

桃采后品质劣变生物学及调控技术研究进展

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摘要:桃常温放置易腐烂变质, 长期的低温冷藏易导致果肉褐变、风味丧失、抗病性降低、有害物质积累等, 是桃产业链的关键性采后问题。前人研究表明, 采后品质劣变症状及相关代谢酶、蛋白、基因对果实衰老和调控技术表现出应答差异性, 为了解研究概况, 笔者对采后品质劣变生物学、调控技术、技术和产品的产业化应用等方面的研究进展进行归纳和分析。目前, 采后品质劣变生物学主要局限于质地、内在品质和冷害及相关基因的挖掘和验证, 调控技术虽然被广泛研究, 但仍未解决长期冷藏导致的果实抗病性降低、风味丧失和货架期缩短的问题。建议后续基于多组学技术, 从超微结构、糖和能量、挥发性物质、内源激素、采后冷害和病害及基因甲基化等方面进行机制解析, 重点从冷链物流体系和抗病防御系统的建立、保鲜剂的研发及配套技术、终端货架和外源激素破休眠技术等方面开展研究。

关键词:桃; 品质劣变; 采后生物学; 调控技术

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Advances in postharvest biology and regulation techniques for prevention of fruit quality deterioration in peach

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Abstract: The total area of peach cultivation in our country is 100 hectares, and more than 80% are produced for fresh sales. Peaches are easy to deteriorate at room temperature, long-term cold storage can result in internal browning (IB), loss of flavor, reduction of disease resistance and accumulation of harmful substances, which are all the key postharvest problems in peach industry. With the upgrading of varieties and the flesh texture diversification of peach [melting (MF), non-melting flesh (NMF), stony hard (SH), and slow ripening (SR)], postharvest quality deterioration symptoms as well as related metabolic enzymes, proteins and genes show different responses to fruit senescence and regulation techniques. To understand the research situation, the author has summarized and analyzed the research progress of postharvest quality deterioration biology, regulation technology, industrial application of fresh-keeping products and technologies, and also put forward the shortcomings and development trends. At present, the biology of postharvest quality deterioration is mainly limited to the excavation and verification in functional proteins and genes of fruit texture, internal quality and chilling injury (CI). Fruit softening is a complex process, including cell wall degradation, ethylene metabolism and other metabolic changes. Among them, the gene *PpPG* is a biomarker of fruit softening and cell wall degradation, and ethylene is the direct factor that leads to fruit softening. Ethylene response factors like *PpERF/ABR1* and *PpERF61*

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can also regulate ethylene biosynthesis and fruit softening by activating the promoter of *PpPG* genes and ripening-related genes. Sugar loss, energy deficiency, active oxygen accumulation, abnormal metabolism of endogenous hormones and gene methylation are the key factors leading to CI by affecting membrane system and ROS. Five structural genes (*PpSS*, *PpINV*, *PpMGAM*, *PpFRK* and *PpHXK*) and eight transcription factors (*PpMYB1/3*, *PpMYB-related 1*, *PpWRKY4*, *PpBZIP 1/2/3* and *PpbHLH2*) jointly regulate the sugar metabolism and cold resistance. Down-regulating the expression of *PpVIN2* can improve the sucrose content and inhibit CI, and *PpeSOT3* may be a potential key gene affecting sorbitol metabolism and chilling resistance. Plant endogenous hormones such as ethylene, abscisic acid (ABA), β -aminobutyric acid (BABA) and salicylic acid (SA) also play an important role in regulating fruit senescence and CI. Postharvest disease is one of the key problems that cause post-harvest loss. *Phomopsis* sp., *Botrytis cinerea*, *Colletotrichum siamense*, *Rhizopus* sp., *Fusarium* sp. and *Aspergillus* sp. are the main pathogens causing postharvest rot. The decrease of lactone, ester and linalool contents and the accumulation of aldehyde and alcohol can be used as predictors of quality deterioration. The metabolism of lignin and aldehydes is the key metabolic pathway to regulate postharvest diseases. Based on the above background, the following suggestions are put forward: (1) Reveal the relationships among cell wall ultrastructure, softening markers, factors affecting ethylene metabolism, as well as interaction mechanism. (2) Expound the regulation mechanism of sugars, acids (pay more attention to the regulation mechanism of sugar metabolism and energy. Acid is also the important substrate of postharvest metabolism that makes great contributions to fruit flavor, energy metabolism and cold resistance, however, its metabolic mechanism is seldom studied.) and volatile substances (especially the accumulation mechanism of alcohols and aldehydes) on postharvest quality. (3) Determine the regulation of cold resistance by sugar and energy metabolism, antioxidant system, endogenous hormones (especially key genes and related factors of ABA metabolism) and key genes methylation. (4) Disclose the mechanism of lignin metabolism and the accumulation of alcohols and aldehydes in the prediction and regulation of postharvest diseases, which can provide a theoretical foundation for the development and application of regulation technology. Temperature, 1-MCP, UV, gas, exogenous hormone and biocontrol bacteria treatment have been applied in peach storage. Among them, storage temperature is the first factor affecting the fresh-keeping efficacy. For example, near-freezing temperature (NFT), low temperature conditioning (LTC), intermittent warming (IW), heat shock treatment (HST) and cold shock treatment (CST) can prolong storage period by inhibiting fruit softening and enhancing the cold tolerance. 1-MCP has a significant regulatory effect on fruit softening, flavor loss, postharvest diseases, especially on softening, by reducing the activities of PG, PME and PEL, down-regulating the expression of *PpPG1, 2*, *PpPME1, 2* and *PpPEL1, 2* under different storage conditions. Proper concentration of gas and exogenous hormones can improve the cold resistance. CO₂ and NO treatment can reduce CI and improve the cold resistance by regulating cell wall and lipid metabolism, such as by regulating the expression of LOX, ADH, FAD and related genes, activating the antioxidant system, and maintaining higher energy charge. Exogenous hormone treatment can also significantly improve the cold resistance during cold storage, among which MeJA, SA, γ -aminobutyric acid (GABA), melatonin (MT) and jasmonic acid (JA) have better effects. Although the postharvest storage technologies have been widely studied, it has not solved the problems of fruit disease resistance reduction, flavor loss and shelf life shortening caused by long-term cold storage, and its application in industry still has some limitations. It is suggested that the industrialization application of technologies and products should start from the followings in the future: (1) The establishment of cold chain logistics system for peach harvest, which integrates classification, packag-

ing, pre-cooling, storage, transportation and shelf-life technical parameter. (2) The research and development of compound antistaling agent and the matching technologies, as well as combination of new anti-staling agent with post-harvest packaging materials to improve the application of technology and products in industry. (3) The research and development of terminal shelf-life technology and exogenous hormone dormancy breaking technology, in order to solve the problem that the fruit shelf cannot break dormancy normally at room temperature after long-term low-temperature storage. (4) The establishment of cold resistance and disease prevention system technology and the breeding of cold-resistant varieties, in order to prolong the supply period of high-quality fresh peaches and solve the technical bottleneck problem of “the Belt and Road” (15–30 days ocean transportation and terminal shelf technology) of domestic fresh peaches.

Key words: Peach; Quality deterioration; Postharvest biology; Regulation techniques

据统计,2022年中国桃栽培总面积100 hm²,80%以上用于鲜食销售^[1]。桃果实采后常温放置易腐烂变质,长期的低温冷藏可导致果肉褐变、风味丧失、抗病性降低、有害物质积累等品质劣变症状,是桃产业中面临的关键性采后问题^[2]。随着国内桃品种更新换代和肉质类型多元化(软溶质、硬溶质、慢溶质、脆肉、不溶质等)的快速推进,采后品质劣变症状及相关代谢酶、蛋白、基因对不同肉质类型果实衰老和调控技术表现出应答差异性,致使桃果实品质劣变症状呈现多元化趋势,鲜果贮藏保鲜与运输面临更多挑战。解析桃采后品质劣变生物学基础,开发与之匹配的品质调控技术和保鲜材料是桃产业减损增效、提升产品竞争力和促进产业可持续发展的重要环节。

近年来,国内外学者关于桃采后品质劣变生物学研究主要集中在果实质地^[3-4]、糖酸^[5-6]、挥发性物质^[7-8]、内源激素^[9-10]、抗氧化物质^[11-12]及采后病害^[13-14]等板块,解析了品质劣变采后生物学机制,挖掘了关键功能基因和代谢通路,并进行了功能验证。针对桃产业中存在的问题,基于采后生物学研究基础,采后品质劣变调控技术被学者广泛研究。其中1-甲环丙烯(1-methylcyclopropene, 1-MCP)^[15-17]、气体^[18-20]、温度^[21-22]、辐照^[23-24]、外源激素^[25-29]、生防菌^[30-32]、植物精油^[33-35]和酚酸类物质^[36-38]处理均可有效缓解桃果实采后品质劣变进程,但仍未解决长期冷藏导致的果实抗病性降低、风味丧失和货架期缩短的问题。目前,多数综述局限于对果实采后质地和冷害的总结,为了解研究概况,笔者对采后品质劣变生物学、调控技术、技术和产品的产业化应用等方面的研究进展进行归纳和分析,提出了研究中存在的不足及发展趋势,

同时对未来的研方向提出建议,以期为解析桃采后品质劣变机制、研发调控技术和保鲜材料提供理论依据和技术支撑,也为采后保鲜贮运技术的应用和物化提供新的观点和思路。

1 桃采后生物学研究进展

1.1 果实质地变化

果实采后软化是一个复杂的过程,包括细胞壁的降解、乙烯代谢及其他代谢变化^[39]。细胞壁中果胶的溶化及中胶层、胞间层的溶解和初生壁的破坏导致果实采后软化;硬度与水溶性果胶含量呈负相关,与原果胶含量、原果胶指数(PI)呈正相关^[3]。多聚半乳糖醛酸酶(polygalacturonase, PG)基因(*PpPG*)为桃果实软化和细胞壁降解的生物标志物,其中,*PpPG1*和*PpPG21*、*PpPG22*分别是影响非溶质桃和溶质桃软化的关键基因^[40];多聚半乳糖醛酸酶抑制蛋白(polygalacturonase-inhibiting protein, PGIP1)基因(*PpPGIP1*)与液泡转化酶(vacuolar invertase, VIN)基因(*PpVIN2*)通过互作抑制桃果实软化^[41]。乙烯是导致桃果实软化的直接影响因子,可独立诱导*PpPG*基因的表达而调控果实软化^[42];乙烯反应因子(ethylene response factor, *PpERF/ABR1*)可激活*PpPG*基因的启动子、促进*PpPG*的表达,导致果实软化^[43];*PpERF61*-*PpSEPI*(a transcriptional activator)调控桃果实乙烯生物合成和质地变化^[44];1-氨基环丙烷羧酸合成酶(1-aminocyclopropane carboxylic acid synthase, ACS)基因(*PpACSI/4*)、1-氨基环丙烷羧酸氧化酶(1-aminocyclopropane carboxylic acid oxidase, ACO)基因(*PpACO1*)^[45]、ACO基因

(AF319166)^[46]、铜锌超氧化物歧化酶基因(copper-zinc-superoxide dismutase gene, *PpCuZnSOD*)^[47]、木葡聚糖内糖基转移/水解酶3基因(xyloglucan endotransglucosylase/hydrolase gene, *PpXTH33*)^[48]可通过介导乙烯代谢间接调控果实采后软化。除此之外,通过瞬时过表达桃醛酮还原酶基因(aldehyde keto-reductase gene, *PrupeAKR2*)可加速果实软化^[49]、沉默铜胺氧化酶基因(ketamine oxidase gene, *PpCuAO4*)^[50]和9-顺式环氧类胡萝卜素双加氧酶家族基因(9-*cis*-epoxycarotenoid dioxygenase gene, *PpNCED*)^[51]可减缓桃果实软化,桃果肉中细胞色素82A(CYP450 82A)和UDP糖昔二磷酸葡萄糖-4-表异构酶1(UDP-arabinose 4- epimerase 1)的下调和甲基化亦可调控果实软化^[52]。

1.2 果实糖含量变化

果实采后糖代谢是一个复杂的过程,涉及多种途径,主要包括蔗糖代谢、己糖代谢、山梨醇代谢和淀粉代谢。蔗糖合成酶基因(sucrose synthase gene, *PpSS*)、蔗糖磷酸合成酶基因(sucrose phosphate synthase gene, *PpSPS*)、蔗糖转运蛋白基因(sucrose transporter gene, *PpST*)与果实采后蔗糖、果糖、葡萄糖和山梨醇代谢密切相关。5个结构基因(*PpSS*、*PpINV*、*PpMGAM*、*PpFRK*和*PpHXK*)和8个转录因子(*PpMYB1/3*、*PpMYB-related1*、*PpWRKY4*、*PpbZIP1/2/3*和*PpbHLH2*)共同调控桃果实采后糖代谢和抗冷性^[5]。采后贮藏期间,*PpaSPS2*、*PpaSSI*和*PpaST3*的表达量与桃果实果糖含量显著相关,*PpaSPS2*和*PpaSST2*的表达量与葡萄糖含量显著相关^[6]。过表达*PpCBF6*可以通过下调*PpVIN2*表达量来提高桃果实的蔗糖含量;锌指蛋白基因(zinc finger protein gene, *PpZAT10*)通过抑制桃果实中的*PpVIN2*和增强VIN酶活性来调控蔗糖代谢^[53-54]。山梨醇转移蛋白基因(sorbitol transfer protein gene, *PpeSOT3/5/7*),尤其是*PpeSOT3*,可能是影响果实山梨醇代谢和抗冷性的潜在关键基因^[55]。

1.3 挥发性物质变化

醛类、醇类、酯类和内酯类化合物为桃果实的特征挥发物质,其中 γ -辛内酯、 δ -癸内酯、 γ -十二内酯、芳樟醇可赋予桃果实典型“桃香”气味,其含量与桃果实采后风味相关^[56]。长期低温冷藏可导致果实酯类、内酯类和萜类物质含量降低,醛醇类物质的积累,可作为果实冷害程度的预测因子^[57]。果实的腐

败变质导致乙醇和乙酸乙酯含量剧增,褐腐菌侵染桃果实可产生异丁醇、乙酸丙酯和异戊酸乙酯,以上挥发性物质可作为桃果实腐烂程度的标记物^[7]。环氧化物水解酶(EH)为桃果实内酯芳香物质合成的关键酶,其中7个EH家族成员基因(*PpEHI~7*)参与了桃果实内酯物质合成,其表达量与内酯芳香物质的积累呈负相关^[58]。脂氧合酶(lipoxygenase, LOX)、脂肪酸去饱和酶(fatty acid desaturase, FAD)、氢过氧化物裂解酶(hydroperoxide lyase, HPL)、醇脱氢酶(alcohol dehydrogenase, ADH)是醇、醛类物质代谢关键酶^[57, 59-60]。醇醛基转移酶(alcoholaldehyde transferase, AAT)是酯类物质代谢关键酶^[61],类胡萝卜素裂解酶双加氧酶(carotenoid lyase dioxygenase, CCD)是芳樟醇等萜类物质合成的关键酶^[59]。除此之外,烯氧化环化酶(alkene oxidative cyclase, AOC)、环氧丙烷合酶(allene oxide synthase, AOS)、12-氧化植物二烯酸还原酶(12-oxophytodienoic acid reductase, OPR)可与LOX通过蛋白互作共同诱导果实采后脂肪酸、酯类和内酯类物质的合成^[59]。

1.4 内源激素变化

植物内源激素乙烯、脱落酸(abscisic acid, ABA)、 β -氨基丁酸(β -aminobutyric acid, BABA)、水杨酸(salicylic acid, SA)等在调控果实成熟和衰老中起重要作用。采后贮藏期间,桃果实产生的乙烯和ABA均与果实硬度呈负相关,ABA含量的提高先于乙烯生成,可激活乙烯的产生,最终导致果实软化^[9];除此之外,乙烯还参与采后桃果实中类胡萝卜素积累和果实着色的调节^[62]。ABA可诱导4 °C冷藏期间中桃9号果实乙烯生物合成基因和乙烯含量上调,从而引起果实软化^[10]。*PpNCED*是果实内ABA合成途径的限速基因,同时也会受到外源ABA的调控^[51],其中*PpNCED1*、*PpNCED5*协同调控桃果实ABA的生物合成和果实软化^[10]。*PpMADS2*通过SA依赖的致病相关基因(*NPRI*)激活和ABA信号相关胼胝质积累的协同作用正向调节BABA诱发的桃果实抗病防御^[63]。

1.5 抗氧化物质变化

桃果实中的多酚、类黄酮和花色苷含量是资源评价和品种选育的重要因素,具有清除1,1-二苯基-2-三硝基苯肼(DPPH)自由基和一氧化氮(NO)自由基的能力。其中,原花青素三聚体C1、原花青素三

聚体异构体1/2、原花青素二聚体B1/2、原花青素二聚体异构体、李属抑制剂b和根皮苷等抗氧化活性化合物,与果实品质和耐贮性密切相关^[12]。20℃贮藏期间,桃果实总酚含量呈先上升后下降的趋势,总黄酮、总花色苷以及类胡萝卜素含量则随贮藏时间的延长而缓慢下降^[64]。与室温贮藏相比,长期的低温贮藏通过下调 CCD 的表达抑制类胡萝卜素积累,其中3个 $PpWRKYs$ 、2个 $PpMYBs$ 和1个 $PpNAC$ 为调节贮藏期间油桃果实中类胡萝卜素代谢的潜在转录因子^[11]。通过抑制乙烯的积累,可调控采后贮藏期间果实花青素生物合成相关酶的活性、基因表达和上游转录因子,影响花青素的合成进程^[65]。

1.6 采后病害

采后病害是引起果实采后损耗的关键因子,其中,拟茎点霉属真菌属(*Phomopsis* sp.)、灰葡萄孢菌(*Botrytis cinerea*)、炭疽病菌(*Colletotrichum siamense*)、根霉属(*Rhizopus* sp.)、镰刀菌属(*Fusarium* sp.)及曲霉属(*Aspergillus* sp.)6种霉菌为引起桃果实采后腐烂的主要病原菌,拟茎点霉属于真菌属最为关键的病原菌^[14]。特定的TGA家族成员可直接响应激发子诱导和病原菌侵染,通过与 $PpNPR1$ 蛋白相互作用在防卫反应中发挥调控作用^[66]。外源ABA-BABA处理可介导 $PpMAPKK5$ 的表达,提高 $PpTGA1$ 的DNA结合活性并激活SA反应性 PR 基因,提高抗病性^[67];BABA处理可提高TGA转录因子($PpTGA1$)和NPR1基因($PpNPR1$)的表达量,以及还原型烟酰胺腺嘌呤二核苷酸磷酸(NADPH)和谷胱甘肽(glutathione, GSH)含量,增强软腐病抗性^[13]。皮西亚酵母处理可介导 $PpMYB308$ 和 $PpMYB306$ 的表达,提高苯丙氨酸解氨酶(phenylalanine ammonia lyase, PAL)和4-香豆酸-CoA连接酶(4-coumarate-CoA ligase, 4CL)的活性和基因表达,增强对根霉菌的抗性^[68];抑制 $PpMYB306$ 介导的木质素生物合成相关基因的转录抑制,提高抗病性^[69]。茉莉酸甲酯(methyl jasmonate, MeJA)处理可介导桃果实 $PpWRKY46$ 和 $PpWRKY53$ 的相互作用,诱导抗病防御系统^[25]。

1.7 采后抗冷性

桃果实采后冷害主要与膜系统、活性氧自由基(reactive oxygen species, ROS)、DNA基因甲基化等直接相关。目前,在桃中鉴定了22个B-box基因家族成员,其中 $PpBBX3/6/12/15/20/26$ 的表达与桃果

实冷害发生呈显著负相关^[70]。钙依赖蛋白激酶基因家族($PpCDPK$)基因 $PpCDPK2/7/10/13$ 与桃采后冷害有关,其中, $PpCDPK7$ 与 $PpRBOH$ 的互作可能是钙信号和ROS信号传导的交汇点^[71]。NADPH为ROS和活性氮自由基(reactive nitrogen radical, RNS)的关键辅酶,桃果实抗冷性是通过维持ROS和RNS的稳态来实现的^[72];冷适应蛋白(cold-regulated, COR3)基因($PpCOR3$)的表达与 H_2O_2 含量呈正相关,并参与桃果实采后冷害调控^[73]。DNA甲基化在调节与冷害相关的基因表达中起关键作用,进而影响桃果实在低温贮藏中的品质和抗冷性^[74];冷害果实的甲基化水平高于非冷害果实,转录因子 $PpNAC1$ 及其下游基因 $PpACS1$ 、 $PpExp1$ 和 $PpAAT1$ 的转录丰度和启动子DNA甲基化呈现反向模式^[75]。ERF转录因子 $PpRAP2.12$ 可激活桃果实中 $PpVIN2$ 的表达而降低采后抗冷性^[53],可作为桃果实采后冷害研究的靶标;Cys79和Tyr396分别是S-亚硝基化和硝化最可能的靶标。通过延缓磷脂的降解、FAD的上调和脂肪酸去饱和的过程可延缓桃果实冷害的发生^[76]。

2 调控技术研究进展

2.1 1-MCP处理

1-MCP处理对果实软化、风味丧失、采后病害等品质劣变症状均有显著的调控作用,众多学者对其调控机制进行了解析。1-MCP处理可通过降低PG、果胶甲基酯酶(pectin methyl esterase, PME)和果胶裂解酶(pectin lyase, PEL)的活性,下调 $PpPG1,2$ 、 $PpPME1,2$ 和 $PpPEL1,2$ 的表达^[4],延缓桃果实软化;并可介导生长素相关的基因(吲哚乙酸、生长素响应转录因子等)和细胞壁修饰相关的基因($PpPG1,2,24$ 和 $PpPME1$)的表达,调控桃果实的软化^[77]。1-MCP处理通过调控与糖、酸代谢相关的基因表达,维持软溶质和不溶质桃果实蔗糖含量和贮藏品质的稳定^[78];并可抑制桃果实甜味、酸味和鲜味的丧失^[11];且可使果实保持较高的β-月桂烯和芳樟醇含量^[4],以及较少的内酯、苯甲醛和组氨酸含量^[8],贮藏风味佳。1-MCP处理主要通过上调 $PpSPS4$ 基因和下调 $PpNI3$ 、 $PpNI4$ 基因的表达,从而调控贮藏期间桃果实的糖代谢,维持更高的蔗糖水平^[16]。1-MCP处理通过提高脯氨酸和多胺的含量^[17];下调生长素反应因子($PpARF1$)、生长素反应基因($PpAUX1$)

IAA1、*PpSAURI* 和 *ppg H3-1*) 和生长素受体蛋白 (*PpTIR1*) 的表达, 调节 IAA 生物合成、生长素信号转导和细胞壁降解^[4], 提高桃果实的抗冷性。1-MCP 与一些保鲜手段结合, 具有协同作用, 如: 1-MCP 联合乙烯吸附剂处理^[79]或结合激光微孔膜包装^[80]可显著抑制果实软化; 1-MCP 结合 CaCl_2 处理可促进桃果实中糖的积累和贮藏品质的保持^[81]; 结合纳米材料包装 (1-MCP-NA) 可显著抑制黄肉桃果实酯类和醛类含量的下降及乙醇含量的积累^[82]。

2.2 气体处理

气体的成分、比例和含量可调控桃果实采后贮藏品质和冷害, CO_2 和 O_2 的处理参数与品种、贮藏条件相关。适宜浓度的 CO_2 和 O_2 处理可抑制桃果实冷害 (CI)、延长贮藏期^[18], 3%~5% CO_2 结合 3%~5% O_2 可上调蟠桃果实丙酮酸脱羧酶 (pyruvate decarboxylase, PDC1/2)、SS 及 V 型质子 ATP 酶亚基的蛋白表达, 维持高能荷状态和蔗糖水平, 抑制果实褐变^[2]; 5% O_2 和 10% CO_2 结合 0 °C 低温贮藏可使桃果实保持较高的酯类和内酯类挥发性物质含量, 尤其是与 LOX 途径相关的化合物, 这些挥发性化合物与消费者接受度呈正相关^[83]; 5% O_2 可介导基因 *PpADH1* 和 *PpPDC2* 的表达, 调控果实乙醇和乙醛积累, 有效减轻桃果实冷害^[84]。

适宜浓度的 NO 处理通过调节细胞壁和脂质代谢来减轻桃果实的冷害^[19]。NO 熏蒸处理可调控霞晖 6 号桃果实 *PpFAD*、*PpLOX*、*PpHPL*、*PpADH*、*PpAAT* 和 *PpACX* 的基因表达, 增加 4 °C 冷藏期间 C6 醛、C6 醇、直链酯和内酯等挥发物含量^[85]; 调控桃果实采后花青素、黄酮醇和黄酮类代谢, 激活抗氧化酶, 延缓霞晖 8 号桃果实衰老^[86]; 降低冷藏期间桃果实的线粒体耗氧量和细胞色素含量, 提高线粒体膜流动性以及呼吸链的细胞色素通路和抗氰通路的活性^[87], 抑制 H_2O_2 含量和 O^{\cdot} 产生速率、诱导氰化物抗性呼吸途径^[88], 提高采后抗冷性。硫化氢 (H_2S) 处理可诱导三磷酸腺苷酶 (ATPases)、琥珀酸脱氢酶 (succinodehydrogenase, SDH) 和细胞色素 C 氧化酶 (cytochrome c oxidase, CCO) 活性, 增加 ATP 和能荷的水平, 减轻采后冷害^[20]; 并通过调节细胞壁修饰酶、酚类物质和脯氨酸代谢, 延缓果肉褐变^[72]。

2.3 温度和辐照处理

贮藏温度是影响果实采后保鲜期的第一因素, 通过对贮藏温度的调控可延缓果实冷害、延长保鲜

期。冰温贮藏 (near-freezing temperature, NFT) 可诱导果实糖和能量的代谢, 提高油桃果实采后品质和抗冷性^[21]。低温预贮 (low temperature conditioning, LTC) 亦可锻炼桃果实抗冷性, 但不同品种的桃对温度的敏感性不同, 最佳预贮温度为 9 °C~12 °C, 预贮时间为 6~10 d^[89]。间歇升温 (intermittent warming, IW) 处理 (每周在 20 °C 放置 1 d 后转移至 5 °C 贮藏) 可抑制黄桃果实酯类物质的降低, 延缓果肉褐变^[90]。热空气处理通过调控花色苷相关基因的表达, 提高果实花色苷含量, 延缓糖酸和酚类物质含量的下降^[91]; 热水处理 (HW) 可调控 *PpHSFA4c* 表达量介导热处理蛋白 (HSP) 和活性氧途径, 减轻果实冷害^[22]; 热空气+1-MCP (HM) 处理通过推迟高峰呼吸, 提高谷胱甘肽过氧化物酶 (GPX) 活性, 上调 *PpaGPXs* 基因的表达, 延缓桃果实的采后衰老^[92]。冷激处理通过调节 *PpbZIP9* 和 *PpVPI1* 介导的呼吸代谢进程, 增强桃果实的耐冷性^[93]。

短波紫外线 B (UV-B) 处理可引起桃果肉中萜类、苯丙烷类、植保素和脂肪酸代谢物含量的提高^[23]; 短波紫外线 C (UVC) 预处理可上调 *PpaSSI* 基因的表达, 保持果实贮藏品质^[6]; 热空气结合 UVC 处理可上调苯丙氨酸解氨酶的酶活性和基因表达, 增强花色苷还原酶、二氢黄酮醇还原酶、UDP-葡萄糖和类黄酮 3-O-葡萄糖基转移酶的活性, 提高 1 °C 冷藏桃果实的花青素、原花青素 (PAs) 和花青素-3-葡萄糖苷 (Cya-3-G) 含量^[94]。45.5 W 微波处理 7 min 可通过抑制膜脂降解和蔗糖积累维持膜稳定性, 降低总酚含量, 抑制冷害引起的果肉褐变^[24]。蓝光 LED 处理可促进油桃果实中果糖和葡萄糖的积累, 白光 LED 处理可显著促进蔗糖的代谢^[95]。

2.4 外源激素处理

外源激素处理可显著提高采后冷藏期间桃果实的抗冷性, 其中 MeJA、SA、 γ -氨基丁酸 (GABA)、褪黑素 (MT)、茉莉酸 (JA) 的处理效果较佳。MeJA 处理可促进贮藏期间果实蔗糖合成^[96], 提高抗冷性^[25]; 上调转录因子 *PpNAC1* 和 *PpMYC2.2* 的表达、下调基因组甲基化水平, 延缓果实冷害^[75]; 同样可以诱导 *PpLOX*、*PpAOS*、*PpAOC*、*PpACOX* 和 *PpFadA* 的基因表达, 激活 α -亚麻酸和茉莉酸信号通路而延缓果实冷害的发生^[26]。SA 处理可促进醇类、脂肪族酯类、内酯和萜烯的释放^[97], 提高 *PpLOXI*、蔗糖合酶基因 (*PpSUS4*)、中性转化酶基因 (*PpNINV8*) 和单糖转运

蛋白基因(*PpTMT2*)的转录水平,减缓果实冷害^[27]。JA处理可诱导桃果实乙烯释放,抑制可溶性总糖含量下降,提高果实抗冷性^[28];且SA和JA处理在减轻桃果实冷害方面存在协同效应^[28]。ABA处理可通过调节金秋红蜜桃果实蔗糖的代谢而缓解0℃下的冷害症状^[29];IAA处理通过调控ABA和GA代谢基因的转录水平,降低ABA和GA水平,提高抗冷性^[29]。GABA处理可上调与抗坏血酸(AsA)和谷胱甘肽(GSH)代谢相关的基因和转录因子,提高桃果实中AsA和GSH的含量^[100],增强果实采后抗冷性^[101]。BABA处理通过调节*PpWRKY40*与调节蛋白*PpNPR1*的互作关系,以及*PpWRKY40*对蔗糖代谢酶基因的激活进程,保持适中的可溶性糖含量,维持果实在适应性和防御之间的平衡^[67]。MT处理可显著提高桃果实不饱和脂肪酸/饱和脂肪酸比例和内源性水杨酸含量,调节抗氧化系统和细胞壁代谢^[102];上调GABA生物合成基因(*PpGADI*和*PpGAD4*)的表达,抑制GABA降解基因(*PpGABA-T*)的表达^[103],提高果实抗冷性。外源2,4-表油菜素内酯(EBR)通过调节*PpGATA12*介导的蔗糖代谢相关基因(*PpSS*和*PpNI*)和能量代谢相关基因(*PpCCO*、*PpSDH*和*PpH⁺-ATPase*)的转录水平^[104];通过*PpHDT1*调节油菜素类固醇代谢^[105],提高桃果实的抗冷性。甘氨酸甜菜碱(GB)处理通过调节精氨酸代谢、GABA分流途径的基因表达和酶活性,提高脯氨酸、多胺和GABA的含量,增强桃果实抗冷性^[106]。

2.5 生防菌

虽然国内关于防治采后病害的生防制剂研究众多,但生产实践中使用的生防制剂仅有Aspire、Shemer、Candidfruit等产品,因此筛选和研发可推广使用的生防制剂意义重大。罗伦隐球酵母+间型假丝酵母组合处理可显著抑制水蜜桃果实霉变和腐烂^[30]。杰米拉类芽孢杆菌W51能有效抑制桃果实采后匍枝根霉的孢子萌发及菌体生长,诱导抗病相关基因的表达,降低软腐病的发病率和病斑直径^[31]。内生真菌蓝状菌属(*Talaromyces*)ZJ-4通过抑制褐腐菌丝的生长,使孢子表面粗糙凹陷、畸形,抑制桃采后褐腐病发生^[107]。桃园土壤中的特基拉芽孢杆菌(*Bacillus tequilensis*)B-23可使菌丝顶端膨大、表面粗糙,孢子边缘干瘪、粗糙且皱缩,同时细胞壁降解、细胞器消失、液泡变形,对褐腐病菌的抑菌

率达到73.68%^[108]。拮抗细菌CE抑菌物质可引起桃褐腐病菌菌丝细胞膜透性变化、菌丝和分生孢子形态异常、分生孢子不能萌发,抑制桃褐腐病菌的侵染^[32]。地衣芽孢杆菌菌株W10菌液及其产生的抗菌蛋白对贮藏期桃褐腐病都有较强的抑制作用,0.1%Ca(NO₃)₂可提高W10菌液及抗菌蛋白对桃果实褐腐病的防治效果,能明显推迟始病时间^[109]。

2.6 植物精油和酚酸类化合物处理

茶树油具有显著的抗真菌活性,可影响孢囊霉细胞膜的组成,改变菌丝形态和膜透性,延缓桃采后病害的发生^[110];茶树油固体脂体质可有效抑制桃褐腐病,保持果实固有品质^[33]。50 μg·mL⁻¹的艾叶、高良姜和白鲜皮精油(EOs)可显著抑制5种采后病原体活性(黄曲霉菌*A. Flavus*、扩展青霉菌*Penicillium Expansum*、灰葡萄孢菌*B. cinerea*、链格孢菌*Alternaria* Nees、美澳型核果链核盘菌*Monilinia fructicola*);其中,三种中草药CP EOs复合制剂(M-CP EOs)对抗真菌活性具有协同作用^[34]。柠檬草、香茅、白唇草和美洲罗勒等精油可显著抑制桃果实采后炭疽菌、灰葡萄孢和褐腐菌真菌活性,其中柠檬草精油对褐腐菌的抑制效果更为显著^[111]。绿薄荷、胡椒薄荷、百里香CT香芹酚和百里香CT百里香酚精油可通过破坏立枯丝核菌的细胞膜来抑制其生长,减轻桃果实上的立枯丝核菌导致的腐烂^[112]。植物基精油(rosewood)处理可显著降低室温和低温条件下水蜜桃被寄生毛霉(*Mucor nidicola*)感染导致的病斑直径和腐烂率^[35]。

苯丙氨酸处理可显著促进贮藏前期桃果皮中花色苷合成相关结构基因(*PAL*、*F3H*、*DFR*、*UFGT*)和调节基因(*MYB10.1*、*bHLH3*、*WD40-1*)的表达,促进果皮花色苷合成^[36]。亚精胺处理可上调桃果实*PpSAMDC*、*PpSPDS*、*PpADC*基因并同时下调*PpACSI*、*PpACOI*基因的转录水平,促进总酚、总黄酮和花色苷等抗氧化物质及活性氧的积累,显著降低白凤水蜜桃果实腐烂率和褐变度^[113]。外源脯氨酸和L-半胱氨酸处理通过降低氧化应激,增强抗氧化酶活性和促进抗氧化成分的积累,减轻蟠桃果实的冷害症状^[37]。茶多酚^[114]或对羟基肉桂酸(P-CA)^[38]处理均可提高总酚、花青素和黄酮含量,增强DPPH自由基和羟自由基清除能力和抗氧化能力,延长果实保鲜期。绿原酸处理通过激活茉莉酸信号途径抑制桃采后青霉菌扩展,减轻果实采后腐

烂的发生^[115]。

3 保鲜技术和产品应用中存在的问题

3.1 保鲜贮运技术应用中存在的问题

基础低温冷藏^[2]、低温预贮^[89]、冰温贮藏^[21]、热预处理^[22,91]、UV 处理^[23]、气调处理^[18]等物理保鲜技术在桃果实保鲜贮藏中有一定的推广应用,但存在较多局限性。(1)冰温贮藏可显著抑制果实冷害,但精准控温是冰温贮藏技术成功与否的关键制约因子,低于冰温会对细胞组织造成冻害,高于冰温会缩短贮藏寿命^[89];(2)预贮温度和预贮时间是制约低温预贮技术的关键因子,不适操作易造成果实软化和褐变加速^[116];(3)1-MCP 处理及复合保鲜技术在抑制果实软化方面效果显著,但存在操作复杂、密闭空间熏蒸时间长、浓度过高果实不能正常软化等问题^[117];(4)热处理和 UV 辐照^[23]技术效果佳,参数易控,但如何与固定的贮藏设备或分选设备相结合,是影响其产业应用的关键因素^[118];(5)气调处理可显著抑制果实褐变和风味丧失,但设备造价昂贵、能耗高,且气调贮藏的果实对终端货架参数要求较高^[2];(6)产业中应用率较高的仍然为非冷害温度的低温贮藏及集果实分级、包装、预冷、贮藏、运输、货架为一体的桃采后冷链物流技术。

3.2 保鲜剂应用中存在的问题

1-MCP^[79-80,82]、外源激素^[96,101-102]、酚酸类^[115]化合物等生理调节剂,生防菌^[108-109]、植物精油^[33,115]等生物保鲜剂在桃果实保鲜贮运中效果显著,但仍存在以下问题:(1)处理效果不持久,作用效果会随着贮藏期的延长而减弱,无法实现果实的长期贮存^[108-109];(2)功能单一,多数采后处理通常只具备延缓成熟、抑菌、减轻冷害、减少失水等单一的作用效果^[79,102,108];(3)安全性有待评估,目前,1-MCP 是应用较为广泛、认可度较高的保鲜剂,大多数化学和生物保鲜剂的安全性仍然受到消费者的质疑,在实际应用中存在限制^[119]。(4)制备方法有待改进,多数保鲜剂存在溶解度小、易降解等制约因素^[120]。如外源激素处理、生防菌处理、植物精油处理可显著提高果实采后抗冷性,但是多以浸泡和喷雾的形式处理,易导致果实采后腐烂严重,且大众接受度低,较难推广。研发成本低、安全性高、效果持久、复合功效的保鲜剂是突破桃采后保鲜技术应用瓶颈的重要发展策略。

4 展望

笔者对相关文献进行了综合对比和阐述,认为引起桃果实采后品质劣变的关键因子为:(1)*PpPG*为桃果实细胞壁代谢和软化的标志物,乙烯和乙烯响应因子是影响果实软化的关键因素;(2)内酯类、酯类和芳樟醇物质含量的降低以及醛和醇的积累,可作为品质劣变程度的预测因子;(3)木质素和醇醛类挥发性物质代谢是调控果实采后病害的关键代谢途径;(4)能量缺失、活性氧积累、内源激素代谢异常、基因甲基化是导致果实冷害和褐变的关键因子。建议后续从细胞壁超微结构、软化标志物、直接和间接影响乙烯代谢的因子、互作机制与果实软化的关联性;糖酸(前人多关注糖代谢对果实风味调控机制的研究,酸是果实采后生命活动的底物,对果实风味、能量代谢和抗冷性均有较大贡献,应对调控机制进行挖掘)和挥发性物质(尤其是醇醛类物质)对采后风味的调控机制;糖和能量代谢、抗氧化系统、内源激素(尤其是ABA 代谢关键基因及关联因子)及关键基因甲基化程度对抗冷性的调控;木质素代谢和醇醛类物质的积累对采后病害的预测和调控作用等方面进行机制解析,为调控技术的研发和应用奠定理论基础。

桃采后品质劣变调控技术虽然被广泛研究,但仍未解决长期冷藏导致的果实抗病性降低、风味丧失和货架期缩短的问题,在产业中的应用仍有一定的局限性。建议未来在技术和产品的产业化应用中从以下几个方面着手:(1)集分级、包装、预冷、贮藏、运输、货架为一体的冷链物流体系的建立;(2)复合保鲜剂的研发及配套技术的集成,将新型保鲜剂与采后包材相结合,提高技术和产品在产业中的应用率;(3)终端货架技术和外源激素破休眠技术的研发,解决长期低温冷藏后的果实常温货架不能正常破休眠的问题;(4)抗冷性和病害防御系统技术的建立及耐冷性品种的选育,延长高品质鲜桃的供应期,解决国产鲜桃一带一路(15~30 d 的远洋运输和终端货架技术)的技术瓶颈问题。

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