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桃果实肉质研究进展

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摘 要:桃果实以皮薄肉厚、味道鲜美、营养丰富等优点而深受国内外消费者喜爱。然而桃果实属于呼吸跃变型果实,且成熟期集中在夏季高温季节,采后迅速软化,导致果实品质下降、不耐贮藏及货架期短,是制约桃产业可持续发展的关键问题。前人研究发现桃果实具有不同的肉质类型,这其中也包含较耐贮运的肉质,为了解桃果实肉质的研究概况,笔者归纳总结了国内外关于桃果实肉质类型的分类及遗传定位、桃果实不同肉质形成的分子机制等方面的研究进展,并提出了存在的不足以及未来研究趋势。指出目前桃果实肉质的研究局限于果实成熟软化过程中细胞壁结构和相关物质的变化、细胞壁降解相关酶的活性变化,以及这些酶的基因克隆,认为未来激素调控桃果实成熟软化的转录调控机制,同时结合基因组、转录组、蛋白组和代谢组等多组学的研究将是桃果实肉质研究的重点方向。

关键词:桃;果实肉质;激素;转录调控

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Research process on peach fruit flesh texture

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Abstract: The fruit of peach (*Prunus persica* L. Batsch) is popular with domestic and foreign consumers, based on thin skin, delicious taste and abundant nutrition. However, the fruit firmness declined rapidly during peach ripening and post-harvest storage, resulting in the decrease of the fruit quality and storability, which is one of the major bottleneck constraints of peach industry development. To understand the research survey of peach fruit texture, and provide a reference to further study the mechanism of fruit ripening and softening of peach fruits, this paper summarized the classification and genetic mapping of peach fruit texture, molecular mechanism of peach fruit texture formation. Flesh texture of peach was classified into melting (MF) and non-melting flesh (NMF), most of the table peaches belong to melting flesh. The melting-type fruit soften rapidly during ripening, non-melting type peaches showed slow softening rate and no notable decrease in flesh firmness, even when overripe. This texture has been also referred to as rubbery. Besides MF and NMF, several other flesh types including stony hard (SH), and slow ripening (SR) were found in current peach cultivars and breeding materials. Peach melting flesh and flesh adhesion to stone (endocarp) are simply inherited and controlled by the F-M locus on linkage group (LG) 4. A number of studies have been conducted to identify potential candidate genes for melting flesh and stone adhesion in peach. Initially, biochemical studies revealed that an endopolygalacturonase (endoPG) is highly expressed in ripe MF peaches, but extremely low in NMF peaches. Thus, the endoPG gene is deemed to be a candidate for the M locus in peach. Two genes encoding endopolygalacturonase (endoPG) in the F-M locus, designated *PpendoPGF* and *PpendoPGM*, are associated with the melting flesh and stone adhesion traits. *PpendoPGM* controls melting flesh while *PpendoPGF* has pleiotropic effects on both melting flesh and stone adhesion. However, recombination between the M and the endoPG gene was observed in three

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progeny derived from a cross between NMF and MF cultivars. The F-M locus has three allelic copy number variants of endoPG, H1 (*PpendoPGF* and *PpendoPGM*), H_2 (*PpendoPGM*), and H_3 (null). The H_2 haplotype may represent the ancestral one while the H_1 and H_3 haplotypes are two variants due to duplication and deletion of *PpendoPGM*, respectively. Accessions with H_1H_1, H_1H_2, or H_1H_3 genotypes show the freestone or semi-freestone and melting flesh phenotype, while both H_2H_2 and H_2H_3 accessions have the clingstone and melting flesh phenotype. The H_3H_3 accessions have the clingstone and non-melting flesh phenotype. The genetic separation of the flesh texture characteristics in F1 and F2 offspring from the cross of non-melting and stony hard cultivars indicated that the stony hard trait was controlled by a single gene, and inherited independently of melting flesh/non-melting flesh traits. The fruit of melting and non-melting cultivars showed increased ethylene production and softer flesh, although their variation degrees differed. Conversely, the stony hard texture was characterized by the absence of both ethylene production and postharvest softening in mature fruit, while the firmness of the stony hard peach decreased effectively with continuous ethylene treatment. The fruit of melting-flesh peach cultivars produce high levels of ethylene caused by high expression of *PpACS1* (an isogene of 1-aminocyclopropane-1-carboxylic acid synthase), resulting in rapid fruit softening at the late-ripening stage. In contrast, the fruit of stony hard peach cultivars do not soften and produce little ethylene due to low expression of *PpACS1*. Recently study showed that suppression of *PpACS1* expression at the late-ripening stage of stony hard peach may result from a low level of IAA and that a high concentration of IAA is required to generate a large amount of system 2 ethylene in peaches. It is suggested that a YUCCA flavin mono-oxygenase gene (*PpYUC11*, ppa008176m), a key gene in auxin biosynthesis, displayed an identical differential expression profile to the profiles of IAA accumulation and *PpACS1* transcription: the mRNA transcripts increased at the late ripening stage in melting flesh peaches but were below the limit of detection in mature fruits of stony hard peaches. In addition, the strong association between intron TC microsatellite genotypes of *PpYUC11* and the flesh texture (normal or stony hard) is described in 43 peach varieties, indicating that this locus may be responsible for the stony hard phenotype in peach. These findings support the hypothesis that *PpYUC11* may play an essential role in auxin biosynthesis during peach fruit ripening and is a candidate gene for the control of the stony hard phenotype in peach. The paper pointed out that the current research of fruit ripening and softening of peach were concentrated in the changes of cell wall material composition and structure, enzyme activity changes of cell wall degradation related enzyme, and the gene cloning and function analysis of cell wall degradation enzyme, and proposed the research directions. Transcriptional regulation mechanism of hormone regulation on ripening and softening of peach fruit, the combination of genomics, transcriptomics, proteomics, and metabolomics studies will be the development direction of peach fruit texture research.

Key words: Peach; Fruit texture; Hormone; Transcriptional control

桃(*Prunus persica* L. Batsch)是蔷薇科(Rosaceae)李属(*Prunus* L.)桃亚属(*Amygdalus* L.)多年生落叶果树。桃果实以皮薄肉厚、味道鲜美、营养丰富等优点而深受国内外消费者喜爱,然而果实在成熟后迅速软化,不仅大大缩短了果实的贮藏时间,而且果实软化后极易受到病原微生物的侵染,造成大量的经济损失,成为制约桃产业可持续发展的关键问题之一。因此,研究桃果实肉质形成机制,选育耐贮运的桃品种,以延迟果实软化和延长果实货架期,一直是人们关注的焦点。果实成熟软化是一个非常复杂的过程,其间经历了一系列的生理生化变化,包括细胞壁的降解、乙烯的释放以及其他的代谢变化[1]。尽管植物果实成熟软化已有不少研究[2-5],但至今尚未有全面介绍桃果实肉质研究进展的综述,不利于研究者的查阅借鉴。笔者对目前桃果实肉质类型的分类及遗传定位、不同肉质类型形成的分子机制等方面的研究进展作一综述,同时对未来研究应关注的重点方向提出建议,以期为探明果实成熟软化机

制和制定桃果实保鲜技术研究方案提供参考和理论依据。

1　桃果实肉质分类与遗传

国内传统上按桃果实成熟软化的特点将果肉的质地分为软溶质、硬溶质、不溶质、面和硬脆5种类型[6]。国外则最早由Connors[7]将果实的肉质定义为3种类型:不适于运输,且果实成熟过程中迅速软化的软溶质型(melting flesh ,MF);商业运输能保持较高的硬度,但成熟即软的硬溶质型(比如'J. H. Hale');成熟后不变软,且果肉具有韧性的不溶质型(non-melting flesh,NMF)[8-10]。Yoshida[11]报道了一种新的桃肉质类型——硬质(stony hard,SH),该类型果实成熟期及采后均不变软,能正常着色,并且积累较高的可溶性固形物含量。除上述这些肉质类型之外,目前桃栽培种和育种种质资源中还包括缓慢成熟型(slow ripening,SR)、缓慢溶质型(slow melting flesh,SMF)。

1.1　桃果实肉质类型

1.1.1　*溶质类型(MF)*　溶质型桃在鲜食桃消费市场中占据主导地位。中国是世界上最大的桃生产地,80%的栽培桃品种为溶质型[12]。Yoshida[11]认为溶质类型包含4种肉质:软、较硬、硬和SH。尽管Bailey等[13]认为软溶质对硬溶质为显性,但Yoshida[11]推测软溶质和硬溶质肉质的差异取决于多基因的剂量效应以及这些基因之间的互作。Connors[7]和Weinberger[14]发现溶质型桃果实肉质坚硬的程度从软到硬可以划分为多个等级。经典的软溶质类型比如'Champion' '玉露水蜜' '爱保太'等,硬溶质类型比如'J. H. Hale' '白凤' '锦绣'等,还有一种称为非常硬的溶质类型,称为缓慢溶质型(SMF),特点是果实成熟期具有相当高的硬度,并具有较长的货架期[15-16]。目前,多个国家将SMF型桃列入育种计划,且催生出一系列的品种(比如'Big Top' 'Rich Lady' 'Diamond Princess' 'White Country' 'White Diamond'等),他们表现为成熟早期果实硬且脆,但最后会释放乙烯,从而变软[17-18]。SMF型桃'Big Top'的果实硬度比硬溶质型'Bolero'在果实成熟期明显更硬,然而采后室温放置5 d后果实变得非常软,最终果实硬度与'Bolero'类似。'Bolero'在果实成熟期采收后便迅速释放乙烯,而SMF型'Big Top'在果实成熟期采收4 d后才开始释放乙烯[16]。同时发现SMF型延迟释放乙烯与乙烯合成限速酶ACC(1-aminocyclopropane-1-carboxylic acid)合成酶(ACC synthase,ACS)基因的延迟表达有关。截止到目前,还没有开发出区分MF和SMF类型的分子标记。

1.1.2　*不溶质类型(NMF)*　NMF类型早期一直以黏核(clingstone)、缓慢变软(slow-softening)或者罐头桃(canning peach)等来命名,这种类型桃果实在成熟阶段仅稍微变软,没有经历第4阶段的溶质化过程,因此最终以NMF命名。NMF类型通常是黏核,肉质具有韧性,适合制作罐头,但将NMF命名为罐头桃类型存在误导,因为目前不溶质类型有广泛的变异,不仅可以用来制作罐头,而且鲜食消费市场中也有很多的NMF品种[19]。通过感官和生理生化比较MF和NMF类型的研究发现,NMF果实更加坚硬,少汁,通常肉质更富有弹性,但风味、苯酚化合物和可溶性固形物含量在2者之间没有明显的差异[20]。早前El-Agamy等[21]认为NMF类型果实成熟期之所以没有溶质化过程,可能是由于该类型仅释放少量乙烯,然而Haji等[22]和Ghiani等[23]发现不管是果实成熟期还是采后NMF型果实的乙烯释放量均高于MF型。

1.1.3　*硬质类型(SH)*　目前所知,最早的SH型品种是北京林果所1970年选育出的'京玉',其果实表现为白肉,离核,硬度高,由于这种类型具有优良的贮运能力和长货架期,早先为了将它们与'NMF'和'MF'区分,将其命名为离核NMF型[24]。SH型果肉相当硬脆,Yoshida[11]最早报道SH类型,推测和MF对NMF为显性一样,MF同样对SH为显性,同时SH由单基因控制。Liverani等[25]也发现SH类型是隐性遗传,成熟的果实仅释放少量或基本不释放乙烯,呼吸速率很低,但果实大小、着色、可溶性固形物含量与其他肉质类型均无显著差异。Goffreda等[26]发现所有的SH型桃果实硬度远胜于MF型,但是在乙烯处理或者低温贮藏的条件下,SH型桃果实会迅速变软。鉴于SH类型良好的贮运能力和长货架期,意大利等多个国家将SH类型也列入了育种计划,并已推出了一系列的SH类型,比如意大利的'Ghiaccio'(冰)系列,韩国的'Yumyeong'('有名'),日本的'Manami'('真奈美')、'Odoroki'('惊讶'),中国的'秦王' '京玉' '霞脆' '中油桃16号' '莺歌桃'等。

1.1.4　*缓慢成熟类型(SR)*　1984年,加利福尼亚的美国农业部农业研究组织(USDA-ARS)在核果类育

种计划中从溶质型油桃‘Fantasia’的杂交后代中筛选出单株，发现其果实延迟成熟且果实硬度非常高，并将其命名为SR类型，这种类型果实硬脆，虽然采后贮藏果实硬度下降非常显著，但采收期硬度要比溶质型‘Fantasia’高60%[27]。它的双亲均为MF类型，且没有发现中间型，据Begheldo等[28]介绍，SR型果实在硬核期后便停止生长，果个小，果实仅释放极少量乙烯且不变软。这类品种含有更高的酚类物质、pH值、可溶性固形物，二氧化碳和乙烯释放量低，是呼吸跃变型果实，但是呼吸跃变准备时间非常长，比正常的果实具有更高的硬度，果面更绿，甚至在秋天落叶后还相当硬。Brecht等[27]推测果实乙烯释放受到抑制是由于乙烯合成前体物质ACC不足所致。尽管SR类型不太适合作为商业化的品种广泛栽培，但是可以作为研究桃果实成熟软化机制的优良试材。

1.2 遗传和定位

尽管不同肉质型桃在果实硬度方面有着非常大的变异，但桃果实肉质的几种主要类型均属于质量性状。

桃果肉质地的溶质/不溶质(M/m)受1对等位基因控制，且溶质(M)对不溶质(m)为显性遗传[13,29]。除此之外，桃果实的特殊性状——黏离核性状，黏/离核(*f/F*)也受1对等位基因控制，离核(*F*)对黏核(*f*)为显性，依据果实的肉质和黏离核状况，桃果实分为黏核溶质桃、黏核不溶质桃和离核溶质桃，离核不溶质这种类型目前尚未有报道。多项研究表明控制黏/离核性状(*f/F*)、溶质/不溶质性状(*M/m*)的基因处于同一个位点，并定位在第4连锁群44 cM处[30-32]。

Haji等[33]利用不溶质的‘Tishiki’和SH型的‘Yumyeong’杂交，F_1代40个个体全部为溶质，F_1自交得到的72个个体中，有53株为非硬质，19株为硬质。在53株非硬质桃中，溶质类型为40株，不溶质类型为13株，19株硬质单株的果实在用乙烯处理后，有15株果实变软(溶质)，4株果实不变软(不溶质)。桃SH型由隐性单基因(*hdhd*)控制，该基因独立于溶质(melting flesh，*M_*)/不溶质(nonmelting flesh，*mm*)遗传，并且对*M/m*基因具有上位性。应用外源乙烯处理SH型桃果实时，其表现型中又可区分为处理后快速软化和处理后缓慢变软的溶质、不溶质表现型，且推断分别由*hdhdM_*和*hdhdmm*两种基因型控制。这一研究清晰地展示了不同肉质类型桃的遗传及交互作用，溶质/不溶质为1对等位基因，溶质为显性，硬质/非硬质为1对等位基因控制，硬质为隐性，且硬质对溶质/不溶质有显性上位作用，即硬质与溶质或不溶质类型结合，后代均表现为硬质类型，独立于溶质/不溶质性状遗传。

SR类型遗传上受单基因隐性(*sr/sr*)控制，研究发现该性状定位在第4条染色体，更深入的分析发现在第4条染色体的11 111 981和11 137 943位点有1段26.6 kb的缺失，导致2个基因(NAC转录因子ppa008301m和预测的转座子ppa021959m)的缺失，推测控制SR肉质类型的候选基因是ppa008301m[34]。

并不是所有肉质性状均为质量性状，果实的肉质受到细胞壁的降解、激素的诱导及其他代谢变化的影响，是多因素造成的。Ogundiwin等[32]通过不溶质型‘Dr. Davis’和离核溶质型‘Georgia Belle’杂交，利用杂种后代分离群体构建连锁图谱，筛选与果实性状紧密连锁的标记，其中，关于肉质的数量性状位点(QTL，quantitative trait locus)主效基因分别是位于LG1的果胶酶(PL2，Pectate lyase)和果胶甲酯酶(PME1，pectinesterase)，位于LG4的成熟抑制子(RIN，Ripening inhibitor)转录因子和内切多聚半乳糖醛酸酶(Endo-PG，endo-polygalacturonase)，位于LG5的α-L-阿拉伯糖呋喃糖苷酶(Ara，Alpha-L-arabinofuranosidase)，位于LG7的果胶甲酯酶(PME5，pectinesterase)和位于LG8的内切多聚半乳糖醛酸酶(Endo-PG4，endo-polygalacturonase)。

2 桃果实不同肉质形成的分子机制研究

果实质地软化主要是由细胞壁结构的改变和细胞壁组分的降解所引起，胞壁物质的降解和果胶-纤维素-半纤维素(P-C-H)结构的破坏是果实质地软化的开端[35-36]。果实的细胞壁多糖组分主要由果胶、半纤维素和纤维素构成。果胶是胞间层的主要成分，果胶溶解是桃果实成熟软化和肉质差异的最根本和最重要的特性[37]。细胞壁超微结构的研究发现，在果实成熟后期，微纤丝间的果胶和纤维素逐渐被细胞水解酶水解，微纤维丝结构变得散乱、细胞壁变薄、细胞变圆且趋于分散[38-40]。目前普遍认为，在一系列水解酶的作用下，果肉细胞壁多糖的降解或解聚是果实质地改变的主要原因[2]。桃果实肉质分

子机制的研究多以溶质型和不溶质型桃以及非SH型桃和SH型桃的对比研究为主。

2.1　溶质型和不溶质型桃分子机制研究

果实成熟软化时在细胞壁中发生的最显著变化是果胶物质的溶液化。果胶是果实细胞壁中胶层的重要组成成分,对细胞间的粘连起着重要作用,果胶的降解特别是多聚醛酸的降解,能造成细胞黏度下降,最终导致果实的软化。

参与果胶降解最关键的酶是PG,多聚半乳糖醛酸酶(PG)分为外切酶(ex-PG)和内切酶(endo-PG)2种。前者水解果胶分子非还原端的α-(1,4)-半乳糖醛酸键,后者随机水解α-(1,4)-半乳糖醛酸键[41]。研究发现溶质桃果实成熟后的软化与Endo-PG酶活性增强直接相关,目前对桃PG的分析,国外主要集中在不溶质和溶质之间,研究发现不溶质桃成熟过程中Endo-PG酶活性始终处于极低的水平,而溶质桃随着果实的成熟,Endo-PG酶活性显著上升[42],因此,*Endo-PG*被认为是控制桃果实*M*位点的候选基因[43-45]。

后续研究发现,不溶质桃成熟过程之所以缺乏内切多聚半乳糖醛酸酶活性,是由于*Endo-PG*基因部分片段缺失突变所致[10,46-47]。遗传学研究发现控制黏/离核性状和溶质/不溶质性状的基因处于同一个位点,随后研究表明*Endo-PG*基因不仅控制桃果实的肉质,还控制果实的黏离核[29,43],称此为F-M基因座。为了解释这一理论,Peace等[47]提出了假设,认为F-M基因座存在至少2个拷贝的*Endo-PG*基因,其中一个控制桃果实的溶质性状,而另一个控制黏离核,黏核和不溶质类型是由于*Endo-PG*基因簇的缺失导致。

然而,直至桃基因组[48]公布前,关于控制桃溶质和离核性状的*Endo-PG*基因簇的证据尽管充分但似乎还不清晰。随着桃基因组的公布,发现定位于第4连锁群44 cM处存在4个*PG*基因。最近,Gu等[49]揭示了其中2个串联排列基因*EndoPGF*和*EndoPGM*分别控制桃果肉溶质和离核性状,这2个基因相似性很高。该研究推测桃祖先种仅含有*EndoPGM*基因,果实表现为黏核溶质;之后*EndoPGM*基因发生了缺失和复制2种突变事件,分别导致了黏核不溶质和离核溶质性状的出现。此外,*EndoPGF*基因除控制果肉黏离核性状外,还引起果肉溶质的多效性,这导致离核不溶质性状无法形成。

2.2　非SH型桃和SH型肉质桃分子机制研究

桃是呼吸跃变型果实,乙烯是桃果实的成熟衰老调控中必不可少的激素。在高等植物中,乙烯生物合成途径已经相当清晰,首先由甲硫氨酸(Methionine,Met)合成S-腺苷甲硫氨酸(S-Adenosylmethionine,SAM),然后SAM在ACC(1-aminocyclopropane-1-carboxylic acid)合成酶(ACC synthase,ACS)的作用下合成ACC,最后ACC在ACC氧化酶(ACC oxidase,ACO)作用下生成乙烯[50]。溶质桃和不溶质桃在果实成熟后期均释放大量乙烯,而SH型桃无论是果实成熟期还是采后均不释放乙烯,果实不变软,在外源乙烯处理后SH型桃能正常软化,因此,推测SH型的乙烯合成受到抑制是导致果实不变软的原因[21,51]。

Haji等[52]采用乙烯的合成前体ACC处理SH桃果实可以促进果实内源乙烯的释放,同时,Tatsuki等[53]通过比较SH型桃和溶质型桃乙烯合成途径相关基因的表达发现*PpACS1*基因在溶质型桃‘Akatsuki’果实成熟期的表达也明显高于SH型桃果实成熟期,表明*PpACS1*基因的转录在SH型桃果实成熟期受到抑制。在桃中存在多个基因编码ACS,目前已经确认仅*PpACS1*参与桃果实成熟软化的乙烯跃变[53-54],表明*PpACS1*在SH型桃果实成熟期的低表达是其不释放乙烯的原因。然而,*PpACS1*不是在所有情况下表达量均很低,逆境处理(伤害和低温)SH桃果实能诱导*PpACS1*的表达,从而释放乙烯[53,55]。这些现象表明,SH桃*PpACS1*基因的上游调控路径发生了阻断,从而抑制了*PpACS1*基因的表达。

Tatsuki等[56]发现溶质型桃与SH型桃相比,在果实成熟期不仅表现出乙烯合成的差异,吲哚乙酸(IAA)含量也呈现出巨大的差异,且生长素和乙烯的跃变出现在同一时间点。转录组学的研究显示,成熟果实中果皮的生长素响应因子(auxin response factor,ARF)、生长素/3-吲哚乙酸(auxin/indole-3-acetic acids,Aux/IAA)等生长素相关基因表达量均明显上调,表明桃果实成熟过程会响应生长素信号[57]。采用生长调节剂萘乙酸(NAA)处理SH型桃能快速诱导*ACS1*表达的提升,果实产生大量乙烯并最终软化[56,58]。因此,SH型桃成熟期*ACS1*的低表达可能是其果实中合成较少的IAA所致,推测桃果实成熟期乙烯的生物合成需要大量的IAA介导。

Pan等[59]进一步通过对比溶质型桃和SH型桃成熟过程中生长素代谢调控基因的表达模式，并分析差异表达基因在SH桃中对外源NAA处理的响应模式，结合基因功能分析，筛选出一个生长素合成路径的限速酶基因*PpYUC11*（类黄素单加氧酶基因），发现该基因的表达水平与成熟阶段溶质型和SH型果实中IAA含量高度一致。同时，通过对14个不同肉质类型桃品种的研究发现，成熟阶段果肉中*PpYUC11*的表达与IAA含量、*PpACS1*表达以及果实乙烯释放量存在协同性变化。进一步对该基因及其启动子区的多态性位点的分析发现，其内含子中的SSR位点可以准确区分品种的基因型是否属于SH类型，表明*PpYUC11*是调控SH性状的候选基因。因此，通过SH型桃的研究揭示了由IAA介导的乙烯跃变调控桃果实成熟和衰老的路径。

3 存在问题及趋势

果实质地的变化是果实成熟的重要特征之一，不同肉质类型对桃果实运输、贮藏具有重要的影响。果肉的松实、脆韧、粗腻等均影响桃果实的商品价值，随着人们生活水平的不断提高，对桃果实的肉质提出了更高的要求，然而目前国内外关于肉质的研究大多局限于硬度的改变，桃果实具有丰富的肉质类型，因此，有必要对桃果实的肉质类型进行进一步的细分。

桃果实的软化一直是研究的重点之一，然而对于桃果实肉质的研究，国内大多集中于比较软溶质和硬溶质桃，主要针对细胞壁解体、细胞壁相关酶的活性变化及编码相关酶单个基因的克隆等，尽管近些年随着桃基因组的公布，关于细胞壁相关酶多基因家族的研究也取得了一定的进展，仍存在以下不足：(1)关于桃果实肉质的研究主要集中于果实成熟软化过程中细胞壁结构和物质的变化，以及细胞壁降解相关酶的活性变化，对于果实成熟软化过程这些酶之间具体参与的功能以及各种酶之间的相互作用还鲜有报道；(2)激素是调控桃果实成熟软化的关键因子之一，生长素和乙烯均扮演着重要的角色，围绕生长素和乙烯调控桃果实成熟软化的研究才刚刚起步，接下来有必要对生长素和乙烯转录调控机制进行深入的研究；(3)目前已有一些涉及果实成熟软化的功能基因组学研究，然而研究的内容还局限于比较原始的技术手段，测序和质谱等技术的发展为挖掘更多肉质软化相关的基因提供了可能。

未来对于桃果实肉质的研究应关注以下几个方面：(1)研究不同肉质类型成熟软化过程中果实细胞壁结构及细胞壁物质成分的变化情况，明确果实成熟软化过程中细胞壁物质成分降解的顺序，以及其与桃果实肉质之间关联性；(2)对不同肉质类型开展基因组重测序，并结合果实成熟软化不同阶段的功能基因组学（比如转录组学、蛋白组学、代谢组学等），以全面系统地探明果实成熟软化过程中的生理生化变化过程；(3)和其他果实类作物不一致的是，生长素一般认为是抑制果实的成熟，然而在桃果实成熟软化过程中生长素有明显的促进作用，那么生长素如何调控乙烯的合成？同时生长素仅通过调控乙烯的合成从而调节果实的软化，还是桃果实的软化存在不依赖乙烯的生长素的调控模式，这些问题均有待发掘；(4)桃是呼吸跃变型果实，乙烯在果实成熟软化中扮演着重要的角色，尽管其他果实类作物对于乙烯在果实成熟软化的调控机制有很多报道，但是乙烯在桃果实的成熟转录调控还鲜有研究，因此，探究乙烯的转录调控机制将有助于进一步明确乙烯在桃果实成熟软化中的作用。

综上所述，利用功能基因组学系统研究果实成熟软化过程中的生理生化变化过程，采用现代分子生物学技术分析蛋白的相互作用，揭示果实成熟软化的基因调控网络图，有利于深入了解果实成熟软化的生理生化变化及其分子机制，对调控果实的成熟软化、培育耐贮运新品种和延长果实保鲜期等都具有十分重要的意义。

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