

Molecular Mechanisms and Natural Selection of Flower Color Variation

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Abstract

Flower color plays a key role in attracting pollinators, and a staggering variety of flower color variations including color parameters and pigmentation pattern exist in nature. Though many studies have been done on the molecular mechanisms of flower color variation, there is still much unknown, especially for pigmentation pattern. The contributions of pollinator and non-pollinator agents to natural selection on floral color variation are also unclear. The review discusses recent data on genetic mechanisms and natural selection of flower color variation. The summary may assist us to further analyze molecular mechanisms of flower color diversity and role of natural selection in flower color variation.

Keywords

Anthocyanin, Floral Color Variation, Pollinators, Fitness, Natural Selection

花色表型变异的分子机制及自然选择

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摘要

花色对吸引传粉者具有非常重要的作用。自然界的花色具有多样性, 主要包括色调和着色模式的变异。虽然前人对花色变异的物质和遗传基础做了大量的研究, 但许多花色变异模式特别是着色模式的分子机制还不清楚。传粉者与非传粉者因素介导的自然选择对花色表型变异的选择机制也有许多未解之谜。本文主要对已知花色表型变异的分子机制及自然选择对花色表型的选择作用进行综述, 以便进一步地探索花色多样性存在的机制和自然选择对花色进化方向的影响。

关键词

花青素, 花色变异, 传粉者, 适合度, 自然选择

1. 引言

花部性状特别是花色在吸引传粉者方面起着非常重要的作用。花色的呈现具有一定的遗传基础, 且需要环境的参与。植物生理生化环境和花青素代谢途径上结构或调控基因的突变均可能带来花色表型的变异。自然界花色表型具有多样性, 主要体现在花色参数和着色模式上。但许多花色变异模式的存在机理还不清楚, 花色变异与自然选择之间的关系也需要深入研究。本文就花色呈现的生理生化基础、已知的花色变异遗传机制和传粉者及非传粉介质(如基因多效性、环境因子、病原菌、啃食者等)对花色进化的影响进行总结, 以利于探讨花色多样性存在的机制。

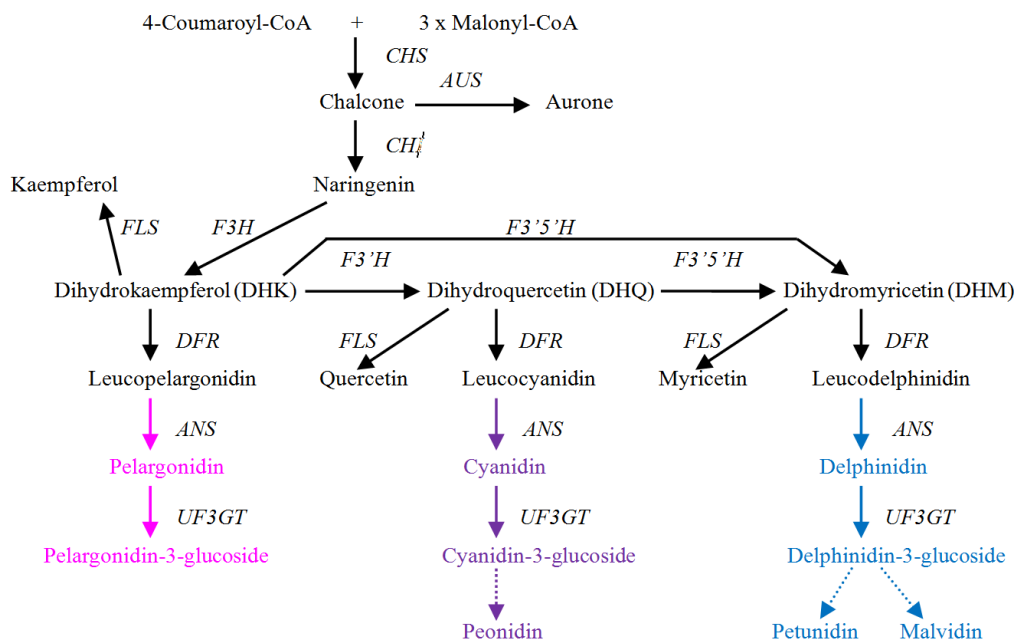
2. 花色呈现的分子基础

2.1. 花色呈现的生化生理基础

花色呈现物质主要有三大类: 甜菜碱(betalains)、类胡萝卜素(carotenoids)和类黄酮(flavonoids) [1] [2] [3]。其中甜菜碱、类胡萝卜素和部分类黄酮(如黄酮、黄酮醇、橙酮)可使花色呈现黄、红等色, 类黄酮中的花青素是花色多样性最主要的物质基础。不同类型的花青素可使花呈现红、粉、紫、蓝等颜色。花青素在细胞质中不稳定而主要以花色苷(配糖体)的形式存在于植物液泡中[1] [4]。花青素苷元主要有天竺葵素(pelargonidin)、矢车菊素(cyanidin)、飞燕草素(delphinidin)、芍药花素(peonidin)、碧冬茄素(petunidin)和锦葵素(malvidin) 6 大类[5] [6] [7]。它们均具有 C6-C3-C6 的基本骨架[3] [8] [9], 结构上的不同主要体现在 B-环上羟基化、甲基化的程度。羟基越多, 花色越蓝; 甲基多则花色趋红。花青素苷元还会发生不同程度的糖基化和酰基化使其更稳定。糖基化使花色发生轻微红移; 被香豆酸、肉桂酸等芳香族氨基酸酰化会使花色发生蓝移[3] [10]。羟基化、甲基化、糖基化和酰基化等修饰使花青素种类丰富多样, 赋予了花色的多样性。随着技术的进步, 越来越多的花青素被分离鉴定[11] [12] [13]。至 2007 年, 自然界共有约 500 种花青素被鉴定[14]。除了花青素类别, 花瓣细胞形状[15] [16] [17]、液泡 pH [18]-[25]、细胞共色素及金属离子的存在[3] [12]都会影响花色的呈现。如飞燕草素在较高的 Fe^{3+} 下会使郁金香(*Tulipa gesneriana*)呈现蓝色[26] [27]。

2.2. 花色呈现的遗传基础

花青素的合成是研究比较清楚的一个次生代谢通路(图 1) [3] [28] [29]。它以香豆酰辅酶 A(4-coumaroyl-CoA)



CHS: 查尔酮合酶(chalcone synthase); **CHI:** 查尔酮异构酶(chalcone isomerase); **F3H:** 黄酮-3-羟化酶(flavanone 3-hydroxylase); **F3'H:** 类黄酮-3'-羟化酶(flavonoid 3'-hydroxylase); **F3'5'H:** 类黄酮-3'5'-羟化酶(flavonoid 3'5'-hydroxylase); **DFR:** 二氢黄酮醇还原酶(dihydroflavonol reductase); **ANS:** 花青素合酶(anthocyanidin synthase); **UF3GT:** 尿苷二磷酸-葡萄糖-类黄酮-3-葡萄糖基转移酶(UDP glucose flavonoid-3-glucosyltransferase)

Figure 1. Anthocyanin biosynthetic pathway (modified from [132])

图 1. 花青素代谢途径(修改自[132])

和丙二酰辅酶 A(malonyl-CoA)为底物, 由结构基因(*CHS*、*CHI*、*F3H*、*F3'H*、*F3'5'H*、*DFR* 和 *ANS*)编码的一系列酶催化合成, 并经糖基化、甲基化和酰基化等修饰后被转运至液泡中。其中 *F3H*、*F3'H* 和 *F3'5'H* 为花青素代谢途径的三个分支酶, 其合成产物分别对应于天竺葵素、矢车菊素和飞燕草素。这些酶基因在许多植物中均已被克隆[6] [28]。它们可能是以多酶复合物的形式在内质网膜上行使催化功能[2] [3] [30]。花青素代谢与初级代谢之间具有密切的联系。来自圆叶牵牛的数据显示其底物香豆酰辅酶 A 与丙二酰辅酶 A 分别来自于苯丙氨酸(phenylalanine)合成途径和糖酵解(glycolysis)过程[31]。

已知花青素代谢途径由 *MYB*、碱性螺旋-环-螺旋(bHLH)和 *WD40* 重复蛋白(WDR)三类调控因子主要以 *MBW* 三元复合物的形式调控[3] [22]。其中 *WDR* 的表达具有广泛性, 而 *MYB* 和 *bHLH* 的表达却仅限于特定组织[32]-[38]。除参与花青素代谢途径外, 不同组合的 *MBW* 复合物还参与液泡 pH 的控制、原花青素的合成、根毛形成、表皮细胞形状的决定和着色模式等过程。其中 *MYB* 决定了其功能的特异性[33] [34] [39]。在 *MBW* 复合物中, *MYB* 和 *bHLH* 可分别特异地结合结构基因启动子区的 *cis* 元件——*ANCNNCC* (MRE, *MYB*-recognizing element)和 *CACN(A/C/T) (G/T)* (*BRE*, *bHLH*-recognizing element), 且 *MRE* 与 *BRE* 之间偏爱 6 bp 的间隔[29] [40] [41]。

但一些 *MYB* 可单独起作用。如在玉米(*Zea mays*)中, *P1*(subgroup7)可单独激活花青素合成的一部分基因(*CHS*、*CHI*、*DFR*、*FLS*)而促进玉米粒中鞣酐(phlobaphene)的合成[25] [36] [42] [43]。在拟南芥(*Arabidopsis thaliana*)中, *CHS*、*CHI*、*F3H*、*F3'H*、*FLS* 可被一些冗余的 *R2R3MYB* (*MYB11*、*MYB12*、*MYB111*) (subgroup7)单独激活[44]。

3. 常见花色表型变异的遗传机制

花色表型多样性不仅体现在花色参数上, 多样的着色模式(图 2)更加丰富了花色的多态。这些变异可



a. 色折(color break): 水仙(*Narcissus pseudonarcissus*) [61]。b-f. 彩斑(variegation): b. 圆叶牵牛(*Ipomoea purpurea*) [62]; c-e. 裂叶牵牛(*I. nil*) [63]; f. 大丽花(*Dahlia variabilis*) [64]。g-j. 缘环(marginal picotee): 矮牵牛(*Petunia hybrid*) [65]。k. 双色花(bicolor)大丽花(*Dahlia variabilis*) [66]。l. 星状(star-type): 矮牵牛(*Petunia hybrid*) [67]。m-n. 紫外模式(UV/bull's eye): 黑心金光菊(*Rudbeckia hirta*): m. 可见光下; n. 紫外光下[68]。o-q. 脉色(venation): o. 金鱼草(*Antirrhinum majus*) [69]; p. 矮牵牛(*Petunia hybrid*); q. 大花蕙兰(*Cymbidium hybrida*) [70]。r-s. 芽红(bud flush): r. 苹果(*Malus × domestica*) [71]; s. 岷江百合(*Lilium regale*) [71]。t-v. 斑点(spot): t. 细长山字草(*Clarkia gracilis*) [72]; u. 郁金香(*Tulipa gesneriana* cv. Murasakizuisho) [27]; v. 蝴蝶兰(*Phalaenopsis* spp. I-Hsin Sun Beauty “KHM1065”) [73]。w. 抬升的斑点(raised spot): 东方百合(Oriental hybrid lily “Le Reve”) [74]。x. 飞溅的斑点(splatter spot): 亚洲百合(Asiatic hybrid lily “Latvia”) [74]。y. 束状斑点(brushmarks): 亚洲百合(Asiatic hybrid lily “Centrefold”) [74]。z. 晕状斑点(spot-halo): 毛地黄(*Digitalis purpurea*) [69]

Figure 2. Reported types of pigmentation pattern

图2. 已报道的花色着色模式类型

能有利于增加植物的环境适应性。花色的变异具有一定的遗传基础，花青素代谢途径上结构或调控基因的突变(包括编码区和调控区)都或多或少会影响基因的功能或表达量而影响花色，基因的组织特异性表达或功能分化也会影响花色表型。

3.1. 花色的获得

花青素代谢为类黄酮的一个代谢分支，根据类黄酮类物质和代谢途径基因类似片段的的存在与否，人们推断类黄酮代谢途径应该起源于植物登陆[45]。一些基因功能的获得可能源于基因重复后的功能分化，如 *CHI* 被推测起源于脂肪酸合酶基因功能分化[46]。从产物类别来看，在原始植物角苔类(liverworts)、苔藓(mosses)和石松类(club mosses)中发现有黄烷酮、黄酮和黄酮醇物质的出现[47]。在蕨类(ferns)植物里出现原花青素[47]，而花青素则从在松柏类裸子植物中出现到广泛存在于被子植物中[48] [49]。在调控基因方面，由于 *MYB* 较强的功能和组织特异性，花色素从无到有或从少到多的获得转换有可能通过 *cis* 或 *trans* 的方式使激活型 *MYB* 高表达[50] [51] [52] [53] [54]或抑制型 *MYB* 低表达[55]来实现(表 1)。

3.2. 从蓝/紫色到红/粉色的花色变异

花色从蓝/紫色到红/粉色的变异通常是由于花青素从飞燕草素或矢车菊素到天竺葵素的转变，即花青素羟基数目的减少，因而常伴随羟基化酶基因 *F3'H* 或 *F3'5'H* 的功能失活或表达量降低(表 2)。牵牛花仅含有矢车菊素和天竺葵素[56] [57] [58]，对于本身就具有蓝/紫色花的物种如圆叶牵牛(*Ipomoea purpurea*)、

Table 1. Summary of *MYB* mutations for gain of pigment**表 1.** 花色获得的基因突变形式

物种名	基因名	突变形式	表型变异	参考文献
<i>Mimulus aurantiacus</i> ssp. <i>puniceus</i>	<i>MaMYB2</i>	Higher expression (CIS)	Yellow to red	[54]
<i>M. luteus</i> ssp. <i>cupreus</i>	<i>PLA1 (R2R3-MYB)</i>	?	Yellow to orange red	[52]
<i>M. luteus</i> ssp. <i>variegatus</i>	<i>PLA2 (R2R3-MYB)</i>	?	Yellow to purple	[52]
<i>M. cardinalis</i>	<i>ROI1 (R3-MYB)</i>	Lower expression (CIS or Trans)	Light pink to dark red	[55]
<i>Phlox drummondii</i>	<i>R2R3-MYB</i>	Higher expression (CIS)	Light blue to dark red	[53]
<i>Antirrhinum majus</i> ssp. <i>Pseudomajus</i>	<i>ROSEA^{et}</i>	Gain of an activator (?)	Light yellow to dark red	[51]
<i>A. majus</i> ssp. <i>Majus</i>	<i>ROSEA^{et}</i>	Gain of an activator (?)	Light yellow to dark red	[50]

COD 代表编码区的突变; CIS 代表 *cis* 调控区的突变; Trans 代表反式作用转录因子的改变; “?” 代表原因不详。

Table 2. Summary of mutations causing flower color changes from blue/purple to red/pink**表 2.** 花色由蓝/紫色到红/粉色变化的基因突变形式

物种名	基因名	突变形式	表型变异	参考文献
<i>Ipomoea purpurea</i>	<i>F3'H</i>	550-bp <i>Tip201</i> insertion in exon3 (COD)	Blue to pink	[59]
<i>I. purpurea</i>	<i>F3'H</i>	402-bp DNA sequences insertion in exon3 (COD)	Blue to pink	[60]
<i>I. nil</i>	<i>F3'H</i>	C to T mutation in exon3 (COD)	Blue to pink	[59]
<i>I. tricolor</i>	<i>F3'H</i>	T insertion in exon2 (COD)	Blue to pink	[59]
<i>I. quamoclit</i>	<i>F3'H</i>	Lower expression in flower (CIS and tissue specific regulatory)	Blue to red	[75] [76] [77]
	<i>DFR-B</i>	15,3,3,6-bp in-frame and 98-bp DNA sequences insertion in 3'-flanking; Substrate specificity change (COD)		
<i>I. horsfalliae</i>	<i>F3'H</i>	Lower expression in flower (CIS and tissue specific regulatory)	Blue to red	[76]
<i>I. coccinea</i>	<i>F3'H</i>	Lower expression in flower (CIS and tissue specific regulatory)	Blue to red	[77]
<i>Ipomoea</i> ssp. <i>gesnerioides</i>	<i>F3'5'H</i>	A premature stop codon in exon1 and a 136-bp out-of-frame deletion in exon2 (COD)	Blue to red	[78] [79]
	<i>DFR-B</i>	Substrate specificity change (COD)		
	<i>F3'H</i>	Lower expression in flower (Tissue specific regulatory)		
<i>Penstemon barbatus</i>	<i>F3'5'H</i>	A premature stop codon at amino acid 407; 11 nonsynonymous mutations (COD)	Blue to red	[80] [81]
	<i>F3'5'H</i>	Low activity on DHK and very low activity on DHQ		
<i>P. labrosus</i>	<i>F3'5'H</i>	No activity on DHK and very low activity on DHQ	Blue to red	[81]
<i>P. subulatus</i>	<i>F3'5'H</i>	Two or more premature stop codons, large deletions, or frameshifting indels (COD)	Blue to red	[81]
<i>Penstemon</i> (10 species)	<i>F3'5'H</i>	Lower expression (CIS)	Blue to red	[53]
<i>Petunia hybrida</i>	<i>F3'5'H</i>	A <i>Spm</i> -like transposon (<i>PstI</i>) insertion in exon2 (COD)	Blue to red	[82]
<i>P. hybrida</i>	<i>F3'5'H</i>	Transposon insertion in exon3 (COD)	Blue to red	[83]
<i>Gentiana scabra</i>	<i>F3'5'H</i>	Two independent transposons insertion in exon1 (COD)	Blue to pink	[84]
<i>Antirrhinum majus</i>	<i>F3'5'H</i>	Lose of function (COD)	Blue to red	[85]
<i>Glycine max</i>	<i>FLS</i>	Single base deletion in coding region (COD)	Purple to magenta	[86]

COD 代表编码区的突变; CIS 代表 *cis* 调控区的突变; Trans 代表反式作用转录因子的改变; “?” 代表原因不详。

裂叶牵牛(*I. nil*)、三色牵牛(*I. tricolor*)而言, 其红/粉色变异通常是由于 *F3'H* 的编码区突变造成[59] [60]。对于同属内蓝/紫色到红/粉色的转变, 若蓝/紫色由飞燕草素决定, 通常会伴随 *F3'5'H* 的功能失活[78] [80]-[85] [87]或表达量下降[53], 有时也伴随 *F3'H* 在花组织中表达量的下降[78] [80] [81]; 若蓝/紫色由矢车菊素决定, 通常红/粉花中 *F3'H* 的启动子序列(*cis* 调控)与蓝/紫花相比会发生变异而导致其表达量下调, 且组织特异性表达调控使其仅降低花组织而不影响营养组织中矢车菊素的含量[75] [76] [77] [87] [88]。这是因为矢车菊素除了贡献于花色外, 在紫外防御、抵御病原菌侵染或动物啃食、生长素极性运输等方面还具有重要的作用, 所以 *F3'H* 的功能失活可能会影响整个植株的生长, 组织特异性表达调控可以降低其有害多效性(*deleterious pleiotropy*)。统计数据表明植物营养组织中的花青素主要为矢车菊素, 很少有植物会缺少有功能的 *F3'H* 拷贝, 而 *F3'5'H* 会在许多科属如蔷薇科(*Rosaceae*)、菊科(*Asteraceae*)、拟南芥属(*Arabidopsis*)、番薯属(*Ipomoea*)、紫罗兰属(*Matthiola*)、郁金香属(*Tulipa*)植物中缺失[45] [87]。

由于 *F3'H* 或 *F3'5'H* 分支被阻断, 花青素代谢通路只能走 *F3H-DFR* 的路径, 所以花色从蓝/紫色到红/粉色的变异有时还伴随着 *DFR* 底物特异性的改变, 即对底物 *DHK* 亲和性的提高, 对 *DHQ* 和 *DHM* 亲和性的降低[77] [78] [79]。*FLS* 表达量下降导致的黄酮醇含量下降也会使花由蓝紫色变为红色[86]。

3.3. 从蓝/紫/红色到白/黄色的花色变异

花色从蓝/紫/红色到白/黄色的变异通常被认为是花青素从有到无的变异, 是质的变化。这些变化可能来自花青素代谢途径一个或多个步骤的阻断(表 3)。代谢通路上结构基因的转座子插入[62] [63] [89] [90] [91]或移码突变[92]导致的功能失活或 *cis* 突变导致的表达量下降[95] [96]均会使植物产生白花。但结构基因的突变通常会使整个植物都无法产生花青素, 最上游基因的突变可以让植物连黄酮、黄酮醇、黄烷酮等类黄酮物质也无法产生, 会因而产生较多的有害多效性, 降低植物适合度(e.g. [93] [94])。*R2R3-MYB* [50] [51] [96]-[103]、*bHLH* [104] [105]和 *WDR* [99]的突变均可以造成花青素代谢途径上结构基因的表达下调而阻断花青素的合成, 但由于 *R2R3-MYB* 具有较高的组织表达特异性和功能分化[33] [34] [39] [50] [103] [106] [107], 所以其突变具有较低的有害多效性。有观点认为自然选择应该偏爱 *R2R3-MYB* 的突变[88]。这与 *R2R3-MYB* 较 *bHLH* 和 *WDR* 及结构基因具有较高的异义和同义突变比率(ω)是一致的[98] [108] [109] [110] [111]。

花青素量的变化可能与花青素代谢途径基因的表达量变化有关, 但具体机制还不清楚。在亚洲百合(*Asiatic hybrid lilies Liliium spp.*)中, *MYB12* 的表达量与花瓣中花青素的积累量呈正比[112]。*R2R3-MYB* 的表达量可解释小天蓝绣球(*P. drummondii*) (深红)与其近缘种 *P. cuspidate* (浅蓝色)杂交 F2 代群体中花色的深浅[53] [113]。

3.4. 花着色模式的变异

花的着色式样主要有断色、彩斑、缘环、星状、紫外模式、斑点、脉色和芽红等(图 2)。目前已知的花色着色模式成因主要有四种: 病毒感染、转座子的插入及部分回复突变、siRNA 介导的基因转录后沉默、基因特别是调控基因的时空特异性表达(表 4)。黄水仙花(*Narcissus pseudonarcissus*)由于水仙花叶病毒的感染会产生断色现象[61]。通常转座子在基因内部的插入和部分回复突变会使花色呈彩斑状[62] [63] [64] [89] [90] [102]。双色花(包括缘环和星状)的形成通常是由于白色区域 *CHS* 的表达下调(主要由 siRNA 介导的其在转录后 mRNA 的降解造成) [65] [67] [114] [115] [116], 或有色区域 *FLS* 的表达上调(原因未知) [65]。UV 模式、斑点、脉色和芽红等表型通常与花青素代谢途径的结构或调控基因的时空表达模式和不同拷贝数有关。在圆叶牵牛中, *CHS-D* 主要在花檐中表达而控制整个花檐的着色, 而 *CHS-E* 主要在花筒、花脉和花药中表达, 可能与花筒的脉色和花脉上有色斑点的形成有关[117] [118] [119]。黑心金光菊(*Rudbeckia hirta*)在花瓣基部有 *F3H*、*F3'H*、*FLS*、*F6H*、*F7GT* 的高量表达使 UV 吸收类的黄酮醇类物质

Table 3. Summary of known mutations for flower color changes from blue/purple/red to white/yellow
表 3. 花色由蓝/紫/红色到白/黄色变化的基因突变形式

物种名	基因名	突变形式	表型变异	参考文献
<i>Ipomoea purpurea</i>	<i>CHS-D</i>	One copy of 3.9-kb <i>Tip100</i> insertion in intron (COD)	Purple to white, flaked	[62]
<i>I. purpurea</i>	<i>CHS-D</i>	Two copies of <i>Tip100</i> insertion in intron (COD)	Purple to stable white	[62]
<i>I. purpurea</i>	<i>CHS-D</i>	Rearrangement of DNA sequences between exon1 and an adjacent <i>Tip100</i> (COD)	Purple to stable white	[90]
<i>I. purpurea</i>	<i>CHS-D</i>	One copy of <i>Tip100</i> insertion in 5'-flanking (COD)	Purple to white, flaked	[90]
<i>I. purpurea</i>	<i>MYB1</i>	6-bp and 19-bp deletions (COD)	Purple to white flowers with colored rays	[98]
<i>I. purpurea</i>	<i>bHLH</i>	<i>IpMu1</i> insertion in exon2 and <i>IpMu2</i> insertion in intron5 (COD)	Bright blue to pale blue	[105]
<i>I. nil</i>	<i>CHS-D</i>	5.57-kb <i>Tpn3</i> insertion in intron (COD)	Purple to white flowers with colored tubes	[91]
<i>I. nil</i>	<i>CHI</i>	<i>Tpn2</i> insertion in intron2 and a speckled-activator (COD)	Purple to white, speckled	[63]
<i>I. nil</i>	<i>DFR-B</i>	<i>Tpn1</i> insertion in intron2 (COD)	Purple to white, flecked	[89]
<i>I. nil</i>	<i>MYB1</i>	AG insertion in exon2 (COD)	Blue to white	[99]
<i>I. nil</i>	<i>bHLH</i>	583-bp tandem duplication derived from exons 5 and 6 (COD)	Bright blue to pale blue	[104]
<i>I. nil</i>	<i>WDR1</i>	7-bp (GGAGTAC/TCCGTAC) insertion (COD)	Blue to white	[99]
<i>Torenia fournieri</i>	<i>F3H</i>	A LTR-type retrotransposon (<i>TORE1</i>) insertion in the promoter (CIS)	Violet to white	[96]
<i>T. fournieri</i>	<i>MYB1</i>	A <i>En/Spm</i> -like transposon (<i>Tif1</i>) insertion in intron2 (COD)	Purple to white, flecked	[102]
<i>Petunia axillaris</i>	<i>AN2</i>	Frameshift and nonsense mutations (COD)	Red to white	[97]
<i>Parrya nudicaulis</i>	<i>CHS</i>	Lower expression (CIS)	Purple to white	[95]
<i>Mimulus lewisii</i>	<i>DFR</i>	A frameshift in exon2 (COD)	Pink to white	[92]
<i>Antirrhinum majus</i> ssp. <i>striatum</i>	<i>ROSEA</i> ^{el}	Lose of an activator (?)	Dark red to light yellow	[51]
<i>A. majus</i> ssp. <i>Latifolium</i>	<i>ROSEA</i> ^{el}	Lose of an activator (?)	Dark red to light yellow	[50]
<i>A. majus</i> ssp. <i>Meonanthemum</i>	<i>ROSEA</i> ^{el}	Lose of an activator (?)	Dark red to light yellow	[50]
<i>Antirrhinum</i> (3 species)	<i>ROSEA</i>	Lose of function (COD and CIS)	Red to pale or yellow	[50]
<i>Aquilegia</i> spp.	<i>R2R3-MYB?</i>	?	Purple to white or yellow	[100]
<i>M. cardinalis</i> SM	<i>PELAN</i>	Gene deletion (?)	Red to yellow	[103]
<i>M. cardinalis</i> CI	<i>PELAN</i>	Lower expression (?)	Red to yellow	[103]
<i>M. guttatus</i>	<i>PELAN</i>	No expression (?)	Red to yellow	[103]
<i>Oriental Lilium</i> spp.	<i>MYB12</i>	Two amino acid substitutions (COD)	Pink to white	[74] [101]

COD 代表编码区的突变; CIS 代表 *cis* 调控区的突变; Trans 代表反式作用转录因子的改变; “?” 代表原因不详。

Table 4. Summary of known mutations that cause pigmentation patterns
表 4. 已报道的花着色模式相关变异

物种名	基因名	突变形式	表型变异	参考文献
<i>Narcissus pseudonarcissus</i>	<i>Narcissus mosaic virus</i>	Viral infection	Color break (figure 2a)	[61]
<i>Ipomoea purpurea</i>	<i>CHS-D</i>	One copy of 3.9 kb <i>Tip100</i> insertion in intron (somatic excision of transposon)	Variation (white, flaked) (figure 2b)	[62]
<i>I. purpurea</i>	<i>CHS-D</i>	One copy of <i>Tip100</i> insertion in 5'-flanking (somatic excision of transposon)	Variation (white, flaked)	[90]
<i>I. nil</i>	<i>CHI</i>	<i>Tpn2</i> insertion in intron2 and a speckled-activator (somatic excision of transposon)	Variation (white, speckled) (figure 2c)	[63]
<i>I. nil</i>	<i>DFR-B</i>	<i>Tpn1</i> insertion in intron2 (somatic excision of transposon)	Variation (white, flecked) (figure 2d, e)	[89]
<i>Dahlia variabilis</i>	<i>bHLH</i>	A 5.4-kb CACTA transposon (<i>Tdv1</i>) insertion in intron4 (somatic excision of transposon)	Yellow ray florets with orange variegation (figure 2f)	[64]
<i>Torenia fournieri</i>	<i>MYB1</i>	A <i>En/Spm</i> -like transposon (<i>Ttf1</i>) insertion in intron2 (somatic excision of transposon)	Variation (white, flecked)	[102]
<i>Petunia hybrida</i>	<i>CHS-A</i>	Lower expression in white margin (siRNA directed silencing in exon2)	White marginal picotee (figure 2g, h)	[65] [116]
<i>P. hybrida</i>	<i>FLS</i>	Higher expression in white center (?)	Colored marginal picotee (figure 2i, j)	[65]
<i>Dahlia variabilis</i>	<i>CHS</i>	Lower expression in white regions (siRNA directed silencing in exon2)	Red-white bicolor (figure 2k)	[66]
<i>Camellia japonica</i> "Tamanoura"	<i>CHS</i>	Lower expression in white regions (?)	White Marginal Picotee	[114] [67]
<i>P. hybrida</i>	<i>CHS-A</i>	Lower expression in white stripe (siRNA directed silencing in exon2)	A star-type red and white bicolor pattern (figure 2l)	[115] [116]
<i>Rudbeckia hirta</i>	<i>F3H, F3'H, FLS, F6H, F7GT</i>	Higher expression in the basal part (?)	UV/bull's eye pattern (figure 2m, n)	[68]
<i>I. purpurea</i>	<i>CHS-D</i>	Tissue specific expression	Flower limb pigmentation	[117] [118]
	<i>CHS-E</i>	Tissue specific expression	Flower tube, ray, and anthers pigmentation	[119]
<i>Clarkia gracilis</i>	<i>F3'H1, F3'5'H1, DFR1, DFR2</i>	Early expression of <i>F3'H1-A</i> throughout the petal and <i>DFR2-A/B</i> in spots; later expression of <i>F3'5'H1-A/B</i> and <i>DFR1-A/B</i> in the petal background (?)	A single red-purple spot against a pink background (figure 2t)	[72] [120]
<i>Paeonia suffruticosa</i> cultivar "Jinrong"	<i>CHS, F3'H, DFR, ANS</i>	Higher expression in the purple spot (?)	Purple spot at the base of white petal	[121]
Pansy (<i>Viola × wittrockiana</i> Gams.)	<i>F3H, F3'5'H, DFR, ANS</i>	Higher expression in the cyanic blotches (?)	Cyanic blotches on the yellow petal	[122]
<i>Antirrhinum</i> ssp.	<i>VENOSA</i>	Tissue specific expression	Petal lobe and tube venation pigmentation (figure 2o)	[50] [124]
<i>Antirrhinum</i> ssp.	<i>ROSEA^{el}</i>	Tissue specific expression	Petal lobe and tube pigmentation	[50]
<i>P. hybrida</i>	<i>DPL</i>	Tissue specific expression	Tube venation pigmentation (figure 2p)	
	<i>AN2</i>	Tissue specific expression	Flower limb pigmentation (figure 2p)	
	<i>AN4</i>	Tissue specific expression	Flower tube and anthers pigmentation	[106]
	<i>PHZ</i>	Tissue specific expression (light induced)	Vegetative tissue pigmentation and bud blushing	

续表

<i>Mimulus lewisii</i>	<i>PELAN</i>	Tissue specific expression	Petal lobe pigmentation	[103]
<i>M. lewisii</i> , <i>M. guttatus</i>	<i>NEGAN</i>	Tissue specific expression	Spot formation in the nectar guide	[103]
	<i>MYB2</i>	Tissue specific expression	Full-red pigmentation in tepals	
<i>Phalaenopsis</i> spp.	<i>MYB11</i>	Tissue specific expression	Red spots in sepals, petals and lip (figure 2v)	[73]
	<i>MYB12</i>	Tissue specific expression	Venation pattern in the sepals, petals and the full pigmentation pattern in the central lobe of the lip	
<i>Lilium regale</i>	<i>MYB15</i>	Tissue specific expression (light induced)	Vegetative tissue pigmentation and bud blushing (figure 2s)	[71]
Asiatic <i>Lilium</i> spp.	<i>MYB12</i> <i>Mon/Ren/Lan</i>	Tissue specific expression	Full-pink pigmentation in tepals	[74] [112] [123]
Asiatic <i>Lilium</i> spp.	<i>MYB6</i>	Tissue specific expression	Vegetative tissue pigmentation and raised spot in tepals	[123]
Asiatic <i>Lilium</i> spp. cv “Latvia”	<i>MYB12-lat</i>	Tissue specific expression	Splatter spot in tepals (figure 2x)	[126]
Oriental <i>Lilium</i> spp.	<i>MYB12</i>	Tissue specific expression	Full-pink and raised spot pigmentation in tepals (figure 2w)	[74] [101]
Apple “Honeycrisp”	<i>MYB10</i>	Lower expression in green stripes (higher methylation in promoter of green stripes)	Red and green stripes on fruit skin	[125]
	<i>MYB10</i>	Higher expression in red regions (light induced)	Blushed fruit skin	
	<i>RED LEAF</i>	Tissue specific expression	Red leaf, red midrib, and red fleck	
<i>Trifolium</i> spp.	<i>RED V</i>	Tissue specific expression	V-broken yellow and red leaflet	[107]
	<i>RED LEAF</i> <i>DIFFUSE</i>	Tissue specific expression	Diffuse red leaf	
<i>Tulipa gesneriana</i> cv. Murasakizuisho	<i>Vit1</i> (coding a vacuolar iron transporter)	Tissue specific expression at the bottom of purple perianth	Blue spot at the bottom of the inner purple perianth (figure 2u)	[26] [27]
	<i>FER1</i> (coding an Fe storage protein)	Tissue specific expression at the upper of purple perianth		[129]

COD 代表编码区的突变; CIS 代表 *cis* 调控区的突变; Trans 代表反式作用转录因子的改变; “?” 代表原因不详。

高积累而形成类似蜜导的 UV 模式[68]; *F3'HI-A* 在整个花瓣和 *DFR2-A/B* 在斑点的早表达及 *F3'5'HI-A/B* 和 *DFR1-A/B* 在花瓣中的晚表达可能是形成细长山字草(*Clarkia gracilis*)粉色带红色斑点表型的主要原因, 但决定斑点位置的因子还有待确定[72] [120]。同样, 花青素代谢途径结构基因在牡丹(*Paeonia suffruticosa* Cultivar “Jinrong”) [121]和三色堇(*Viola × wittrockiana* Gams.) [122]斑点位置出现高表达, 这对它们花瓣上形成斑点具有很重要的作用。因为在斑点的形成过程中通常涉及多个结构基因的协同表达, 且结构基因的表达受调控基因的影响, 所以结构基因的时空特异性表达很大程度上可能是由调控基因的时空表达特异性决定的。许多研究表明 *R2R3-MYB* 的时空特异性表达对不同部位的着色具有非常重要的影响(表 4) [50] [69] [71] [73] [74] [101] [103] [106] [107] [112] [123] [124] [125] [126]。周围有光环的斑点表型(图 2z)可能与斑点周围激活型因子(WDR)的移除或抑制型因子(R3-MYB)的流入有关[68]。R3-MYB 和 WD40 均具有细胞间可移动性[69] [106]。在斑点处 MBW 复合物可促进 R3-MYB 的产生[127] [128], 斑点周围区域 R3-MYB 的流入与 WDR 的流出使其花青素合成较少或无, 故呈光环型斑点的表型。另外, 细胞形状[15] [17] [69] 和 Fe³⁺转运和存储蛋白的组织特异性表达[26] [27] [129]也可能影响花色斑点的形成。

目前 *MYB* 的时空特异性表达机制并不清楚。影响营养组织和芽红着色的 *R2R3-MYB* 通常会受光的诱导而高表达, 且抑制型的 *R3-MYB* 会被激活参与该过程以避免过激反应[106] [127], 但环境特别是光诱导

花青素合成的分子机制并不清楚。*R2R3-MYB* 启动子区甲基化程度的不同会决定其表达与否而影响花青素合成部位, 但 DNA 甲基化的组织特异性机制也未知[125]。

4. 花色表型变异的自然选择机制

花色的变异可能会带来传粉者或其访问频率的变异, 传粉者与花色的相互关系对花色进化具有重要的意义。长期以来, 人们对传粉者在花色亿万年的选择中发挥的作用十分好奇。此外, 非传粉者因素(自然环境、病原菌、啃食者、基因多效性等)也会影响花色多态性[132] [180] [181]。

4.1. 花色转换方向与传粉者偏好

在陆地植物中发生过多次独立的花色从蓝/紫色到红/粉色或花色从蓝/紫/红色到白/黄色的转换, 如曼陀罗属(*Iochroma*)、番薯属(*Ipomoea*)、钓钟柳属(*Penstemon*)、耧斗菜属(*Aquilegia*) (图 3a-d)、闭鞘姜属(*Costus*) [45] [75]-[81] [87] [92] [130] [131] [132]。在这些属中蓝紫色常为原始色, 花色从蓝/紫色到红/粉色和蓝/紫/红色到白/黄色的转换比较常见, 而反向转换则较少[92] [132] [133]。已记录的反向转换包括在苦苣苔科(*Gesneriaceae*)的三个属(*Sinningia*, *Paliavana* 和 *Vanhouttea*)中曾发生过多次数花色从红色到蓝色的转换[134], 在黄蕊花属(*Dalechampia*)和枫属(*Acer*)中曾分别发生过三次花色从绿色或黄色到红色或紫色的转换[135], 在沟酸浆属(*Mimulus*)中也发生过花色从黄色到红色或粉色的转换(图 3e) [52]。花色转换方向的不对称性对花色的进化方向具有很大的限制[132]。目前对于花色着色模式的进化转换研究较少。仅有研究认为金鱼草的脉色可能为祖先性状, 在全红的花瓣背景下脉色的作用被红色掩盖进而导致脉色消失[50] [124]。

通常, 花色从蓝/紫色到红/粉色的转换伴随传粉者从蜂类(bees)到蜂鸟(hummingbirds)的转换, 从蓝/紫/红色到白/黄色的转换伴随传粉者从蜂类或蜂鸟到蛾类(moths)的转换[45] [87] [132] [136]。花色的质变导致的传粉者类型的改变在许多科属如番薯属[75]、沟酸浆属[137] [138] [139]、耧斗菜属[100]、碧冬茄属(*Petunia*) [140]、假番薯属(*Ipomopsis*) [141] [142]中均观察到。通常为了避免对同种传粉者的竞争, 同域分布的两近缘种(异域分布时通常具有相同花色)会分化出不同的花色[53] [113] [143] [159] [160] [161] [162]。传粉者对花色的量变是否具有区分能力还存在许多不确定性[144] [145] [146]。着色模式的变化通常会影响传粉者的访问频率, 具有较明显斑点或花蜜指示标志的花色类型[147]-[152]会受到偏爱。

4.2. 传粉者介导的自然选择对花色进化的影响

传粉者对花色表型变异的区别访问是否对花色的进化产生选择性作用, 通常要看该区别访问是否造成不同花色类型植物适合度(fitness)的不同[132]。植物适合度组分(fitness components)包括结果率、结籽率、萌发率、存活率、可育率等生活史性状。适合度反映一个个体能够产生的有活力的后代数量。

多数研究缺乏对不同花色变异的适合度的评估(e.g. [75] [100] [124] [137] [138] [140])。一些研究只测量了部分适合度成分但未检测到传粉者对花色的选择作用(e.g. [113] [143] [154] [156])。还有的研究注意到不同花色类型间适合度成分有差异且传粉者有偏爱, 但无确切的实验和分析证据表明该差异是由传粉者造成(e.g. [72] [139] [152] [164] [166] [169] [175] [191])。但相当数量的研究观测到传粉者的区别访问会带来不同花色类型植物适合度组分的不同(表 5)。不同传粉者对不同花色类型的偏爱可能会使得同一属不同物种或同种物种不同个体间基因流减少, 导致花色的歧化选择(disruptive selection) [141] [142] [157] [158]。在同域地区为了避免对同种传粉者的竞争, 花色也会发生歧化[159]。同种传粉者对不同花色类型访问次数及取食时间的差异导致的花粉输出与沉积量的差异对花色多样性的维持具有重要作用[153] [167]。传粉者对花色某一类型的偏爱性可导致花色的方向性选择(directional selection) [145] [146] [151] [165] [168] [170] [172]或稳定性选择(stabilizing selection) [163]。有时, 某一花色类型在受到传粉者低访问时自交率的增加会维持其基因频率在一定水平, 对花色产生平衡选择(balancing selection) [168] [169] [170] [177] [178] [179], 从而维持花色多态性。

Table 5. Effects of flower color on pollinator visits and fitness components**表 5.** 花色对传粉者和适合度组分的影响

物种名	比较的花色 或着色模式	传粉者	适合度成分	传粉者偏爱性	传粉者介导的 自然选择	非传粉者 因素介导的 自然选择	参考文献
<i>Penstemon digitalis</i>	White, white with purple striping	Small-to large-bodied bees	Fruit set, seed number	-	No	-	[154]
<i>Phlox drummondii</i> , <i>P. cuspidate</i>	Light/dark blue, light/dark red	Butterflies, moths, and hawkmoths	Fruit set, seed number, survival rate	Light blue	No	-	[113] [143]
<i>Wahlenbergia albomarginata</i>	Blue to white	Solitary bees	Seed number , pollen export	No	No	-	[155]
<i>Iris atropurpurea</i> , <i>I. haynei</i>	Purple, dark brown	Male bee shelters	Seed set	Dark brown	No	-	[156]
<i>Mimulus aurantiacus</i>	Red , yellow	Hummingbirds and hawkmoths	Survival rate , plant size	Hummingbirds for red, hawkmoths for white	-	Red morphs had higher survival rate and plant size than yellow morphs at both coast and inland regions	[139]
<i>Malva moschata</i>	Red, white	Bumblebees and honeybees	Fruit set , seed number	Bumblebees preferred for red, honeybees had no preferences	-	Honeybee abundance may maintain flower color polymorphism	[166]
<i>Bixa orellana</i>	White, amaranth rose , petunia purple, cobalt violet	Honeybees, carpenter bees, ants, and small flies	Fruit set , mature fruit number , seed number , seed mass	Amaranth rose	-	Increased selfing rate of morphs under lower visits may maintain flower color polymorphism	[169]
<i>Clarkia gracilis</i> ssp. <i>sonomensis</i>	Spotted /unspotted pink flowers	<i>Evyalaeus pullilabris</i>	Sired seed number , seed number	Weak preference for spotted flowers	-	Small postpollination siring advantages for spotted plants	[72] [164] [191]
<i>Ursinia calenduliflora</i>	spotted , unspotted yellow flowers	Male <i>Megapalpus capensis</i>	Pollen export , number of fertilized ovules	Spotted flowers	-	Herbivores (preference for spotted morph); Low latitude and high altitude were beneficial to spotted morph	[152]
<i>Aquilegia coerulea</i>	White to blue	Bumblebees and hawkmoths	Seed set	Bumblebees for blue, hawkmoths for white	Whiter flowers were associated with the annual presence of hawkmoths.	Higher altitude was correlated with bluer flowers	[157] [158]
<i>Ipomopsis aggregata</i> , <i>I. tenuituba</i>	Red, pink (hybrids), white	Hummingbirds and hawkmoths	Fruit set, seed set , sired seed number	Hummingbirds for red, hawkmoths for white	Disruptive selection	-	[141] [142]
<i>M. bicolor</i>	All yellow, white and yellow bicolor	Small-bodied bees	Pollen deposition , seed number	No	Avoidance of pollinator competition with <i>M. guttatus</i> in sympatric area, disruptive selection	Latitude explained 52% of the variation in morph frequency across sites	[159]
<i>Antirrhinum majus</i>	Red, yellow, white	Bumblebees	Pollen receipt and export , fruit set	Yellow or white	Maintenance of flower color polymorphism	-	[153] [167]

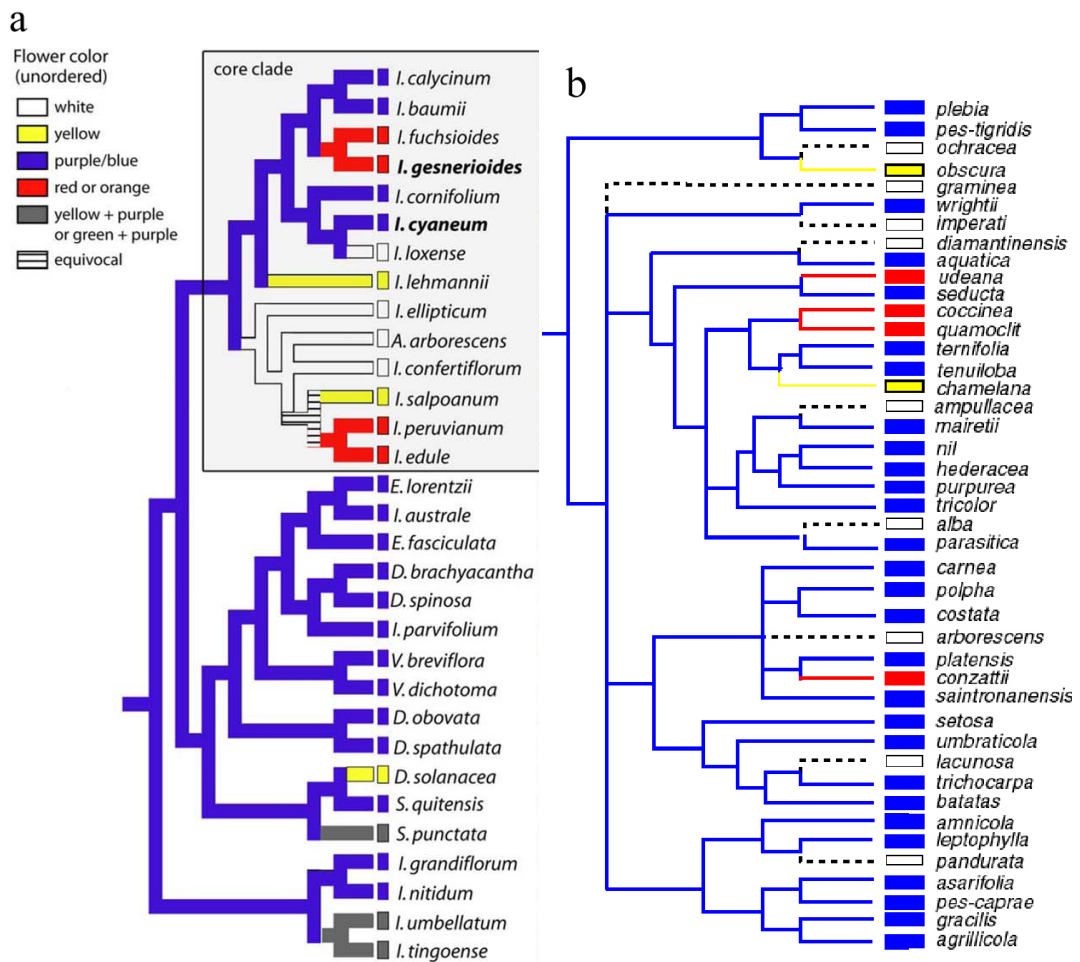
续表

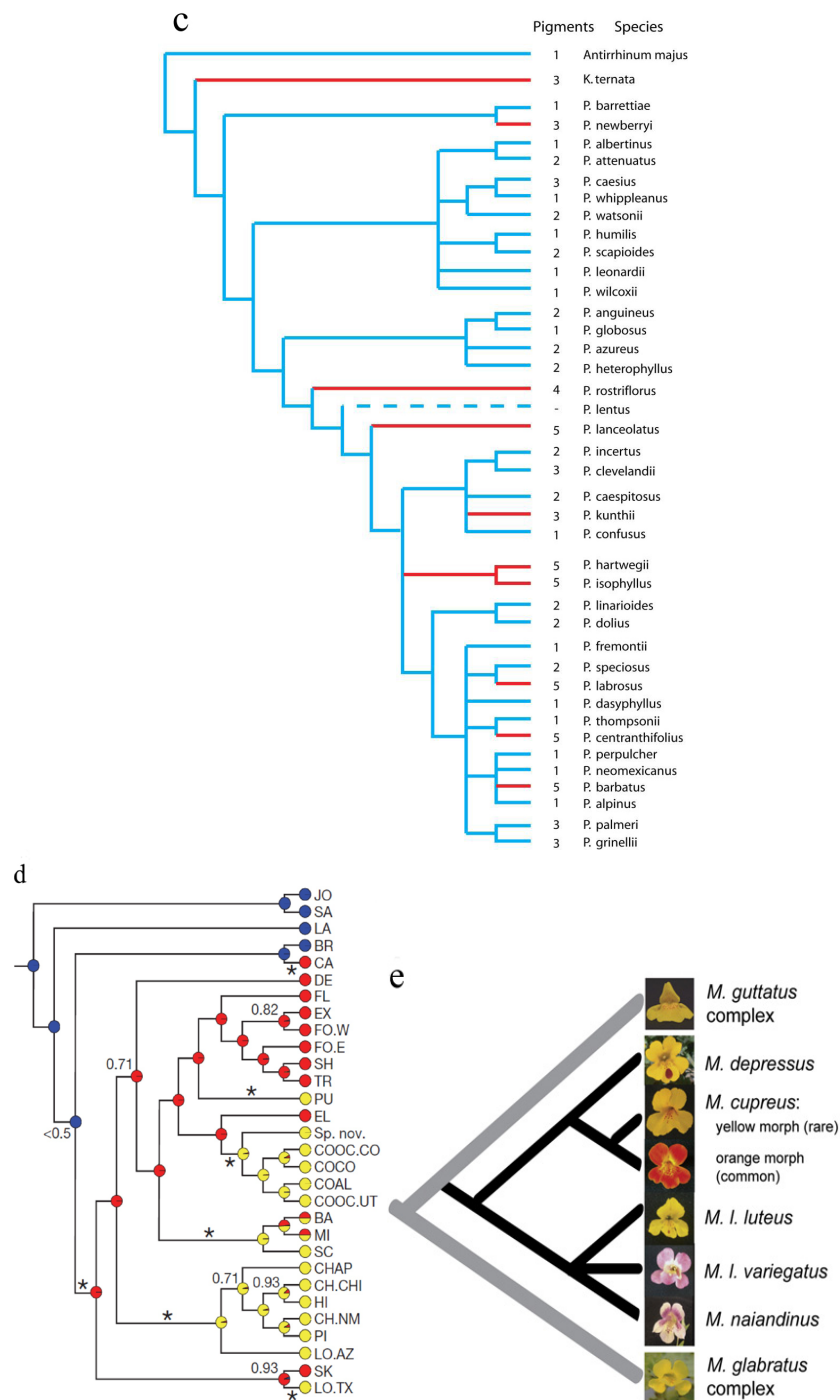
<i>Claytonia virginica</i>	White to red	<i>Andrena erigeniae</i>	Fruit production, fruit set	-	Directional selection for redness (marginal significant)	Intermediately colored flowers set more fruit than white or red-flowered plants, balancing selection; Herbivores (preferring red morph) showed selection antagonistic to pollinators; Pathogen (preferring infection of white morph) showed selection opposing to herbivores.	[165]
<i>Lapeirousia oreogena</i>	With or without white arrows-markings	long-proboscid nemestrinid fly <i>Prosoeca</i> sp. nov.	Pollen export, fruit set, seed set	Flowers with white arrows-markings	Directional selection	-	[151]
<i>Centaurea cyanus</i>	Violet-blue (dark, violet and strong UV reflective)	Bumblebees	Fertilization rate, seed number	-	Directional selection	-	[145]
<i>Lysimachia arvensis</i>	Blue, red	Solitary bees and <i>Bombus terrestris</i>	Germination, seedling survival, seedling mass, ovule and pollen production, pollen export, seeds per fruit, seed set	Blue	Directional selection for blue in blue biased population	Dry and hot were beneficial to blue morphs; Delayed selfing may exert balancing selection on red morph in blue biased population	[168] [170]
<i>Gentiana lutea</i>	Yellow to orange	Bumblebees	Seed number	Yellowness in Torrestí'o population	Directional selection in Torrestí'o population; Variation in pollinator communities among populations may maintain color polymorphism	Seed predators avoided yellow flowers in Torrestí'o population, same directional selection with pollinators; Orangeness increased westward	[171] [172]
<i>Anacamptis morio</i>	Violet-blue (lighter, strong contrast)	Bumblebees	Fruit number, fruit mass	-	Directional selection	-	[146]
<i>Delphinium nelsonii</i>	Blue, white	Hummingbirds and bumblebee queens	Seed set	Blue	Stabilizing selection	-	[163]
<i>I. purpurea</i>	Dark purple (<i>MYB1MYB1</i>), light purple (<i>MYB1myb1</i>), white (<i>myb1</i>)	Bumblebees	Flower number, fruit number, seed mass, seed number, survival rate	When white phenotypes constitute 25% of the population, pollinators were against visiting white flowers; no preference for dark and light flowers	Negative frequency dependent selection	Increased selfing rate of white morph under lower visits and overdominance of heterozygote exerted balancing selection	[173] [174] [177] [178] [179]
<i>Cosmos bipinnatus</i>	Purple, pink , white	Bumblebees and honeybees	Fruit set and seed number per capitulum	Pink	-	Overdominance of heterozygote exerted balancing selection	[175]

续表

<i>Sisyrinchium</i> sp.	Purple (<i>dd</i>), white (<i>DD, Dd</i>)	Bees, hover flies, and thrips	Fruit set, size of mature fruit, seed number Flower number, fruit set, seed number, germination, survival rate, fecundity, relative fitness	-	-	Overdominance of heterozygote exerted balancing selection	[176]
<i>P. drummondii</i>	Red, white	Butterflies, moths, and hawkmoths	Flower number, survival rate, fecundity, germination	No	No	Pleiotropy, purifying selection for white individual	[188]
<i>I. purpurea</i>	Purple (<i>CHS-D-</i>), white (<i>chs-d</i>)	Bumblebees	Flower number, survival rate, fecundity, germination	No	No	Pleiotropy, purifying selection for white individual	[93] [94] [189]
<i>Linanthus parryae</i>	Blue, white	Beetles	Seed number	No	No	High spring precipitation was beneficial to white morph, fluctuating selection	[190]

“比较的花色或着色模式”中粗体部分表示该花色类型适合度较高；“适合度成分”中粗体部分表示有显著差异的适合度成分；“-”表示无实验证据。





a. 曼陀罗属(*Lochroma*) [78]; b. 番薯属(*Ipomoea*) [45]; c. 钓钟柳属(*Penstemon*) [132]; d. 耧斗菜属(*Aquilegia*) [131]; e. 沟酸浆属(*Mimulus*) [52]; d 中的星号表示推断的传粉综合征之间的转换。

Figure 3. Some generic phylogenies showing flower color transitions

图 3. 一些属植物花色转换系统树

在进化过程中, 植物为适应不同的传粉者会使花部特征特异化。如被蜂鸟传粉的花通常为红色、具有较长的花筒、较窄的花檐、外突的雄蕊和柱头、分泌大量但糖浓度较低的花蜜, 被蜂类传粉的花大多为蓝紫色、具较宽的花筒和花檐、内嵌的雄蕊和柱头、分泌少量但高浓度的花蜜, 而被蛾类传粉的花则

多为白色、花筒较长、有芳香气味且经常在夜间开放, 具低浓度高量花蜜[132] [136] [182] [183]。花色与其他花性状之间具有高度的相关性(e.g. [184] [185] [186]), 对其他花性状的选择也可能会影响花色的变异。性状之间的相互关联和权衡是限制花色方向性进化的一个因素[187]。

4.3. 非传粉者因素介导的自然选择对花色进化的影响

非传粉者因素对不同花色类型的适合度也具有一定的影响(表 5)。因为不同的花色类型对光照、降水量、温度、海拔、经纬度等环境的适应能力可能不同, 所以环境的异质性可导致不同花色类型在不同地区分布的差异[152] [157] [158] [159] [168] [170] [171] [190], 可能会介导花色的歧化或动态选择(fluctuating selection)。啃食者与传粉者偏爱的相同可能带来与传粉者作用相反的拮抗选择(antagonistic selection) [152] [165]。环境因子、啃食者或病原菌在花色的多态性维持方面起着非常重要的作用, 其通常还会限制花色的方向性进化[165] [168] [170] [171] [172]。

基因的多效性也会影响花色。有时, 杂合体花色表型会表现出超显性(overdominance) [165] [173] [174] [175] [176]而维持等位基因频率的平衡, 对花色产生平衡选择。由于突变基因的有害多效性, 一些白花个体与有色花相比, 通常具有较低的萌发率、存活率、可育率或抵御啃食者和病原菌的能力较差, 因而具有较低的适合度而受到纯化选择(purifying selection), 结果在群体中占有较低的频率[93] [94] [165] [188] [189]。

5. 展望

花色表型的丰富变异既存在于种间, 也存在于种内。花色表型变异的分子机制和自然选择的研究对探究生物多样性的存在机制具有重要意义。目前对种内的数量变异研究相对较少。传粉者或非传粉者因素对花色变异所起的选择作用有可能影响花色的进化, 但其作用机制还需要更多研究。已有的研究结果多数还需要生态学的调查加以确认。花色表型变异导致的植物-传粉者关系的变化如何影响物种的分化, 进而影响生态系统的动态变化尚需更多关注。特别是随着气候变化的加剧, 自然环境对植物性状和传粉者访花行为的影响将越来越受重视。显然, 相关研究将会深化我们对未来气候下动植物互作关系的认识。

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