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特邀综述

观赏植物分子育种研究进展

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摘要 分子育种技术在跨越种间隔离障碍、加速育种进程和获得新奇特变异方面具有传统育种技术无法比拟的优势。将其用于观赏植物育种将会极大地提升产品品质并可增强产业竞争力。该文综述了近10年来观赏植物分子育种的研究进展, 希望能为国内观赏植物研究者提供一份参考资料。

关键词 观赏植物, 观赏性状, 分子育种

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观赏植物作为重要的栽培植物, 在社会经济发展中起着重要作用。观赏植物产业被誉为21世纪的“朝阳产业”, 是农村经济新的增长点。20世纪80年代以来, 以植物细胞培养和组织培养技术、分子标记技术和转基因技术等为核心的现代生物技术, 广泛应用于观赏植物种质资源遗传分析、新品种培育和优质新产品开发, 大大加快了全球观赏植物产业的发展, 现已形成了一整套观赏植物生物技术。随着全球经济的发展和人们生活品质的提高, 人们对色彩鲜艳、花型奇特、气味芳香、品质优良的观赏植物产品需求进一步增加, 同时人们的环保意识也进一步加强, 培育生长快速、节约资源、抗逆性强和环境效益好的观赏植物新品种已成为必然。

传统的观赏植物育种技术在观赏植物品种培育历史上发挥过重要作用。以分子标记辅助育种、转基因育种、体细胞培养和试管再生等为核心的现代观赏植物育种技术, 克服了常规育种方法周期长、预见性差及选择效率低的缺点, 且能够打破物种界限, 克服生殖隔离困难, 实现优良基因重组, 定向选育优质、高抗观赏植物新品种。将以这些现代生物技术为平台的分子育种技术与传统技术相结合, 会极大地拓展观赏植物育种的范围。近10年来, 国内外观赏植物分子育种研究取得了令人瞩目的成绩。本文综述这一发展概况, 希望能为国内观赏植物研究者和生产企业提供一份参考资料。

1 花色改良

具有新异花色的花卉往往经济价值可观。利用基因工程技术培育新异花色品种是花卉分子育种研究的热点之一, 也是目前最成功的观赏植物性状改良的范例之一(表1)。随着人们对花色素代谢途径的解析、相关基因的分离以及转基因技术的不断成熟, 改变观赏植物花色已成为可能(徐清烯和戴思兰, 2004)。同时, 花色素代谢途径还为基因工程效率的研究提供了模式(Tanaka and Ohmiya, 2008)。

植物的花色主要由三大类色素决定: 类黄酮(包括花青素)、类胡萝卜素和甜菜色素。花青素是类黄酮家族中的主要呈色物质(胡可等, 2010; Tanaka and Brugliera, 2013)。通过对花青素合成分支途径的关键节点基因进行调控, 人们成功地获得了一些花色改良的观赏植物新品种。Van der Krol等(1988)首次将花青素合成途径上游的*CHS*基因反义导入矮牵牛(*Petunia hybrid*), 抑制生成花青素苷的前体柚皮素等的合成, 引起矮牵牛花色改变, 为分子育种改良花色带来希望。随后, 科学家应用抑制基因表达的方法在多种观赏植物中获得了花色明显变化的转基因株系(Nakatsuka et al., 2008, 2010; Boase et al., 2010; Chen et al., 2011b)。导入单个外源基因使花色发生改变的尝试, 近年来有许多成功的案例, 尤其是在缺

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表1 观赏植物花色改良分子育种一览表

Table 1 The improvement of flower colour using molecular breeding method in ornamental plants

受体植物	分子设计	性状变化	参考文献
矮牵牛(*Petunia hybrid*)	抑制内源*CHS*表达	粉色变为白色	Van der Krol et al., 1988
	抑制内源*F3′5′H*表达	蓝色、紫色变为浅蓝色、浅粉色	Shimada et al., 2001
	过表达长春花*F3′5′H*	红色变为深红色，紫色花斑	Mori et al., 2004
	抑制内源*F3′H*表达+过表达月季*DFR*	红色变为橙色	Tsuda et al., 2004
	过表达*PH5*	紫色变为红色	Verweij et al., 2008
龙胆(*Gentiana* sp.)	通过RNAi抑制*CHS*表达	蓝色变为白蓝-白	Nakatsuka et al., 2008
	通过RNAi抑制*F3′5′H*和*A5*/*3′AT*表达	蓝色变为淡紫-白蓝	Nakatsuka et al., 2010
仙客来(*Cyclamen persicum*)	通过RNAi抑制*F3′5′H*表达	紫色变为红-粉	Boase et al., 2010
蝴蝶兰(*Phalaenopsis amabilis*)	通过RNAi抑制*PeUFGT3*表达	红色变为白色	Chen et al., 2011b
月季(*Rosa chinensis*)	过表达三色堇*F3′5′H*+鸢尾*DFR*+月季*DFR* RNAi	红-白青变为浅蓝色	Katsumoto et al., 2007
菊花(*Chrysanthemum morifolium*)	月季*CHS*启动子+三色堇*F3′5′H*+菊花*F3′H* RNAi	粉色变为蓝色	Brugliera et al., 2013
	菊花花特异型*F3H*启动子+风铃草*F3′5′H*+乙醇脱氢酶5′UTR区作为增强子	红-紫变为蓝紫色	Noda et al., 2013
	通过RNAi抑制*CmCCD4a*表达	白色变为黄色	Ohmiya et al., 2006
烟草(*Nicotiana tabacum*)	抑制内源*F3′H*和*FLS*+过表达非洲菊*DFR*	粉色变为红色	Nakatsuka et al., 2007
	过表达瓜叶菊*F3′5′H*	粉色变为紫色	Sun et al., 2013a
蓝目菊(*Arctotis stoechadifolia*)	*F3′5′H* RNAi+过表达非洲菊*DFR*	洋红色变为浅红色	Seitz et al., 2007
郁金香(*Tulipa gesneriana*)	*TgVIT1*+*TgFER* RNAi	紫色变为深蓝色	Shoji et al., 2010
夏堇(*Torenia fournieri*)	抑制内源*F3′H*和*F3′5′H* +过表达月季*DFR*	蓝紫色变为粉色	Nakamura et al., 2010
琴叶榕(*Ficus lyrata*)	过表达葡萄*VvMybA1*基因	绿色变为紫色	Zhao et al., 2013

乏蓝色系的物种中导入有“蓝色基因”之称的*F3′5′H*基因，开启了蓝色花育种的大门(Shimada et al., 2001; Mori et al., 2004; Huang et al., 2013)。目前的研究热点是通过多基因导入完成分支途径的重建。对飞燕草素苷合成途径上的多个基因进行调控，已经成功实现分支途径的重建，获得了花色偏蓝的香石竹(*Dianthus caryophyllus*)、月季(*Rosa chinensis*)和菊花(*Chrysanthemum morifolium*)等观赏植物新品种(Fukui et al., 2003; Katsumoto et al., 2007; Brugliera et al., 2013; Noda et al., 2013)。使用相似的方法也获得了能够有效积累天竺葵素和飞燕草素的矮牵牛、烟草(*Nicotiana tabacum*)、蓝目菊(*Arctotis stoechadifolia* var. *grandis*)和夏堇(*Torenia fournieri*)转基因株系(Tsuda et al., 2004; Nakatsuka et al., 2007; Seitz et al., 2007; Nakamura et al., 2010; Sun et al., 2013a)。除了对花色素生物合成途径上的相关酶基因进行调控外，随着对花色呈色机理的深入了解，目前的花色改良研究已经扩展到影响花色素呈色的其它相关基因。Zhao等(2013)通过向琴叶榕(*Ficus lyrata*)转入编码葡萄花青素苷合成调控因子的*VvMybA1*基因，获得了紫色叶新品种。Shoji等(2010)通过将与铁离子转运和贮藏相关的基因*TgVit1*和*TgFER1*过表达和抑制，使郁金香(*Tulipa gesneriana*)细胞中铁离子含量明显升高，成功地将紫色郁金香转变为深蓝色。Verweij等(2008)向矮牵牛植株中导入编码P_{3A}-H^+-ATPase的基因*PH5*，使花瓣液泡pH值降低，从而获得了花色从紫色向红色转变的变化表型。

以类胡萝卜素为主要呈色物质的花色变化主要受到类胡萝卜素积累量的影响，因此与类胡萝卜素合成相关基因的分离以及其合成机制成为类胡萝卜素研究的热点。在研究类胡萝卜素的过程中，人们也获

得了许多花色表型具有明显变化的转基因株系。Ohmiya等(2006)利用RNAi干扰白色菊花中*CmCCD4a*基因的表达, 获得了花色为黄色的转基因后代。

甜菜色素仅存在于石竹目(除粟米草科和石竹科外)的植物中, 由于在相同的植物中其不与花青素同时出现, 故往往作为化学分类的指标。甜菜色素主要呈现黄色和紫色(Tanaka et al., 2008)。对于甜菜色素的生物合成途径及该途径上涉及的关键酶基因和调控因子的研究尚不够深入, 虽然近年来的研究已经基本确定了其合成的关键步骤, 但目前的实验普遍证实其合成途径中还应该存在多种生物化学反应过程(Gandía-Herrero and García-Carmona, 2013)。因此需要进一步阐明甜菜色素的合成过程, 以便为以甜菜色素为主要呈色物质的物种进行花色改良研究奠定基础。

2 花型

观赏植物的花型是指植物的花器官形态, 包括各部分器官的形状、数量、大小和对称性等。利用分子育种技术进行花型改良也取得了一些进展(表2)。目前, 国内外关注的焦点是花瓣形态建成的分子机制(王小菁和杨玉萍, 2013)。Bowman等(2012)的研究认为虽然花的外形多种多样, 但是各类花器官的发育是以一整套高度保守的同源异型基因(花器官发育ABC模型)为基础, 通过保守的组合模式起作用。在观赏植物育种中, 利用同源异型基因的突变可以培育出具有独特花型的新品种。Broholm等(2008)通过抑制非洲菊(*Gerbera jamesonii*)中B类基因*GGLO1*、*GDEF1*和*GDEF2*的表达, 获得了过渡类花瓣消失和外轮舌状花完全退化的新花型株系。而针对C类基因的基因工程育种往往是形成重瓣花卉新品种的重要来源, 牵牛花(*Ipomoea nil*)、月季和小银莲花(*Anemone rossii*)均是由于内源C类基因正常功能被抑制获得的(Iwasaki and Nitasaka, 2006; Dubois et al., 2010; Galimba et al., 2012)。矮牵牛中2个C类基因*PMADS3*和*FBP6*的双突变体表现出第3轮花器官向花瓣强烈转变, 并且第4轮花器官丧失了花分生组织决定性, 产生了多层新的花瓣类器官(Heijmans et al., 2012; Mach, 2012)。Sage-Ono等(2011)通过抑制矮牵牛内源*DP*基因(C类基因*AG*的同源基因)的表达, 获得了具双花结构的转基因株系。

花的形状不仅仅是由器官特征决定的, 同一轮中的花器官形状也可能不同, 即花部对称性差异。通过对花瓣对称性决定基因*CYC*和*DICH*的转基因育种, 能够改变花瓣形态建成。在非洲菊中, 过表达*Gh-CYC2*基因造成了中间过渡类型花向舌状花转变(Broholm et al., 2008)。在露地菊品种火焰中过表达*SQU*基因(*CYC*的同源基因)后舌状花畸形率下降, 更好地保证了两侧对称的花型(罗冉, 2011)。在仙客来(*Cyclamen persicum*)中过表达*TCP*基因家族中的*CpTCP1*基因, 花瓣出现褶皱和卷曲现象, 形成了特异花型的转基因株系(Tanaka et al., 2011)。

由于ABC模型中的成员和花对称性决定因子多以转录因子家族形式存在, 且绝大多数观赏植物为异源多倍体, 控制其花型的转录因子数量较多, 使用传统的转基因技术难以克服转录因子间的冗余性, 育种难度较高。近年来, 基于植物特异转录因子抑制子基序发展起来的嵌合抑制子沉默技术(chimeric repressor ear silencing technology, CREST)可以克服这一缺点。Tanaka研究组通过构建*35S:AatTCP3: EAF-motif*(*TCP3SRDX*)嵌合蛋白超表达载体转化了多种观赏植物, 获得了多种花型改变的转基因株系, 如花瓣边缘呈波浪状的月季(Gion et al., 2011)、菊花和夏堇转基因株系(Narumi et al., 2011)。利用月季ABC模型中的B类基因*SEP3*构建*RhSEP3SRDX*嵌合蛋白超表达载体转化月季, 获得了花瓣完全消失、仅留存萼片的“绿色月季”; 而使用拟南芥(*Arabidopsis thaliana*)中控制细胞扩展的基因*AtYAB1*构建YAB1SRDX载体转化月季, 获得了株型和花型完全改变的“奇异”月季转基因株系(Ishiguro et al., 2012)。

3 花香

花香化合物主要由萜类、苯类/苯丙素类、脂肪酸衍生物和一些含氮或硫化合物等组成(Pichersky and Dudareva, 2007; Dudareva and Pichersky, 2008; 向林和陈龙清, 2009; 岳跃冲和范燕萍, 2011; 孔滢等, 2012)。Dudareva等(1996)从仙女扇(*Clarkia breweri*)中克隆了编码萜类合成途径上芳樟醇合成酶的*LIS*基因。*LIS*也是最早用于转基因花香育种的目的

表2 观赏植物花型改良分子育种一览表

Table 2 The improvement of flower shape using molecular breeding method in ornamental plants

受体植物	分子设计	性状变化	参考文献
非洲菊 (*Gerbera jamesonii*)	抑制内源基因*GGLO1*、*GDEF1*和*GDEF2*表达	过渡类花瓣消失, 外轮舌状花完全退化	Broholm et al., 2010
	过表达内源基因*GhCYC2*	中间过渡类型花向舌状花转变	Broholm et al., 2008
矮牵牛(*Petunia hybrid*)	转座子*Tpn102*插入*FE*形成突变体	多种不同的花部变异	Iwasaki and Nitasaka, 2006
	利用CRES-T技术抑制内源*DP*表达	双花结构	Sage-Ono et al., 2011
月季 (*Rosa chinensis*)	抑制内源基因*RhAG*表达	双花结构	Dubois et al., 2010
	*RhSEP3SRDX*嵌合蛋白超表达载体将内源*SEP3*转化月季	花瓣完全消失, 仅留存萼片	Ishiguro et al., 2012
	*YAB1SRDX*整合蛋白超表达载体将拟南芥*AtYAB1*转化月季	株型和花型完全改变	Ishiguro et al., 2012
小银莲花(*Anemone rossii*)	抑制内源基因*ThtAG1*表达	双花结构	Galimba et al., 2012
矮牵牛(*Petunia hybrid*)	*PMADS3*和*FBP6*的双突变体	产生多层新的花瓣类器官	Heijmans et al., 2012; Mach, 2012
露地菊(*Chrysanthemum morifolium*)	过表达内源基因*SQU*	舌状花畸形率下降	罗冉, 2011
仙客来(*Cyclamen persicum*)	过表达内源基因*CpTCP1*	花瓣出现褶皱和卷曲	Tanaka et al., 2011

基因, 但将该基因转入矮牵牛和香石竹后, 虽然芳樟醇含量显著提高, 但该类物质无法被人类嗅觉所识别(Lücker et al., 2001; Lavy et al., 2002)。第1个花香育种成功的案例来自Lücker等(2004)对烟草的实验, 他们将柠檬(*Citrus limon*)中3个不同的单萜基因同时转入烟草, 转基因烟草的叶和花中都释放出β-蒎烯、柠檬烯、γ-萜品烯以及很多花香化合物的副产品, 引起了花香的强烈改变。Aranovich等(2007)将从仙女扇中克隆的*BEAT*基因导入洋桔梗(*Eustoma grandiflorum*), 转基因株系只能在有外源添加物质的情况下才产生乙酸苄酯。矮牵牛中异源表达月季*RhAAT*基因(乙醇-乙酰转移酶(alcohol acetyltransferase)基因)产生了芳香物质乙酸苄酯和乙酸苯乙酯, 育成了芳香型矮牵牛转基因株系(Shalit et al., 2003)。

除上述萜类物质合成相关基因的转化外, 改变苯类/苯丙素类化合物途径的分支代谢模式, 亦能增加目的产物的合成, 增强花香。该途径以莽草酸(shikimic acid)为前体, 经苯丙氨酸(phenylalanine)形成反式肉桂酸(*trans*-cinnamic acid), 然后经过一系列甲基转移酶和酰基转移酶的作用甲基化或酰基化, 形成挥发性化合物。在矮牵牛中, 抑制该通路的*BSMT*、*BPBT*、*PAAS*和*CFAT*基因的表达均能部分或完全抑制相应化合物的合成, 产生无香味的转基因株系(Underwood et al., 2005; Kaminaga et al., 2006; Orlova et al., 2006; Dexter et al., 2007)。这些研究结果表明, 上述基因是花香化合物合成途径上分支代谢节点基因。向矮牵牛中转入*ODORANT1*基因, 使得转基因植株经由莽草酸途径合成的芳香物质前体含量减少, 明显降低了花香主要成分(苯类化合物)的释放水平(Verdonk et al., 2005), 表明该基因是花香合成通路的负调节因子。而正调节该基因的2个编码MYB类转录因子的基因, *EOBI*和*EOBII*(*EMISSION OF BENZENOIDS I* and *II*)已被克隆, 矮牵牛的*EOBI*和*EOBII*抑制株系中, 苯类化合物含量较对照降低, 花香变淡(Spitzer-Rimon et al., 2010, 2012; Yuan et al., 2013)。由于苯丙素途径是花青素合成和莽草酸代谢的共同途径, 故对某些花色代谢基因的调控亦能够产生花香新品种。通过在香石竹中反义抑制花青素代谢关键酶编码的*F3H*基因可阻碍花青素的生物合成, 使得代谢转移到苯甲酸的产生上, 导致苯甲酸甲酯的合成量增加, 产生能被人类嗅觉识别的芳香气味(Zuker et al., 2002)。向矮牵牛中转入拟南芥花青素合成途径调节基因*AtPAP1*, 在改变花色的同时, 其体内的苯乙醛含量增加, 增加了转基因矮牵牛的芳香性(Zvi et al., 2008)。将该基因转入月季, 亦能够使转基因月季的挥发类物质萜类化合物的含量增加(6.5倍), 且该变化可被人类嗅觉所区分(Zvi et al., 2012)。

综上所述, 花香分子育种的难度很大, 复杂的代谢网络、代谢通量的变化、受体中底物的特异性以及人类嗅觉的分辨程度差异均有可能导致花香分子育

种的效果不明显。调控花香产生和释放的机制无论理论上还是技术上都仍处于初级阶段(表3)。观赏植物在长期进化过程中, 挥发类物质对植物吸引传粉者和规避害虫均具有非常重要的作用。但由于长期杂交和选择育种, 目前适用于商业化生产的芳香观赏植物产品并不多(Dudareva and Pichersky, 2008), 因此使用转基因手段在商品花卉中重建挥发类香气物质的代谢途径变得非常重要。

4 株型

株型是指植株地上部分的形态特征和空间排列方式, 影响株型的主要因素包括: 株高、分枝数、分枝角度和叶片着生角度等(库丽霞等, 2010)。植物株型形成的遗传调控网络极其复杂, 其精细的调控机理尚未解析。目前, 研究者通过分析突变体并借助转基因技术等方法已分离出一些影响株型的基因(表4)。这些基因主要包括以下几类: 细胞分裂素合成酶基因*IPT3*(于静等, 2012); 独脚金内酯合成和信号转导通路中的*MAX4*/*RMS1*/*DAD1*/*HTD*/*CCD8*/*D10*基因(Johnson et al., 2006; Simons et al., 2007; Crawford et al., 2010; Liang et al., 2010; Domagalska and Leyser, 2011); *TCP*基因家族的*TB1*/*BRC1*/*FC1*基因(Hubbard et al., 2002; Takeda et al., 2003; Chen et al.,

表3 观赏植物花香改良分子育种一览表

Table 3 The improvement of flower scent using molecular breeding method in ornamental plants

受体植物	分子设计	性状变化	参考文献
烟草(*Nicotiana tabacum*)	将3个不同的单萜基因同时转入烟草	引起花香的强烈改变	Lücker et al., 2004
矮牵牛 (*Petunia hybrid*)	过表达月季*RhAAT*基因	产生芳香物质乙酸苄酯和乙酸苯乙酯	Shalit et al., 2003
	通过乙烯调节*PhBSMT1*基因表达	产生无香味的转基因株系	Underwood et al., 2005
	抑制内源基因*BPBT*表达	产生无香味的转基因株系	Orlova et al., 2006
	通过RNAi抑制*PhIGS1*基因表达	产生无香味的转基因株系	Dexter et al., 2007
	抑制*PAAS*基因表达	产生无香味的转基因株系	Kaminaga et al., 2006
	过表达*ODORANT1*基因	降低花香主要成分苯类化合物的释放水平	Verdonk et al., 2005
	过表达拟南芥*AtPAP1*基因	增加苯乙醛含量	Zvi et al., 2008
洋桔梗(*Eustoma grandiflorum*)	过表达仙女扇*BEAT*基因	产生乙酸苄酯	Aranovich et al., 2007
香石竹(*Dianthus caryophyllus*)	抑制内源基因*F3H*表达	导致苯甲酸甲酯的合成量增加	Zuker et al., 2002
月季(*Rosa chinensis*)	过表达拟南芥*AtPAP1*基因	使萜类化合物的含量增加	Zvi et al., 2012

表4 观赏植物株型改良分子育种一览表

Table 4 The improvement of plant type using molecular breeding method in ornamental plants

受体植物	分子设计	性状变化	参考文献
矮牵牛(*Petunia hybrid*)	过表达*LIF*基因	植株变矮, 侧枝增多	Nakagawa et al., 2005
菊花(*Chrysanthemum morifolium*)	过表达*Ls*基因	植株变矮, 侧枝增多, 株型更加紧凑	Han et al., 2007; Jiang et al., 2010; Huh et al., 2013
	过表达*rolC*基因	植株变矮, 侧枝增多, 株型更加紧凑	Mitiouchkina and Dolgov, 2000
	过表达*BRC1*基因	植株变矮, 侧枝增多, 株型更加紧凑	Chen et al., 2013b
香石竹(*Dianthus caryophyllus*)	过表达*rolC*基因	植株发生矮化, 花径变小, 花更加紧凑	Zuker et al., 2001
长寿花 (*Kalanchoe blossfeldi*)	过表达*KxhKN5*基因和*AtSHI*基因	株型紧凑, 花序数目明显增加	Lütken et al., 2011; Lütken et al., 2010
一品红 (*Euphorbia pulcherrima*)	过表达*AtSHI*基因	植株矮化, 节间长度变短, 节间数目和苞片数目减少, 苞片面积减小	Islam et al., 2013

2013b); GRAS蛋白家族的LAS/MOC1/Ls转录因子(Li et al., 2003b; Yang et al., 2005, 2012; Jiang et al., 2010; Huh et al., 2013); 细胞色素P450家族中的*SPS*、*BUSHY*和*Dwarf2*基因(Reintanz et al., 2001; Tantikanjana et al., 2001; 张伟强等, 2011); 毛根农杆菌*rol*基因(Zuker et al., 2001); MYB转录因子家族的*RAX*/*BL*基因(Keller et al., 2006); *SHI*基因家族的*SHI*/*STY1-2*/*LRP1*/*SRS3-8*基因(Islam et al., 2013); HD-ZIPIII转录因子家族的*REV*基因(Talbert et al., 1995); TFIIIA-type锌指蛋白家族的*SUP*/*TIF*/*ZFP*基因(Nakagawa et al., 2005); *LAZY1*基因(Li et al., 2007)和*TAC1*基因(Yu et al., 2007)等。株型对观赏植物来说既是观赏性状又是重要的经济性状。观赏植物的株型对其经济价值具有决定性作用。目前的研究热点是培养株型矮小、紧凑且能够自然分枝的盆栽花卉以及侧芽少、枝干挺立的鲜切花品种(周晓阳等, 2012)。在矮牵牛中过表达*LIF*基因的转基因株系植株变矮、侧枝增多(Nakagawa et al., 2005)。菊花中过表达*Ls*基因(Han et al., 2007; Jiang et al., 2010; Huh et al., 2013)、*rolC*基因(Mitiouchkina and Dolgov, 2000)和*BRC1*基因(Chen et al., 2013b)后, 其转基因株系植株变矮、侧枝增多且株型更加紧凑。在香石竹中过表达*rolC*基因使植株发生矮化, 花径变小, 花更加紧凑(Zuker et al., 2001)。在长寿花(*Kalanchoe blossfeldi*)中过表达*KxhKN5*基因(Lütken et al., 2011)和*AtSHI*基因(Lütken et al., 2010), 其转基因株系株型紧凑、花序数目明显增多。在一品红(*Euphorbia pulcherrima*)中过表达*AtSHI*基因, 其植株矮化, 节间长度变短, 节间数目和苞片数目减少, 苞片面积减小(Islam et al., 2013)。这些研究结果表明, 利用转基因技术可以改变株型这一观赏性状。

5 开花期

观赏植物的开花期是构成其观赏价值的重要内容之一。在观赏植物的生产中, 控制产品的开花期, 适时上市可直接影响其在市场上的价格。因此花期始终是观赏植物品种改良的重要目标性状之一(王翊等, 2010)。通过对模式植物拟南芥开花调控网络的研究, 发现目前主要有6条成花调控途径: 光周期途径和春化途径响应季节变化过程中日长和温度的变化(Kobayashi and Weigel, 2007); 环境温度途径响应栽培环境中的温度变化(Lee et al., 2007); 自主途径、赤霉素途径和年龄途径响应自身生长发育状况的变化(Amasino and Michaels, 2010; Fornara et al., 2010; Andrés and Coupland, 2012)。在不断变化的外部环境条件和内部生理条件下, 这些途径通过一些主要的整合因子(如*SOC1*、*FT*和*LFY*等)的作用实现对拟南芥开花时间的精确调控(Lee and Lee, 2010)。目前人们研究的热点是分离观赏植物的整合因子基因, 并希望通过转基因技术获得开花期提前的转基因株系, 真正实现花期可控。*LFY*基因是最早研究的整合子之一, 向欧洲山杨(*Populus tremula*)(Weigel and Nilsson, 1995)、菊花(邵寒霜等, 1999)、杨树(*P. trichocarpa*)(Rottmann et al., 2000)和大岩桐(*Sinningia speciosa*)(Zhang et al., 2008)中转入*LFY*的同源基因均获得了开花期提前的转基因株系。此外, *LFY*的同源基因还可决定花由营养生长向生殖生长转变(Ma et al., 2008b)。近几年来的研究结果表明, FT蛋白就是“成花素”, 可以通过韧皮部从叶片运输到茎端分生组织, 与bZIP转录因子FD互作, 共同激活花分生组织基因*AP1*的表达, 从而促进拟南芥成花转换并启动花发育过程(Abe et al., 2005; Corbesier et al., 2007; Notaguchi et al., 2008; Li et al., 2009; Matsoukas et al., 2012; Xu et al., 2012; Taoka et al., 2013)。因此, 人们逐渐将研究的热点转移到*FT*基因的功能研究上。在草本观赏植物菊花中过表达*CsFTL3*基因(Nakatsuka et al., 2009; Oda et al., 2011)、三花龙胆(*Gentiana triflora*)中过表达*GtFT1*和*GtFT2*基因或抑制*GtTFL1*基因(Imamura et al., 2011)、牵牛花中过表达*FT2*基因(Hayama et al., 2007)的转基因株系开花均提前。相对草本观赏植物而言, 木本观赏植物转基因提前开花的效果更加明显。欧洲山杨中过表达*PtFT1*基因的转基因株系仅需4周即可成花, 而未转基因植株则需要8–12年才能开花(Böhlenius et al., 2006)。美洲黑杨(*Populus deltoides*)幼龄期植株过表达*FT2*基因的转基因株系1年即可开花(Hsu et al., 2006)。因此, 通过分子育种技术改良木本植物的开花期应用前景非常广阔。此外, 目前还有一些关于MADS-box基因改变观赏植物花期的报道。石斛兰(*Dendrobium nobile*)中过表达*DOSOC1*基因(Ding et al., 2013)、文心兰(*Oncidium*)中过表达*OMADS1*基因

(Thiruvengadam et al., 2012)、菊花中过表达*AP1*基因(Shulga et al., 2011)、洋桔梗中过表达麝香百合(*Lilium longiflorum*)*LMADS1-M*基因和文心兰*OMADS1*基因(Thiruvengadam and Yang, 2009)均可导致转基因株系提前开花。通过转基因技术获得开花期推后的转基因株系则报道较少。表5为观赏植物花期改良分子育种的研究进展。

6 抗逆性

6.1 非生物胁迫

在现代切花和盆花生产中, 由于精细栽培设施和智能光温系统的推广, 非生物胁迫对观赏植物的影响已经越来越小(Chandler and Brugliera, 2011)。但要实现高效节能的集约化生产, 提高抗逆性仍是改良观赏植物品质的重要内容。在露地栽培和园林景观营造中, 抗非生物胁迫则始终是观赏植物育种的一项重要内容。

高等植物通过转录因子、各类信号转导途径识别和传递逆境信号, 继而通过编码活性氧清除系统、离子平衡系统和渗透保护物质抵御逆境、获得抗性(Gechev and Hille, 2012)。目前, 已在多种观赏植物中分离到了上述“识别”和“抵御”逆境的功能基因, 并在模式植物中得到了功能验证。

DREB类转录因子是调控高等植物抗干旱、耐盐渍和低温最重要的一类转录因子, 也是抗逆基因工程中最常被选择的目标基因, 其在多种观赏植物抗非生物胁迫过程中发挥“节点”基因的作用(Yang et al., 2009; Chen et al., 2011a; Huang et al., 2012)。转拟南芥*AtDREB1A*基因的菊花品种Fall Color, 在高温胁迫下能够快速积累热激蛋白(Hong et al., 2009); 在干旱和盐碱胁迫下脯氨酸的积累量增加, 过氧化物酶的活性增强(Hong et al., 2006)。Yang等(2009)从菊花品种神马中分离得到2个*DREB*的同源基因*CgDREBa*和*CgDREBb*, 转*CgDREBa*的菊花品种神马在盐胁迫下抗活性氧能力亦显著增强(Chen et al., 2011a)。另有报道, 将抗寒信号通路DREB-CBF途径的*ICE1*、*CBF*和*DREB1C*等基因转入菊花、矮牵牛和月季中(Chen et al., 2010, 2012; Chandler and Sanchez, 2012), 均能够提高转基因植株的抗冷性, 且转基因植株的其它观赏特性不变。

表5 观赏植物开花期改良分子育种一览表

Table 5 The improvement of flowering period using molecular breeding method in ornamental plants

受体植物	分子设计	性状变化	参考文献
欧洲山杨 (*Populus tremula*)	过表达*LFY*基因	开花期提前	Weigel and Nilsson, 1995
	过表达*PtFT1*基因	转基因株系仅需4周即可成花, 而未转基因植株则需要8–12年才能开花	Böhlenius et al., 2006
杨树(*P. trichocarpa*)	过表达*LFY*基因	开花期提前	Rottmann et al., 2000
大岩桐(*Sinningia speciosa*)	过表达*LFY*基因	开花期提前	Zhang et al., 2008
菊花(*Chrysanthemum morifolium*)	过表达*CsFTL3*基因	开花期提前	Nakatsuka et al., 2009; Oda et al., 2011
	过表达*AP1*基因	开花期提前	Shulga et al., 2011
三花龙胆 (*Gentiana triflora*)	过表达*GtFT1*基因	开花期提前	Imamura et al., 2011
	过表达*GtFT2*基因	开花期提前	Imamura et al., 2011
	抑制*GtTFL1*基因	开花期提前	Imamura et al., 2011
牵牛花(*Petunia hybrid*)	过表达*FT2*基因	开花期提前	Hayama et al., 2007
美洲黑杨(*P. deltoides*)	过表达*FT2*基因	转基因株系1年即可开花	Hsu et al., 2006
石斛兰(*Dendrobium nobile*)	过表达*DOSOC1*基因	开花期提前	Ding et al., 2013
文心兰(*Oncidium*)	过表达*OMADS1*基因	开花期提前	Thiruvengadam et al., 2012
洋桔梗 (*Eustoma grandiflorum*)	过表达麝香百合*LMADS1-M*基因	开花期提前	Thiruvengadam and Yang, 2009
	过表达文心兰*OMADS1*基因	开花期提前	Thiruvengadam and Yang, 2009

除转录因子的转基因育种外，还有一些关于导入结构基因培育抗逆观赏植物的报道。Xu等(2009)将拟南芥钠氢反转运体基因(*AtNHX1*)转入矮牵牛，转基因植株在盐胁迫下维持较高水势、钠钾离子平衡和脯氨酸含量。Sun等(2013b)将赤霉素代谢途径基因*GASA14*转入非洲菊，发现其不仅能够调节叶片伸展大小，还能够提高转基因植株的抗非生物胁迫能力。将拟南芥和水稻(*Oryza sativa*)的脯氨酸合成基因*P5CS*转入矮牵牛，获得了在干旱胁迫下正常生长的转基因株系(Yamada et al., 2005)。

6.2 生物胁迫

真菌、细菌、病毒、病原体以及虫害会对花卉生产及销售的各个环节带来毁灭性打击。传统的育种方法和化学药剂防治均不能在真正意义上实现抗生物胁迫花卉新品种的培育，转基因育种是一条经济可行的育种策略。综合国内外报道，培育抗镰孢菌、葡萄孢属真菌、锈病、黑斑病、白粉病和蚜虫的观赏植物新品种，是现代花卉生产中抗生物胁迫最为重要的育种目标(Chandler and Tanaka, 2007)。

植物对病毒和真菌的识别主要通过3种方式实现，即“基因对基因”模式、“激发子/受体”模式和防卫模式。目前，转基因育种的策略有2种。第1种是转入植物自身编码的抗病毒基因，这类基因以编码小分子蛋白和次生代谢物质类基因为主。如转山蒜菜防御素基因(*wasabi defensin gene*)的蝴蝶兰(*Phalaenopsis amabilis*)，转商陆抗病毒蛋白(pokeweed antiviral protein, PAP)基因的矮牵牛，二者均获得了抗胡萝卜软腐病和黄瓜花叶病毒(*Cucumber mosaic virus*)的免疫(Sjahril et al., 2006; Li et al., 2012)。向矮牵牛中转入拟南芥编码参与植物抗毒素合成的*AtACT*基因，获得了抗葡萄孢菌的矮牵牛品系(Muroi et al., 2012)。于淼等(2010)采用农杆菌介导法将梅(*Prunus mume*)的多聚半乳糖醛酸酶抑制蛋白基因(*PGIP*)转入菊花，获得了抗真菌病的菊花株系。Li等(2003a)将洋葱(*Allium cepa*)转脂蛋白基因*Ace-AMP1*转入月季，获得了对蔷薇单丝壳菌(*Sphaerotheca pannosa*)抗性提高的转基因月季株系。在马蹄莲(*Zantedeschia elliottiana*)中异源表达铁氧化还原蛋白类似基因(*plant ferredoxin-like protein gene*, *PFLP*)，增强了转基因株系对软腐病的抗性(Yip et al., 2007)。Sen等(2013)将水稻几丁质酶基因(*CHILL*)转入菊花，也获得了抗*Septoria obesa*以免疫叶斑病的菊花品种(Sen et al., 2013)。第2种育种策略是利用源于病毒编码的基因，如衣壳蛋白基因(*coat protein*, *CP*)、RNA复制酶基因和反义链RNA等。Clarke等(2008)利用病毒介导的发卡RNA法成功抑制了一品红内源的猩猩木花叶病毒(*Poinsettia mosaic virus*)，获得了抗性飞跃式提高的转基因株系。将病毒的衣壳蛋白基因转化到植物细胞内，可使*CP*基因在植物细胞内表达，进而使转基因植物获得抗该病毒的能力。抗蕙兰花叶病毒(*Cymbidium mosaic virus*)的兰花品种和蝴蝶兰品种(Chang et al., 2005)、抗齿舌兰环斑病毒(*Odontoglossum ringspot virus*)的卡特兰(*Cattleya*)品种(Zhang et al., 2010)及抗黄瓜花叶病毒和菊花B病毒的菊花品种(Mitiouchkina et al., 2004; Kumar et al., 2012)均是通过该方法获得。除转化衣壳蛋白基因外，还可将病毒的RNA复制酶基因向目的植物转化以提高该植物的抗病性，如抗黄瓜花叶病毒的百合品种Acapulco即是通过这种方法获得(Azadi et al., 2011)。Xu等(2010)将黄单孢菌属内源$hpaGX_{oo}$基因转入菊花，获得了抗链格孢叶斑病的菊花品系。

目前，Bt基因已成为抗虫基因工程研究和应用最多的基因。Bt蛋白质晶体由*cry*和*cyt*编码，能在一些昆虫体内活化成有毒性的蛋白，并与昆虫中肠上皮细胞的特异性受体结合，使其产生穿孔，从而杀灭昆虫。将*cry1AcFm*导入紫罗兰(*Matthiola incana*)增强了其对小菜蛾(*Plutella xylostella*)的抗性(Mii et al., 2011)。将*cry1Ab*、*cry1Ac*和*cry1Ca*转入菊花，获得了抗夜蛾(*Spodoptera litura*)和粘虫(*Spodoptera exigua*)的转基因株系(Shinoyama et al., 2008; Rattan, 2010; Teixeira da Silva et al., 2013)。Shinoyama等(2012)还通过过表达*cry1Ab*基因，抑制菊花内源减数分裂重组酶基因(*meiosis-specific recombinase gene*)，获得了对多种害虫具有广谱抗性的菊花品种，但其作用机理尚不清楚。目前，关于通过非转Bt类基因获得抗虫观赏植物的报道还不多见。Kim等(2011a)将咖啡碱合成途径中的3个甲基转移酶基因转入菊花，培育出了能合成咖啡碱的转基因株系，含有咖啡碱的菊花叶片对甜菜粘虫(*Spodoptera exigu*)和棉蚜(*Aphis gossypii*)表现出较强的

抗性, 同时也发现转基因菊花的叶片中水杨酸含量大幅度提高, 对一些真菌病原的抗性也明显增强(Kim et al., 2011b)。根据这些研究结果开展的观赏植物抗逆性改良的分子育种研究也取得了很好的进展(表6)。

7 采后保鲜品质

切花生产中, 花枝瓶插寿命长短是最为重要的农艺性状和育种目标。近年来分子育种技术也被用于鲜切花采后保鲜品种改良的育种研究(表7)。鲜切花被剪下离

表6 观赏植物抗逆性改良分子育种一览表

Table 6 The improvement of stress resistance using molecular breeding method in ornamental plants

受体植物	分子设计	性状变化	参考文献
菊花 (*Chrysanthemum morifolium*)	过表达拟南芥*AtDREB1A*基因	高温胁迫下能够快速积累热激蛋白; 干旱和盐碱胁迫下脯氨酸的积累和过氧化物酶活性增强	Hong et al., 2006, 2009
	过表达*CgDREBa*基因	盐胁迫下抗活性氧能力显著增强	Chen et al., 2011a
	过表达异色菊*ICE1*基因	转基因植株耐热性、抗旱性和耐盐性提高	Chen et al., 2012
	过表达梅*PGIP*基因	转基因株系对黑斑病有不同程度的抗性	于淼等, 2010
	过表达水稻几丁质酶基因	获得免疫叶斑病的品种	Sen et al., 2013
	过表达CVB衣壳蛋白基因	获得抗菊花B病毒的品种	Mitiouchkina et al., 2004
	过表达CMV衣壳蛋白基因	获得抗黄瓜花叶病毒的品种	Kumar et al., 2012
	过表达黄单孢菌属内源*hpaGX$_{oo}$*基因	获得抗链格孢叶斑病的品系	Xu et al., 2010
	过表达*cry1Ab*、*cry1Ac*和*cry1Ca*基因	获得抗夜蛾和粘虫的转基因株系	Shinoyama et al., 2008; Rattan, 2010; Teixeira da Silva et al., 2013
	过表达*cry1Ab*基因, 并抑制菊花内源减数分裂重组酶基因	获得对多种害虫具广谱抗性的菊花品种	Shinoyama et al., 2012
	过表达3个甲基转移酶基因	转基因株系对甜菜粘虫和棉蚜表现出较强的抗性	Kim et al., 2011a, 2011b
矮牵牛 (*Petunia hybrid*)	过表达*CBF*基因	转基因植株抗冷性提高	Chandler and Sanchez, 2012
	过表达拟南芥*AtNHX1*基因	转基因株系抗盐和抗旱性提高	Xu et al., 2009
	过表达拟南芥或水稻*P5CS*基因	干旱胁迫下转基因株系脯氨酸积累量增加, 生长正常	Yamada et al., 2005
	过表达拟南芥*AtACT*基因	获得抗葡萄孢菌的品系	Muroi et al., 2012
月季 (*Rosa chinensis*)	过表达蒺藜苜蓿*DREB1C*基因	转基因植株抗冷性提高	Chen et al., 2010
	过表达洋葱*Ace-AMP1*基因	获得对蔷薇单丝壳菌抗性提高的转基因株系	Li et al., 2003a
蝴蝶兰 (*Phalaenopsis amabilis*)	转山蒿菜防御素基因	获得抗胡萝卜软腐病的抗性	Sjahril et al., 2006
马蹄莲 (*Zantedeschia elliottiana*)	异源表达*PFLP*基因	转基因株系对软腐病的抗性增强	Yip et al., 2007
一品红 (*Euphorbia pulcherrima*)	病毒介导的发卡RNA法抑制内源猩猩木花叶病毒	获得抗性飞跃式提高的转基因株系	Clarke et al., 2008
石斛兰 (*Dendrobium nobile*)	过表达衣壳蛋白基因	获得抗蕙兰花叶病毒的品种	Chang et al., 2005
卡特兰 (*Cattleya labiata*)	过表达齿舌兰环斑病毒复制酶基因	获得抗齿舌兰环斑病毒的品种	Zhang et al., 2010
紫罗兰(*Matthiola incana*)	过表达*cry1AcFm*基因	增强植株对小菜蛾的抗性	Mii et al., 2011

表7 观赏植物分子育种改良采后保鲜品质一览表

Table 7 The improvement of disease of postharvest asparagus using molecular breeding method in ornamental plants

受体植物	分子设计	性状变化	参考文献
香石竹 (*Dianthus caryophyllus*)	使用矮牵牛花部特异性启动子*fbp1*转化*etr1-1*基因	获得瓶插寿命长且不影响其它观赏品质的香石竹转基因株系	Bovy et al., 1999
矮牵牛 (*Petunia hybrid*)	转化*etr1-1*基因	*etr1-1*在调控花朵衰败时间上呈现完全显性	Clevenger et al., 2004
	使用衰老阶段特异作用启动子*SAG12*转化异戊烯转移酶基因*IPT*	转基因株系花冠衰老延迟, 对乙烯敏感性降低	Chang et al., 2003
菊花(*Chrysanthemum morifolium*)	转化突变型乙烯受体基因*mDG-ERS1*	培育出乙烯不敏感型切花品种	Narumi et al., 2005
月季 (*Rosa chinensis*)	利用VIGS沉默*RhNAC2*或*RhEXPA4*基因	月季花瓣的耐失水性和扩展能力降低	Dai et al., 2012
	利用VIGS沉默*RhNAC100*基因	沉默该基因的表达明显促进了月季花瓣面积的增加和细胞的扩展	Pei et al., 2013
	使用衰老阶段特异作用启动子*SAG12*转化异戊烯转移酶基因*IPT*	转基因株系叶片衰老延迟, 对外源乙烯抗性增强	Zakizadeh et al., 2013
丛生风铃草 (*Campanula carpatica*)	使用矮牵牛花部特异性启动子*fbp1*转化*etr1-1*基因	获得乙烯不敏感株系	Sriskandarajah et al., 2009
长寿花 (*Kalanchoe blossfeldiana*)	使用矮牵牛花部特异性启动子*fbp1*转化*etr1-1*基因	获得乙烯不敏感株系	Sanikhani et al., 2008

开母体后, 会发生失水胁迫, 导致乙烯生成量升高, 加速花朵的衰老和脱落, 抑制花瓣的扩张。因此, 乙烯是造成切花采后损失的重要因素。降低切花对乙烯的敏感性或抑制乙烯的合成是提高采后品质的主要手段(Chandler and Sanchez, 2012)。

传统的化学保鲜处理大量使用银离子和其它有害人体健康的化学试剂(Lütken et al., 2012)。通过转基因育种培育瓶插寿命长且绿色环保的切花品种能够有效解决这一问题。对香石竹、三色堇(*Viola tricolor*)和圣诞秋海棠(*Begonia×cheimantha*)等植物内源乙烯合成基因*ACC*或*ACO*进行抑制, 均得到不释放内源乙烯的转基因株系, 但转基因株系仍能受到空气中乙烯的影响, 切花瓶插寿命并未明显改变(Hvoslef-Eide et al., 1995; Savin et al., 1995; Aida et al., 1998)。为此, 研究者将目光转向了植物识别乙烯信号的受体上, 乙烯受体是植物感受乙烯的关键因子, 是乙烯信号转导途径的首要环节。拟南芥中乙烯受体*ETR1*的显性突变基因*etr1-1*丧失了对乙烯信号的识别, 突变植株对乙烯极不敏感(Bleecker et al., 1988)。将这类*etr1-1*突变型基因转入香石竹、兰花、矮牵牛、菊花和龙面花(*Nemesia strumosa*)中, 均培育出了乙烯不敏感型切花品种, 其采后保鲜时间长且叶片衰老和黄化现象降低(Bovy et al., 1999; Clevenger et al., 2004; Narumi et al., 2005; Raffeiner et al., 2009)。

近年来, 研究者发现月季中的*Agos*基因、水通道蛋白基因(*Rh-PIP1;1*, *Rh-PIP2;1*)及扩展蛋白基因*RhEXPA4*均位于乙烯信号转导途径的下游, 在乙烯对花瓣细胞扩展的抑制中起重要作用, 抑制该类基因均能够促进月季花瓣的扩展(Ma et al., 2008a; Chen et al., 2013a; Lü et al., 2013)。而*NAC*基因家族的2个成员*RhNAC2*和*RhNAC100*有可能是乙烯信号转导通路的正、负调控因子, *RhNAC2*可以直接调节*RhEXPA4*的表达, 抑制该基因显著降低月季花瓣的耐失水性和花瓣的扩展能力(Dai et al., 2012), 而RhNAC100是细胞扩展的负调节因子, 抑制该基因的表达明显促进月季花瓣面积的增加和细胞的扩展(Pei et al., 2013)。

由于乙烯是重要的植物内源激素, 在抗病和营养繁殖方面发挥着重要作用, 因此对该信号通路的基因转化有可能影响其它生物学过程(Lütken et al., 2012)。Bovy等(1999)使用矮牵牛花部特异性启动子*fbp1*连接*etr1-1*, 获得了瓶插寿命长且不影响其它观赏品质的香石竹转基因株系。继而这一策略被成功地

应用于丛生风铃草(*Campanula carpatica*)(Sriskandarajah et al., 2009)、长寿花(Sanikhani et al., 2008)、齿舌兰(*Odontoglossum crispum*)和文心兰(Raffeiner et al., 2009)等观赏植物中。

除了降低乙烯的生物合成, 延长瓶插寿命的另一策略是增加衰老过程中的细胞分裂素合成。将衰老阶段特异作用启动子*SAG12*(Gan and Amasino, 1997)与异戊烯转移酶基因*IPT*连接转化矮牵牛和月季(Chang et al., 2003; Zakizadeh et al., 2013), 均得到了瓶插时间长的新品种。

8 问题与展望

综上所述, 目前国际上在观赏植物分子育种研究领域取得了可喜的进展。已有34种花卉成功获得转基因株系, 累计导入约90个基因, 分子育种研究几乎覆盖所有观赏性状(表1–表7)。研究较多的受体植物主要有菊花、月季、矮牵牛和香石竹, 较为成功的实例主要集中在花色的改良上。这些研究成果说明, 利用分子育种技术进行观赏植物品质改良是可行的, 但是目前尚存在很多问题需要进一步探讨。

8.1 观赏性状形成的遗传调控机理有待深入研究

从上述研究进展来看, 观赏性状形成的遗传调控机理还有待深入研究。例如, 尽管关于花色素合成的机理研究得较为透彻, 但是关于色素呈色的机理还远没有被清楚阐释, 转基因改良花色的物种和花色改良的程度还很有限。关于其它观赏性状形成的机理也远没有彻底明晰, 很多转基因育种工作仅仅凭借人们对模式植物的理解进行。而观赏植物复杂的遗传背景往往使得这些转基因植物的观赏品质改良的效果不够明显。因此, 对受体植物遗传背景的解析还是观赏植物研究领域一项长期的任务。对特定物种重要观赏性状的遗传调控机理研究是开展转基因育种的基础。

8.2 转基因的受体系统尚待进一步完善

观赏植物分子育种的复杂性还在于建立不同品种和品系的再生和转化体系并非易事。目前, 只有月季、菊花和香石竹等几种花卉的再生和转化体系相对容易建立, 但是要获得不同基因型的再生和转化系统尚需要开展大量的实验工作。

8.3 寻找更加有效的外源基因

对已有观赏植物转基因成功的案例进行分析, 发现不同来源的外源基因导入受体植物获得表型性状改良的程度不同, 这不仅涉及结构基因, 还涉及调控序列。因此, 挖掘有效的基因资源用于观赏植物品种改良也是一项长期而艰巨的任务。

随着模式植物功能基因组学、代谢组学、蛋白质组学和表观遗传学等研究的不断深入, 以及新技术和新方法的不断涌现, 观赏植物品质形成机理的研究正在向纵深方向发展, 这些研究将会为观赏植物分子育种工作的开展奠定更为坚实的理论基础。

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Advances in Molecular Breeding of Ornamental Plants

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Abstract Molecular breeding of plants has great advantages over traditional breeding in breaking the isolation among species, accelerating the process of breeding and achieving new and unique mutants. Its application in breeding ornamental plants will increase the quality of products and enhance the competence of relevant industries. This paper summarizes advances in research into molecular breeding of ornamental plants in the last decade.

Key words ornamental plants, ornamental traits, molecular breeding

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