

# 辣椒果实主要品质性状遗传和代谢物组成研究进展

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**摘要:** 辣椒果实含有的辣椒素、类胡萝卜素、维生素、类黄酮和挥发性有机化合物等代谢物质, 决定了辣椒果实颜色、营养和风味等品质性状。本文综述了辣椒素合成的遗传及调控、辣椒果色的遗传和类胡萝卜素合成、果实类黄酮含量 QTL 定位和风味物质种间转育等研究进展。

**关键词:** 辣椒; 果实品质; 果色; 风味; 代谢组

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## Genetic Control and Metabolite Composition of Fruit Quality in *Capsicum*

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**Abstract:** Pepper fruit contains capsaicinoids, carotenoids, vitamins, flavonoids and volatile organic compounds, which are responsible for the fruit color, nutritional and flavor quality. This paper reviews the genetic regulation of capsaicinoid biosynthesis, genetic control of fruit color and carotenoid synthesis, QTL analysis of flavonoids and interspecific introgression for flavors.

**Keywords:** *Capsicum*; fruit quality; fruit color; flavor; metabolome

辣椒属 (*Capsicum* spp.) 有一年生辣椒 (*Capsicum annuum*)、中国辣椒 (*C. chinense*)、灌木状辣椒 (*C. frutescens*)、浆果状辣椒 (*C. baccatum*) 和绒毛辣椒 (*C. pubescens*) 5 个栽培种。辣椒果实含有丰富的辣椒素类物质、类胡萝卜素、维生素以及有机酸、糖类、类黄酮和挥发性代谢产物 (表 1), 其种类和含量决定了辣椒果实颜色、营养和风味等品质, 以及抗氧化、降糖、降脂和消炎等保健功能 (Yahia et al., 2001; Sun et al., 2007; Paran & Fallik, 2011; Tundis et al., 2011, 2013; Zimmer et al., 2012)。

辣椒素为辣椒果实特有, 决定辣椒的辣味 (辛辣刺激性灼痛感), 并有抗癌、镇痛和减肥等医疗和保健作用 (Fraenkel et al., 2004; Luo et al., 2011; Ludy et al., 2012; Lau et al., 2014; Whiting et al., 2014)。辣椒含有丰富的类胡萝卜素, 其种类和含量决定辣椒成熟果实颜色, 其中辣椒红素还是优良的天然红色素 (Arimboor et al., 2015)。辣椒果实中的糖类主要是葡萄糖和果糖 (Jarret et al.,

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2009), 有机酸主要是苹果酸和柠檬酸 (Eggink et al., 2012a), 维生素 C 的含量是蔬菜中最高的 (Isabelle et al., 2010), 维生素 E 也很丰富 (Meckelmann et al., 2015a, 2015b)。辣椒果实中主要的类黄酮物质是槲皮素 (quercetin) 和木犀草素 (luteolin) (Miean & Mohamed, 2001; Bae et al., 2014; Meckelmann et al., 2015a, 2015b)。另外已在辣椒果实中检测出 300 多种可挥发性物质 (Rodríguez-Burrueto et al., 2010; Bogusz Junior et al., 2015; Patel et al., 2016)。

辣椒果实的风味是其所含代谢物在人们食用时引起的味觉 (糖、有机酸)、嗅觉 (挥发性酯类、萜类等) 和辛辣痛觉 (辣椒素类物质) 等综合感受, 这些物质不但能提供人体所需的营养, 还在抗氧化、调节人体代谢和维持生理功能等方面发挥重要作用。近年来已初步探明了辣椒不同栽培种及种内不同材料的主要品质相关代谢物组成 (Ritota et al., 2010; Wahyuni et al., 2013b; van Zonneveld et al., 2015; Patel et al., 2016; Aranha et al., 2017; Becerra-Martínez et al., 2017; Morales-Soriano et al., 2018; Tripodi et al., 2018)。有的代谢产物影响辣椒多个品质性状, 如决定辣椒果实颜色的类胡萝卜素, 不仅具有生物抗氧化活性 (Hervert-Hernández et al., 2010; Alvarez-Parrilla et al., 2011), 而且  $\beta$ -胡萝卜素、 $\alpha$ -胡萝卜素和  $\beta$ -隐黄素是维生素 A 原 (Wahyuni et al., 2013a), 具有保健功能和营养价值。虽然辣椒果实营养成分和风味物质的代谢谱解析已取得显著进展, 但辣椒果实感官评价 (sensory evaluation) 还有待完善, 以及受辣椒种间杂交障碍等因素制约, 辣椒品质育种有待深入推展。本文综述了辣椒果实辣椒素、果色、风味、营养等品质性状的遗传和相关代谢物组成成分的研究进展。

表 1 辣椒果实重要品质成分含量较高的材料及含量

Table 1 The important compounds of pepper fruit quality and their higher metabolite containing germplasm in *Capsicum* spp.

代谢物 Metabolite	材料 Material	含量 Concentration	参考文献 Reference
类胡萝卜素 Carotenoid	<i>C. annuum</i> ‘Nambe’	(10.76 ± 2.54) mg · g <sup>-1</sup> DW	Guzman et al., 2010
	<i>C. annuum</i> ‘Pulla’	(1 173 ± 49) µg · g <sup>-1</sup> FW	Wall et al., 2001
辣椒红素 Capsanthin	<i>C. annuum</i> ‘NuMex Nematador’	(4.01 ± 2.86) mg · g <sup>-1</sup> DW	Guzman et al., 2010
	<i>C. annuum</i> ‘BRS Sarakura’	(177 ± 2) µg · g <sup>-1</sup> FW	Agostini-Costa et al., 2017
维生素 A 前体 Provitamin A	<i>C. annuum</i> ‘Amish Chicken’	208.40 IU · g <sup>-1</sup> FW <sup>a</sup>	Kantar et al., 2016
	<i>C. chinense</i> ‘Seriema’	(2.99 ± 0.32) µg · g <sup>-1</sup> FW <sup>b</sup>	Agostini-Costa et al., 2017
维生素 C Vitamin C	<i>C. annuum</i> ‘Paprika B58’	(2817.2 ± 16.2) µg · g <sup>-1</sup> FW	Bae et al., 2014
维生素 E Tocopherols	<i>C. annuum</i> ‘No. 1’	29.1 µg · g <sup>-1</sup> DW	Meckelmann et al., 2015b
葡萄糖 Glucose	<i>C. annuum</i> ‘Hybrid 3’	38.1 µg · g <sup>-1</sup> FW	Eggink et al., 2012a
果糖 Fructose	<i>C. annuum</i> ‘Line M’	37.4 µg · g <sup>-1</sup> FW	Eggink et al., 2012a
苹果酸 Malic acid	<i>C. annuum</i> ‘Piquillo’	5 423 µg · g <sup>-1</sup> FW	Eggink et al., 2012a
柠檬酸 Citric acid	<i>C. annuum</i> ‘Line N’	1 592.7 µg · g <sup>-1</sup> FW	Eggink et al., 2012a
黄酮类 Flavonoids	<i>C. frutescens</i> ‘Bird Chili’	1 663.0 µg · g <sup>-1</sup> DW <sup>c</sup>	Miean & Mohamed, 2001
	<i>C. annuum</i> ‘PA137’	(86.6 ± 2.8) µg · g <sup>-1</sup> FW <sup>d</sup>	Bae et al., 2014
总酚 Total phenolic	<i>C. baccatum</i> ‘Butanol’	(187.51 ± 2.34) mg · g <sup>-1</sup> DW <sup>e</sup>	Zimmer et al., 2012

注: a. 用酶联免疫吸附法测定。b. 以视黄醇活性当量计算得到。c. 包括槲皮素、木犀草素和杨梅素 3 种黄酮类物质。d. 包括槲皮素、木犀草素、山奈酚和杨梅素 4 种黄酮类物质。e. 没食子酸当量。

Note: a. Enzyme-Linked Immunosorbent Assay. b. RAE (retinol activity equivalents). c. It contains quercetin, luteolin and myricetin. d. It contains quercetin, luteolin, kaempferol and myricetin. e. Gallic acid equivalent.

## 1 辣椒辣味相关基因与辣椒素合成调控

### 1.1 辣椒辣味遗传与基因定位

目前已报道的辣椒辣味基因有 *Pun1* (Stewart et al., 2005)、*Pun2* (Stellari et al., 2010)、*Pun3*

(Han et al., 2019; Zhu et al., 2019)、假定氨基转移酶基因 (*putative aminotransferase, pAMT*) (Lang et al., 2009) 和假定酮脂酰 ACP 还原酶基因 (*putative ketoacyl-ACP reductase, CaKRI*) (Koeda et al., 2019) 等。其中 *Pun1*、*pAMT* 和 *CaKRI* 为辣椒素生物合成途径相关基因, *Pun3* 为辣椒 MYB 转录因子基因, *Pun2* 在辣椒野生种 (*C. chacoense*) 中发现, 但尚未见 *Pun2* 相关候选基因的报道。

*Pun1* 编码辣椒素生物合成最后一步的催化酶——脂肪酰转移酶 Acyltransferase (AT, Stewart et al., 2005; Aza-González et al., 2011; Ogawa et al., 2015), 其基因表达影响其他结构基因 (Arce-Rodríguez & Ochoa-Alejo, 2015), 并在辣椒素合成积累中起主导作用 (Ogawa et al., 2015)。先前报道的辣椒栽培种中有 3 种 *Pun1* 基因的突变体, 一年生辣椒 *pun1<sup>1</sup>* (Stewart et al., 2005)、中国辣椒 *pun1<sup>2</sup>* (Stewart et al., 2007) 和灌木状辣椒 *pun1<sup>3</sup>* (Stellari et al., 2010)。最近 Kirii 等 (2017) 在甜椒一年生辣椒 ‘Nara Murasaki’ 中发现了 1 个新的突变体 *pun1<sup>4</sup>*, 其在 *Pun1* 第 2 外显子区有单碱基 (A) 插入。pAMT 在辣椒素合成苯丙氨酸途径的末尾催化香草醛 (Vanillin) 合成香草基胺 (Vanillylamine)。Lang 等 (2009) 报道低辣味的一年生辣椒 ‘CH-19 Sweet’ 的 *pAMT* 在 1 291 bp 处发生单碱基 (T) 插入突变, 形成终止密码子, *pAMT* 失去功能, 从而合成辣椒素酯类物质。辣椒素酯类的功能与辣椒素相近, 但无辣味, 是辣椒素的优良替代品, 因此低辣度、高辣椒素酯类的辣椒材料及其 *pAMT* 的研究受到了关注。目前已经一年生辣椒、中国辣椒和灌木状辣椒材料中发现 11 个 *pamt* 基因型 (表 2), 为辣椒素酯类生物合成和应用研究奠定了基础。

表 2 辣椒高辣椒素和辣椒素酯类材料及其含量与 *pamt* 位点类型  
Table 2 High Capsaicinoid and capsinoid containing germplasm and *pamt* type in *Capsicum* accessions

辣椒种 Species	参考文献 Reference	材料 Material	含量 ( $\mu\text{g} \cdot \text{g}^{-1}$ DW) Content		<i>pamt</i> 位点 <i>pamt</i> allele
			辣椒素 Capsaicinoid	辣椒素酯 Capsinoid	
一年生辣椒 <i>C. annuum</i>	Tanaka et al., 2010a	CH-19 Sweet	110 ± 3	5 825 ± 286	<i>pamt<sup>1</sup></i>
		Himo	未测出 Not detected	1 240 ± 105	<i>pamt<sup>2</sup></i>
中国辣椒 <i>C. chinense</i>	Tanaka et al., 2010b	Belize Sweet	微辣 Mildly pungent	732	<i>pamt<sup>3</sup></i>
		Zavyory Hot	微辣 Mildly pungent	1 812	<i>pamt<sup>4</sup></i>
	Tanaka et al., 2015	Aji Dulce strain 2	微辣 Mildly pungent	1 797	<i>pamt<sup>5</sup></i>
		7-Pot	23 303 ± 1560.4	915 ± 39.8	
		Trinidad scorpion	19 853 ± 2 404.6	754 ± 26.0	
		moruga yellow			
		Red Habanero	15 008 ± 786.1	296 ± 54.3	
		Bhut Jolokia	7 751 ± 928.3	308 ± 53.5	
	Koeda et al., 2014; Tanaka et al., 2015	LP6	54 ± 8.4	680 ± 26.9	<i>pamt<sup>7</sup></i>
	Jang et al., 2015	No. 80	40 ± 1.9	1 761 ± 146.5	<i>pamt<sup>6</sup></i>
		SNU11-001	50.09 ± 17.94	7 441.81 ± 693.84	两种突变 Two types
灌木状辣椒 <i>C. frutescens</i>	Tanaka et al., 2017	No. 4043	未测出 Not detected	456.9 ± 52.40	<i>pamt<sup>9</sup></i>
	Park et al., 2015	S3212	9.0 ~ 11.9	415.5 ~ 607.6	<i>pamt<sup>8</sup></i>

*CaKRI* 基因 (Koeda et al., 2019) 是从无辣味的中国辣椒 ‘No.3341’ 中图位克隆得到的, 参与辣椒素生物合成过程中支链脂肪酸合成循环途径。Koeda 等 (2019) 报道在辣椒 ‘No.3341’ 中, 该基因第一内含子插入 4.5 kb 的转座元件 (transposable element, TE) 导致转录不完整, 蛋白缺少重要的功能活性保守区域; 果实中也检测不到支链脂肪酸合成循环途径的代谢产物 8 - 甲基癸酸 (8-methyl-6-nonenoic acid)。

*Pun3* 属 MYB 转录因子基因 (Han et al., 2019; Zhu et al., 2019)。Arce-Rodriguez 和 Ochoa-Alejo (2017) 从一年生辣椒 ‘Tampiqueño 74’ 中同源克隆得到辣椒 *CaMYB31* 基因。而后 Han 等 (2019) 利用无辣味的一年生辣椒 ‘YCM334’ 和有辣味的一年生辣椒 ‘Tean’ 构建的 F<sub>2</sub> 群体, 将 *Pun3* 定

位在辣椒 7 号染色体，并预测 *CaMYB31* 为 *Pun3* 候选基因。Zhu 等(2019)利用极辣的中国辣椒‘740’和微辣的一年生辣椒‘CA1’构建的 F<sub>2</sub> 群体，发现了与辣椒素含量相关的主效 QTL (*Capsaicinoid 1*, *Cap1*)，获得候选基因 *MYB31*，指出 *Cap1* 与先前报道的辣椒素含量相关数量遗传位点 *cap* (Blum et al., 2003)、*cap7.2* (Ben-Chaim et al., 2006) 和质量遗传位点 *Pun3* (Han et al., 2019) 是一致的，*Cap1* (*MYB31*)、*CaMYB31* (Arce-Rodriguez & Ochoa-Alejo, 2017) 和 *Pun3/CaMYB31\_Tean* (Han et al., 2019) 的核苷酸和蛋白质序列高度相似。

辣椒的辣味，即辣椒素含量的高低呈数量遗传特征。利用辣椒种内和种间杂交群体，在辣椒 12 条染色体上发现多个控制辣椒素、二氢辣椒素或总辣椒素类物质（辣椒素和二氢辣椒素之和）含量的 QTL 位点 (Blum et al., 2003; Ben-Chaim et al., 2006; Paran et al., 2010; Yarnes et al., 2013; Lee et al., 2016; Han et al., 2018; Zhu et al., 2019)。利用辣椒栽培种自然群体和全基因组关联分析 (genome-wide association study, GWAS), Nimmakayala 等 (2014, 2016) 发现了 1 个与总辣椒素（辣椒素和二氢辣椒素）含量显著相关的 SSR 标记 (CAMS-142)，25 个与辣椒素、二氢辣椒素和总辣椒素（辣椒素和二氢辣椒素）含量显著相关的 SNP 位点；Han 等 (2018) 报道了 99 个与辣椒素显著相关的 SNP 位点，通过比较已报道的辣椒素和二氢辣椒素相关 QTL 和 SNP 位点的物理位置，从中发现了 pAMT、肉桂酸 - 4 - 羟化酶 (cinnamate 4-hydroxylase, C4H)、4 - 香豆酰 - CoA 连接酶 (4-coumaroyl-CoA ligase, 4CL)、酰基 - ACP 硫酯酶 (acyl-ACP thioesterase, FAT) 和咖啡酰莽草酸酯酶 (caffeooyl shikimate esterase, CSE) 基因等 5 个已知或可能参与辣椒素生物合成、影响辣椒素含量的基因，实现了部分数量遗传位点的基因预测。

## 1.2 辣椒素生物合成的调控

辣椒素类物质由苯丙氨酸和支链脂肪酸两条途径于果实胎座和隔膜上的腺体细胞中合成 (Aza-González et al., 2011)，辣椒素和二氢辣椒素约占辣椒果实中总辣椒素类物质含量的 80% 以上 (Kozukue et al., 2005)，其在果实中的积累受基因型、果实生长阶段和栽培环境的影响 (Zewdie & Bosland, 2000; Gurung et al., 2011, 2012; Kim et al., 2014; Qin et al., 2014; Arce-Rodriguez & Ochoa-Alejo, 2015; Deng et al., 2016; Jeeatid et al., 2018a, 2018b)。研究发现，辣椒素的生物合成由结构基因决定并受转录因子的调控 (Keyhaninejad et al., 2014; Zhang et al., 2016; Arce-Rodríguez & Ochoa-Alejo, 2015, 2017; Han et al., 2019; Zhu et al., 2019)。

Arce-Rodríguez 和 Ochoa-Alejo (2015) 报道辣椒果实中酰基转移酶基因 *AT3* (*Pun1*) 的表达与辣椒素的合成时序性相关，沉默 *AT3* 后，辣椒素生物合成的结构基因 *pAMT*、支链氨基酸转移酶 (branched-chain amino acid transferase, BCAT)、 $\beta$ -酮脂酰 - ACP 合成酶 ( $\beta$ -ketoacyl-ACP synthase, KAS) 和酰基载体蛋白 (acyl carrier protein, ACL) 等基因表达显著降低。Sarpras 等 (2016) 研究了辣椒素合成相关基因苯丙氨酸裂解酶 (phenylalanine ammonia lyase, PAL)、*C4H*、咖啡酸转甲氧基酶 (caffeoic acid O-methyl transferase, COMT)、酰基 - CoA 合成酶 (acyl-CoA synthetase, ACS)、*pAMT*、BCAT、KAS、ACL、FAT 和 *Pun1* 的基因在不同辣度辣椒果实中的表达情况，结果表明多数基因在高辣度中国辣椒‘Acc23’（总辣椒素含量 64 377.0  $\mu\text{g} \cdot \text{g}^{-1}$  DW）中的表达较中辣度的灌木状辣椒‘Acc65’（总辣椒素含量 30 277.1  $\mu\text{g} \cdot \text{g}^{-1}$  DW）和低辣度的一年生辣椒‘Acc95’（总辣椒素含量 168.5  $\mu\text{g} \cdot \text{g}^{-1}$  DW）呈倍数增加。Tanaka 等 (2017) 报道辣椒胎座中 *Pun1*、*pAMT*、*KAS* 和 *BCAT* 的表达显著上调，且在高辣辣椒‘Trinidad Moruga Scorpion Yellow’（完整果实和果皮得辣椒素含量分别为 23.1 和 29.0  $\text{mg} \cdot \text{g}^{-1}$  DW）的果皮中稳定表达，但在辣椒‘Red Habanero’（完整果实和果皮的辣椒素含量分别为 13.2 和 3.7  $\text{mg} \cdot \text{g}^{-1}$  DW）果皮中几乎检测不到。这些研究表明，辣椒

素合成相关的结构基因在辣椒果实胎座尤其是在果皮中的上调表达可能是辣椒素含量提高的原因之一。

Keyhaninejad 等 (2014) 报道, 与植物次级代谢相关的转录因子 AP2/ERF 家族中的 *Erf* 和 *Jerf* 基因在辣椒开花后 16~20 d 果实胎座中表达, 其表达量在一年生辣椒、中国辣椒和灌木状辣椒的 9 份材料中与其辣度相关, 从而认为 *Erf* 和 *Jerf* 参与调控辣味的强弱。最近, 研究者利用不同的辣椒材料, 分别证实了辣椒 MYB 转录因子相关基因 *CaMYB31* (Arce-Rodriguez & Ochoa-Alejo, 2017)、*Pun3/CaMYB31\_Tean* (Han et al., 2019) 和 *Cap1* (*MYB31*) (Zhu et al., 2019) 参与调控辣椒辣味 (辣椒素含量) 的高低。辣椒 MYB 转录因子基因在不同辣度材料的转录水平与辣椒素合成途径相关基因 *AT3*、*pAMT*、*C4H* 和 *KAS* 等的转录水平以及辣椒果实中辣椒素类物质的积累进程和含量正相关; 沉默 *CaMYB31* 后显著降低辣椒素合成相关基因的表达和辣椒素的含量 (Arce-Rodriguez & Ochoa-Alejo, 2017; Zhu et al., 2019)。Zhu 等 (2019) 进一步发现 *MYB31* 启动子变异和其转录活性相关, 决定辣椒种间材料启动子活性差异的关键区域, 在极辣的中国辣椒 ‘740’ 中有 1 个正常的 W-box 元件, 该 W-box 可以被一个胎座特异表达的 WRKY9 转录因子识别使得 *MYB31* 转录被强烈激活, 进而极大增强其果实中辣椒素类物质的合成。

## 2 辣椒果色遗传和类胡萝卜素合成

### 2.1 辣椒果色遗传及相关基因

辣椒果实颜色在生理成熟前后有明显变化, 主要由果肉细胞中叶绿素、类胡萝卜素和花青素等的种类和含量决定 (张宝玺 等, 1996; 吴雪霞 等, 2005; Paran & van der Knaap, 2007; Lightbourn et al., 2008)。花青素和叶绿素是辣椒未成熟果实的主要色素, 也影响成熟果实颜色 (薛林宝 等, 2005; Borovsky & Paran, 2008)。类胡萝卜素是成熟果实主要色素来源 (Ha et al., 2007)。一般随着辣椒果实发育至生理成熟, 橙色和红色的类胡萝卜素不断累积, 而叶绿素和花青素逐渐降解 (吴雪霞 等, 2005; 戴雄泽 等, 2009; Guzman et al., 2011)。

辣椒未成熟果实有绿色 (green)、象牙色 (ivory)、紫色 (violet) 乃至近黑色 (nearly black) 等 (Lightbourn et al., 2008)。紫色辣椒由单显性基因 *A* (*Anthocyanin*) 控制 (Peterson, 1959)。辣椒 *A* 基因与矮牵牛 *An2* (*Anthocyanin2*) 基因同源, 后者为 R2R3 MYB 转录因子基因, 参与调节花青素的生物合成 (Borovsky et al., 2004)。象牙色或硫磺白色 (sulfury white) 由 *sw1* (*sulfury white*) 控制, 莴苣色 (lettuce) 或黄绿色 (yellow green) 由 *sw2* 控制, 深绿色 (dark green) 或雪松绿 (cedar green) 由 *sw3* 控制 (Wang & Bosland, 2006)。目前已发现 *APRR2-Like* (Pan et al., 2013)、*CaGLK2* (Brand et al., 2014) 和 *CcLOLI* (Borovsky et al., 2019) 3 个控制辣椒绿色果实颜色深浅变化的基因。Brand 等 (2012) 利用深绿色果实的一年生辣椒 ‘1154’ 和浅绿色果实的中国辣椒 ‘PI152225’ 为亲本构建 F<sub>2</sub> 代群体, 经叶绿素含量测定和分子标记分析, 定位了 *pc8.1* 和 *pc10.1* 两个控制辣椒果实叶绿素含量的主效 QTL。Pan 等 (2013) 同源克隆了辣椒 *APRR2-Like* 基因, 该基因和 *pc8.1* 位于遗传图谱相同区域, *APRR2-Like* 基因序列在白色果实中因单碱基置换 (G/A) 形成终止密码子, 此 SNP 与辣椒分离群体中果实的颜色 (绿色和白色) 紧密相关。Brand 等 (2014) 进而利用番茄 *u* (*uniform ripening*) 突变体 *SIGLK2* 基因信息, 利用辣椒转录组和基因组数据挖掘辣椒 *CaGLK2* 基因, 经分子标记和无效等位基因遗传分析、以及基因表达分析证实 *CaGLK2* 为 *pc10.1* 位点候选基因, 其通过调控叶绿体大小而控制辣椒果实叶绿素含量及未成熟果实颜色。Borovsky 等 (2019) 利用一年生辣椒

‘1154’和‘NIL86-45’(‘1154’和‘PI152225’回交自交BC<sub>4</sub>F<sub>3</sub>后代,包含pc1区域)构建的F<sub>2</sub>分离群体,经集群分离分析法(bulk segregant analysis, BSA),获得pc1(pc8.1)的候选基因CcLOL1,其为锌指转录因子基因,在辣椒果实绿果期作用于多种光合作用和氧化还原相关基因,从而影响果实叶绿素含量。

辣椒生理成熟果实常见的颜色有红色、黄色和橙色,另外还有棕色(brown)、紫色(purple)和橄榄绿(olive green)等(Lightbourn et al., 2008)。研究表明,3个独立遗传的基因位点Y,CI和C2(Hurtado-Hermamdez & Smith, 1985)决定辣椒果实红色、黄色、橙色和白色等(表3)。棕色果实由cl基因决定(Borovsky & Paran, 2008),紫色果实由A基因决定(Borovsky et al., 2004)。辣椒果实红色(Y)对黄色或橙色(y)为显性,由于红色果实主要含有辣椒红素和辣椒玉红素两种红色素,Y位点被认为是控制辣椒素和辣椒玉红素合成的基因位点。连锁分析发现辣椒红素和辣椒玉红素合成酶基因Ccs(capsanthin-capsorubin synthase)与Y共分离,从而认为Ccs为Y的编码基因(Lefebvre et al., 1998; Popovsky & Paran, 2000);八氢番茄红素合成酶基因Psy(phytoene synthase)与C2共分离,为C2候选基因(Thorup et al., 2000; Huh et al., 2001)。

**表3 辣椒成熟果色及其可能基因型**  
**Table 3 Color and proposed genotypes of ripe fruit in *Capsicum* spp.**

参考文献 Reference	基因型 Genotype			果色 Fruit color
	Ccs	/	Psy	
Thorup et al., 2000	Y	CI	C2	红色 Red
	Y	cl	C2	红色 Red
	Y	CI	c2	桃红色 Peach
	Y	cl	c2	桃红色 Peach
	y	CI	C2	橙色 Orange
	y	cl	C2	橙色 Orange
	y	CI	c2	奶油色 Cream
	y	cl	c2	奶油色 Cream

辣椒果实成熟过程中若叶绿素不能降解,造成果实因同时含有红色素和叶绿素而呈棕色,此突变体由隐性单基因cl(chlorophyll retainer)控制(Smith, 1950)。Borovsky和Paran(2008)报道,若辣椒同时含有隐性y基因和cl基因,则果实至成熟期时仍为绿色,因辣椒cl突变体与其他植物sgr(stay green)突变体具有相同的特征,从而同源克隆得到辣椒CasGR基因。另外,Wang等(2015)克隆了1个辣椒光敏基因CarbcL,并经病毒诱导的基因沉默(virus-induced gene silencing, VIGS)证实其参与果实叶绿素和辣椒红素的合成代谢。

## 2.2 辣椒成熟果实类胡萝卜素的种类及含量

辣椒是类胡萝卜素含量最丰富的蔬菜之一(Kopsell & Kopsell, 2006),在干辣椒和鲜辣椒中胡萝卜素的含量最高分别可达10.76 mg·g<sup>-1</sup>(Guzman et al., 2010)和1173 μg·g<sup>-1</sup>(Wall et al., 2001)。红色辣椒主要含有辣椒红素、β-隐黄素、β-胡萝卜素、辣椒玉红素、玉米黄素、花药黄质和α-胡萝卜素等色素,黄色辣椒含有紫黄质、叶黄素、α-胡萝卜素、β-胡萝卜素、玉米黄素、花药黄质和β-隐黄素等色素,橙色辣椒含有辣椒红素、β-隐黄素、玉米黄质、紫黄质、α-胡萝卜素、β-胡萝卜素和玉米黄素(Marín et al., 2004; Ha et al., 2007; Guzman et al., 2010; Wahyuni et al., 2011; Kim et al., 2016)。红色辣椒的总类胡萝卜素含量比黄色辣椒和橙色辣椒高,且不同的辣椒材料之间差异较小(Ha et al., 2007; Guzman et al., 2010; Kim et al., 2016; Agostini-Costa et al., 2017)。

辣椒红素是红辣椒的主要色素,其在干辣椒和鲜辣椒中的含量分别为0.04~4.01 mg·g<sup>-1</sup>

(Guzman et al., 2010) 和  $68 \sim 177 \mu\text{g} \cdot \text{g}^{-1}$  (Agostini-Costa et al., 2017), 占总类胡萝卜素的 75%~80% (Ha et al., 2007; Kim et al., 2016)。黄色和橙色辣椒果实中含有较高的  $\beta$ -胡萝卜素和叶黄素 (Ha et al., 2007), 但不同材料之间存在较大差异。例如 Agostini-Costa 等 (2017) 报道紫黄质是 3 个黄色 ‘Jalapeño’ 辣椒的主要色素 ( $34 \sim 100 \mu\text{g} \cdot \text{g}^{-1}$  FW), 但其中 1 个黄色辣椒同时含有较高的玉米素 ( $36 \mu\text{g} \cdot \text{g}^{-1}$  FW); Wahyuni 等 (2013a) 发现黄色辣椒中  $\beta$ -胡萝卜素、叶黄素、花药黄质和玉米素含量最高。橙色辣椒中类胡萝卜素的种类和含量变化较大, Wahyuni 等 (2011) 报道橙色辣椒中没有检出玉米素和  $\beta$ -胡萝卜素, 但 Kim 等 (2016) 指出橙色一年生辣椒 ‘Paprika’ 的主要色素为玉米素 ( $850.6 \sim 1\,513.9 \mu\text{g} \cdot \text{g}^{-1}$  DW), 占总类胡萝卜素的 80%以上。Guzman 等 (2011) 报道橙色辣椒总类胡萝卜素含量为  $0.05 \sim 3.67 \text{ mg} \cdot \text{g}^{-1}$  DW, 高低相差 73 倍; Kim 等 (2016) 发现 1 个红果一年生辣椒 ‘Mini Goggal Red’ 的辣椒红素含量仅为  $39.8 \mu\text{g} \cdot \text{g}^{-1}$  DW, 而玉米素含量却高达  $1\,214.1 \mu\text{g} \cdot \text{g}^{-1}$  DW, 并认为此类高玉米素的红果辣椒品种具有潜在的保健价值。

辣椒红色素是食品、化妆品等优良的天然着色剂, 其含量高低是决定色素辣椒商品性的重要指标 (Wahyuni et al., 2013a)。目前辣椒红色素评价标准主要有美国香料贸易协会 ASTA (American Spice Trade Association) 和中国国家标准 (GB 1886.34-2015)。Meckelmann 等 (2015a, 2015b) 报道了 32 份来自秘鲁的绒毛辣椒的 ASTA 为 2~66; 23 份 1 年生辣椒、浆果状辣椒、中国辣椒和灌木状辣椒材料的 ASTA 为 3~94。van Zonneveld 等 (2015) 发现来自玻利维亚和秘鲁的 186 份辣椒材料, ASTA 最高分别可达 107 (1 年生辣椒)、36 (浆果状辣椒)、146 (中国辣椒)、69 (灌木状辣椒)、16 (绒毛辣椒) 和 33 (野生种)。中国报道的辣椒色素品种国家标准色价为 15 左右 (霍建泰等, 2015; Luo et al., 2016), 而杨志刚等 (2015) 报道的 92 份辣椒杂交种和自交系的国家标准色价最高可达 20.62, 表明辣椒品种的色价还有提升的空间。

### 2.3 辣椒果实类胡萝卜素合成的调控机制

目前有关辣椒类胡萝卜素合成的调控, 主要是针对八氢番茄红素合成酶 (PSY)、番茄红素环化酶 (LCYb 和 LCYe)、 $\beta$ -胡萝卜素羟化酶 (Crtz) 和辣椒红素合成酶 (CCS) 基因等的结构、表达及其蛋白产物进行研究, 以揭示辣椒成熟果实颜色变化的遗传调控机制。

*Ccs* 编码辣椒红素合成酶, 是辣椒红果基因, 且对辣椒黄果和橙果为显性遗传, 其结构存在丰富的多样性 (Rodriguez-Uribe et al., 2014; Ha, 2015; Tian et al., 2017)。黄色或橙色果实辣椒不含 *Ccs* 或因其序列变异而失去功能 (Lefebvre et al., 1998)。Lang 等 (2004)、Popovsky 和 Paran (2000) 报道, 在黄色果实辣椒中 *Ccs* 基因 3'端分别发生了 211 和 220 bp 的缺失。Guzman 等 (2010) 报道橙色果实一年生辣椒 ‘Fogo’ 的 *Ccs* 编码区发生移码突变造成转录提前终止, 其果实主要含有  $\beta$ -胡萝卜素和玉米黄质, 而不含辣椒红素和辣椒玉红素。Li 等 (2013) 报道在黄色果实一年生辣椒 ‘CK7’ 存在 *Ccs*, 但该基因在转录起始位点下游 1 095 bp 处发生了单碱基 (C/G) 突变导致形成提前终止密码子, 并在翻译起始位点下游 1 265 bp 处发生了 1 bp 的缺失造成移码突变, 此突变与橙色果实辣椒 ‘Fogo’ (Guzman et al., 2010) 的移码突变相同。Ha 等 (2007) 报道黄色果实中国辣椒 ‘Y2’ 的 *Ccs* 基因在 1 431 bp 处插入 8 bp, 造成移码突变, 转录提前终止; 中国辣椒 ‘Y3’ *Ccs* 在 599 bp 处发生单碱基 (C/A) 突变, 形成提前终止密码子。另外, Borovsky 等 (2013) 报道了红色果实一年生辣椒 ‘Maor’ 经 EMS 诱导的橙色果实突变体 ‘E-172-3’, 其  $\beta$ -胡萝卜素羟化酶 2 ( $\beta$ -CHY2,  $\beta$ -CAROTENE HYDROXYLASE2) 基因第 709 位碱基发生突变, 橙色果实的  $\beta$ -胡萝卜素含量为红色果实的 3.2 倍, 而类胡萝卜素总量则降低了 58.3%。

Guzman 等 (2010) 报道 *Psy*, *Lcyb*, *Crtz-2* 和 *Ccs* 基因位点控制不同的酶合成，并与果实积累特定类胡萝卜素相关。Rodriguez-Uribe 等 (2012) 报道橙色果实辣椒 ‘Fogo’ 中 *Ccs* 的突变基因 *ccs-3* 有转录但无蛋白合成；‘Orange Grande’ 和 ‘Oriole’ 辣椒中虽含有 *Psy*、*Lcyb*、*Crtz-2* 和 *Ccs* 基因，但无 *Ccs* 转录，也无红色素积累；‘Canary’ 辣椒中的 4 个基因都有转录但无 CCS 蛋白和红色素合成。Tian 等 (2014) 利用 VIGS 方法，将辣椒 *Ccs*、*Psy*、*Lcyb* 和 *Crtz* 基因单个沉默后，果实由红色变为黄色或橙色，当多个基因同时沉默后，果实着色同样表现异常。单个基因或多个基因沉默后，辣椒红素明显降低，而且其合成底物  $\beta$ -胡萝卜素、 $\beta$ -隐黄质或玉米黄素也表现不同程度的降低。Kilcrease 等 (2015) 报道总类胡萝卜素含量增长与  $\beta$ -胡萝卜素和紫黄质增长相关，*Psy* 和 *Crtz-2* 的表达水平与特定的类胡萝卜素含量相关。Tian 等 (2015) 报道 *Psy*、*Lcyb*、*Crtz* 和 *Ccs* 参与辣椒红素的合成，其表达影响辣椒成熟果颜色。

上述研究表明，辣椒 *Ccs* 等类胡萝卜素合成基因存在丰富的多态性，相同果色的辣椒材料，其类胡萝卜素的种类和含量可能不同，相关基因亦存在转录或翻译变化。根据果实颜色，选择某种类胡萝卜素含量较高的辣椒材料可能是无效的，但可利用类胡萝卜素合成途径相关基因标记进行高  $\beta$ -胡萝卜素等材料的选择。

### 3 辣椒营养和风味代谢物组成成分

#### 3.1 维生素种类及含量

辣椒果实所含维生素主要是四萜类化合物类胡萝卜素中的维生素 A 原 ( $\alpha$ -胡萝卜素、 $\beta$ -胡萝卜素和  $\beta$ -隐黄质)、酚类化合物维生素 E ( $\alpha$ -生育酚、 $\beta$ -生育酚、 $\gamma$ -生育酚和  $\delta$ -生育酚等)、维生素 C 和叶酸等。其含量与材料基因型、生长季节、栽培方式和果实发育时期等相关 (Antonious et al., 2009; Jarret et al., 2009; Bae et al., 2014; Agostini-Costa et al., 2017)。

维生素 C 是辣椒果实中含量最丰富的维生素，且成熟果实高于未成熟果实 (Bae et al., 2014)，Kantar 等 (2016) 指出一些辣椒果实维生素 C 含量超过了猕猴桃。各栽培种中，一年生辣椒维生素 C 含量最高可达  $2.517 \text{ mg} \cdot \text{g}^{-1}$  FW (paprika PA137) (Bae et al., 2014)，中国辣椒 (Trinidad 7 Pot) 达  $1.958 \text{ mg} \cdot \text{g}^{-1}$  FW (Kantar et al., 2016)，浆果状辣椒 (Bird's eye hot pepper) 达  $50.44 \text{ mg} \cdot \text{g}^{-1}$  DW (Perla et al., 2016)，灌木状辣椒 (Lombok & Tabasco) 的小于  $0.50 \text{ mg} \cdot \text{g}^{-1}$  DW (Wahyuni et al., 2011)。

Kantar 等 (2016) 用酶联免疫吸附法 (Enzyme-Linked Immunosorbent Assay, ELISA) 测定一年生辣椒、浆果状辣椒、中国辣椒和绒毛辣椒的维生素 A 含量，分别为每  $100 \text{ g}$  鲜质量  $303 \sim 20\,840$ 、 $32\,003 \sim 18\,065$ 、 $15\,253 \sim 20\,240$  和  $10\,355$  IU。Agostini-Costa 等 (2017) 报道露地栽培辣椒的维生素 A 含量较温室栽培的高，且露地栽培的一年生辣椒 ‘CNPH 25.313’ 和中国辣椒 ‘Seriema’ 维生素 A 的含量以视黄醇活性当量计算 (retinol activity equivalents, RAE) 最高分别可达  $(2.22 \pm 0.17)$  和  $(2.99 \pm 0.32) \mu\text{g} \cdot \text{g}^{-1}$ 。

一年生辣椒、浆果状辣椒、中国辣椒和灌木状辣椒间的  $\alpha$ -生育酚和  $\beta$ -生育酚含量存在差异， $\alpha$ -生育酚是维生素 E 的主要形式。辣椒果实中维生素 E 总量介于  $0.23$  (浆果状辣椒)  $\sim 29.1 \mu\text{g} \cdot \text{g}^{-1}$  DW (一年生辣椒)，鲜果中的含量可达  $163.2 \mu\text{g} \cdot \text{g}^{-1}$  (AC2212, 中国辣椒)，辣椒 ‘AC1979’ (一年生辣椒) 同时含有较高的  $\alpha$ -生育酚 ( $95.3 \mu\text{g} \cdot \text{g}^{-1}$  FW) 和  $\beta$ -生育酚 ( $42.4 \mu\text{g} \cdot \text{g}^{-1}$  FW) (Wahyuni et al., 2013b; Meckelmann et al., 2015b)。

### 3.2 糖和有机酸含量

辣椒果实糖和有机酸含量与辣椒基因型和果实不同成熟期相关 (Perla et al., 2016)。Eggink 等 (2012a) 报道 24 个无辣味的一年生辣椒成熟果中葡萄糖含量为  $17.9 \sim 38.1 \mu\text{g} \cdot \text{g}^{-1}$  FW, 果糖含量为  $18.9 \sim 37.4 \mu\text{g} \cdot \text{g}^{-1}$  FW, 柠檬酸含量为  $117.1 \sim 1592.7 \mu\text{g} \cdot \text{g}^{-1}$  FW, 苹果酸的含量为  $1857 \sim 5423 \mu\text{g} \cdot \text{g}^{-1}$  FW。Perla 等 (2016) 报道 123 份浆果状辣椒果实还原糖 (*D*-葡萄糖和 *D*-半乳糖) 含量介于  $41 \sim 700 \text{ mg} \cdot \text{g}^{-1}$  DW; 辣椒未成熟果实还原糖含量较成熟果实低, 例如浆果状辣椒 ‘VI028794’ 未成熟果实还原糖含量为  $40.99 \text{ mg} \cdot \text{g}^{-1}$  DW, 成熟时则上升到  $177.33 \text{ mg} \cdot \text{g}^{-1}$  DW。Jarret 等 (2009) 报道 216 份中国辣椒成熟果的总糖 (蔗糖、葡萄糖和果糖) 含量为  $1.98 \sim 15.43 \text{ mg} \cdot \text{g}^{-1}$  FW, 柠檬酸含量为  $2.44 \sim 8.18 \text{ mg} \cdot \text{g}^{-1}$  FW。

### 3.3 挥发性香味物质

目前辣椒 5 个栽培种中一共检测到挥发性化合物 300 多种, 主要为酯类和萜类, 其中含量较高的有戊酸己酯 (hexyl pentanoate)、异戊酸己酯 (hexyl isopentanoate)、*Z*-异戊酸-3-己烯酯 (*Z*-3-hexenyl isopentanoate)、2-甲基丁酸己酯 (hexyl 2-methylbutanoate) 和 3,3-二甲基环己醇 (3,3-dimethylcyclohexanol) 等 (Pino et al., 2007, 2011; Forero et al., 2009; Rodriguezo-Burruzeo et al., 2010; Gahungu et al., 2011; Eggink et al., 2012b; Bogusz Junior et al., 2015; Cuevas-Glory et al., 2015; Patel et al., 2016)。其种类和含量因辣椒不同栽培种、果实发育时期和果实部位等存在差别 (Rodriguezo-Burruzeo et al., 2010; Kollmannsberger et al., 2011; Moreno et al., 2012)。辣椒未成熟果实可挥发性化合物含量高于成熟果实, 随着果实的发育成熟, 一些主要的挥发性化合物含量逐渐降低, 甚至消失 (Pino et al., 2006; Forero et al., 2009; Bogusz Junior et al., 2012)。Pino 等 (2007) 报道 *C. chinense* 辣椒橙色和棕色果实中的挥发性化合物含量高于红色果实。Moreno 等 (2012) 报道辣椒胎座组织中含有较高的挥发性化合物, 辣椒杂交种果实胎座中的挥发性物质含量是其果肉的 14 倍。对不同种类辣椒果实挥发性化合物以及风味的研究, 有助于育种者通过遗传转化培育风味独特的辣椒品种。

Moreno 等 (2012) 通过对 8 个 1 年生辣椒和 2 个中国辣椒材料以及 6 个种内杂交种和 2 个种间杂交种果实挥发性组分的研究, 发现辣椒杂交后代挥发性物质含量较亲本材料明显提高。Eggink 等 (2014) 利用辣椒种间杂交回交群体 (*C. annuum* × *C. baccatum* var. *pendulum*), 通过代谢谱分析和感官评价, 定位了多个辣椒果实挥发性风味物质 (volatile and flavor) 和萜类化合物 (terpenoid) QTL 位点, 并实现了辣椒风味的种间渐渗转育。

### 3.4 类黄酮含量及 QTL 定位

辣椒果实中类黄酮主要包括黄酮醇类 (flavonols) 的山奈酚 (kaempferol)、槲皮素 (quercetin)、杨梅素 (myricetin) 和黄酮类 (flavone) 的木犀草素 (luteolin) 和芹菜素 (apigenin) 等。研究发现, 辣椒果实中黄酮类物质的含量与材料种类、生长环境和果实发育时期密切相关 (Marín et al., 2004; Lee et al., 2005; Butcher et al., 2012; van Zonneveld et al., 2015)。据报道, 一年生辣椒、中国辣椒、浆果状辣椒和灌木状辣椒果实中黄酮类物质含量分别可达  $892.0 \mu\text{g} \cdot \text{g}^{-1}$  DW (或  $86.6 \mu\text{g} \cdot \text{g}^{-1}$  FW)、 $138 \mu\text{g} \cdot \text{g}^{-1}$  DW (或  $11.9 \mu\text{g} \cdot \text{g}^{-1}$  FW)、 $128 \mu\text{g} \cdot \text{g}^{-1}$  DW、 $1663.0 \mu\text{g} \cdot \text{g}^{-1}$  DW, 其中槲皮素和木犀草素是辣椒果实中主要黄酮类物质 (Miean & Mohamed, 2001; Bae et al., 2014; Meckelmann et al., 2015a, 2015b); 未成熟果实总类黄酮含量是成熟果实的 4~5 倍 (Howard et al., 2000; Marin et al., 2004; Bae et al., 2014)。

Wahyuni 等 (2014) 利用一年生辣椒 ‘AC1979’ 和中国辣椒 ‘No. 4661 Selection’ 的杂交  $F_2$  代在辣椒 6 个染色体的不同位置共定位了 11 个槲皮素、木犀草素和芹菜素相关代谢数量性状位点 (metabolite quantitative trait locus, mQTL) 和辣椒 MYB12 转录因子基因 (*Ca-MYB12*)、查尔酮合成酶基因 (*CHS-2*)、查耳酮异构酶基因 (*CHI-2* 和 *CHI-4*)、黄酮合酶基因 (*FS-2*) 等 5 个类黄酮代谢途径基因表达 QTL (expression QTL, eQTL)，发现 *Ca-MYB12* 和 *FS-2* 分别调控辣椒果实中柚皮苷查尔酮 (naringenin chalcone) 和黄酮-C-糖苷类 (flavone C-glycosides) 含量。

## 4 问题与展望

### 4.1 多组学解析辣椒种间或种内果实风味多样性

糖和有机酸是鲜食无辣味辣椒 (青椒和彩椒) 的主要风味物质，辣椒素类物质为辣椒特有并使其具有辛辣刺激性，酯类和萜类等挥发性香味物质赋予辣椒香味，上述各物质种类和含量决定了辣椒果实的不同风味。目前，研究者已通过遗传作图定位了多个控制辣椒品质相关代谢物遗传位点 (Popovsky & Paran, 2000; Huh et al., 2001; Keyhaninejad et al., 2014; Wahyuni et al., 2014; 张正海 等, 2014; Arce-Rodriguez & Ochoa-Alejo, 2017)，并已初步开展了辣椒风味物质杂交转育研究 (Moreno et al., 2012; Eggink et al., 2014; Tanaka et al., 2014)。利用气相色谱—质谱联用 (Gas Chromatography – Mass Spectrometer, GC – MS)，高效液相色谱 (High Performance Liquid Chromatography, HPLC) 和核磁共振 (Nuclear Magnetic Resonance, NMR) 等代谢谱测定方法，以及主成分分析 (Principal Components Analysis, PCA) 和偏最小二乘法判别分析 (Partial least squares discriminant analysis, PLS-DA) 等方法，对辣椒不同栽培种及种内不同材料的代谢谱多样性和主要化合物组成、含量进行了研究 (Patel et al., 2016; Becerra-Martínez et al., 2017; Morales-Soriano et al., 2018)。然而，前期研究大多基于图位克隆或遗传分析，与番茄相比 (杜敏敏 等, 2017)，辣椒风味相关基因挖掘，风味表型与代谢谱、基因型的关联分析较薄弱。基于辣椒基因组学研究基础 (Kim et al., 2014; Qin et al., 2014)，随着表型组 (辣椒风味感官评价等)、代谢组 (GC – MS, HPLC 和 NMR 等) 和基因组 (BSA, GWAS 等) 等组学分析的应用，将推动辣椒种间和种内果实风味差异的表型、代谢物解析和遗传调控等相关研究。

### 4.2 品质相关性状遗传调控研究助力辣椒品质育种

蔬菜品质研究正从传统的食用品质向外观、风味品质和功能性营养物质等多角度研究转变 (喻景权, 2014)，而辣椒作为人们喜食的蔬菜和调味品，其品种必然要面临满足不同食用方式和加工目的等多样化需求。以前辣椒育种追求品种丰产性、耐贮运性，忽视了口感、色泽等品质，近年来不同栽培条件下专用型辣椒品种需求增加，而且消费者更加注重口感、风味等优良品质 (耿三省 等, 2015)。高品质辣椒品种的培育，离不开高辣椒素、辣椒红素、维生素 C 等相关风味和营养物质种质资源的挖掘及相关代谢物的遗传调控等基础性研究。目前已在辣椒果色和辣椒红素遗传 (Popovsky & Paran, 2000; Thorup et al., 2000; Huh et al., 2001; Brand et al., 2012, 2014; Pan et al., 2013; Wang et al., 2015)，辣味遗传和辣椒素合成调控 (Keyhaninejad et al., 2014; Arce-Rodríguez & Ochoa-Alejo, 2015, 2017; Lee et al., 2016; Nimmakayala et al., 2016; Zhang et al., 2016; Han et al., 2018, 2019; Koeda et al., 2019; Zhu et al., 2019)，果实风味 (Bae et al., 2014; Bogusz Junior et al., 2015; Loizzo et al., 2015; Meckelmann et al., 2015b; van Zonneveld et al., 2015; Patel et al.,

2016; Sandoval-Castro et al., 2017) 等方面取得进展。然而辣椒在低温、弱光环境下的均匀着色仍是育种者面临的挑战, 辣椒素和辣椒红素含量的遗传调控及高辣椒素和高辣椒红素材料培育仍需加强, 与辣椒风味品质相关的遗传和代谢组解析还有待深入开展。

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