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植物叶色突变体分类、变异机制与应用的研究进展

周夏雯^{1,2}, 石从广², 周芳伟², 徐 梁², 杨少宗², 何秋伶¹

(1. 浙江理工大学 生命科学与医药学院 浙江省植物次生代谢调控重点实验室, 浙江 杭州 310018; 2. 浙江省林业科学研究院, 浙江 杭州 310023)

摘要: 植物叶色变异是自然界中一种常见并且容易识别的现象, 叶色变异通常会影响植物的光合作用效率, 导致生长不良, 因此曾被认为是不良变异而逐渐被淘汰。但近年来, 随着社会的发展和园林绿化的需求, 叶色突变体逐渐受到关注。叶色突变体受到分子水平的调控, 导致叶绿体结构异常, 光合作用受抑制, 色素合成代谢通路异常, 因此是研究色素代谢、叶绿体发育分化、光合作用等途径的理想材料, 也可为品种改良提供重要信息。综述了近年来植物叶色突变体的研究进展, 明确高等植物叶色突变体主要来源于自然突变和人工诱变, 叶色突变体按颜色可分为黄化、黄绿、绿黄、绿白、白化、浅绿、白翠、条纹等几种类型; 按叶色变化方式可分为单色突变、杂色突变和阶段性失绿, 其遗传方式通常分为细胞核遗传、细胞质遗传和核质互作遗传; 与正常绿色叶片植株相比, 大多数叶色突变体叶片的净光合速率、气孔导度和蒸腾速率都下降, 二氧化碳的利用率降低; 叶绿素、类胡萝卜素、类黄酮(主要是花青素)合成与代谢相关基因的突变以及与叶绿体分化发育相关基因的突变可解释叶色突变体发生的分子机制。叶色突变体可应用于园林绿化, 并作为优良的实验材料广泛应用在基础研究和育种工作中。参 112

关键词: 叶色变异; 叶绿素; 叶绿体; 类胡萝卜素; 类黄酮; 综述

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Research progress on classification, variation mechanism and application of plant leaf color mutants

ZHOU Xiawen^{1,2}, SHI Congguang², ZHOU Fangwei², XU Liang², YANG Shaozong², HE Qiuling¹

(1. Zhejiang Province Key Laboratory of Plant Secondary Metabolism and Regulation, College of Life Sciences and Medicine, Zhejiang Sci-Tech University, Hangzhou 310018, Zhejiang, China; 2. Zhejiang Academy of Forestry, Hangzhou 310023, Zhejiang, China)

Abstract: Leaf color variation in plants is a common and easily recognized phenomenon in nature, which affects the photosynthetic efficiency of plants and leads to poor growth, so it was once considered to be an undesirable variation and gradually eliminated. But in recent years, social advancements and increased demand for ornamental landscaping have brought renewed attention to leaf color mutants. Leaf color mutants are generally regulated at the molecular level, resulting in abnormal chloroplast structure, inhibited photosynthesis, and abnormal pigment synthesis and metabolic pathways. Therefore, they serve as ideal materials for studying pigment metabolism, chloroplast development and differentiation, photosynthesis, and related pathways, and can also provide important information for variety improvement. This paper reviews the research progress of

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作者简介: 周夏雯(ORCID: 0009-0006-1942-6548), 从事分子生物学研究。E-mail: xiaxia7051129@163.com。通信作者: 石从广(ORCID: 0000-0001-5566-4507), 副研究员, 从事珍稀濒危植物保护与林木遗传育种研究。E-mail: 419782450@qq.com。何秋伶(ORCID: 0000-0002-9000-6726), 副教授, 从事植物分子生物学研究。E-mail: qlhe@zstu.edu.cn

leaf color mutants in recent years, and clarifies that leaf color mutants in higher plants mainly come from natural mutation and artificial mutation. Leaf color mutants can be divided into several types based on color, such as yellowing, yellow green, green yellow, green white, albino, light green, white emerald, stripe and so on. According to the way of leaf color change, leaf color mutants can be divided into monochromatic mutation, variegated mutation and stage chlorosis. Its inheritance mode is generally divided into nuclear inheritance, cytoplasmic inheritance and nucleocytoplasmic interaction inheritance. Compared with normal green leaf plants, the net photosynthetic rate, stomatal conductance, transpiration rate of most leaf color mutants decrease, so does the utilization rate of carbon dioxide. Mutations in genes related to synthesis and metabolism of chlorophyll, carotenoids, and flavonoids (particularly anthocyanins), as well as genes involved in chloroplast differentiation and development, can explain the molecular mechanism underlying leaf color mutants. Leaf color mutants can be applied in landscaping and widely used in basic research and breeding as excellent experimental materials. The findings of this review can provide theoretical reference for further research on leaf color variation. [Ch, 112 ref.]

Key words: leaf color variation; chlorophyll; chloroplast; carotenoid; flavonoid; review

植物叶片含有叶绿素、叶黄素、花青素、类胡萝卜素等多种色素，正常生育期的叶片中叶绿素占据绝对优势而使得叶片呈现绿色^[1]。叶片颜色变异是高等植物中一种普遍且易于识别的性状变异。由于自然突变或人工诱变，植物体内色素合成代谢相关基因发生变化，直接或间接地影响包括叶绿素在内的多种色素的合成或降解，使得叶色突变体中这些色素的质量分数和比例发生变化，植物叶片随之呈现不同的颜色^[2]。通常叶色突变体的叶绿体结构会发生改变，叶绿体发生形变、外膜破损等，使得叶绿体无法维持正常功能，叶绿素的合成减少，光合作用减弱，导致植物生长发育不良甚至死亡^[3]。因此，在很长一段时间内叶色变异被认为是没有价值的有害变异^[4]，直至有研究利用普通小球藻 *Chlorella vulgaris* 绿色突变体 W5 证明原卟啉Ⅲ是叶绿素合成的前体后^[5]，叶色突变体又得到重视，作为优良的实验材料在叶色调控机制、色素合成代谢途径、叶绿体结构、光合作用机制等基础研究中发挥着重要作用。另外，调控叶色的基因可作为选择标记基因应用在分子育种和杂交育种中；具有观赏性的叶色突变体也是优秀的彩叶植物种质资源，可被应用于园林绿化中。本研究对近些年叶色突变体在来源、叶色性状分类、光合特性、叶色变异分子机制、应用价值等方面的研究进行综述，以期对叶色突变体研究提供依据和新的思路。

1 叶色突变体的来源、叶色性状分类及光合特性

高等植物的叶色突变体主要来源于自然突变和人工诱变。相较于人工诱变而言，自然突变的数量较少，人工诱变是植物叶色突变体的主要来源方式，人工诱变又可分为化学试剂诱导^[6]、物理射线诱导^[7]和转基因诱导^[8]等。

叶色变异普遍在苗期就表现出不同的叶色变化，因此一般以苗期的叶色为依据对叶色突变体进行分类。GUSTAFSSON^[9]将叶色突变体分为白化、浅绿、黄化、条纹和斑点等 5 种类型。而后，AWAN 等^[10]进行了更加详细的分类，将叶色突变体分为黄化、黄绿、绿黄、绿白、白化、浅绿、白翠和条纹。WALLES^[11]则根据突变体的叶片在其整个生育期颜色的变化方式，分为三大类：单色突变、杂色突变、阶段性失绿。单色突变表现为仅出现黄、白或浅绿中的一种颜色；杂色突变表现为斑点、白绿等多种颜色；阶段性失绿则在生育期的某一阶段表现出突变性状，一段时间后又恢复为绿色，如大麦 *Hordeum vulgare* 突变体 *whs18* 在苗期表现为绿色，从第 7 叶或第 8 叶开始黄化，而后短时间出现白化叶，在拔节前长出的新叶呈现条纹白色，而后又逐渐长出正常的绿叶^[12]；常绿则是在生育末期仍保持绿色的性状且不易黄化，如在拟南芥 *Arabidopsis thaliana* 中由于编码脱镁叶绿素水解酶的基因 *PPH* 发生突变，使得叶绿素降解途径中脱镁叶绿素转化为脱镁叶绿素酸 a 过程受到阻碍而出现的常绿突变体^[13]。

植物叶色突变体的遗传通常分为细胞核遗传、细胞质遗传和核质互作遗传等 3 种方式。大多数叶色突变体为细胞核遗传，如绿豆 *Vigna radiata* 叶绿素缺乏突变体^[14]、黄瓜 *Cucumis sativus* 黄叶突变体^[15]等

都为细胞核遗传。叶绿体具有相对独立的基因表达和调控系统^[16],部分叶色突变体表现为细胞质遗传,如玉米 *Zea mays* 条纹叶突变体^[17]、小麦 *Triticum aestivum* 紫条纹叶色突变体 *psl1*^[18]等。叶绿体的发育代谢等过程需要核基因与叶绿体基因的协调作用,核基因突变会影响叶绿体基因的表达^[19-20],因此,在少部分情况下叶色突变体表现为核质互作,如经 2-4-氯苯巯基三乙胺 (CPTA) 处理得到的大麦叶色突变体^[21]。

与正常绿色叶片植株相比,由于叶色突变体叶片色素比例的改变、叶绿体结构的形变及叶绿体数量的减少,突变体的光合作用受到抑制^[22]。大多数叶色突变体叶片的净光合速率下降、二氧化碳利用率降低,从而使得叶片的细胞间二氧化碳摩尔分数增加,并且净光合速率和蒸腾速率都与气孔导度呈现正相关^[23-24],如牡丹 *Paeonia suffruticosa* 黄叶突变体的光合参数明显低于野生型牡丹,相较于野生型,突变体的净光合速率、气孔导度、蒸腾速率都下降了 50% 以上,胞间二氧化碳摩尔分数则增加了 15.1%^[25]。

2 叶色突变体叶色变异的分子机制

2.1 光合色素生物合成与代谢相关基因突变

2.1.1 叶绿素生物合成相关基因突变 叶绿素的生物合成途径由一系列酶催化的合成步骤组成^[26],反应以谷氨酸酰-tRNA 为起始,在谷氨酰胺 tRNA 还原酶的催化下转化为谷氨酸-1-半醛,紧接着经过 3 步酶催化反应合成胆色素原。研究表明:催化合成胆色素原的胆色素原脱氨酶 (PBGD) 的缺陷会引起玉米的叶色变化,突变体中编码 PBGD 的基因发生突变,PBGD 的催化活性降低,叶绿素合成量减少,最终形成浅绿色的斑纹叶片^[27]。经过尿卟啉原Ⅲ合成酶、尿卟啉原Ⅲ脱羧酶、粪卟啉原Ⅲ氧化酶等酶催化的一系列酶促反应后,胆色素原转化为镁原卟啉Ⅸ单甲酯。镁原卟啉Ⅸ单甲酯在镁原卟啉单甲酯Ⅸ环化酶 (MgPCY) 的催化下转化为二乙烯原叶绿素酸酯,在原叶绿素酸酯还原酶 (POR) 和联乙烯还原酶 (DVR) 的催化下合成单乙烯叶绿素 a。研究证明:编码 MgPCY^[28]、POR^[29]、DVR^[30-31] 的基因发生突变,使得酶功能丧失,叶绿素合成受阻,植物叶片则表现出不同程度的失绿。单乙烯叶绿素 a 在叶绿素合酶的催化下合成叶绿素 a,在叶绿素酸酯 a 加氧酶 (CAO) 和叶绿素 b 还原酶的催化下最终合成叶绿素 b。在大白菜 *Brassica rapa* ssp. *pekinensis* 浅绿叶突变体中,编码 CAO 的基因发生单核苷酸突变,蛋白质翻译提前结束,CAO 活性显著降低,叶绿素 b 合成量减少^[32]。叶绿素生物合成途径中催化反应进行的酶,尤其是叶绿素生物合成途径中的关键酶受损后,植物体叶绿素的合成随之受到抑制。催化卟啉原Ⅸ转化为镁卟啉原Ⅸ的镁螯合酶是叶绿素生物合成的限速酶和关键酶,它由 3 个亚基组成,分别为镁螯合酶 I 亚基 (CHLI)、镁螯合酶 D 亚基 (CHLD)、镁螯合酶 H 亚基 (CHLH)^[33-34]。编码这 3 个亚基的基因发生突变的植物,镁螯合酶的正常功能受损,叶绿素的生物合成受阻,叶片都表现出黄色或黄绿色的性状^[35-37]。镁螯合酶催化反应需要能量,CHLI 具有 ATP 酶活性,能够水解 ATP,促进反应的进行^[38]。基因组解偶联 4 蛋白 (GUN4) 是一种核基因编码的蛋白,它与卟啉原Ⅸ结合形成复合物,再与 CHLH-GUN5 复合物结合,刺激镁螯合酶的活性,促进镁离子插入卟啉原Ⅸ形成镁卟啉原Ⅸ^[39-40]。INAGAKI 等^[41]在水稻 *Oryza sativa* 中发现:GUN4 的合成受到光敏色素 B 的转录调控,突变体中的 GUN4 基因受到强烈抑制,镁螯合酶活性减弱,水稻叶片呈现淡绿色。GUN4 表现出光依赖性。在黑暗中,拟南芥中的 GUN4 受 GUN4 激酶调节,当其 C 端被磷酸化,GUN4 失去活性,拟南芥叶片出现褪绿现象^[42]。叶绿素生物合成途径中的任意一个合成步骤受到各种因素的影响而中断都会影响叶绿素的生物合成,随之植物体内的叶绿素质量分数降低,从而导致植物叶色的改变^[43]。

2.1.2 叶绿素代谢相关基因突变 在植物体内,叶绿素的合成和代谢是同步进行的,维持着动态平衡。当代谢过程中相关基因发生突变,这种动态平衡的改变会引起植物叶色的变化^[44]。目前,已经有许多叶绿素分解代谢相关基因被发现,包括 *SGR1* (也被称为 *NYE1*)、*SGR2* (也被称为 *NYE2*)、*NYC1*、*NOL*、脱镁叶绿酸 a 加氧酶基因 (*PAO*)、脱镁叶绿酸 a 水解酶基因 (*PPH*) 等,并且这些基因受到不同的转录因子及转录调控机制的调控^[45-52]。茉莉酸被认为是植物衰老的诱导剂,可调控叶绿素的降解,转录调控因子 MYCs 是茉莉酸诱导的叶绿素降解途径的关键调控节点^[46-47]。MYCs 可通过与 *PAO* 的启动子结合,直接促进叶绿素降解。同时 MYCs 可与转录调控因子 ANACs 结合,形成复合物,激活 *NYE1* 和 *NYC1* 的表达,从而促进叶绿素的降解。ANACs 也可直接激活叶绿素代谢相关基因,促使叶绿素降解^[46-48]。*PIF4/5* 是一种光敏色素作用因子,在光信号转导中的起着重要的调控作用,对叶绿素降解具有正向调控

作用^[49]。PIF4/5 可直接调控叶绿素代谢相关基因，如 *SGR*、*NYC1*、*NOL* 等，促进叶绿素降解^[50]。另外，在黑暗及高温条件下，PIF4/5 能够正向调控转录因子 *ORE1*^[50]。*ORE1* 在衰老过程中激活乙烯生物合成基因 *ACS2* 的表达，随后激活乙烯介导的叶绿素降解网络^[51]。乙烯不敏感 3(EIN3) 是乙烯信号传导的主要正调节因子，可以与 *NYE1*、*NYC1*、*PAO* 的启动子物理结合以激活其表达来直接促进叶绿素降解，同时 EIN3 也可直接靶向 *ORE1*，从而激活叶绿素降解相关基因的表达^[51]。植物叶绿素代谢过程中的基因上调或下调都会影响叶绿素的代谢过程，使得植物叶片出现失绿或常绿的现象^[53]。

2.1.3 类胡萝卜素合成相关基因突变 类胡萝卜素是使植物呈现黄色、橙色或红色的一类色素。根据化学结构的不同可以将类胡萝卜素分为 2 类：一类是胡萝卜素，如 α -胡萝卜素、 β -胡萝卜素和番茄红素；另一类是叶黄素，如玉米黄素、叶黄素和虾青素^[54]。类胡萝卜素的生物合成由香叶基香叶基焦磷酸酯 (GGPP) 开始，经过一系列的酶促反应后合成上述 2 类类胡萝卜素。八氢番茄红素合成酶 (PSY) 催化类胡萝卜素生物合成的第 1 步反应，而后八氢番茄红素在八氢番茄红素脱氢酶 (PDS) 的催化下转化为顺式番茄红素。研究表明：*PSY* 基因和 *PDS* 基因缺陷的植物，其类胡萝卜素生物合成途径受阻，同时影响叶绿素生物合成途径，植物叶片出现白化现象^[55-56]。合成途径分支处的类胡萝卜素异构酶 (CRTISO) 是类胡萝卜素生物合成中的关键酶，它催化顺式番茄红素转化为全反式番茄红素^[57]。SU 等^[58] 和 LI 等^[59] 研究发现：大白菜突变体中的类胡萝卜素异构酶基因 *BrCRTISO* 存在不同程度的片段缺失以及单核苷酸突变，类胡萝卜素异构酶的功能缺失导致顺式番茄红素大量积累，然而这一步反应可在光诱导下进行非酶反应，因此突变体的外叶呈现绿色，因没有光照无法继续合成叶黄素、玉米黄素等类胡萝卜素，顺式番茄红素大量积累，故内叶呈现橙色。类胡萝卜素叶绿体调节剂 1 基因 *CCR1* 编码组蛋白甲基转移酶 (SET 结构域 8, SDG8)，SDG8 能与 *CRTISO* 的启动子结合，调控类胡萝卜素的生物合成^[60-61]。

2.1.4 类黄酮色素合成代谢相关基因突变 类黄酮是在植物中普遍存在的色素，通常为浅黄色或无色，偶尔表现为橙黄色，同时也是一种重要次生代谢物，大多数类黄酮具有显著的生理及药理活性^[62]。迄今为止，从植物中分离得到的黄酮类化合物有 9 000 多种^[63]。类黄酮生物合成途径非常复杂，通过苯丙氨酸途径将苯丙氨酸转化为各种黄酮类化合物^[64]。苯丙氨酸氨裂解酶 (PAL)、查尔酮合成酶 (CHS)、查尔酮还原酶 (CHR)、查尔酮异构酶 (CHI) 等催化类黄酮生物合成的酶的变化会使得植物叶片中黄酮类化合物的质量分数发生变化，导致叶片颜色的变化^[65-66]。花青素是一类广泛存在于植物中的水溶性类黄酮色素，在不同的 pH 下会使植物呈现不同的颜色，并且对植物抗氧化应激具有重要的调节作用^[67]。类黄酮生物合成途径分支处的柚皮苷查尔酮在 CHI、黄酮 3' 羟化酶 (F3'H)、二氢黄酮醇 4 还原酶 (DFR) 以及花青素还原酶 (ANS) 的催化下合成花青素。有研究比较了枫香 *Liquidambar formosana* 转色期的基因表达量，发现花青素合成途径中的 *CHS*、*CHI*、*F3'H*、*DFR*、*ANS* 等酶基因的表达量显著增加^[68]。结构基因的转录调控是植物中调节花青素生物合成的重要机制，在紫叶茶 *Camellia sinensis*^[69]、紫叶芥菜 *Brassica juncea*^[70]、紫叶大琴叶榕 *Ficus lyrata*^[71] 和具有斑纹叶片的蒺藜苜蓿 *Medicago truncatula*^[72] 中都发现了这种调节机制，即 MYB 转录因子与 bHLH 转录因子结合并招募 WD40 重复蛋白，形成 MYB-bHLH-WD40 复合物，调节花青素的合成，MYB 转录因子的过度表达使得花青素的合成增加，出现紫色叶片。在蒺藜苜蓿中，拮抗性的 MYB 转录因子与促进花青素生物合成的 MYB 转录因子竞争性结合 bHLH 转录因子，导致形成斑纹叶片^[72]。

2.2 与叶绿体分化发育相关基因的突变

叶绿体是植物所特有的“能量转换器”，植物的光合作用在此进行，将光能转换为植物体可利用的化学能，在植物的生长发育过程中发挥着重要的作用^[73]。许多研究表明：叶色的变化往往伴随着叶绿体结构的改变，可表现为叶绿体液泡化^[74]，叶绿体数量减少，并伴随着不同程度的形变^[75]，其外膜也出现不同程度的破损^[76]，叶绿体内基粒的数量及基粒片层数量减少，基粒排列不整齐，变得松散^[77-78]。叶绿体结构的变化及叶绿体的缺失可能会影响叶绿素等光合色素的质量分数和比例，这是导致植物叶色变化的重要原因之一^[79-80]。

叶绿体蛋白由核基因与叶绿体基因编码合成，是叶绿体膜的重要组成部分，参与叶绿体的分化与发育。类囊体是组成叶绿体内膜系统的单位，类囊体膜上含有多种蛋白质，包括细胞色素 b6/f 复合体、铁

氧化还原蛋白、黄素蛋白、光系统 I 复合物、光系统 II 复合物等^[81]。Snowy Cotyledon 2(SCO2) 蛋白是一类参与类囊体膜生物合成, 并与光捕获叶绿素结合蛋白 LHCB1 相互作用的蛋白^[82]。SCO2 基因的缺失影响了叶绿体蛋白的合成, 导致类囊体膜上的 PS II 蛋白复合体的组装和修复受阻, 从而导致百脉根 *Lotus japonicus* 和拟南芥子叶白化, 真叶出现杂色^[82]。五肽重复序列 (PPR) 蛋白是一类参与细胞器基因表达的转录后调控的蛋白质, 在叶绿体发育中起着重要作用^[83-84]。在拟南芥^[85-86] 和水稻^[87-88] 中都发现了多种 PPR 蛋白, 并且水稻编码 PPR 蛋白的基因缺失突变体表现出白化叶片的表型^[89-90]。多器官 RNA 编辑因子 (Morf) 是另一类参与转录后调控的蛋白, 它可以与 PPR 蛋白形成复合物参与调节叶绿体基因的表达^[91-92]。如在水稻中 *OsMORF9* 可以与五肽重复家族成员 *OsSLA4* 和 *DUA1* 相互作用, 参与 RNA 剪接和编辑过程, 影响叶绿体的发育^[93]。

2.3 草本与木本植物叶色变异的异同

草本植物大多为 1 年生或 2 年生, 其茎部木质化程度较低。草本植物茎部含有叶绿体, 能进行光合作用^[94], 在叶色变异时往往会伴随着茎部颜色的变化。木本植物为多年生, 茎部木质化程度高, 具有保护作用的周皮由死亡的细胞组成^[94]。木本植物叶色变异时, 在其茎秆上往往观察不到颜色的变化。从根本上来说, 草本植物与木本植物叶色变异都是由于色素合成代谢相关基因的变异, 加上环境因素, 直接或间接地影响色素的合成代谢, 使得叶片中各种色素的质量分数及比例改变, 最终形成不同的叶色^[95]。

3 叶色突变体的应用价值

3.1 应用于基础研究

近些年, 叶色突变体是遗传模式^[96]、色素合成^[97]、光合作用^[98]、细胞结构与发育等基础研究的理想材料, 并成为分子生物学和发育生物学的热点研究领域之一^[99]。如从籼稻品种 ‘TN1’ 的甲磺酸乙酯诱变群体中分离出的稳定遗传的白色类病突变体, 其叶绿体超微结构发生改变, 叶绿素代谢和叶绿体发育相关基因的调控发生改变, 可作为研究叶绿体超微结构、叶绿素合成代谢、叶绿体发育和遗传模式的优良材料^[100]。目前, 水稻、拟南芥等模式植物叶色突变体的研究比较深入, 有许多涉及叶绿素生物合成的基因已被克隆, 如水稻中编码叶绿素生物合成途径中的关键酶——镁螯合酶的 *ChlD* 亚基的同位基因 *YGL*^[101]、*Chl1*^[102]、*YGL7*^[103] 等。

3.2 应用于育种工作

叶色常在苗期表达, 并且极易识别, 在育种中可以简化良种繁育^[104] 和杂交育种^[105] 过程, 缩短育种年限, 促进育种进程和提高种质资源利用效率。叶色变化可被肉眼轻易观察到, 与叶色相关的基因可作为分子标记应用于选择标记系统。将目的基因和相关叶色基因同时调控, 可实现通过观察叶片颜色筛选出表达目的基因的转基因植株^[106]。核编码的 δ 因子对于植物叶绿体编码基因的转录调控至关重要。在玉米中, 由于 δ 因子 *ZmSig2A* 的缬氨酸残基缺失导致形成可逆黄化/白化叶突变体^[107], 利用该突变基因进行杂交育种时, 可在苗期时就识别和消除假杂种。敲除植物体内 *PDS* 基因会引起叶片白化, 所以常被用于检测基因编辑体系是否成功^[108]。近年来, 利用 *PDS* 基因与成簇的规律间隔的短回文重复序列 (CRISPR/Cas9) 基因编辑技术对植物进行基因编辑, 在植物遗传改良及种质创新等方面广泛应用^[109]。

一些叶色突变体在产量、风味、观赏等方面具有优异表现, 许多叶色突变体被认为是优良种质资源。可利用一些作物叶片常绿的性状延缓衰老、增加作物的产量, 如水稻的叶绿素代谢途径受阻, 叶片保持常绿, 种子中的多种营养物质含量增加^[110]; 或因叶片颜色变化使得代谢物含量不同, 从而具有独特的风味, 如茶树 *Camellia sinensis* 白化品种 ‘玉金香’ 叶色金黄, 叶片中槲皮素和儿茶素质量分数增加使其更具有茶味^[111]。一些彩叶植物颜色绚丽、枝叶繁茂, 作为观赏植物在园林绿化中得到广泛应用, 常见的有金叶女贞 *Ligustrum × vicaryi*、金边黄杨 *Euonymus japonicus* ‘Aurea-marginatus’、枫香、银杏 *Ginkgo biloba* 等^[112]。

4 展望

由于叶色突变体大多表现为失绿, 影响植物体的光合作用, 进而影响植物的生长发育, 因此在最初被认为是不良性状, 对于叶色突变体的研究较少。直到发现叶色突变体是研究色素合成、叶绿体结构、

光合作用等的优良材料，对叶色突变体的研究才逐渐增多。叶色变异在植物中非常广泛，虽然有关叶色突变体的研究已较多，但是大多集中在模式植物拟南芥以及水稻、玉米等经济作物上，并且大多利用转录组、蛋白质组、代谢组等大数据联合分析的方法对叶绿素生物合成代谢途径上的基因进行研究，而对叶色变异的关键基因的上游调控机制的研究较少，如一些具有调控作用的非编码 RNA 在叶色变异中的作用。因此，后续的研究应利用更丰富的分子生物学手段，从多方面进一步解析叶色变异的机制，为更多植物叶色突变体的研究提供理论依据。

5 参考文献

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