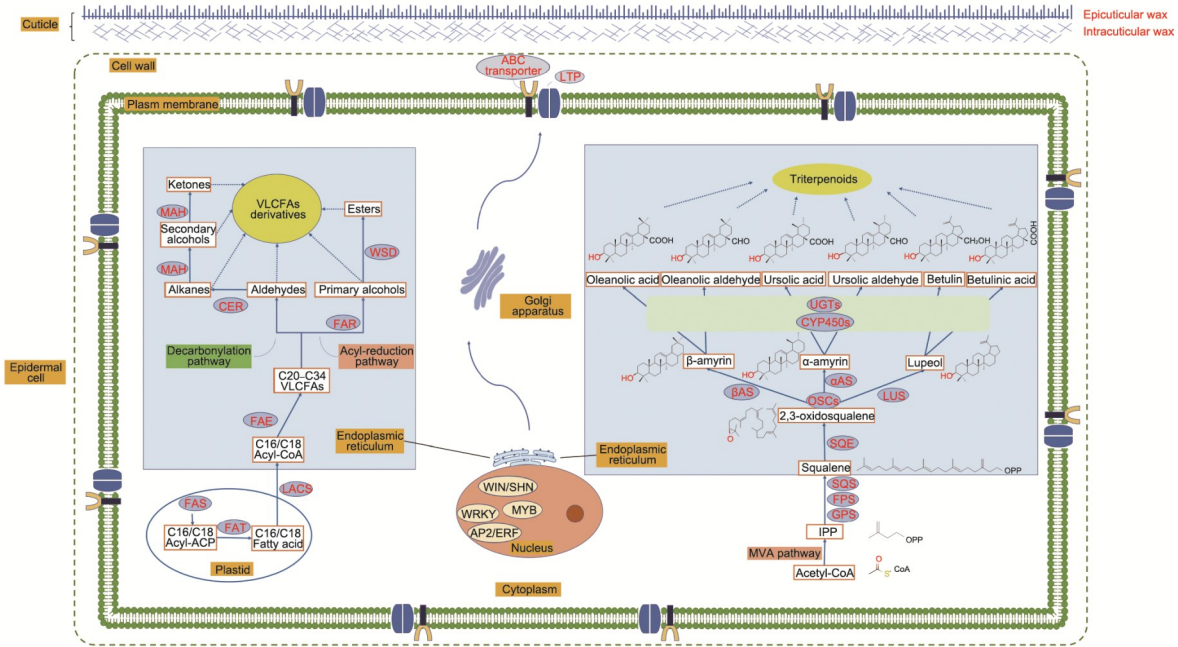


图2. 果实蜡质合成及转运。LTP: 脂质转移蛋白; FAS: 脂肪酸合成酶复合物; FAT: 酰基-ACP 硫酯酶; LACS: 长链酰基辅酶A (CoA) 合成酶; FAE: 脂肪酸伸长酶复合物; ABC: 转运蛋白; FAR: 脂肪酰辅酶A 还原酶; WSD: 蜡酯合成酶/二酰甘油酰基转移酶; CER: 脂肪醛脱羧酶; MAH: 中链烷烃羟化酶; MVA 途径: 甲羟戊酸途径; IPP: 异戊烯焦磷酸; GPS: 香叶基焦磷酸合成酶; FPS: 法尼基焦磷酸合成酶; SQS: 角鲨烯合成酶; SQE: 角鲨烯环氧化酶; QSC: 氧化鲨烯环化酶; LUS: 羽扇豆醇合成酶;  $\alpha$ AS:  $\alpha$ -amyrin 合成酶;  $\beta$ AS:  $\beta$ -amyrin 合成酶; CYP450s: 细胞色素 P450 单氧化酶; UGTs: 糖基转移酶。WIN/SHN、WRKY、MYB、AP2/ERF 是转录因子。

因及其功能[23,28,46,60–77]。其中，来自 CER 家族的结构基因被广泛研究。Albert 等[60]成功克隆出 4 个在苹果果皮中特异表达的结构基因 (*CER1*、*CER4*、*KCS7/2* 和 *LACS2*)。 *KCS7/2* 和 *LACS2* 基因在 VLCFAs 的合成中发挥重要作用，而 *CER1* 和 *CER4* 基因分别调控烷烃和初级醇的合成。 *CsCER1* 基因的过表达能促进黄瓜烷烃生物合成和耐旱性[61]; *CsCER4* 基因与脂肪醇的生物合成有关

[62]，类似的结论在苹果[60]和柑橘[46]中得到验证。研究发现番茄 *LeCER6* 缺失突变体的表皮蜡质中 C28 以上的 VLCFAs 含量显著低于野生型[63]。 *CsCER6* 基因还参与蜡质生物合成途径，影响柑橘果皮的光滑度[64]。表皮蜡质组分的运输和分泌需要 ABC 转运蛋白和 LTP 的参与。柑橘中 *CsABCG11* 基因表达量的降低会影响脂肪族化合物的含量[64]。

表3 与果皮蜡质合成和转运调控相关的结构基因和转录因子(TFs)

Gene name	Species	Gene function	References
<i>LeSITTS1</i>	Tomato	$\beta$ -Amyrin synthesis	[65]
<i>LeSITTS2</i>	Tomato	Oxidosqualene cyclase	[65]
<i>PaCER1</i>	Sweet cherry	Formation of very long-chain (VLC) alkanes	[66]
<i>CsCER1</i>	Cucumber	–	[61]
<i>CsCER3</i>	Citrus	–	[64]
<i>CER4</i>	Citrus	Formation of VLC primary alcohols	[60,67]
<i>CsCER4-like1/CsCER4-like3</i>	Citrus	–	[46]
<i>CsCER4</i>	Cucumber	Formation of VLC primary alcohols	[62]
<i>LeCER6</i>	Tomato	$\beta$ -ketoacyl-CoA synthase VLCFA elongation	[63]
<i>CsCER6</i>	Citrus	$\beta$ -ketoacyl-CoA synthase Affects the smoothness of citrus fruit epidermis	[28,64]
<i>MdCER6</i>	Apple	$\beta$ -ketoacyl-CoA synthase VLCFA elongation	[67]

Gene name	Species	Gene function	References
<i>CS-FAD</i>	Cucumber	$\omega$ -3-fatty acid desaturase Regulating the conversion of linoleic acid to linoleic acid	[68]
<i>PaKCR1</i>	Sweet cherry	$\beta$ -ketoacyl-CoA reductase VLCFA elongation	[66]
<i>MdKCS</i>	Apple	$\beta$ -ketoacyl-CoA synthetase VLCFA elongation	[69]
<i>CsKCS19/CsKCS20/kcs11-like1</i>	Citrus	Biosynthesis of VLC acyl-CoA	[64]
<i>KCS9/KCS20</i>	Pear	$\beta$ -ketoacyl-CoA synthetase	[23]
<i>MAH1</i>	Pear	Mid-chain alkane hydroxylase Accumulation of secondary alcohols and ketones	[23]
<i>MdMAH1</i>	Apple	–	[67]
<i>PaLACS2</i>	Sweet cherry	Long-chain acyl-CoA synthetase Biosynthesis of C16 or C18 acyl-CoA	[66]
<i>LACS2</i>	Apple	–	[60]
<i>LACS2</i>	Pear	–	[23]
<i>LACS4</i>	Citrus	Long-chain acyl-CoA synthetase	[64]
<i>CsCER7</i>	Cucumber	3'-5' exoribonuclease Accumulation of fruit cuticular wax	[70]
<i>CER2</i>	Pear	Participation in carbon atom distribution	[23]
<i>MdWSD1</i>	Apple	Wax ester synthase (WS) and diacylglycerol acyltransferase	[67]
<i>CsABCG11</i>	Citrus	Secretion and transport of aliphatic wax components	[64]
<i>LTPG1</i>	Apple	Secretion and transportation of wax components	[60]
<i>LTPG1</i>	Pear	–	[23]
<i>LTP4</i>	Pear	Encoding lipid transfer protein	[23]
<i>MdMYB30</i> (MYB)	Apple	TFs related to wax accumulation	[71]
<i>MYB96</i> (MYB)	Citrus	–	[28]
<i>MYB16/96/106</i> (MYB)	Pear	–	[23,72]
<i>WRKY20/89</i> (WRKY)	Pear	–	[72]
<i>WIN1</i> (WIN1/SHN1)	Apple	–	[60]
<i>MdSHN3</i> (WIN1/SHN1)	Apple	–	[73]
<i>SISHN1</i> (WIN1/SHN1)	Tomato	–	[74]
<i>CpSHN1/CpSHN2</i> (WIN1/SHN1)	Papaya	–	[75]
<i>WRI4</i> (AP2/SHEN)	Pear	–	[72]
<i>McWRI1</i> (AP2/SHEN)	Apple	–	[76]
<i>MdERF2</i> (AP2/ERF)	Apple	–	[77]

### 3.3. 蜡质代谢调控

近年来,许多研究表明植物蜡质的合成和转运可以在转录水平[10,78]进行调控。MYB、WRKY、AP2/SHEN等家族的多种转录因子参与调控植物蜡质合成与转运(表3)。Zhang等[71]从苹果中鉴定到一个MYB家族的新成员*MdMYB30*。*MdMYB30*与*MdKCS1*基因启动子结合来激活*MdKCS1*基因转录表达,促进表皮蜡质积累。*MYB96*在纽荷尔脐橙中的表达量高于温州蜜柑,暗示*MYB96*在柑橘果实蜡质沉积的调控中可能起着至关重要的作用[28]。其他MYB家族成员如MYB16/96/106与多个品种的

梨果蜡质合成调控相关[23,72]。尽管*WRKY20*、*WRKY89*和*WRI4*(AP2/SHEN家族)的表达量与3个梨品种蜡质含量变化并不一致,推测这些基因可能通过其他水平,如转录后和翻译后水平调控蜡质积累[72]。苹果的*McWRI1*激活*McKCS*、*McLAC*和*McWAX*基因的启动子并上调其表达水平,导致烷烃积累和果实表面蜡质结构改变[76]。研究发现,*MdERF2*基因的过表达可以上调愈伤组织和果实中的*MdLACS2*、*MdWSD1*、*MdCER4*和*MdCER6*基因的表达水平,从而导致总蜡质、烷烃和醇含量上升,酸和酯含量下降,果实表皮蜡质的微观结构发生改变[77]。编码

SHN1/WIN1 转录因子的 *MdSHN3* 基因也被发现能正向调控苹果表皮蜡质沉积[73]。

除转录调控外, 转录后和翻译后水平的调控在植物蜡质生物合成和转运过程中也发挥着重要作用。然而, 很少有研究关注这些转录后调控机制[78]。拟南芥中的一些研究结果表明表皮蜡质的生物合成受到RNA外泌体和RNA介导的基因沉默机制的调控[79–80]。此外, 拟南芥、水稻 (*Oryza sativa*) 和小麦 (*Triticum turgidum* ssp. *Durum*) 中 SUPERKILLER (Ski) 复合体的组分、胞质外泌体辅助因子和 microRNAs 也参与表皮蜡质生物合成的调控[81–82]。至于表皮蜡质生物合成的翻译后修饰机制, 有证据表明蛋白质泛素化和 26S 蛋白酶体系统也参与其中[83–84]。然而, 目前还没有关于果实表皮蜡质转录后和翻译后调控的研究报道, 这些领域还需要进一步探索。

## 4. 贮藏条件对果实蜡质的影响

角质层蜡质的合成和运输不仅发生在果实发育和成熟阶段, 也在果实采后贮藏过程中进行。许多采后贮藏条件, 如温度、相对湿度 (RH)、气体环境和外源激素等会影响采后果实表皮蜡质代谢。

### 4.1. 温度

研究表明, 温度会影响果实贮藏期间表皮蜡质的形态和组成[2]。室温贮藏 (25 °C) 比低温贮藏 (4 °C) 的苹果果实中总蜡含量更高。在 4 °C 贮藏过程中, 苹果表皮蜡质晶体由扁平的片状变为小颗粒状, 再变为熔融形态; 相对而言, 在 25 °C 贮藏后, 苹果表皮蜡质晶体由扁平的片状变为小颗粒状[2]。推测室温贮藏期间蜡质积累较多可能是由于较高的温度诱导脂肪酸生物合成和脱羧途径。长期冷藏期间果实蜡质的减少似乎是通过脂肪酸延伸复合物和 ECERIFERUM 蛋白 1 和 3 (CER1 和 CER3) 的基因表达下调所介导[85]。此外, 与 20 °C 贮藏的果实相比, *PpCER1*、*PpLACS1* 和 *PpLipase* 基因在桃果实冷藏期间的表达受到抑制[46]。

### 4.2. 相对湿度

先前的研究揭示了果实角质层——更具体地说, 表皮蜡质层的组成——与采后果实品质密切相关[5]。在关注库尔勒香梨中从母体脱离后引起果实脱水的 RH 条件后, 研究还发现失水胁迫影响果实蜡质组分[49]。库尔勒香梨在高湿贮藏条件下, 能保持蜡质 (如烷烃和醛类) 的组分和含量以及蜡晶形态的完整性, 有利于保持水分和延缓果

实衰老[49]。然而, 也有研究发现 RH 并不影响柑橘果实总蜡含量; 反而改变了蜡的化学组成。与高 RH 环境相比, 低 RH 环境下的果实贮藏有助于增加果实蜡质中醇类和脂肪酸的比例, 同时减少萜类和烷烃, 导致烷烃/萜类比值较低, 这与较高的果实失重率和角质层渗透率值有关[53]。但目前在番茄中的研究表明, 采后脱水条件虽然会导致果实品质劣变, 但是果实蜡质含量和化学组分并未发生明显变化[86]。

### 4.3. 气调贮藏

二氧化碳 (CO<sub>2</sub>) 冲击诱导 ‘October Sun’ 桃角质层组分的变化和角质层相关基因 (*PpCER1*、*PpLACS1* 和 *PpLipase*) 的表达[46]。此外, 与常规环境 (0 °C, 90% RH) 相比, 在控制气调环境 (1.5% O<sub>2</sub>, 2.5% CO<sub>2</sub>, 0 °C, 90% RH) 中苹果角质层的微裂纹和表皮蜡质形态发生明显变化[87]。此外, Klein 等[37]研究苹果在气调 (CA) 和动态气调 (DCA) 贮藏后货架期间蜡质含量和组成的变化。他们发现, 与 CA 相比, DCA 处理的苹果总蜡含量增加, 油腻感降低。DCA 贮藏的果实表现出更低的呼吸作用和较好的品质; 因此, DCA 被认为是一种最佳的贮藏方式。

### 4.4. 乙烯和 1-甲基环丙烯

果实蜡质组分和含量变化主要受乙烯类植物激素的调控[88–90]。4 μL·L<sup>-1</sup> 乙烯处理 4 d 的晚熟脐橙 (Navelat) 中, *CsCER4/CsFAR3* (醇形成) 和 *CsABCG11/WBC11* (蜡质转运) 基因的表达量高于对照果实, 而 4 μL·L<sup>-1</sup> 乙烯处理 8 d 的晚熟脐橙 (Navelat) 中这些基因的表达量下调[90]。作为乙烯类似物的乙烯利, 能增加新红星苹果 (Starkrimson) 冷藏期间表皮蜡密度, 加速蜡质晶体融化和果实衰老[67], 而上调 *MdCER6* (VLCFAs 合成)、*MdCER4* 和 *MdWSD1* (醇形成) 等基因的表达。乙烯受体抑制剂 1-甲基环丙烯 (1-MCP) 在表皮蜡质调控方面的作用往往与乙烯相反。1-MCP 处理的梨在整个贮藏期间蜡质含量均低于对照果实, 表明 1-MCP 处理有效抑制梨果表皮蜡质的积累[91]; 1-MCP 还能降低马溪嘎啦苹果 (Maxi Gala) 中脂肪酸和 10-二十九烷醇的含量[56]。此外, 在 20 °C 贮藏 70 d 后, 1-MCP 处理的粉红佳人苹果 (Cripps Pink) 蜡质中液态组分的积累和果皮油腻化被显著抑制[89]。Yang 等[92]研究发现 1-MCP 对蜡质组分存在的另一个负面影响, 即 1-MCP 显著延缓金冠苹果 (Golden Delicious) 在 20 °C 贮藏期间 α-法尼烯的产生。



#### 4.5. 其他

其他植物激素，如 $\beta$ -氨基丁酸（BABA）[24]、茉莉酸甲酯（MeJA）[72]、脱落酸（ABA）[53]等已被证明可以调控采后果实蜡质合成和转运相关基因的表达。Wang等[24]研究发现，与对照相比，BABA处理的甜樱桃具有更光滑的角质层和更完整的皮下细胞，BABA处理还能减少果实失水，延缓细胞膜透性的增加和果实硬度的下降。ABA处理介导了甜橙果实高或低RH下蜡质组分的变化[53]。此外，还有研究表明VLCFAs（十六烷酸和二十六烷酸）影响梨中蜡质覆盖率和结构，并调控蜡质结构基因和TF基因的表达[72]。采后热处理也被证明会影响桃果实表皮蜡质代谢[46]。

### 5. 蜡质在果实采后品质保持中的作用

角质层蜡质不仅仅作为物理屏障阻止果实免受环境和病原菌入侵；其与果实品质也密切相关[93]。角质层蜡质的组成、含量和结构直接影响果实的贮藏品质和抗病性，如图3所示，下面分节进行说明。

#### 5.1. 蜡质与果实失水

某些特定类型的果实成熟后表面无气孔。因此，角质层被认为是控制水分蒸腾的唯一屏障，通过角质层调节水分平衡，维持果实表面完整性[94]。蜡质层可以防止植物组织中水分的非气孔性散失，这与蜡质的疏水性和复杂的空间结构有关。在番茄*LeCER6*蜡质缺失突变体的表皮细胞中发现蜡质生物合成的脱羧途径受阻，从而加速果实表

皮角质层的水分散失[95]。蜡质含量，尤其是烷烃含量是采后辣椒（*Capsicum spp.*）水分渗透的重要决定因素[96]。对苹果蜡质组分与贮藏品质的相关性分析也发现，蜡质组分尤其是烷烃类物质在贮藏期内是维持苹果果实品质所必需的[38]。烷烃也被发现在降低西葫芦果实冷藏期间的失水和冷害中起着重要作用[97]。

尽管内蜡和外蜡都会影响水分扩散，但内蜡为主导因素[6]。脱蜡的番茄果实角质层失水比未脱蜡果实更严重[98]。番茄表皮蒸腾失水主要由内蜡中的脂肪族化合物决定，而外蜡中的脂肪族化合物起次要作用。与外蜡去除相比，内蜡脂肪族含量的降低能造成更严重的果实失水。甜橙（*Citrus sinensis*）和温州蜜桔（*Citrus unshiu*）蜡质中的醛、脂肪酸、烷烃和初级醇对果实失水起重要作用[28]。研究发现，欧洲李果实的失重主要是由表皮角质层失水（95%）引起的，而非气孔蒸腾作用。完整果实的持水能力强于脱蜡（通过物理方法或化学方法）果实。贮藏温度越低，果实失水越慢[7]。在其他水果如桃[99]、柑橘[28]、蓝莓[12]中也得到类似的结果。

#### 5.2. 蜡质与果实软化

除细胞壁结构外，角质层能在一定程度上维持果实硬度，而角质层蜡质也能有效延缓果实软化进程。研究发现，蓝莓表皮蜡质的存在显著降低细胞壁降解酶（即果胶酶、多聚半乳糖醛酸酶和纤维素酶）活性，从而延缓原果胶和纤维素的降解，减少细胞壁降解，维持果实硬度；相比之下，果实在去除蜡质之后，软化和衰老过程加剧[12]。一些在贮藏过程中硬度和失重率变化不大

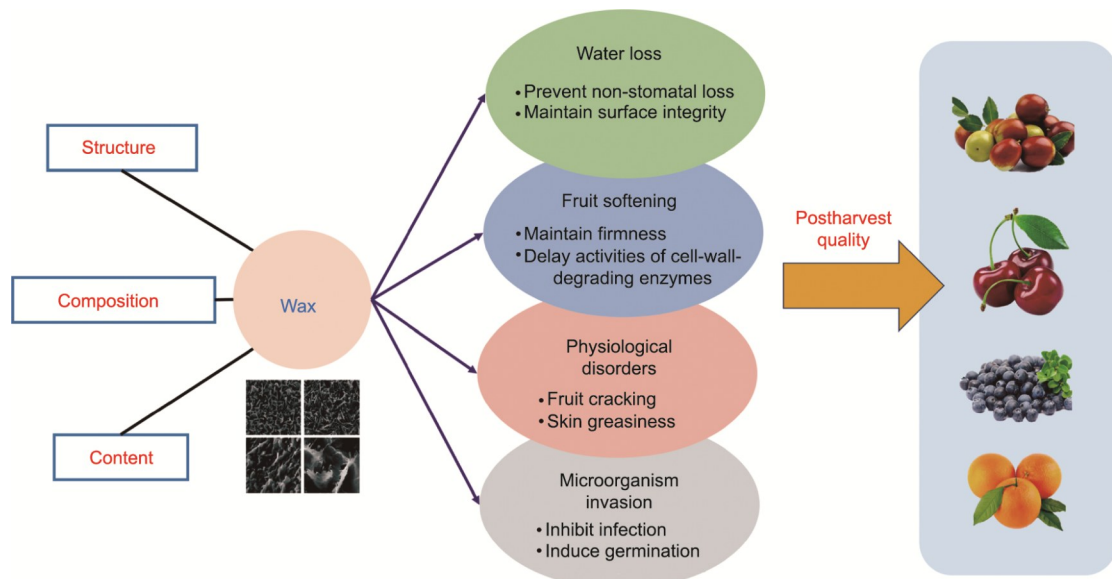


图3. 蜡质在果实采后品质保持中的作用。角质蜡对果实品质保持的四个方面有影响：果实失水、果实软化、果实生理失调和微生物入侵。

的苹果品种具有较厚且致密的角质层，角质层的厚度与果实贮藏期间的硬度呈显著正相关[100]。结合梨果上类似结果表明，角质层的性质，包括耐酸碱性和非渗透性，可有效地保持表皮细胞的完整性，从而在一定程度上维持果实硬度[101]。

### 5.3. 蜡质与果实生理失调

裂果是造成番茄、荔枝、樱桃等多种水果经济损失的常见原因之一。不同品种的樱桃对裂果的耐受性不同[102]。裂果主要是由于果实成熟期多雨高湿的环境造成。雨水通过表皮角质层渗入果实细胞。角质层蜡质中的烷烃含量影响角质层的通透性，其中，烷烃含量越高，角质层通透性越低，水的渗透性也越弱，使得果实对裂果有更大的耐受性[6]。苹果虎皮病的发生也被认为与表皮蜡质变化有关。苹果蜡中含有 $\alpha$ -法尼烯等成分， $\alpha$ -法尼烯及其氧化产物的积累可能是引起虎皮病的原因。高温和缺水会加速 $\alpha$ -法尼烯氧化产物的积累，从而增加虎皮病的发生率[103]。低温下果皮蜡质中脂肪酸、酯类和抗氧化物质含量的增加，在一定程度上抑制不饱和脂肪酸的氧化，从而增加细胞膜通透性，减少虎皮病发生[103]。

此外，苹果、梨等水果在采后贮藏过程中，果皮变得油腻[27,104]。果皮油腻化是一种严重影响果实感官品质的生理性病害，可能与果皮表皮蜡质组成和微观结构变化有关[27]。Christeller和Roughan [105]发现苹果油腻化的发生与法尼醇的长链不饱和脂肪酸酯有关。随后，Yang等[27]研究表明，贮藏过程中苹果的这种令人不愉快的油腻感的产生是由液态蜡质成分，尤其是(E,E)-法尼醇酯类化合物的积累引起。此外，蜡醇和脂肪醇可能影响蜡从固态到液态的相变。常温下贮藏的苹果表面会产生新的蜡质，与油腻化程度呈正相关。值得注意的是，苹果油腻化的发生并不依赖于新蜡的产生；相反，某些特定蜡质成分的变化会影响果皮油腻化[106]。另外，新蜡的产生是由于果实自身启动了蜡质生物合成还是由于其他角质层组分转化而来，还有待进一步研究。

### 5.4. 蜡质与病原菌侵染

植物角质层是病原菌入侵植物宿主的第一道屏障。一方面角质层的特殊结构作为天然屏障对病原微生物起到物理阻挡的作用；另一方面角质层的组分疏水性强，能够在一定程度上抑制病原菌孢子的侵染附着[107]。某些特定的蜡质抗真菌组分如三萜化合物、烷烃、甾醇等也能够抑制菌丝生长[108]。葡萄感病品种和抗病品种的果实和叶片的总蜡含量没有显著差异，但是特定的抗真菌成分（对

白粉菌孢子抑制率达到75%以上）只有在抗病品种中存在，这些成分包括脂肪酸、烷烃、萜、吡啶衍生物、酮、胺、酚、甾醇等[4]。

然而，还有研究表明，植物表皮的蜡质组分还能被病原菌特异性识别，其疏水性特点反而诱导病原菌生长（如孢子萌发、芽管伸长以及附着孢分化等）[109–111]。椪柑（*Citrus reticulata* Blanco）果实的角质层蜡能够促进青霉菌分生孢子的萌发和芽管伸长，抑制菌丝生长[9]。而在温州蜜橘（*Citrus unshiu*）外蜡中的脂肪酸、烷烃以及萜类物质能显著促进青霉菌的菌丝生长（离体实验），外源蜡质喷洒果实却能抑制菌丝生长（体内实验）[29]。此外，Tang等[111]也发现梨果表皮蜡质组分和疏水性有助于链格孢霉侵染结构的形成。这两种看似完全相反的结果，也说明蜡质组分在病原菌侵染植物过程中发挥的独特作用。造成这种差异的原因可能是由于不同品种的柑橘蜡质组分不同，对病原菌生长产生的作用也不尽相同。确定病原菌如何与蜡质成分相互作用和信号传导可以帮助解释这种差异。同时，病原菌所处的不同环境（果实表面和培养基）也可能造成病原菌菌丝生长存在差异。

## 6. 结论与展望

角质层蜡质是覆盖在植物表皮细胞外的一层特殊结构。由于其在维持果实品质方面的重要作用，近几十年来一直是植物研究的重点。表皮蜡质的结构与组成、合成与转运调控以及对果实品质的影响等方面的研究取得了重要突破。尽管蜡质组分和含量都与角质层的蒸腾损失有关，但正如本文所述，蜡质组分相比总含量要发挥更主要的作用。因此未来应进一步研究如何通过蜡质干预去改良果实品质。未来对水果蜡质的研究应注重蜡质成分与晶体结构的关系。“什么样的蜡质组分决定了蜡晶形态？”“蜡质含量是否影响蜡晶形态？”等问题还有待研究。

此外，表皮蜡质在果实抗病性中的多重作用有待进一步揭示。一方面，蜡质组分抑制病原菌的生长；另一方面，蜡质也能促进病原菌的侵染——这两个看似相反的结果，未来可能需要进一步探索。为了回答这些问题，蜡质缺失突变体果实的挖掘将有利于学者们能够精准评估表皮蜡质在果实货架期和抗病性中的作用。

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