果 树 学 报 2024,41(1):155-161
Journal of Fruit Science

DOI:10.13925/j.cnki.gsxb.20230394

红花草莓育种及花瓣呈色机制研究进展

才 智,岳静宇,王钰雯,景天惠,雷家军,薛 莉*

(沈阳农业大学园艺学院,沈阳 110866)

摘 要:草莓属植物均开白花。红花草莓是一种新型草莓,其果红花亦红,能观赏兼鲜食,可作为多年生草本花卉,用于地栽、盆栽等景观美化,具有较高的经济价值和观赏价值。概述了红花草莓的起源、育种历史和现状及新近育成的种子型品种的研究进展,并对红花草莓花瓣呈色物质、转录调控等分子机制研究进展进行了综述,期望能为红花草莓新品种选育和种质创新提供新思路。

关键词:红花草莓;花色;杂交育种;种子型品种;花青苷;呈色机制

中图分类号:S668.4 **文献标志码**:A **文章编号**:1009-9980(2024)01-0155-07

Advances in research on breeding and petal coloration mechanism of red-flowered strawberry

CAI Zhi, YUE Jingyu, WANG Yuwen, JING Tianhui, LEI Jiajun, XUE Li*

(College of Horticulture, Shenyang Agricultural University, Shenyang 110866, Liaoning, China)

Abstract: The strawberry, belonging to the *Fragaria* genus of the Rosaceae family, is a perennial herbaceous plant with global significance as a berry fruit crop. Nearly all strawberry plants have white flowers. The red-flowered strawberry is a result of distant hybridization, which can be viewed in addition to fresh food due to its vibrant red flowers. China has a robust foundation in strawberry cultivation, and its area and yield ranks first in the world, which is of significant economic benefits. With the rapid development of China's economy and the improvement of material level, people have higher and higher requirements for the selection of strawberry cultivars, "good-looking, delicious and healthy" is the current new demand for strawberry consumption. In recent years, red-flowered strawberries have garnered a global attention from scholars and breeders, which have coloration and morphological characteristics such as Pink Panda, Toscana, Pretty Beauty and Summer Breeze series. In addition, the red-flowered strawberry has a strong ability to reproduce; its green leaves, red flowers and red fruits have a high ornamental value, and can be used for landscaping and potted viewing. The red-flowered strawberry is highly popular due to its vibrant color and edible fruit, commanding a significantly higher market price compared to ordinary white strawberry cultivars, and thereby exhibiting immense and economic value. In China, the red-flowered strawberry can flower all year round in the southern region where the temperature is suitable, and in the cold northern region, it can also flower from April to October. Most red-flowered strawberries are not cold resistant, and its application in the open field in Shenyang area in China needs cold protection to overwinter, which seriously limits its growing area. Flower color is the main ornamental trait of the red-flowered strawberry, which is distinguished from cultivated strawberries with white flowers by its diverse petal colors, including gradients from light pink to deep red. There are many reasons affecting the formation of red color. The most important factor is the type and content of

收稿日期:2023-10-16 **接受日期**:2023-11-29

基金项目:辽宁省科技厅面上项目(2023-MS-211);沈阳市种业创新项目(Z20230379)

作者简介:才智,女,在读硕士研究生,从事观赏植物种质资源与遗传育种研究。E-mail:c18342801098@163.com

*__通信作者__ Author for correspondence. E-mail:lixue@syau.edu.cn

pigments. The flower color of the red-flowered strawberry hybrid covers the whole red series, from light pink to red, which provides an ideal material for studying the mechanism of flower color formation. At present, there have been many studies on the molecular mechanism of petal coloration in red-flowered strawberry. The results show that the structural genes of anthocyanin synthesis pathway and some *MYB* transcription factors play a role in flower color of red-flowered strawberry. In addition, molecular markers related to flower color of red-flowered strawberry have also been developed, which can effectively accelerate molecular breeding of red-flowered strawberry. Modern red-flowered strawberry breeding has a history of more than 60 years. With the joint efforts of breeders at home and abroad, new cultivars of red-flowered strawberry have come out continuously. At present, seed cultivars with different petal colors of red-flowered strawberry have been obtained, which will lay a good foundation for its popularization and application. The breeding of red-flowered strawberry cultivars in China started relatively late. Shenyang Agricultural University was the first institute to carry out the breeding of red-flowered strawberry in China. According to the different application goals of red-flowered strawberry, it mainly focused on the aspects of large fruit, high quality, bright color and good resistance. Now a series of red-flowered strawberry cultivars with different colors have been obtained. Some breeders obtained decaploid red-flowered strawberry through ploidy breeding, which showed strong plant resistance, large flower, strong reproduction ability and strong resistance. Currently, the majority of red-flowered strawberry cultivars in our country are single-petaled, and they are mainly propagated through asexual reproduction by using stolons. There is still a big gap compared with the cultivars cultivated abroad, especially in the Netherlands. Flower color, type and fruit quality are crucial traits that directly impact the ornamental and economic value of red-flowered strawberry. Therefore, in order to enhance the breeding efforts for red-flowered strawberry in China, it is necessary to broaden the genetic background by introducing excellent foreign cultivars as hybrid parents. This should be accompanied by extensive crossbreeding work and full utilization of abundant resources from related plants within China. Additionally, combining traditional crossbreeding methods with modern molecular biological techniques can cultivate superior red strawberry cultivars with independent intellectual property rights. Simultaneously, future efforts should focus on strengthening promotion and publicity of red-flowered strawberry to increase awareness suitable for both appreciation and consumption purposes. This will facilitate wider adoption of red-flowered strawberry among individuals and businesses. The present paper provides a comprehensive review on the origin, breeding history, current status of red-flowered strawberry, and the research progress made in developing new seed cultivars. Additionally, it delves into the molecular mechanism underlying petal color and explores the transcriptional regulation of red-flowered strawberry. The aim is to offer novel insights for breeding and germplasm innovation in red-flowered strawberry.

Key words: Red-flowered strawberry; Flower color; Cross breeding; Seed type cultivar; Anthocyanin; Coloring mechanism

草莓是蔷薇科(Rosaceae)草莓属(*Fragaria*)的多年生草本植物,作为“水果皇后”,是世界上重要的浆果类果树。我国草莓产业基础雄厚,栽培面积和产量连续多年居世界第一位,经济效益显著。随着我国经济社会的快速发展和物质水平的提高,人们对草莓品种选育的要求也越来越高,“好看、好吃、安全”是目前草莓消费的新需求。现在大规模栽培草莓的花色均为白色,颜色较为单一,而通过远缘杂交手段能够获得花色鲜艳夺目、果面光泽度高且酸甜可口的草莓新品种已经成为草莓品种选育的新方向。红花草莓是通过远缘杂交手段得到的观赏兼食用的多年生草本植物,植株低矮、花色艳丽。花色是红花草莓的主要观赏性状,区别于开白色花的栽培草莓,红花草莓的独特之处在于它的花瓣颜色多样,

包括了从浅粉色到深红色的各个梯度。红花草莓由于具有靓丽的花色和可食用的果实而备受人们欢迎，具有较大的市场潜力和经济价值。随着阳台花卉的流行，世界各国纷纷开展了红花草莓的育种，包括日本、荷兰、德国、美国、韩国、中国等，主要围绕提高红花草莓的花色、花型、果实品质、抗性等，其中荷兰ABZ种子公司育成的品种最多，包括不同花色及不同花型的红花草莓[1]。有关不同植物的花青苷生物合成及转录调控已经进行了许多研究，主要的花青苷呈色物质、转录调控关键基因以及一些转录后调节miRNAs在不同的物种中都有了报道[2-4]。目前，已经从代谢组、转录组等多个层面分析了红花草莓花瓣着色的生理和分子机制。

1　红花草莓的来源

红花草莓（Red-flowered strawberry）是利用远缘杂交将红色花基因导入到栽培草莓中得到的，其花瓣呈现红色系的多种不同颜色，具有很高的观赏价值和商业价值[5-6]。迄今为止，已有两个远缘杂交途径获得了红花草莓，第一个来源途径是1962年，由英国的Ellis用开白花的八倍体凤梨草莓（*F.*× *ananassa*，$2n=8x=56$）与开红花的六倍体沼委陵菜（*Potentilla palustris*，$2n=6x=42$）进行属间杂交，得到了开粉红色花的七倍体杂种植株（$2n=7x=49$），其生长势弱，遂与栽培草莓品种（*F.*× *ananassa*）不断进行回交，直到1989年成功培育出世界上第一个红花草莓品种粉红熊猫（Pink Panda），其花为粉红色，具四季开花性，但果实很小、结实率很低[7-9]；红花草莓的第二个来源途径是，2021年俄罗斯新西伯利亚中央植物园的Ambros和Novikova [10]利用八倍体栽培草莓和开红色花的尼泊尔委陵菜（*P. nepalensis* Hook）（$2n = 4x = 28$）进行远缘杂交获得的粉红花F_1代杂种，其抗寒性强，这是最新发表的利用近缘的委陵菜属植物种质进行属间杂交得到的开红色花的草莓。相信不久之后，将会有更多的途径可以培育出红花草莓，创新更多的红花草莓新种质。

2　红花草莓杂交育种进展

现代红花草莓育种已经有60多年的历史，在国内外育种工作者的共同努力下，红花草莓新品种不断问世，为其推广应用奠定了良好基础。Khanizadeh等[11]在加拿大魁北克利用（Raritian × K74-12）×（SJ9616-1 × Pink Panda）杂交，成功培育了两个日中性红花草莓新品种玫瑰波丽（Roseberry）和玫瑰丽娜（Rosalyne），花粉色、果实芳香、品质优且抗寒。Olbricht等[12]以粉红熊猫（Pink Panda）和口红（Lipstick）为亲本，经杂交和自交得到了大量花色艳丽、重瓣或半重瓣观赏性强的F_3杂种优系；瑞典科学院细胞学和遗传学研究所也进行了类似的工作，以粉红熊猫和荷兰ABZ种子公司创造的红花杂交品种为亲本，希望能够培育出抗寒的红花草莓品种用于露地栽培，建立了包含5个欧洲选育品种和30个杂交品系的大果粉花草莓基因库[10]。

红花草莓具有高度杂合性，其种子型品种的育成是先通过反复自交，从而获得纯合的育种材料，这一过程因材料和性状的差异，自交次数也有所不同，再配制杂交组合选育而成。1993年，ABZ种子公司开始红花草莓种子型品种育种工作，红花草莓对消费者的吸引力是基于花朵大小、形状、数量和颜色等，他们的育种目标是以观赏特性为主，包括开花早、株型紧凑、花朵吸引人以及果实口感最佳。目前，市场上ABZ种子的F_1杂交草莓品种有23个，这些种子已经出口到六大洲的30多个国家，包括中国、日本、美国等[13]。表1列出了ABZ种子公司在1995—2021年部分培育的12个由种子繁殖型的红花草莓品种，如Roman（罗曼）、Ruby Ann（卢比安）、Tristan（特里斯坦）、Summer Breeze Cherry（夏日微风樱桃）、Summer Breeze Rose（夏日微风玫瑰）等，这些红花草莓品种均是通过种子繁殖，产生匍匐茎较少，植株长势一致，花和果实性状均较好。通过对种子繁殖型草莓品种的推广应用，将会对未来的草莓种苗繁育系统和生产模式产生重要影响。

沈阳农业大学最早在我国开展了红花草莓的选育工作，自1999年从日本引入红花草莓品种粉红熊猫后，展开了系列杂交，主要围绕大果、优质、色艳、抗性等方面进行新品种选育。2011年，培育出了红花草莓新品种粉佳人（花粉色、果实酸甜）和俏佳人（花深粉色、果实品质优）[14]，2014年培育出了新品种粉公主（花粉色、四季开花）和红玫瑰（花深粉色、花大），2016年又培育出新品种小桃红（花红色）和四季红（花红色、四季开花）[15]；同时，还通过倍性育种的手段，用红花草莓品种粉佳人与白花、抗寒且果实芳香的12*x*种间杂种进行杂交，获得了植株高大、花大、繁殖力强的红花草莓新种质[16]。与红花草

莓亲本粉红熊猫相比，沈阳农业大学现在育成的红花草莓品种植株长势旺、花色丰富且果实性状要显著优于亲本粉红熊猫；与市面上ABZ公司的其他红花草莓品种相比，沈阳农业大学育成的品种植株长势更壮、四季开花类型者多、繁殖能力更强，更易于覆盖地面。另外，2017年江苏省农业科学院以红颜为母本，以优良中间育种材料03-01（花粉色）为父本进行杂交，选育成优质的红花草莓新品种紫金红，其花为粉红色、重瓣，适合鲜食与观赏[17]；2021年以优质红花品系08-1-N-5和早熟大果白花品系09-8-S-9进行杂交，又培育出观赏兼鲜食的红花草莓新品种紫金粉玉，其突出性状是早熟、花红色[18]。

表1 1995—2021年荷兰ABZ公司市场上销售的部分F_1杂交红花草莓品种

Table 1 ABZ F_1 hybrid red-flowered strawberry cultivars in the market 1995—2021

品种 Cultivar	选育年份 Released year	花色 Flower color	特性 Characteristics
比甘 Pikan	2002	粉色 Pink	种子发芽快而一致、株型紧凑、果实香甜 The seeds germinate quickly and consistently, the plant is compact, and the fruit is sweet
罗曼 Roman	2004	粉色 Pink	匍匐茎长、大花、半重瓣花、果实芳香 Long stolons, large flowers, semi-double flowers, fragrant fruit
佛罗莱恩 Florian	2004	粉色 Pink	观赏花园用，果实特殊芳香味 For ornamental garden use, the fruit has a special aroma
野马 Tarpan	2006	深粉色 Deep pink	早花、大花、半重瓣花，果实细长形、鲜红 Early, large and semi-double flowers, elongated and bright red fruit
麦伦 Merlan	2008	粉色 Pink	早花、株型紧凑，香甜、丰产 Early flowers, compact plant, sweet fruit, high yield
加桑 Gasana	2010	粉色 Pink	种子发芽快而一致、大花，香甜 The seeds germinate quickly and consistently, large flowers, sweet fruit
特里斯坦 Tristan	2010	深粉色 Deep pink	株型紧凑、开花早，甜 Compact plant, early flower, sweet fruit
托斯卡纳 Toscana	2011	深粉色 Deep pink	种子发芽快而一致、大花，果实多汁、芳香 The seeds germinate quickly and consistently, the flowers are large, and the fruit is juicy and fragrant
福瑞森F_1 Frisan F_1	2012	粉色 Pink	生长旺盛、花量大，高产，果实多汁、香甜 Vigorous growth, large amount flowers, high yield, juicy and sweet fruit
卢比安 Ruby Ann	2015	红色 Red	种子发芽快而一致，株型紧凑，香甜、果大 The seeds germinate quickly and consistently, compact plant, sweet and large fruit
夏日微风玫瑰 Summer Breeze Rose	2018	红色 Red	玫瑰状半重瓣花，株型紧凑，夏季结果、香甜 Rose - shaped semi-double flowers, compact plant, summer fruit, sweet
夏日微风樱桃 Summer Breeze Cherry	2020	粉色 Pink	强壮，生长旺盛、半重瓣花，美味、新鲜 Strong, vigorous, semi-double flowers, delicious and fresh fruit

3 红花草莓花瓣呈色调控研究

近年来，国内外对草莓花青苷的合成及转录调控已进行了较多研究，红花草莓花瓣和果实的主要呈色物质是花青苷，然而它们的主要花青苷种类不同[19-20]。Xue等[19]采用HPLC-MS技术，对红花草莓不同花色的花瓣中花青苷成分进行鉴定，发现了7种花青苷，包括天竺葵素类苷元、矢车元菊素类苷元和飞燕草素类苷元。随着红花草莓花色的加深，花青苷的总含量越高，红花草莓花瓣中还发现了少量的飞燕草素类苷元。矢车菊素-3-葡萄糖苷是红花草莓花瓣的主要呈色物质，而果实中主要的呈色物质是天竺葵素-3-葡萄糖苷，这与栽培草莓果实中的主要呈色物质一致[21]。这表明红花草莓的果实和花瓣中花青苷积累的方式不同，也就是说在红花草莓中有两种以上可调控花青苷积累的模式。

转录因子是位于植物细胞核中调控花青苷积累的重要因子，通过结合花青苷合成代谢途径上结构基因的启动子，进行激活或抑制基因的转录。目前，已经从代谢组、转录组等多个层面分析了红花草莓花瓣着色的原因。Xue等[22]发现，花青苷合成途径的结构基因*FaANS*、*FaBZ1*和*FaUGT75C1*的低表达是红花草莓杂交后代中白色花瓣中花青苷缺失的主要原因，同时，*FaFLS*和*FaDFR*基因的相互作用可能会进一步抑制花青苷的合成；洪燕红等[23]发现在红花草莓莓红的花瓣发育过程中，*FaMYB6*和*FaMYB90*对花青苷的生物合成有正向调控作用，而

*FaMYB82*则与这4个差异表达的结构基因*FaPAL*、*Fa4CL*、*FaDFR*和*Fa3GT*呈极显著负相关；Liu等[24]通过对红花草莓R2R3-MYB基因家族的全基因组分析，鉴定出3个调控红花草莓花瓣中花青苷生物合成的R2R3- FaMYB基因，分别为*FaMYB28*、*FaMYB54*和*FaMYB576*。经系统进化树构建及序列比对分析，这些*FaMYBs*与果实中调控花青苷形成的*FaMYB1*、*FaMYB10*和*FaMYB5*均不同，这说明在红花草莓的不同组织部位的着色上，有不同的机制来影响花青苷的形成[25-26]。

已有大量的研究表明，miRNAs在植物花青苷的生物合成过程中发挥重要作用，主要通过调控花青苷生物合成相关的转录因子，来影响花青苷合成的相关结构基因的表达；或者可以直接负调控花青苷合成途径的结构基因，从而对植物花青苷的含量产生影响。目前已经鉴定到许多miRNAs能够在不同植物花瓣或果实呈色方面起作用，例如miR858[27-28]、miR156[29]、miR7125[30]、miR477[31]、miR5290[32]等。目前草莓中miRNAs的研究已取得一系列进展，主要围绕果实发育、抗性等方面[34-35]。Li等[36]从森林草莓Rugen中发现miR167及其靶基因生长素反应因子6（*ARF6*）可调控草莓根、叶发育，增加草莓根和叶的数量。红花草莓中miRNA调控花瓣着色的相关报道还较少。Yue等[37]利用多组学联合（miRNAs测序、转录组测序和降解组测序）分析等方法，筛选到了4个与红花草莓花瓣颜色调控相关的差异表达的miRNAs，分别为*FamiR858_R-2*、*FamiR828a*、*FamiR396e*和*FamiR156a*。*FamiR156a*、*FamiR396e*和*FamiR858_R-2*分别靶向*FaSPL13A*、*FabHLH79*、*FaMyb308*，而促进红花草莓花瓣中花青苷的积累；*FamiR828a*可能通过靶向*FaMYB114*抑制红花草莓花瓣花青苷的积累。此外，已有研究表明，miR156通过靶向*SPL*转录因子正向调控花青苷的合成，*SPL*通过MYB-bHLH-WD40复合物负调控花青素的积累[38]；miR828和miR858通过调控*VvMYB114*，促进葡萄中花青苷和黄烷醇的积累[27]；Xie等[39]研究发现，在苹果中，miR858、miR828和miR159通过与多个MYBs相互作用形成一个复杂而庞大的调控网络，参与苹果生长和花青苷代谢的调控，并且miR858被预测靶向苹果中高达66个MYB转录因子。这些研究结果为深入解析红花草莓花瓣呈色的分子机制奠定了一些理论基础。

4 展　望

红花草莓的主要特征是观赏性强、花瓣色彩艳丽、一季或四季开花、易于繁殖、管理简便，既可用作园林绿化，又可用作盆栽，且其果实鲜美可食用，具有很高的开发价值。我国红花草莓品种选育工作起步较晚，目前我国自己选育的红花草莓品种多为一轮花瓣，且主要的繁殖方式是利用匍匐茎来进行无性繁殖，这些与荷兰育成的品种相比还存在较大差距。花色、花型以及果实是影响红花草莓品种是否优秀的重要品质性状，这些直接影响到红花草莓的观赏价值和经济价值。因此，在红花草莓育种工作中，我国要在引进国外优良品种的同时，拓宽杂交亲本的遗传背景，开展大量的杂交选育工作，并充分挖掘和利用我国丰富的近缘属植物资源，运用常规杂交育种和现代分子生物育种技术手段相结合，培育出一批具有我国自主知识产权的更优红花草莓新品种。同时，今后应加强红花草莓的推广、宣传工作，以提高对赏食兼用草莓新品种的认知度，并促进红花草莓更广泛的普及。

参考文献 References：

[1] 薛莉，雷家军，刘源 . 红花草莓育种研究进展[J]. 东北农业大学学报，2012，43(10)：172-176.
XUE Li，LEI Jiajun，LIU Yuan. Review on pink-flowered strawberry breeding[J]. Journal of Northeast Agricultural University，2012，43(10)：172-176.

[2] SHANG Y J，VENAIL J，MACKAY S，BAILEY P C，SCHWINN K E，JAMESON P E，MARTIN C R，DAVIES K M. The molecular basis for venation patterning of pigmentation and its effect on pollinator attraction in flowers of *Antirrhinum*[J]. The New Phytologist，2011，189(2)：602-615.

[3] WANG Y L，WANG Y Q，SONG Z Q，ZHANG H Y. Repression of *MYBL2* by both microRNA858a and HY5 leads to the activation of anthocyanin biosynthetic pathway in *Arabidopsis*[J]. Molecular Plant，2016，9(10)：1395-1405.

[4] 曹琳娇，李晓杰，焦棒棒，梁毅，马长生 . 蔬菜花青苷生物合成及转录调控的研究进展[J]. 中国瓜菜，2019，32(12)：1-7.
CAO Linjiao，LI Xiaojie，JIAO Bangbang，LIANG Yi，MA Changsheng. Advances in biosynthesis and transcriptional regulation of anthocyanin in vegetables[J]. China Cucurbits and Vegetables，2019，32(12)：1-7.

[5] BENTVELSEN G，BOUW B. Breeding ornamental strawberries[J]. Acta Horticulturae，2006(708)：455-458.

[6] NIEMIROWICZ-SZCZYTT K. The results of intergeneric pollination of *Fragaria* × *ananassa* Duch. and *Fragaria virginiana*

Duch. by *Potentilla* species[J]. Acta Societatis Botanicorum Poloniae，2014，53(4)：443-454.

[7] 闫玉华，代汉萍，雷家军 . 红花草莓及其杂交育种研究[J]. 沈阳农业大学学报，2005，36(5)：612-614.
YAN Yuhua，DAI Hanping，LEI Jiajun. Study on red-flowered strawberry (*Fragaria* × *Potentilla*) and its breeding[J]. Journal of Shenyang Agricultural University，2005，36(5)：612-614.

[8] MABBERLEY D. *Potentilla* and *Fragaria* (Rosaceae) reunited[J]. Telopea，2002，9(4)：793-801.

[9] SAYEGH A J，HENNERTY M J. Intergeneric hybrids of *Fragaria* and *Potentilla*[J]. Acta Horticulturae，1993(348)：151-154.

[10] AMBROS E，NOVIKOVA T. Productivity characteristics of F_1 ornamental progenies between *Fragaria* × *ananassa* Duchesne ex Rozier. and *Potentilla nepalensis* Hook[J]. BIO Web of Conferences，2021，38：00003.

[11] KHANIZADEH S，DESCHÊNES M，DUBÉ C.‘Roseberry’strawberry[J]. HortScience，2010，45(10)：1545-1546.

[12] OLBRICHT K，POHLHEIM F，EPPENDORFER A，VOGT F，RIETZE E. Strawberries as balcony fruit[J]. Acta Horticulturae，2014，1049：215-218.

[13] BENTVELSEN G，VAN DER VANGE A. Advances in F_1 hybrid day-neutral strawberry breeding at ABZ Seeds，Andijk，The Netherlands[J]. Acta Horticulturae，2021(1309)：241-246.

[14] 雷家军，薛莉，代汉萍，邓明琴 . 红花草莓新品种‘粉佳人’和‘俏佳人’[J]. 园艺学报，2015，42(3)：599-600.
LEI Jiajun，XUE Li，DAI Hanping，DENG Mingqin. Two new pink-flowered strawberry cultivars‘Pink Beauty’and‘Pretty Beauty’[J]. Acta Horticulturae Sinica，2015，42(3)：599-600.

[15] XUE L，LEI J J，DAI H P. Two new pink-flowered strawberry cultivars‘Sijihong’and‘Xiaotaohong’[J]. Acta Horticulturae，2017(1156)：141-144.

[16] XUE L，DAI H P，LEI J J. Creating high polyploidy pink-flowered strawberries with improved cold tolerance[J]. Euphytica，2015，206(2)：417-426.

[17] 王庆莲，赵密珍，王壮伟，吴伟民，钱亚明 . 红花草莓新品种‘紫金红’[J]. 园艺学报，2017，44(12)：2425-2426.
WANG Qinglian，ZHAO Mizhen，WANG Zhuangwei，WU Weimin，QIAN Yaming.‘Zijinhong’，a new red-flowered strawberry cultivar[J]. Acta Horticulturae Sinica，2017，44(12)：2425-2426.

[18] 王庆莲，赵密珍，王壮伟，关玲，刘佳全，蔡伟建，夏瑾，陈志京 . 红花草莓新品种紫金粉玉的选育[J]. 果树学报，2021，38(7)：1214-1216.
WANG Qinglian，ZHAO Mizhen，WANG Zhuangwei，GUAN Ling，LIU Jiaquan，CAI Weijian，XIA Jin，CHEN Zhijing. Breeding report of a new strawberry cultivar with red flower Zijin Fenyu[J]. Journal of Fruit Science，2021，38(7)：1214-1216.

[19] XUE L，WANG Z G，ZHANG W，LI Y X，WANG J，LEI J J. Flower pigment inheritance and anthocyanin characterization of hybrids from pink-flowered and white-flowered strawberry[J]. Scientia Horticulturae，2016，200：143-150.

[20] 王键，张莹莹，薛莉，雷家军 . 红花草莓杂交后代花瓣色素成分分析[J]. 东北农业大学学报，2016，47(11)：9-16.
WANG Jian，ZHANG Yingying，XUE Li，LEI Jiajun. Analysis on flower pigment components in petals of hybrid offspring of pink-flowered strawberry[J]. Journal of Northeast Agricultural University，2016，47(11)：9-16.

[21] KOSAR M，KAFKAS E，PAYDAS S，BASER K H C. Phenolic composition of strawberry genotypes at different maturation stages[J]. Journal of Agricultural and Food Chemistry，2004，52(6)：1586-1589.

[22] XUE L，WANG J，ZHAO J，ZHENG Y，WANG H F，WU X，XIAN C，LEI J J，ZHONG C F，ZHANG Y T. Study on cyanidin metabolism in petals of pink-flowered strawberry based on transcriptome sequencing and metabolite analysis[J]. BMC Plant Biology，2019，19(1)：423.

[23] 洪燕红，叶清华，李泽坤，王威，谢倩，陈清西，陈建清 . 红花草莓‘莓红’花瓣花色苷积累及其 MYB 基因的表达分析[J]. 园艺学报，2021，48(8)：1470-1484.
HONG Yanhong，YE Qinghua，LI Zekun，WANG Wei，XIE Qian，CHEN Qingxi，CHEN Jianqing. Accumulation of anthocyanins in red-flowered strawberry‘Meihong’petals and expression analysis of *MYB* gene[J]. Acta Horticulturae Sinica，2021，48(8)：1470-1484.

[24] LIU J X，WANG J，WANG M Q，ZHAO J，ZHENG Y，ZHANG T，XUE L，LEI J J. Genome-wide analysis of the R2R3-*MYB* gene family in *Fragaria* × *ananassa* and its function identification during anthocyanins biosynthesis in pink-flowered strawberry[J]. Frontiers in Plant Science，2021，12：702160.

[25] PILLET J，YU H W，CHAMBERS A H，WHITAKER V M，FOLTA K M. Identification of candidate flavonoid pathway genes using transcriptome correlation network analysis in ripe strawberry (*Fragaria* × *ananassa*) fruits[J]. Journal of Experimental Botany，2015，66(15)：4455-4467.

[26] SALVATIERRA A，PIMENTEL P，MOYA-LEON M A，CALIGARI P D S，HERRERA R. Comparison of transcriptional profiles of flavonoid genes and anthocyanin contents during fruit development of two botanical forms of *Fragaria chiloensis* ssp. *chiloensis*[J]. Phytochemistry，2010，71(16)：1839-1847.

[27] TIRUMALAI V，SWETHA C，NAIR A，PANDIT A，SHIVAPRASAD P V. miR828 and miR858 regulate *VvMYB114* to promote anthocyanin and flavonol accumulation in grapes[J]. Journal of Experimental Botany，2019，70(18)：4775-4792.

[28] ZHANG B，YANG H J，YANG Y Z，ZHU Z Z，LI Y N，QU D，ZHAO Z Y. Mdm-miR828 participates in the feedback loop to regulate anthocyanin accumulation in apple peel[J]. Frontiers in Plant Science，2020，11：608109.

[29] WANG Y M，LIU W W，WANG X W，YANG R J，WU Z Y，WANG H，WANG L，HU Z B，GUO S Y，ZHANG H L，LIN J X，FU C X. MiR156 regulates anthocyanin biosynthesis through SPL targets and other microRNAs in poplar[J]. Horticulture Re-

search，2020，7：118.

[30] HU Y J，CHENG H，ZHANG Y，ZHANG J，NIU S Q，WANG X S，LI W J，ZHANG J，YAO Y C. The MdMYB16/MdMYB1-miR7125-MdCCR module regulates the homeostasis between anthocyanin and lignin biosynthesis during light induction in apple[J]. The New Phytologist，2021，231(3)：1105-1122.

[31] DONG X N，LIU C R，WANG Y Q，DONG Q，GAI Y P，JI X L. MicroRNA profiling during mulberry (*Morus atropurpurea* Roxb) fruit development and regulatory pathway of miR477 for anthocyanin accumulation[J]. Frontiers in Plant Science，2021，12：687364.

[32] CHEN R C，MAO L C，GUAN W L，WEI X B，HUANG Z H，WU Y Y. ABA-mediated miR5290 promotes anthocyanin biosynthesis by inhibiting the expression of *FaMADS1* in postharvest strawberry fruit[J]. Postharvest Biology and Technology，2022，189：111934.

[33] LIANG Y X，GUAN Y H，WANG S X，LI Y J，ZHANG Z H，LI H. Identification and characterization of known and novel microRNAs in strawberry fruits induced by *Botrytis cinerea*[J]. Scientific Reports，2018，8(1)：10921.

[34] XU X B，MA X Y，LEI H H，YIN L L，SHI X Q，SONG H M. MicroRNAs play an important role in the regulation of strawberry fruit senescence in low temperature[J]. Postharvest Biology and Technology，2015，108：39-47.

[35] ZHENG G H，WEI W，LI Y P，KAN L J，WANG F X，ZHANG X，LI F，LIU Z C，KANG C Y. Conserved and novel roles of miR164-*CUC2* regulatory module in specifying leaf and floral organ morphology in strawberry[J]. The New Phytologist，2019，224(1)：480-492.

[36] LI T Y，WANG S X，TANG X G，DONG X X，LI H. The FvemiR167b-*FveARF6* module increases the number of roots and leaves in woodland strawberry[J]. Scientia Horticulturae，2022，293：110692.

[37] YUE J Y，LIU Z X，ZHAO C，ZHAO J，ZHENG Y，ZHANG H W，TAN C H，ZHANG Z T，XUE L，LEI J J. Comparative transcriptome analysis uncovers the regulatory roles of microRNAs involved in petal color change of pink-flowered strawberry[J]. Frontiers in Plant Science，2022，13：854508.

[38] GOU J Y，FELIPPES F F，LIU C J，WEIGEL D，WANG J W. Negative regulation of anthocyanin biosynthesis in *Arabidopsis* by a miR156-targeted SPL transcription factor[J]. The Plant Cell，2011，23(4)：1512-1522.

[39] XIE K B，SHEN J Q，HOU X，YAO J L，LI X H，XIAO J H，XIONG L Z. Gradual increase of miR156 regulates temporal expression changes of numerous genes during leaf development in rice[J]. Plant Physiology，2012，158(3)：1382-1394.