

硬质桃研究现状及展望

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摘要:提升果实耐贮运性是我国桃育种的重要目标之一。硬质桃最早于1976年报道,但在我国的研究利用较晚,其果实在成熟时不释放乙烯或仅释放少量乙烯,可较长时间保持硬、脆状态。因此,硬质桃具有较长的留树保鲜期和较好的采后贮运性,弥补了我国普遍种植的溶质型桃不耐贮运的短板,适应了桃产业规模发展、远端较长时间运输的需求。笔者对硬质桃的发现及研究现状进行了综述,对其存在的问题和发展方向进行了探讨,以便更好地促进硬质桃的研究与利用。

关键词:桃;硬质;遗传;分子基础

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Research status and perspective for stony-hard peach

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Abstract: Peach is the 3rd largest deciduous fruit in China, which is commercially planted almost all around the country. Traditionally, most of the cultivars planted in China are melting flesh type whose flesh becomes softening very quickly at the end of fruit development and the fruits are difficult to deliver to far markets. In recent years, development of cultivars with good keeping quality has become one of the most important breeding objectives pursued by many peach breeders. Peach is a typical kind of respiratory climactic fruit. Normally, the ethylene production rises gradually with the progress of peach fruit ripening and reaches a peak finally. Owing to the action of ethylene, PG enzymes (including exo- and endo-PG) are catalyzed, which resulted in cell wall degradation. Then, the firmness of the peach fruits declines dramatically and the fruits become soft and juicy soon. However, there are also some other kinds of peach fruit textures. Stony-hard peach is a kind of fruits in which the production of ethylene is blocked, which results in that the fruit can keep hard even on-tree or during post-harvested period. This nature makes it a very good material to make up the shortage of melting flesh type. Stony-hard flesh type was originally reported in 1976 by Yoshida. However in China, there were no reports about this kind of peach until recent years. 'Jingyu' was the first stony-hard peach cultivar selected by Beijing Forestry and Pomology Institute in 1970s. It was widely used in peach breeding programs in China, not for the fruit texture at the beginning but for the carrier of *g* gene for nectarine breeding. There are many stony-hard peach/nectarine cultivars released and commercially planted in China in recent years, such as CN 18, CN 20 and CP 8 bred by Zhengzhou Fruit Research Institute of Chinese Academy of Agricultural Sciences; 'Ruiguang' 'Meiyu' and 'Huayu' bred by Beijing Institute of Forestry and Pomology; and 'Xiacui' bred by Jiangsu Academy of Agricultural Sciences. In addition, there were also some breeders or institutes from Europe, USA, Japan and so on were engaged in several programs for stony-

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hard peach breeding and have released some cultivars for commercial production, such as ‘Ghiaccio’ series, ‘Yumyeong’, ‘Manami’, etc.. Genetically, the stony-hard trait is controlled by a single recessive gene (*hd*), which is epistatic to the melting/non-melting character and inherited independently. Many literatures showed that the stony-hard texture was resulted from a mutation of *PpYUC11* gene, belonging to *YUCCA* gene family, which encodes a flavin monooxygenase-like gene. In melting flesh peach fruits, *PpYUC11* catalyzes the progress of IAA biosynthesis, and then *PpACS1* is induced and catalyzes the production of ethylene, which leads to the softening of peach fruits finally. RT-PCR detection showed that *PpYUC11* gene expressed abundantly in melting or non-melting flesh peach fruits during mature stage but undetectable in stony-hard peach fruit. Analysis of the gene structure indicated there existed a 2.1 kb insertion upstream of the start codon of the *PpYUC11* gene in stony-hard peach, leading to the losing of function. Based on the researches, a molecular marker has been developed to distinguish stony-hard peach from other flesh textures of peach fruit. By detecting some germplasm resources and cultivars, we have found some good resources containing *hd* gene, such as ‘CN5’ ‘Golden Honey 3’ ‘CP5’ ‘Yuhualu’ ‘Baihua’ ‘NJC83’, etc., which can be used for stony-hard peach breeding. ‘CN 15’ ‘CN20’ ‘Xiacui’ ‘Qingwang’, and several other cultivars were verified as stony-hard texture with *hd-hd* genotype. Stony-hard peaches or nectarines were welcomed by some farmers and logistics industry for their good keeping quality. But there are still some problems, such as lack of fragrance, relatively less prominent flavor, post-harvest diseases, etc., which need to be taken into account in future from multiple ways including breeding, cultivation and post-harvest handling.

Key words: Peach; Stony-hard; Inheritance; Molecular basis

桃(*Prunus persica* L. Batsch)是蔷薇科(Rosaceae)李属(*Prunus* L.)植物,是广泛栽培于世界各国的重要核果类果树之一,在我国的栽培历史超过3 000年^[1]。桃为呼吸跃变型果实,在果实发育后期乙烯释放快速增加,形成一个高峰,从而诱发桃果实的呼吸跃变,使果实迅速变软^[2-5]。我国传统的桃品种绝大多数为溶质型,甜美多汁。桃的早期种植多以家庭小规模种植为主,仅在以种植点为中心的小范围内出售,大范围流通很少。改革开放以来,我国的桃产业得到了快速发展,自1993年起,栽培面积和产量就已跃居世界第一。据FAO最新数据,2017年我国桃栽培面积和产量分别达到78.19万hm²和1 429.5万t,占世界总栽培面积和产量的51.2%和58.0%。

近些年来,随着新土地政策的推行,产业结构进一步调整,种植大户不断涌现,产业也逐渐向部分区域集中。如在山东省蒙阴县,形成了一个种植面积4.33万hm²、年产量96万t的集中产区^[6]。由于大规模产区的形成,桃也由过去的区域流通,逐渐往全国性大流通方向发展,甚至销往全球^[7]。在这种情况下,传统柔软多汁的溶质桃往往很难适应

远距离、长时间的物流过程,造成损耗过高或过早采摘,品质无法满足消费者需求等问题。因此,挖掘耐贮运种质、培育耐贮运优质品种对桃产业发展至关重要。

硬质桃是留树及采后均不变软的肉质类型,由于其耐贮运性好,成为解决桃“短腿”问题的重要途径之一。笔者就硬质桃的发现、特点、研究进展等进行了总结,并对其存在的问题和解决途径进行了探讨。

1 硬质桃的发现及主要特点

1.1 我国早期关于桃肉质的研究

桃虽然起源于我国,但国内有关果实肉质类型的研究却不多。1976年浙江省农业科学院园艺研究所桃梨课题组^[8]对桃杂交后代主要性状的遗传倾向进行了分析研究,其中,亲本‘小暑’为脆肉类型,以‘小暑’为父本,‘玉露’和‘大白桃’为母本的组合中,出现了不同比例的脆肉类型,分别为10%和44.4%,且这些后代汁液均较少,但群体均较小,分别为11株和9株。据《中国果树志 桃卷》^[9]第140页,浙江的‘小暑’为‘陆林’,描述为“肉质硬脆,成

熟度高时发面,纤维细,汁液少;……;离核”。此外,在‘仁圃早生’和‘岗山 500’‘黄金’和‘爱保太’组合中还出现了粉质类型的桃,纤维多,汁少。这是我国现有可查文献中关于肉质研究最早的报道,脆肉等描述与现在研究的粘核硬质桃类似,而成熟度高时发面或粉质、汁液少等描述与离核硬质桃的表型类似。

1987年汪祖华等^[10]在《落叶果树》上发表了我国第1篇专门研究桃果实肉质的文章“桃果实肉质研究初报”,文章对不同肉质桃的硬度及果胶物质含量、过氧化氢酶活性及同工酶谱等进行了分析,发现硬度低的溶质品种原果胶含量少,可溶性果胶含量多,硬度高的不溶质品种则相反。

1.2 硬质桃的发现及特点

桃肉质通常分为溶质(Melting flesh, MF)和不溶质(Non-melting flesh, NMF)2类,溶质桃成熟时很快变软,采后软化更快,而不溶质桃成熟时硬度下降较慢,果肉有韧性,有橡皮质感。1976年, Yoshida^[11]报道了一种在留树成熟和采后都几乎不变软的桃,并将其归为“stony hard”类型(缩写 SH, 硬质型)。最早选出的 SH 类型桃品种是‘京玉’^[12],该品

种由北京市农林科学院林果所于1961年以‘大久保’和‘兴津油桃’为亲本,通过杂交选育,1975年定名,成熟时硬度高、离核、白肉,类似“离核不溶质”,具有较好的贮运性和货架期^[13-16]。‘京玉’是我国选育的第一个硬质桃品种,但国内却未见其肉质类型的相关研究报道。2009年,北京市农林科学院林业果树研究所陈青华等发表了“京玉桃在我国桃育种中的应用”一文,概述了‘京玉’桃对我国桃育种的贡献,但在肉质方面,也仅仅提到该品种“果实硬度大,适采期长,耐储运能力强”^[13]。

硬质桃具有很脆的果肉质^[12,17],在加热后可以变得与溶质类型类似^[11]。Liverani 等^[18]发现 SH 类型桃果实成熟时仅释放少量乙烯或不释放乙烯,其他方面与普通桃无显著差异。SH 桃果实硬度远大于溶质桃,用乙烯处理可以使 SH 桃变软^[19];在低温(10℃)冷藏条件下,可以诱导产生乙烯^[20-23]。Haji 等^[24]测定了溶质、不溶质和硬质3种不同肉质桃采后果实硬度和乙烯释放情况,溶质和不溶质桃乙烯释放增加,硬度逐渐下降,尽管幅度有所不同;而硬质桃在贮藏过程中仅产生极少量乙烯或不产生乙烯,且能保持很高的硬度,与前2种肉质明显不同(图1)。

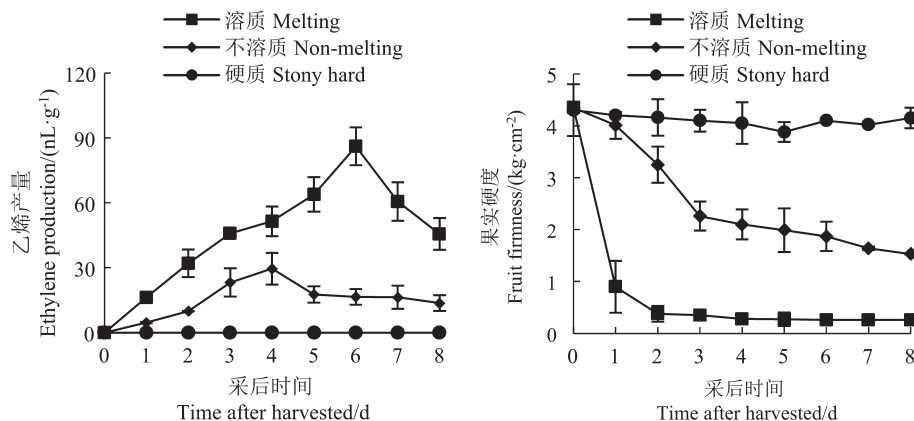


图1 不同肉质桃采后乙烯产量和硬度变化^[24]

Fig. 1 Changes of ethylene production and fruit firmness of different flesh textures^[24]

2 硬质桃的育种利用

2.1 国外硬质桃育种

将 SH 性状纳入美国种质资源圃的工作始于上世纪 70 年代,迄今已实施了若干相关的育种项目^[25-26]。上世纪 80 年代早期,阿肯色大学的育种家 Clark 等从桃杂交群体中发现了不同于溶质和不溶质的果肉类型,一种类型为离核但果肉很硬,在完全成熟时变软,这在后来被称为“慢溶质”(Slow melting);另一种类型为黏核但果肉比不溶质更硬,

后来被称为“不软”(Nonsoftening)的果肉类型^[27]。1999年,美国新泽西州罗格斯大学果树研究与推广中心发布了3个硬质桃,L5-112(黏核)、L2-42(离核)和J19-19,其中,L2-42的父本来自我国的‘京玉’。同时指出,硬质对可溶性固形物含量没有明显不利影响,但可能会影响其他风味成分^[25]。

意大利 CREA-Forli 自 1980 年起就开始通过人工杂交将硬质性状引入到鲜食桃中^[28],并配置了 30 个组合,获得了 3 000 余株杂种实生苗^[29]。Ghiaccio 是意大利育成的系列桃品种,包括‘Ghiaccio 1’

‘Ghiaccio 2’ ‘Ghiaccio 3’等,这些硬质型品种不着色,果肉很硬,货架期可长达 25 d^[12,30-31]。

此外,巴西和我国台湾地区也有以 SH 为目标的桃育种项目,以培育具有更好贮运性和货架期的品种,并同时满足鲜食和加工市场^[26,32]。

2.2 我国硬质桃育种

‘京玉’是我国最早选育的硬质型桃品种^[12],在后期的桃育种中得到了广泛应用。截至 2009 年,以‘京玉’为来源育成了 35 个品种,其中 27 个品种有肉质及硬度方面的描述,包括 6 个软溶质、18 个硬溶质、3 个硬肉,代表性的品种有‘早玉’‘华玉’‘瑞光美玉’‘秦光’‘秦光 2 号’等^[13]。其中的脆肉、高硬度的桃品种很可能都是硬质桃,但由于描述相对模糊,也缺乏遗传方面的分析及相关研究,限制了其在后续育种中的利用。

1999 年,中国农业科学院郑州果树研究所选用油桃优株 89-1-28 为母本,‘中油桃 5 号’为父本,配置杂交组合,共获得 50 株杂种实生苗。其中,编号为‘99-37-46’(即‘中油 15 号’)的单株 6 月中旬果实即开始着色,很快达到全红,但硬度变化较小,可

一直挂树到 7 月上旬仍维持不变软。遗憾的是,由于育种周期限制,很多单株短期内被淘汰,未能对该组合全部后代进行逐一细致评价和深入研究。除此之外,在同年的‘中油桃 5 号’×‘SD9238’、‘89-7-12’(‘京玉’×‘早红 2 号’)×‘中油桃 5 号’等组合中均发现了类似肉质的单株。

通过文献查询和比较,笔者认为这些单株的肉质表型与国外报道的 Stony hard 类型非常类似,即肉质硬脆,留树及采后均不变软。笔者以国外报道的硬质型桃‘Yumyeong’为对照,测定了部分单株果实的乙烯释放情况^[33-34],确认了这些单株均不释放乙烯,为硬质型桃。

2.3 我国育成的部分硬质桃品种及谱系

因国内育成品种很少有肉质类型的准确描述,为更好地定性,我们利用开发的转座子插入标记,对部分品种的基因型进行了检测,结果如下:

转座子插入标记检测为 SH 肉质(基因型为 *hd-hd*)的品种:‘中油 15 号’(图 2)‘中油 18 号’‘中油 20 号’‘中桃白玉’‘霞脆’^[35](图 3)‘秦王’^[36]、‘华玉’^[37]等。

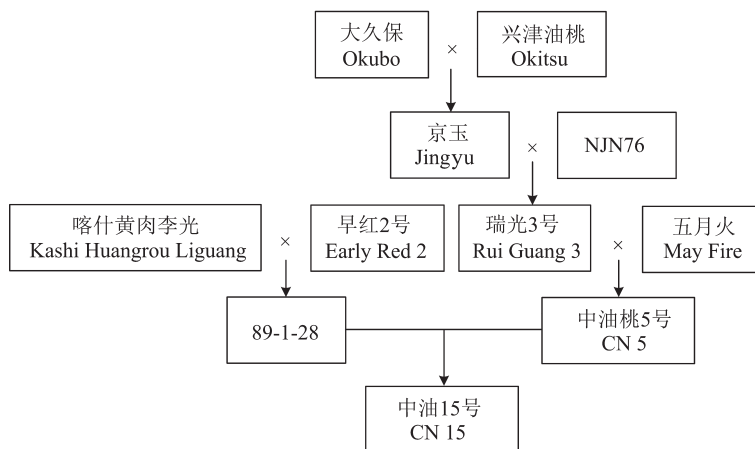


图2 硬质桃品种‘中油 15 号’的系谱

Fig. 2 Genetic lineages of stony hard nectarine cultivar ‘CN15’

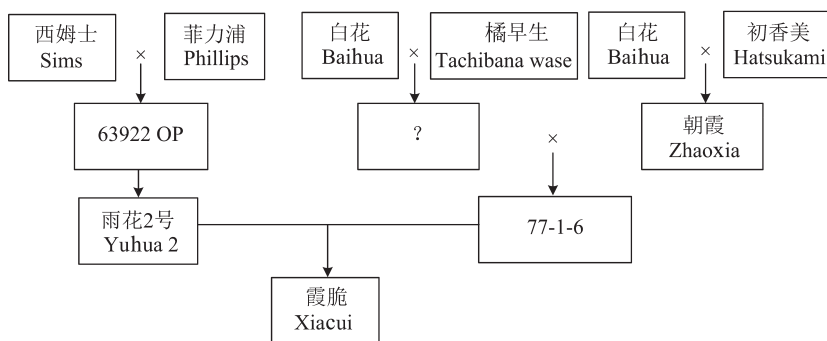


图3 硬质桃品种‘霞脆’的系谱^[35]

Fig. 3 Genetic lineages of stony hard peach cultivar ‘Xiacui’^[35]

转座子插入标记检测含硬质基因(基因型为 *Hdhd*)的品种:‘NJC83’‘寒公主’‘双喜红’[‘瑞光2号’×(‘北京25-17’×‘早红2号’)]^[38]、‘雨花露’(‘白花水蜜’×‘早上海水蜜’)^[39]、‘白花水蜜’‘岗山白’‘兴津油桃’‘大久保’‘中油桃5号’(‘瑞光3号’×‘五月火’)^[40]、‘黄金蜜桃3号’^[41]、‘中桃5号’(‘朝晖’×‘双佛’)(未发表)等。

此外,根据公开的品种特性资料及亲本等信息,我们判断可能是硬质型的品种还有:‘美硕’(‘京玉’实生)^[42]、‘美锦’(‘京玉’自交)^[43]、‘早玉’(‘京玉’×‘瑞光3号’)^[44]、‘瑞光美玉’(‘京玉’×‘瑞光7号’)^[45]、‘秦超’(‘秦王’芽变)^[46]、‘春雨黄桃2号’(‘西尾黄金’实生)^[47]、‘署脆红’(‘超越1号’芽变)^[48]等。

3 硬质桃的遗传及分子基础

3.1 硬质桃的遗传

Yoshida 等^[11](1976)首次报道了 SH 性状,总结出 MF 对 SH 为显性,并受单基因控制。Goffreda^[25,49]和 Liverani 等^[18]也发现 SH 为隐性。硬质性状独立于溶质/不溶质性状遗传,且对溶质/不溶质性状有上位作用^[50]。外源乙烯的使用证明了硬质桃中包含有 MF 和 NMF 类型,SH/MF 果实会软化成溶质质地,而 SH/NMF 果肉不会变“溶质”^[17,24,31-32,50-51]。‘中油15号’‘中油18号’等均为 SH/NMF 类型。

我们于2009年以溶质型的‘黄金蜜桃3号’^[41]和硬质型的‘中油15号’杂交,在98个后代中,溶质和硬质型为52:46,接近1:1。‘黄金蜜桃3号’与‘中桃5号’杂交,后代溶质与硬质分别为60:18,接近3:1(内部数据),这些结果与前人报道的遗传规律相符,同时也说明‘中桃5号’和‘黄金蜜桃3号’均含有硬质基因,可用来培育硬质桃品种。

3.2 硬质桃形成的分子基础

硬质桃是由于乙烯合成受阻所致。植物体内乙烯的合成主要包含2步,SAM(S-adenosyl-L-methionine, S-腺苷蛋氨酸)在 ACC 合酶(ACC synthase, ACS)的作用下合成 ACC(1-amino-cyclopropane carboxylic acid, 1-氨基环丙烷羧酸),ACC 在 ACC 氧化酶(ACC oxidase, ACO)的作用下再生成乙烯^[52]。研究表明,通过简单的喷施 10~20 mmol·L⁻¹ 的 ACC 就可以促进乙烯的合成,并让硬质桃果实变软,更高的浓度可以增加乙烯的释放量,使果实

更快软化^[50]。但乙烯的合成仅仅被限制在 ACC 处理后的 2~3 d,随后果实的软化会停止^[53]。

对硬质桃成熟时 *Pp-ACS1* 的表达分析表明,该基因的表达受到抑制^[54],导致了 ACC 合成受阻,果实不能释放乙烯,无法变软。但有意思的是,同样是 SH 基因型,在衰老的花、受伤的未成熟和成熟果实中,乙烯释放却增加,*Pp-ACS1* 的转录也正常^[55-58]。乙烯诱发的成熟伴随着 PG 基因表达的增加,包括 *endo-*和 *exo-PG* 活性^[55,59],但不发生 *Pp-ACS1* 的积累^[54],且不发生乙烯合成的自动催化。这些发现清晰地表明,硬质基因位点与 *Pp-ACS1* 基因表达的调控有关,而与其他乙烯感知和信号转导途径无关^[57]。

硬质桃乙烯合成受阻是由于果实成熟期生长素(IAA)的含量较低。使用外源萘乙酸(NAA)可以诱导硬质桃 *PpACS1* 的表达,从而产生大量乙烯,导致果实变软^[58-59]。Zeng 等^[60]用生长素处理硬质桃,也导致了 *Pp-ACS1*、*Pp-ACS4* 和 *Pp-ACS5* 等表达的增加,但用乙烯处理抑制了这些基因的转录,这表明乙烯成为 ACS 基因的负反馈调控因子。乙烯处理并没有诱导桃果实中 *Pp-ACS1* 的表达,这表明桃中乙烯的生物合成没有自动催化,也解释了桃中系统 II 乙烯的生物合成需要较高水平的生长素^[58]。

在多数植物体中,生长素的生物合成主要通过吲哚-3-丙酮酸(IPA)途径完成。首先,TAA 家族蛋白(氨基转移酶)催化色氨酸(Trp)转变为吲哚-3-丙酮酸,然后在 YUCCA 基因家族(黄素单加氧酶)的作用下催化 IPA 直接转变成 IAA^[61]。Pan 等^[33]通过 DGE 分析,比较了硬质桃和溶质桃果实成熟后期基因表达的差异,发现一个与生长素生物合成有关的关键基因——*PpYUC11*,在溶质桃果实成熟后期,该基因转录增加,而在硬质桃中,该基因的表达则难以检测。Tatsuki 等^[62]的研究也表明,尽管在成熟时硬质桃中 IAA 的含量较低,但 IPA 的水平较高,表明 YUCCA 的活性受到了抑制,导致 IPA 的积累。用根据序列差异设计的 SSR 引物,对 43 份不同肉质桃品种进行了检测,检测结果与这些品种的基因型相吻合^[33],再次验证了该基因与硬质性状的关联。

这些结果证明了 *PpYUC11* 在桃果实成熟过程的生长素合成中起关键作用。该基因的变异导致果实中生长素不能正常合成,进而使下游 *PpACS1* 受抑制,ACC、乙烯合成受阻,最终果实不能变软。

进一步研究发现,硬质桃中 *PpYUC11* 基因上游启动子区域的一个转座子插入是该基因表达受阻的根本原因^[62-63]。Cirilli 等^[64]也通过基因组关联作图、转录组分析和对 SH 和非 SH 单株的全基因组重测序数据,以及对育种优株和分离群体的标记-性状关联分析等,确认了控制硬质性状的 *hd* 位点位于桃第 6 染色体的 1 个 1.8 Mbp 的区域内,转录组数据的比较分析也再次确认了 SH 果实 *PpYUC11* 的表达缺失。

4 硬质桃存在的问题及未来发展方向

4.1 硬质桃存在的问题

从第 1 个硬质桃品种问世到近几年的明确身份和推广,已过去近半个世纪,早期由于认识不足,并没有明确地将其与其他肉质桃很好地区分,更谈不上利用。近几年,随着‘霞脆’‘中油 15 号’‘中油 18 号’‘中油 20 号’等品种在生产上的推广应用,硬质桃受到种植者及物流业者的欢迎,其持久的高硬度大大减少了软化腐烂带来的损耗,较长的留树时间保证了果农的从容销售,采后硬度的保持也使完全成熟的鲜桃可以送达全国。从另一个方面来看,部分硬质桃还是存在一些不尽如人意之处,主要有以下几个方面:

(1) 香气欠缺:几乎所有的硬质桃都缺乏水蜜桃的香气,虽然其他类型品种的香气也在慢慢丢失,但硬质桃表现得尤其明显。究其原因,可能与乙烯途径阻断导致下游次生代谢物质合成受阻有关,目前还缺乏深入研究。

(2) 品质不及溶质桃:一些消费者反映大部分硬质桃品种口感硬而不甜,或甜而不脆,可能存在多方面的原因。其一,由于硬质桃留树时间长,而生产中习惯性早采,部分产区为了“抢占市场”,果实刚着色但未完全发育就提早采摘上市,导致硬质桃品质充分发育再上市的优势无法体现;其二,由于硬质桃质地较脆,水分相比水蜜桃偏少,口感甜度难免稍次于水蜜桃;其三,当前推广的硬质桃,大多为早熟品种,光合产物积累不足,品质相比中晚熟桃确实有所欠缺,如果生产中再不注意肥水管理及产量控制,很难保证其果实品质。实际上,有些硬质桃品种,如早熟的‘霞脆’、中熟的‘中油 20 号’等,品质不次于同期成熟的其他类型桃品种。

(3) 采后病害:据物流环节反映,硬质桃在物流过程中硬度保持很好,但存在采后病害重、腐烂较

多等问题。我们推测,由于硬质桃质地较脆,采后贮运过程中易磕碰造成伤害,伤害诱导了果实释放乙烯,使果实软化,进而导致腐烂。也可能与部分品种果皮薄,易感染采后病害有关。

4.2 硬质桃未来研究方向

4.2.1 遗传基础与种质创新 桃硬质性状的遗传已基本清楚,其候选基因也已得到克隆^[33],由于缺乏高效的遗传转化体系,使得基因的功能验证存在一定障碍。此外,桃硬质性状与离核、汁液含量、脆度、可溶性固形物含量、香气等相关性状的交互,需要进一步阐明。

虽然目前生产上已有一些明确或不明确的硬质桃品种,但总体上处于初级阶段,已推广的品种也存在类型不够丰富,熟期不配套等问题。未来种质创新需要重点关注:(1) 酥脆多汁:偏硬而汁少的品种,口感有所欠缺,而具有类似酥梨酥脆口感的类型会更受消费者欢迎;同时着重培育具有较好香气,或用乙烯处理变软后有较浓郁香气的品种。(2) 离核硬质:离核硬质桃果实在成熟过程中,开始表现为硬脆,随后伴随着离核过程,汁液变多,硬度逐渐下降,多数这类品种会变粉质。在变粉质之前,硬度中等且汁液较多时,品质及口感最佳。该类型可能是硬质桃品种发展的一个方向,‘京玉’‘华玉’‘早玉’‘中桃 8 号’等品种均为此类型。(3) 熟期配套,类型丰富:培育不同肉色不同成熟期的优质硬质桃、油桃品种,包括蟠桃、油蟠桃品种。

4.2.2 采后保鲜与贮运 在常规条件下,硬质桃自身不释放乙烯,但采后 10 °C 以下低温或机械伤害会刺激乙烯释放。因此,今后需要结合硬质桃独有的特点,加强采后保鲜及贮运方面的深入研究。作者认为,未来硬质桃采后方面的主要研究方向包括:(1) 研发商品化产品,在采后控制硬质桃的硬度和软化速度,使其具有水蜜桃的口感和香气;(2) 探索有效的采后保鲜技术,维持果实采后的硬度和品质;(3) 研究合适的低温保鲜方法,避免果实冷害的发生。

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