

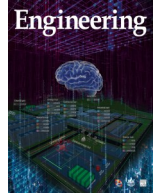


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## 果实采后品质与安全的研究进展及调控策略

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### 摘要

新鲜果实风味鲜美、营养丰富、有益健康,受到全世界消费者的青睐,成为健康膳食结构的重要组成部分。果实采后品质与安全涉及果实自身发育、环境因子和采后病原菌侵染之间的相互作用。解析果实成熟、衰老及抗性应答,以及采后病原菌的分子致病机制,对认知果实品质和安全的分子调控网络至关重要。本文综述了近年来果实采后品质保持的分子机制、主要采后病原真菌(*Botrytis cinerea*和*Penicillium expansum*)致病产毒的分子基础等方面的研究进展及防控策略。相关研究结果将为促进果实产业的可持续发展提供科学依据。

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## 1. 引言

新鲜果实含有丰富的有机酸、糖、维生素、矿物质和其他有益健康的成分,是人类日常膳食结构中不可缺少的组成部分[1-2]。随着人民生活水平的不断提高和消费观念的转变,果实产业对世界经济的贡献在过去几十年显著增加。根据中国农业农村部 and 联合国粮农组织的最新统计,中国果实年产量连续二十多年位居世界首位[3]。但是,在采前和采后阶段,新鲜果实不可避免地会发生品质劣变和病害腐烂。特别是在发展中国家,约有三分之一的新鲜果实损失于采后贮运过程,不能到达消费者餐桌。诱发果实采后损失的因素很多,而果实自身衰老和病原真菌侵染是最主要的诱因[4]。尽管使用化学农药防病至今仍然是控制采后损失的主要方法,但长期高浓度使用化学

农药防病引发的环境污染和食品安全,成为全球关注的热点。此外,有些病原真菌产生的有毒次生代谢物对消费者的健康造成重大威胁。因此,研究果实成熟、衰老机制及病原菌致病产毒的分子基础,对创制有效调控果实衰老和抗病性以及病原菌致病力的精准技术至关重要。本文将重点阐述近年来果实在采后品质维持、抗氧化途径及病原真菌致病产毒的分子基础方面的重要进展及关键调控靶点(图1)。

## 2. 果实成熟、衰老和抗性应答

### 2.1. 果实品质形成与维持

果实成熟和衰老是高度复杂而有序的生理过程,直接关系到果实品质的形成和保持[2,5]。这些过程涉及众多基

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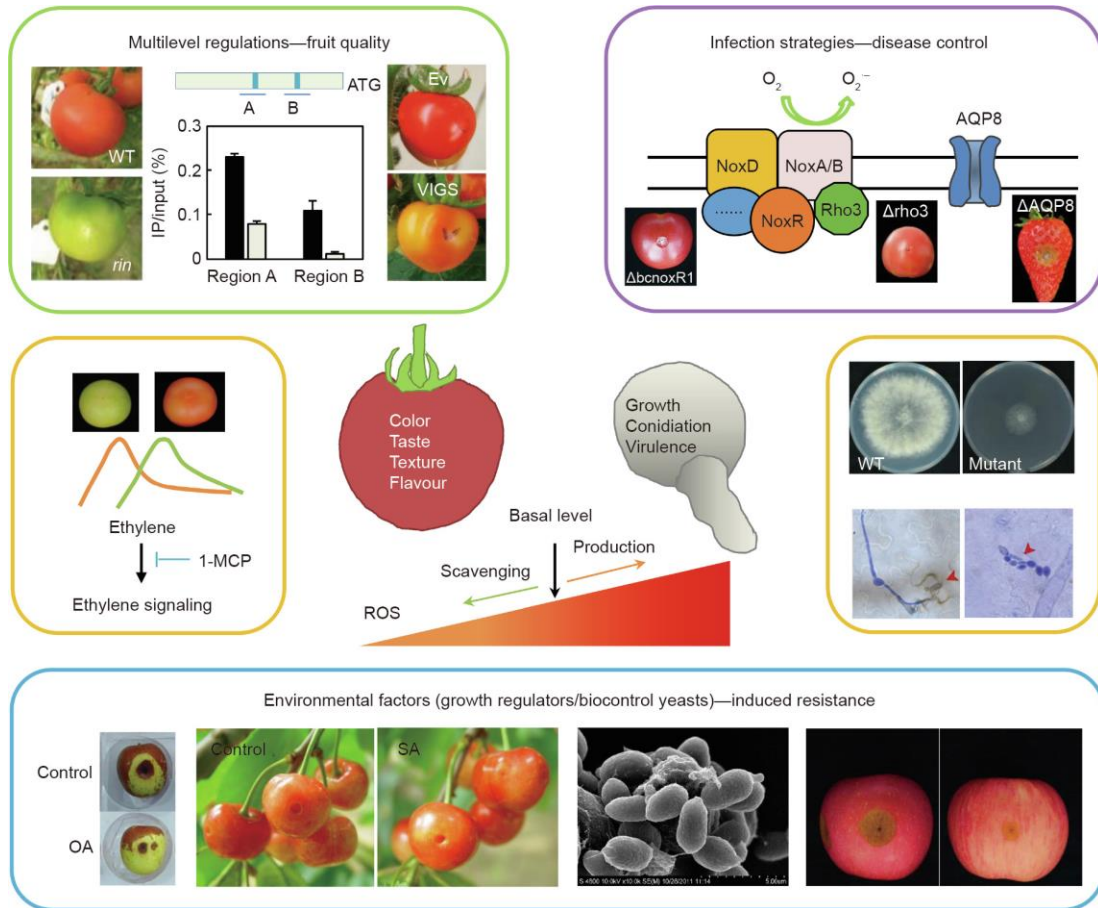


图1. 采后果实、病原真菌与外源因子之间的相互作用。1-MCP: 1-甲基环丙烯; SA: 水杨酸; OA: 草酸; NHS: 非热激处理; ROS: 活性氧; WT: 野生型; *rin*: ripening inhibitor; Ev: 空载对照; VIGS: 病毒诱导的基因沉默; IP: 免疫沉淀; AQP: 水通道蛋白。

因在时间和空间尺度上的重编程，最终引发果实色泽、风味、香气、质地及其他品质性状的变化[6]。成熟果实通常比未成熟果实对采后病害更加敏感[7]，这种敏感性往往会影响果实品质，造成巨大损失；当果实成熟度最高时通常具有最高的商品价值，而此时病原菌侵染造成的损失也更加严重[8]。因此，深入理解病原菌致病与果实成熟之间的关联机制，有助于保持果实采后品质，增强果实抗病性，延长货架期，提高果实商品质量。

果实有两种类型，即呼吸跃变型和非呼吸跃变型。许多呼吸跃变型果实（如番茄、苹果和香蕉）在成熟启动时几乎同时出现呼吸高峰和乙烯高峰[5]。这类果实采收时成熟度相对较低，便于贮藏，出库时进行催熟处理，促进快速成熟，达到可食用的品质。在此过程中，过量使用乙烯会导致果实快速软化和品质劣变。因此，乙烯生物合成或信号转导过程的精细调控，对于延长果实采后货架期和保持果实品质具有重要意义。1-甲基环丙烯（1-methylcyclopropene, 1-MCP）作为乙烯受体的竞争抑制剂，抑制乙烯信号转导反应[9]，因此被广泛用于延缓呼吸跃变型果

实的成熟进程[10-11]。除了在果实成熟进程[10,12]和病原真菌抗性[11,13]调控中的作用之外，1-MCP还通过调控有机酸动态平衡来维持果实风味，调节糖和风味挥发物的水平，进而影响果实的感官品质和内在品质[14]。

番茄是一种重要的经济作物，也是研究果实成熟和衰老分子机制的模式植物。关于调控番茄果实成熟的关键基因[15]已有很多报道，包括 *rin* (ripening-inhibitor) [16]、*nor* (non-ripening) [17]、*Cnr* (colorless non-ripening) [18]、*Gr* (green-ripe) [19]和 *Nr* (never ripe) [20]。其中 MADS-box 转录因子 RIPENING-INHIBITOR (RIN) 在成熟相关基因转录激活中的作用已经得到广泛研究。研究者[21]通过染色质免疫沉淀 (chromatin immunoprecipitation, ChIP) 法分析鉴定了 241 个可能参与果实品质调控的 RIN 直接靶标。随后的研究鉴定了一系列与特定香气产生（如 *TomloxC* 和 *ADH2*）[22]、泛素-蛋白酶体途径（如 *SIUBC32* 和 *PSMD2*）[23]、细胞壁重构和碳水化合物修饰[24]相关的功能基因，这些基因都是转录因子 RIN 直接调控的靶基因。然而，近年的研究表明，*rin* 突变是一种功

能获得性突变，而不是一种功能缺失突变。DNA片段的部分缺失导致转录因子MADS-RIN和MADS-Macrocalyx(MC)发生融合，形成融合蛋白RIN-MC，对下游靶基因产生转录抑制作用[25-26]。因此，RIN的功能还有待于进一步深入分析，需要结合多个等位基因位点的突变进行研究。

果实成熟涉及复杂的生物化学过程和生理代谢变化[27]，特别是果实中糖类和有机酸的含量变化[27-28]。非呼吸跃变型果实成熟过程中的生理代谢变化远低于呼吸跃变型果实。转录组学分析显示，柑橘果实成熟中后期的碳水化合物代谢水平降低，这可能是由于蔗糖磷酸合酶(sucrose phosphate synthase, SPS)和柠檬酸合酶上调所致[29-30]。同时，蔗糖合成酶和SPS直接调控糖的积累[31]，而每种糖所占的比例在不同品种之间和不同成熟阶段存在显著差异[32]。研究证明，蔗糖可以加速非呼吸跃变型果实，如草莓[33]、葡萄[34]、柑橘[35]等的成熟进程。有趣的是，糖类、有机酸和细胞膨压还是促进脱落酸(abscisic acid, ABA)积累的早期信号，而FaABAR/CHLH和FaPYR1信号通路通过ABRE和sigma因子等调控糖和花青素的生物合成[36]。此外，蔗糖通过9-顺式-环氧类胡萝卜素双加氧酶1调控草莓果实中ABA积累的启动[37]。值得注意的是，有机酸含量的变化通常与糖含量的变化相反。当淀粉降解导致糖积累时，果实中有机酸显著减少，此过程受其自身遗传因素和环境因子的协同调控。苹果酸和柠檬酸是呼吸跃变型和非呼吸跃变型果实中含量最丰富的有机酸。有些呼吸跃变型果实以苹果酸作为呼吸底物，而非呼吸跃变型果实在整个成熟过程中则持续积累苹果酸[39]。

果实成熟也会影响次生代谢产物的水平。黄酮类化合物(如酚酸类和花色苷类)主要通过苯丙烷代谢途径合成，是直接影响果实品质和商品价值的关键次生代谢产物。类黄酮的生物合成与MYB转录因子、MYC-like碱性螺旋-环-螺旋(bHLH)转录因子和WD40-repeat蛋白调控的关键酶密切相关[40-41]。MYB和bHLH转录因子的表达模式及其与DNA结合的特异性决定了被激活的基因亚群，而WD40蛋白在MYB-bHLH-WD40(MBW)复合物中仅作为常见的转录因子发挥作用[40]。有的果实能够在果肉和果皮中同时积累花色苷，而另一些果实只在果皮中积累花色苷。此外，在光、温度、干旱、机械损伤等环境因子刺激下，许多果实在果皮中积累花色苷；而不同的环境条件下，果实花色苷的组成和含量存在显著差异[42-43]。果实中花色苷的环境特异性积累机制已经引起了人们的广泛关注[39,41]。然而，目前关于类黄酮合成的关键

因子及其在果实和病原菌相互作用中的功能的研究鲜有报道。

## 2.2. 氧化应激和诱导抗氧化能力

活性氧(reactive oxygen species, ROS)一方面在发育进程和环境刺激响应的多条信号通路中发挥重要作用，另一方面作为氧气消耗产生的副产物产生负面作用[2,44]。ROS可作为信号分子调节众多细胞过程，但过量ROS积累造成的氧化胁迫将诱发果实品质劣变[45-47]。线粒体是细胞内ROS产生的主要细胞器，果实中特定的线粒体蛋白，如电压依赖性阴离子选择性通道蛋白(voltage-dependent anion channel, VDAC)、乌头酸酶和某些抗氧化蛋白(如锰超氧化物歧化酶)容易发生氧化损伤。特别是在果实采后贮藏和运输过程中的不利环境条件下，这种损害会干扰线粒体功能，最终导致果实品质劣变[48]。氧化胁迫将诱发蛋白质羧基化修饰，干扰VDAC功能，影响抗氧化酶活性，进而促进线粒体中超氧阴离子自由基的生成[2,48]。研究表明，通过降低环境温度减少ROS积累可有效降低线粒体羧基化水平，从而延缓果实衰老[49]。在低氧(2%~5%)条件下贮藏也能有效降低ROS水平，并延缓果实衰老；而诱导ROS积累的贮藏条件则产生相反的效果[50]。总的来说，ROS稳态介导的果实对不利环境因子的应答反应，主要是通过诱导果实抗氧化能力和植物激素(如水杨酸、茉莉酸和一氧化氮)、启动磷脂信号和其他防御反应，增强细胞壁和其他物理屏障的重塑产生应答[51]。

诱导果实内在的抗氧化能力和抗病能力是保持果实品质和延缓品质劣变的有效策略，其机制包括：①诱导果实产生与抗性相关的蛋白或次生代谢物(如病程相关蛋白)，以及激活其酶(如植保素、几丁质酶、苯丙氨酸解氨酶、 $\beta$ -1,3-葡聚糖酶和酚类物质)活性；②减轻蛋白氧化损伤；③增强细胞壁屏障。水杨酸作为激活防御反应的重要信号分子，激活系统获得性抗性，进而保护植物(包括采后果实)免受生物和非生物胁迫的影响[52]。外源水杨酸处理可显著诱导桃和甜樱桃果实中抗氧化酶的水平，表明抗氧化蛋白(如过氧化氢酶和谷胱甘肽转移酶)参与果实防御反应[52-53]。同样，草酸可以抑制枣果实的乙醇产生和乙烯代谢，诱导防御反应蛋白表达，延缓果实衰老和提高抗病能力[54]。

## 2.3. 果实采后品质维持研究的新策略

近年来关于番茄果实成熟机制的研究表明，现有的自然突变体背景可能比最初预期的情况更加复杂，往往是由

显性失活突变 (dominant-negative mutation) 或功能获得突变 (gain-of-function mutation) 造成。因此, 利用成簇规则间隔短回文重复序列 (clustered regularly interspaced short palindromic repeats, CRISPR) /CRISPR 相关内切酶9 (Cas9) 技术研究果实成熟相关表型时, 应设计敲除靶点, 并在此基础上产生多个新的等位基因。此外, 由于成熟相关基因可能通过上调或下调表达的方式发挥作用, 添加或删除启动子区域的转录因子结合基序也是调控不同果实中基因表达的一种策略[6]。全面分析与基因表达谱和果实品质性状相关的表观遗传修饰位点, 可能为未来育种研究提供新的候选基因。总之, 更全面的实验设计应该涉及多个调控水平 (如转录水平、转录后和表观遗传调控), 需借助高通量方法和数据挖掘技术, 加深我们对果实品质维持分子机制的理解。

### 3. 采后病害发生机制及调控策略

病原真菌侵染是威胁全球食物链供应的另一个主要因素, 人们一直在努力探索经济、有效、安全的采后病害控制技术[4]。使用方便、成本低廉的化学合成杀菌剂一直是控制采后病害最常用的方法。然而, 杀菌剂的频繁使用引起了公众对食品安全和环境风险的广泛担忧, 而且杀菌剂的高浓度使用也会诱发耐药菌株产生和农药残毒超标, 因此从自然资源中探索高效的抑菌物质来代替/减少化学农药用量是绿色防病的新途径。

#### 3.1. 明确病原菌致病力调控的潜在靶点

大多数果实采后病原真菌都是死体营养型病原真菌, 最初认为这类病原真菌主要利用细胞壁降解酶 (cell wall degrading enzyme, CWDE) 或真菌毒素杀死寄主细胞, 而非效应因子[7]。然而, 近些年研究表明, 事实并非如此。例如, Zhang 等[55]报道拟南芥 (*Arabidopsis*) 中一种受体蛋白 RESPONSIVENESS TO BOTRYTIS POLYGALACTURONASES1 能够识别灰霉菌 (*B. cinerea*) 分泌的一种内聚半乳糖醛酸酶 (Bcpg3), 表明寄主细胞的细胞膜上的受体蛋白和类受体蛋白将 *B. cinerea* 分泌蛋白识别为微生物相关的分子模式, 从而调节寄主的免疫反应。加利福尼亚大学的金海翎团队[56]通过研究小RNA (small RNA, sRNA), 揭示了植物细胞与 *B. cinerea* 之间存在活跃的通信交流, 并赋予了sRNA作为效应因子的新功能, 表明sRNA在病原菌和寄主植物之间的相互作用中可能也具有致病因子的作用。*B. cinerea* 细胞中某些sRNA可以转移到植物细胞中, 利用植物的RNA干扰系统沉默与其免疫过

程相关的特定基因[56]。相反, 植物也能利用胞外囊泡将sRNA转入 *B. cinerea*, 进而抑制致病相关基因的表达[57]。虽然一些先进的技术 (如表面等离子体共振结合串联质谱、分裂泛素酵母双杂交分析和单分子膜蛋白追踪) 已经逐渐应用于分析病原真菌与寄主植物之间的相互作用, 采后病原菌复杂的致病机制仍然值得进一步深入探讨。

许多研究表明, ROS产生系统及其相关组分参与调控 *B. cinerea* 的生长发育和致病力[58-59]。在 *B. cinerea* ROS产生系统的多个组分中, BcNoxA和BcNoxB是人类NADPH (一种辅酶, 指还原型烟酰胺腺嘌呤二核苷酸) 氧化酶催化亚基 gp91<sup>phox</sup> 的同源蛋白, 同时具有跨膜结构域和催化结构域[60-61]。BcNoxD作为接头蛋白 p22<sup>phox</sup> 的同源蛋白, 能够直接与BcNoxA相互作用; 而另一种跨膜蛋白 BcPls1 作为BcNoxB复合物中的p22<sup>phox</sup> 同源蛋白发挥作用[62], 特别是BcNoxR通过调节BcNoxA和BcNoxB的催化功能发挥核心调控作用[61-62]。表型分析表明, 不同Nox亚基的缺失突变体在菌核形成、菌丝生长以及附着胞形成方面存在缺陷[61,63-65], 进而降低 *B. cinerea* 的致病力。这些证据表明, Nox亚基除了在维持细胞ROS产生和转运过程中发挥作用外, 还参与调控 *B. cinerea* 的发育和致病过程[61-62]。因此, 通过调节采后病原菌细胞的ROS稳态来抑制其生长和致病力是可行的[2]。

此外, 研究表明, 扩展青霉 (*Penicillium expansum*) 和指状青霉 (*Penicillium digitatum*) 的寄主专化性可能涉及基因组变异[66]。例如, 与 *P. expansum* 相比, *P. digitatum* 的遗传变异水平相对较低, 这也解释了 *P. digitatum* 对柑橘果实侵染的特异性[66-67]。然而, 特定的环境条件也会影响 *P. expansum* 的致病力。报道显示, pH响应转录因子 PePacC 可以调控致病力和棒曲霉素 (patulin, PAT) 合成, 在 *P. expansum* 对环境pH的响应中发挥重要作用[68]。此外, 对转移DNA (T-DNA) 插入文库的筛选显示, 一种分泌相关蛋白 Blistering1 也可以调控 *P. expansum* 的致病力[69]。

#### 3.2. 采后病害的生物防治

利用拮抗微生物来防控果实采后病害是一种安全有效的技术[70]。近二十多年的研究在拮抗微生物筛选、抑菌机理解析、提高生防效果等方面取得了显著进展。许多酵母菌株已被证明对多种果实采后病害具有明显的抑制作用[71-73], 具有广泛的应用前景; 并且, 它们对营养需求低, 与其他防控措施相容性好, 在不利条件下存活率高[1]。酵母拮抗菌的作用机制主要包括: 竞争生存环境和营养、形成生物膜、与病原菌互作、产生抗真菌物质、诱

导寄主抗性等[74]。在目前报道的分离菌株中,黏红酵母(*Rhodotorula glutinis*)、罗伦隐球酵母(*Cryptococcus laurentii*)和卡利比克毕赤酵母(*Pichia caribbica*)均能够有效控制不同果实的采后病害[75-80]。未来的研究重点应聚焦于提高现有菌株的生物防治效力,并积极探索生物防治与其他有效措施协同作用的潜力。

### 3.3. 筛选天然生物活性物质

经美国食品药品监督管理局(FDA)认证的一些安全物质/天然来源(植物或微生物来源)的物质,如黄酮类、酚酸类、萜类及其衍生物,由于具有较好的抑菌潜力,可作为安全的保鲜剂应用,受到研究人员的广泛关注。事实上,许多外源物质(如肉桂酸[81]、磷酸三钠[82]、苧酸甲酯[83]、壳聚糖[84]和纳他霉素[85])已经被报道能够有效防控苹果、草莓和葡萄等果实的采后病害,其作用机制主要包括提高果实抗氧化能力、诱导磷脂信号和增强细胞壁防御。另外,这些物质能够引起病原菌膜完整性受损、诱导细胞氧化应激以及自噬活性,进而抑制病原菌的细胞活力[86]。今后的研究需要进一步确定针对不同靶标的活性物质是否可以复配,以实现协同作用。

### 3.4. 果实采后致病因子研究面临的挑战

现有研究表明,大多数病原真菌的成功侵染依赖于其分泌活性和调节环境pH条件的能力,进而降解寄主细胞壁,缓解寄主产生的氧化暴发[56,68-69]。因此,病原菌与寄主互动时分泌蛋白谱的时空变化、T-DNA插入文库筛选、缺失突变体表型分析和蛋白质互作分析是今后研究的重点。在侵染早期对植物组织样本的分析也可以为致病因子鉴定和功能分析提供新线索。除了分泌蛋白,sRNA和真菌毒素也可作为潜在的效应因子或毒力因子发挥作用,了解这些致病因子的作用将为阐明果实与病原菌相互作用的机制提供新证据。在自然条件下,病原菌侵染果实的能力很大程度上取决于特定的环境条件,包括环境pH值、光照、温度和养分等。因此,精细调控这些环境因子也是提高果实抗性的重要途径。

## 4. 毒素合成和污染控制措施

### 4.1. 毒素生物合成途径中的关键基因和潜在靶点

丝状真菌能够产生大量次级代谢物[87],其中一部分代谢物在制药工业中具有重要价值,而另一部分代谢物则对食品工业和农业生产有害[88-89]。除了造成果实采后腐烂,有些病原真菌还能产生真菌毒素,这些毒素是食品

中常见的污染物,严重威胁人类健康。棒曲霉素是一种由丝状真菌产生的真菌毒素,可污染新鲜果蔬及其加工产品[90-92]。

考虑到在食品中消除或减少棒曲霉素污染的高成本,阐明棒曲霉素生物合成的分子路径具有重要的应用价值,有助于通过直接阻断毒素合成来控制棒曲霉素污染。有些丝状真菌(如棒曲霉*Aspergillus clavatus*[93]、灰黄青霉*Penicillium griseofulvum*[94]和*P. expansum*[95-97])负责棒曲霉素合成的基因簇已经得到解析。与黄曲霉毒素的合成基因簇不同,*P. expansum*棒曲霉素合成基因簇中的15个基因(*PePatA~PePatO*)都能影响棒曲霉素的生物合成,敲除其中的8个编码催化酶的基因后,棒曲霉素合成被完全抑制[98-99],表明这些基因对于棒曲霉素的生物合成是必不可少的。其中,C6型转录因子*PePatL*是调控棒曲霉素合成的特异性转录因子[97]。除了棒曲霉素生物合成途径的特异性转录因子外,一些全局性的转录因子(如*VeA*、*VelB*和*VelC*)也参与了棒曲霉素合成的调控,它们也是抑制真菌毒素产生的重要潜在靶点[99]。

### 4.2. 毒素污染的防控措施

目前,关于从食品中减少或消除棒曲霉素的研究进展相对缓慢,清洗或清除果实腐烂组织仍然是减少棒曲霉素污染最经济有效的措施[100]。由于酵母菌细胞能够代谢或降解棒曲霉素,因此,通过酵母菌株的发酵作用也能有效减少棒曲霉素的含量,脱除效果通常能达到90%以上[101-102]。然而,酵母菌发酵会影响果实制品的自然风味。一些天然产物(如植物源酚酸)也能显著减少真菌毒素的产生[103]。研究发现酚酸类物质对香豆酸可降低约90%的A型单端孢霉烯毒素T-2和HT-2的积累,以及48%~77%的玉米赤霉烯酮的积累[103],说明这些物质可以通过采前或采后的应用来控制镰刀菌和其他病原真菌导致的毒素积累。今后的研究还可以从新来源(如木材、竹材废料或传统中药材)中广泛筛选天然黄酮类化合物,利用这些资源还有助于减少资源浪费和环境污染。

## 5. 展望

近年来,在采后果实品质与安全调控方面的研究已经取得了重要进展(图2)。然而,自然环境与采后生物学实验条件有很大的不同,尤其在采后运输、贮藏和销售过程方面。此外,大多数实验室的研究是通过在果实表面人为产生伤口来检验抑菌效果,而在商业应用中,抗性应该在果实表面和内部表现出来。因此,今后的研究应着重于

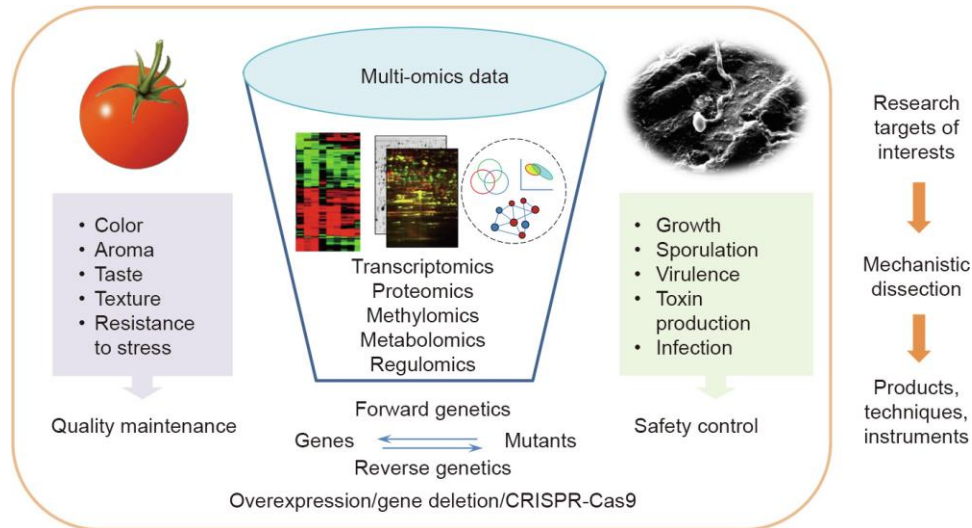


图2. 解析果实品质保持及安全相关机制的研究策略。

以下几方面：①进一步筛选抗菌谱更宽、效果更好的天然活性物质和拮抗微生物；②综合研究果实、病原菌和环境因子之间的相互作用机制和模式；③整合具有不同作用机制的防控策略进而达到协同效应。

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## Compliance with ethics guidelines

Tong Chen, Dongchao Ji, Zhanquan Zhang, Boqiang Li, Guozheng Qin, and Shiping Tian declare that they have no conflict of interest or financial conflicts to disclose.

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