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水稻叶色基因克隆与分子机制研究进展

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摘要: 叶色突变体是研究水稻光合作用、叶绿素合成与降解及其生长发育调控机制的重要材料,而且在水稻杂交制种、提高生物量等方面具有较高的实际应用价值。目前,超过 120 个水稻叶色相关基因被克隆,分布在水稻 12 条染色体上,其中第 3 号染色体克隆的基因最多。水稻叶色调控机制涉及多个调控途径,包括色素生物合成与降解、质体转录复合物、转录后修饰、核质信号转导、叶绿体蛋白酶以及转录因子与表观遗传。本文从水稻叶色遗传机理与基因克隆、分子调控机制及其在水稻育种上的应用进行了总结与展望,以期为水稻高光合育种及挖掘适用于杂交制种的水稻叶色种质资源提供依据。

关键词: 水稻;叶色基因;分子机制;育种

Advances on Gene Isolation and Molecular Mechanism of Rice Leaf Color Genes

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Abstract: Leaf color mutants in rice are important materials for studying the regulatory mechanism of photosynthesis, chlorophyll synthesis and degradation, and plant growth and development, and they are also with high practical value in producing hybrid seeds and improving biomass. To date, over 120 genes modifying the leaf color have been cloned on 12 chromosomes, including chromosome 3 where the most number of genes were reported. Rice leaf color regulation mechanisms were identified, including pigment biosynthesis and degradation, plastid transcription complex, post transcriptional modification, nuclear and cytoplasmic signal transduction, chloroplast protease, transcription factor and epigenetics. In this paper, the genetic mechanism and molecular isolation of leaf color genes, the regulation mechanism and the practical use in rice breeding were summarized and prospected. This might provide a basis for high photosynthetic breeding and the exploitation of leaf color germplasm resources suitable for hybrid seed production in rice.

Key words: rice; leaf color gene; molecular mechanism; breeding

叶绿体是植物最重要的光合细胞器,是植物激素、脂肪、淀粉等代谢物的合成场所。叶色突变体是研究植物叶绿体发育的理想材料,叶色变异主要表现为白化、黄化、淡绿、深绿、条纹、斑马纹。水稻叶色基因的克隆与分子机制解析有助于基因工程育种。叶色作为形态标记,用于保证杂交稻制种和不育系繁殖纯度。此外,一些叶色突变体具有特殊的优良性状,可以为水稻遗传育种提供丰富的种质资源。

1 水稻叶色的遗传机理与基因克隆

水稻叶色变异的遗传机理主要有细胞核遗传突变、细胞质遗传突变以及核-质互作突变。目前,多数水稻叶色突变由核基因控制,且以隐性核单基因控制为主。房贤涛等[1]发现白化转绿突变体 *21W1* 由显性基因控制;钟振泉等[2]发现斑点叶突变体 *spl32* 由一对显性核基因控制。目前,水稻细胞质遗传引起的叶色突变没有报道。核质互作引起的突变是目前叶

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色变异研究的热点。叶绿体的发育依赖于细胞核编码的基因与叶绿体编码的基因之间的协作。

截至2020年1月，超过120个水稻叶色基因已被克隆，分布在12条染色体上，第1、2、3、5、6、8、12号染色体上分别有19、11、23、13、11、4、6个叶色基因，其他染色体叶色基因均为7个。这暗示第1号和第3号染色体可能是水稻叶色基因分布热点（表1）。水稻叶色突变体大多与叶绿素合成、降解或叶绿体发育有关。克隆的水稻叶色突变基因中，白条纹与白化转绿基因有51个，黄化基因有28个，淡绿基因有16个，白化致死基因有12个，深绿（持绿）基因有8个，斑马叶基因有7个（表1）。

表1　已克隆的控制水稻叶色的基因

Table 1　Cloned genes controlling leaf color in rice

基因 Gene	染色体 Chromosome	突变表型 Mutant phenotype	基因功能 Gene function	参考文献 Reference
WFSL1	1	白条纹	参与叶绿体生物合成	[3]
NYC1	1	永绿	叶绿素b还原酶基因	[4]
GLK2	1	深绿	转录因子	[5]
OsPAPST1	1	萎黄	3′-磷酸腺苷5′-磷酰硫酸转运蛋白，参与质核信号传递	[6]
YGL8	1	黄叶	镁原卟啉IX单酯环化酶的催化亚基	[7]
WP3	1	白条纹叶和白穗	线粒体蛋白	[8]
OsCAF1	1	白化致死	叶绿体RNA剪切因子	[9]
WSL	1	白条纹	PPR蛋白，参与叶绿体基因RNA剪切	[10]
PDF1B	1	白化	肽脱甲酰基酶	[11]
ALS3	1	白化致死	PPR蛋白	[12]
ASL1	1	白化致死	叶绿体核糖体蛋白	[13]
WLP1	1	白叶和穗	叶绿体核糖体L13蛋白	[13]
ALR	1	白条纹	dCMP脱氨酶	[14]
TCM1	1	白化	pTAC12	[15]
IspE	1	黄化转绿	异戊二烯生物合成	[16]
GRA78	1	白条纹	硫氰酸合成酶	[17]
OsHAP3A	1	淡绿	HAP复合体的一个HAP3亚基	[18]
WLP2	1	白叶和穗	质体编码的RNA聚合酶相关蛋白	[19]
YGL8	1	黄叶	尿嘧啶核苷酸激酶	[20]
OsGluRS	2	高温黄绿色	谷酰基tRNA合成酶	[21]
LIL3	2	黄化	光捕获蛋白	[22]
YL1	2	黄绿叶	光诱导叶绿体蛋白	[23]
Zebra524	2	斑马叶	番茄红素 β-环化酶	[24-25]
ALS2	2	白化致死	叶绿体50S核糖体蛋白L21	[21]
LAS	2	白化致死	苏氨酸tRNA的合成酶	[26]
GRY79	2	黄化转绿	金属-β-内酰胺酶-三螺旋嵌合体	[27]
WSL4	2	温敏条纹	PPR蛋白，参与叶绿体RNA剪切	[10]
OsDG2	2	黄化转绿	富含甘氨酸蛋白	[28]
IspF	2	淡绿	异戊二烯生物合成	[29]
LYL1	2	黄化	牻牛儿基牻牛儿基还原酶	[22]
cpSRP43	3	黄绿叶	叶绿体信号识别颗粒	[30]
Z3	3	斑马叶	柠檬酸转运蛋白	[31]
OsPDS	3	白化	ABA合成	[24]
OsClpP5	3	淡绿	叶绿体蛋白酶基因	[32]
PHYB	3	淡绿	光敏色素	[33]
V2	3	温敏白化转绿	鸟苷酸激酶	[34]

表1(续)

基因 Gene	染色体 Chromosome	突变表型 Mutant phenotype	基因功能 Gene function	参考文献 Reference
OsCHLH	3	白化	镁离子螯合酶H亚基	[35]
CS3	3	黄化	Ycf54结构域蛋白	[36]
OsDVR	3	黄绿叶	联乙烯还原酶	[37]
OsYLC2	3	黄叶	亚铁血红素加氧酶	[38]
VYL1	3	白化转绿	叶绿体蛋白酶	[32]
AL1	3	白化	八肽重复蛋白	[39]
OsCHLI	3	黄绿	镁离子螯合酶I亚基	[40]
YSA	3	幼苗白化	PPR蛋白	[41]
HSA1	3	高温白化	类果糖激酶蛋白	[42]
NOL	3	永绿	叶绿素b还原酶基因	[4]
V1	3	温敏白化转绿	叶绿体蛋白	[33]
OsFdC2	3	黄绿叶	铁氧还蛋白类似物	[43]
WGL2	3	白化	叶绿体核糖体蛋白	[44]
OsPIL1	3	淡绿	与光敏色素互作的类bHLH因子	[45]
TSV3	3	温敏白化	GTP结合蛋白	[46]
OsCHLD	3	黄化	镁离子螯合酶D亚基	[40]
OspTAC2	3	白化致死	PPR蛋白	[47]
WSP1	4	白条纹叶和白穗	叶绿体基因RNA编辑因子	[48]
MPR25	4	苍绿	PPR蛋白,参与nad5转录本RNA编辑	[49]
OsPORA	4	黄化	原叶绿素酸酯氧化还原酶A	[50]
AM1	4	白化中脉	钾离子外排逆向转运蛋白	[51]
WSL5	4	白条纹	PPR蛋白,参与叶绿体RNA剪切	[52]
YSS1	4	白条纹	DUF3727超家族	[53]
GIC	4	淡绿	PARC6同源蛋白	[54]
Z15	5	斑马叶基因	类受体激酶蛋白	[55]
Hsp70CP1	5	白化转淡绿	热激蛋白分子伴侣	[56]
OsDjA7	5	白化	分子伴侣	[56]
OsDjA8	5	白化	分子伴侣	[56]
YGL1	5	黄绿	叶绿素合成酶	[50]
TCD5	5	温敏白化	单加氧酶	[57]
TCM5	5	高温黄化	Deg蛋白酶	[58]
WSL8	5	白条纹	脱氧核糖核酸激酶	[59]
BGL	5	亮绿叶	乌嘌呤核苷酸交换因子OsRopGEF10	[60]
OsHAP3B	5	淡绿	HAP复合体的一个HAP3亚基	[18]
WSL6	5	白条纹	GTP结合蛋白	[61]
OsHAP3C	5	淡绿	HAP复合体的一个HAP3亚基	[18]
OsPPR6	5	白化致死	PPR蛋白,参与叶绿体RNA编辑与剪切	[62]
RA1	6	白化致死	甘氨酰tRNA合成酶	[63]
ZN	6	斑马叶	类囊体结合蛋白	[64]
V3	6	温敏白化转绿	核糖核酸还原酶大亚基	[33]
St1	6	温敏条纹	核糖核酸还原酶小亚基	[33]
GLK1	6	深绿	转录因子	[5]
NYC3	6	持绿	α/β折叠水解酶家族蛋白	[4]

表 1（续）

基因 Gene	染色体 Chromosome	突变表型 Mutant phenotype	基因功能 Gene function	参考文献 Reference
OsBT1-3	6	白条纹	质体腺嘌呤核苷酸转运蛋白	[65]
YGL2	6	黄叶	血红素加氧酶	[66]
OsAld-Y	6	黄绿叶	果糖 -1, 6- 二磷酸醛缩酶	[67]
SPP	6	白化转绿	基质加工肽酶	[44]
OsBE1	6	白化致死	糖苷水解酶 13 家族蛋白	[68]
WP1	7	白条纹叶和穗	缬氨酸 tRNA合成酶	[69]
OsSLA4	7	白化	PPR 蛋白, 参与 RNA 剪切	[70]
OsZDS	7	白化致死	ζ - 胡萝卜素脱氢酶	[24]
OsCHR4	7	白化	染色质域解旋酶 DNA 结合蛋白	[71]
CHR729	7	浅绿色	染色质域解旋酶 DNA 结合	[71]
OsV4	7	低温白化	PPR 蛋白	[70]
ObgC	7	白化	Sp0B 相关的三磷酸鸟苷结合蛋白	[46]
VAL1	8	白化转绿	嘌呤核苷酸生物合成酶	[72]
Zl16	8	斑马叶	β - 羟脂酰 -ACP 脱水酶	[73]
DYE1	8	持绿	光捕获复合体 I 亚基	[74]
EF8	8	深绿	HAP 复合体的一个 HAP3 亚基	[75]
AL2	9	白化	叶绿体 IIA 型内含子剪接促进因子	[76]
OsV5A	9	黄叶	*OsV$_{5A}$* 与 *OsPORA* 和 *OsPORB* 互作, 调控叶绿素合成	[50]
OsPPR1	9	白化致死	PPR 蛋白	[77]
DUA1	9	低温白化	PPR 蛋白, 参与叶绿体基因 RNA 编辑	[48]
SGR	9	持绿	参与叶绿素分解	[4]
TCD9	9	温敏白化转绿	分子伴侣蛋白亚基	[78]
CYO1	9	白化	子叶叶绿体合成因子	[79]
TCD10	10	温敏白化转绿	三角状五肽重复区蛋白	[78]
WSL3	10	白条纹	质体 RNA 聚合酶的非核心亚基	[80]
OsPORB	10	淡绿	原叶绿素酸酯氧化还原酶 B	[50]
OsHemA	10	淡绿	谷氨酰 -tRNA 还原酶	[81]
OsCAO2	10	敲除无差异	叶绿素 a 加氧酶	[82]
OsCAO1	10	淡绿	叶绿素 a 加氧酶	[82]
Rey（*k2*）	10	黄化转绿	磷酸果糖激酶 B 型碳水化合物激酶	[42]
ETL1	11	黄化	PPR 蛋白	[48]
YGL138（*t*）	11	黄绿叶	信号识别因子 54 kD 蛋白	[30]
OsSIG2A	11	温敏白化	RNA 聚合酶 σ 因子	[83]
OsABCI8	11	白化转绿	ATP 结合盒转运蛋白	[84]
ZEBRA2	11	斑马叶基因	类胡萝卜素异构酶	[24]
CFM3	11	白化致死	叶绿体基因剪切因子	[9]
BGL11（*t*）	11	亮绿叶	硫氧还蛋白超家族	[60]
ETL2	12	黄化	PPR 蛋白	[48]
OsPGL1	12	淡绿	PPR 蛋白, 参与叶绿体基因 RNA 编辑	[85]
CSP41b	12	淡绿	叶绿体茎环结合蛋白	[86]
TCM12	12	低温白化	双磷酸甘油酸非依赖性磷酸甘油酸变位酶	[87]
WSL12	12	白条纹	核苷二磷酸激酶	[88]
TCD11	12	温敏白化转绿	叶绿体核糖体蛋白	[77]

2 水稻叶色调控机制

2.1 参与色素生物合成与降解途径

植物光合色素主要是叶绿素与类胡萝卜素。叶绿素合成从谷氨酰 -tRNA 开始到合成叶绿素 a 和 b 结束，由 27 个基因编码的 15 种酶完成。目前，水稻已经克隆 14 个直接参与叶绿素合成的基因，这些基因突变都会引起叶色异常。*OsCAO1* 编码叶绿素 a 加氧酶，其突变体表现出淡绿叶的表型[82]。*OsCHLH*、*OsCHLD* 和 *OsCHLI* 分别编码 Mg- 原卟啉 IX 螯合酶的 3 个亚基，突变植株均表现为叶片黄化[35,40]。*YGL1* 编码叶绿素合酶，催化叶绿素酸酯 a 转化为叶绿素 a，突变体表现为黄绿叶[50]。类胡萝卜素是一类多异戊间二烯化合物，可以吸收和传递光能，保护叶绿素。水稻参与类胡萝卜素生物代谢途径的 4 个主要基因已被鉴定出，即 *OsPDS*（八氢番茄红素脱氢酶）、*OsZDS*（ζ- 胡萝卜素脱氢酶）、*OsCRTISO*（类胡萝卜素异构酶）及 *β-OsLCY*（番茄红素 β - 羟化酶）[24-25]。这 4 个基因突变都会导致植株体内类胡萝卜素含量降低，引起植株叶色变异[25]。此外，参与血红素生物合成和降解途径的基因突变也会引起植物叶色异常。血红素是一类含铁的四吡咯环，是许多蛋白质的成分，而四吡咯生物合成途径有 2 个分支，一是原卟啉Ⅸ与 Fe^{2+} 螯合形成血红素；二是 Mg^{2+} 螯合产生镁原卟啉Ⅸ并进一步合成叶绿素。血红素含量异常反馈抑制叶绿素合成，进而导致植株叶色变异。*OsYLC2* 与 *YGL2* 编码血红素加氧酶，参与血红素的生物合成，突变体表现为黄化叶[38,66]。

2.2 叶绿体发育相关基因

叶绿体是一种含有遗传物质的半自主细胞器。叶绿体的发育通常分为三个阶段：一是质体的复制和质体 DNA 合成；二是叶绿体遗传系统的建立；三是叶绿体光合作用系统的建立。

2.2.1 质体转录复合物参与叶绿体的发育 质体拟核编码的基因转录主要依赖于核基因编码的 RNA 聚合酶（NEP，nuclear-encoded RNA polymerase）和质体基因编码的 RNA 聚合酶（PEP，plastid-encoded RNA polymerase）。PEP 是一个由质体与核基因共同编码的蛋白质组成的复合物。目前，水稻已经鉴定出了一些核基因编码的 PEP 复合物成分。*WSL3* 编码一个质体 RNA 聚合酶的非核心亚基 OsPAP1/OspTAC3，其突变体表现为白化致死[80]。*OspTAC2* 编码一个含有 10 个 PPR（Pentatricopeptide repeat）结构域的叶绿体蛋白，*OspTAC2* 突变植株表现为白化致死，PEP 活性严重受损[47]。*OsTRXz* 编码一个 Z 型的硫氧还蛋白，其突变体表现为白化致死。OsTRXz 与两个果糖激酶 FLN1 和 HSA1/FLN2 互作，参与 PEP 复合物的形成[42]。*TCM1* 编码一个转录活性染色体（TAC，transcriptionally active chromosome）的叶绿体蛋白，参与调控低温叶绿体发育[15]。PEP 复合物结构极其复杂，鉴定出来的组分较少，对于 PEP 复合物在水稻等单子叶植物中的组成以及调控质体发育的机制有待研究。

2.2.2 转录后修饰调控叶绿体发育 质体基因通常以多顺反子转录单位组成，初级转录本需要通过各种转录后修饰（RNA 剪切、RNA 编辑、RNA 裂解、RNA 稳定）形成成熟的转录本。植物中参与质体基因转录后修饰的蛋白主要有 PPR 蛋白、MORF（MORF，multiple organellar RNA editing factor）蛋白以及一些质体基因剪切因子。在水稻中已经鉴定了 16 个 PPR 蛋白、1 个 MORF 蛋白以及 3 个剪切因子参与质体基因 RNA 编辑与 RNA 剪切（表 1）。*WSL* 编码一个 PLS（Pentatricopeptide repeat long short）亚家族的 PPR 蛋白，其突变导致植株叶片白条纹。进一步研究发现 *WSL* 参与质体 *rpl2* 的内含子剪切[10]。*DUA1* 编码一个 PLS-DYW（Pentatricopeptide repeat long short-Asp/Tyr/Trp）亚家族的 PPR 蛋白，参与低温下 *rpoB* 与 *rps8* 的 RNA 编辑。同时，*DUA1* 与 RNA 编辑因子 MORF 蛋白 WSP1 互作，介导低温下 WSP1 蛋白的稳定[48]。*WSP1* 突变导致植株出现条纹叶与白穗的表型，降低质体基因 *ndhD*、*ndhG*、*rps14* 与 *rpoB* 的 RNA 编辑效率[48]。*AL2* 编码一个叶绿体内含子剪切促进因子，其突变导致植株白化，影响多个质体基因内含子剪切[76]。*OsCAF1* 编码一个含有 CRM 结构域的叶绿体蛋白，参与 6 个质体基因（*atpF*、*ndhA*、*ndhB*、*rpl2*、*rps12*、*ycf3*）的内含子剪切。*OsCAF1* 突变体表现为白化致死，PEP 活性显著下降[9]。水稻基因组有 477 个 PPR 蛋白与 7 个 MORF 蛋白，这些基因的功能没有一一阐明，有待深入研究。

2.2.3 核质信号转导参与质体发育 质体和细胞核之间存在信号传递，细胞核能够随着质体代谢及发育状态的改变而做出相应的反应来调控细胞核基因的表达。水稻 *OsGUN4* 可以与镁离子螯合酶 H 亚基相结合，介导原卟啉到镁原卟啉的生物合成，从而调控叶绿素的合成。因此，镁 - 原叶琳 IX 被认为是

质体与细胞核信号转导的信号分子[35]。*Rey*（*k2*）编码一个磷酸果糖激酶B型叶绿体蛋白，参与核质信号的传递，其突变导致水稻叶片黄化[42]。目前，鉴定出的参与核质互作信号通路的基因较少，需要不断加强研究。

2.2.4 叶绿体蛋白酶调节叶绿体发育 叶绿体蛋白的降解是依赖于自身的蛋白酶体进行的。叶绿体光系统蛋白的降解需要SPP（Stromal processing peptidase）与TPR（Thylakoid processing peptidase）蛋白的参与，而叶绿体中其他蛋白的降解主要依赖于FtsH（Filamentous temperature sensitive）和Clp（Caseinolytic protease）。水稻*SPP*突变体表现为早期叶片白化，植株根的生长受到抑制[44]。Clp是ATP依赖的叶绿体基质丝氨酸蛋白酶，主要负责叶绿体中看家蛋白的降解。在水稻中已克隆了两个Clp基因*OsClp5*和*VYL1*。*OsClp5*突变体表现为叶片淡黄，三叶期后逐渐枯死；*VYL1*编码Clp6，其突变体表现为整个生育期叶片黄化、植株矮化以及籽粒变小[32]。本课题组鉴定了一个叶绿体丝氨酸蛋白酶*OsClp8*，其T-DNA插入突变体表现为苗期白化（未发表）。

2.2.5 转录因子与表观遗传调控叶绿体发育 核基因编码的光敏色素及其互作因子、GLK2蛋白（Golden2-like proteins）以及CAAAT-box结合复合体HAP在调控植物叶绿体发育中起着重要作用。拟南芥*PIF1*和*PIF3*的突变体表现为白化，叶绿体发育迟缓。在连续红光照射下，光敏色素*PHYB*突变体表现出淡绿叶的表型。进一步研究表明*PHYB*调控*CHLH*与*GUN4*的表达，控制叶绿素合成[33]。水稻光敏色素互作的类bHLH因子*OsPIL1*直接调控*OsPORB*与*OsCAO1*的表达，从而控制叶绿素生物合成，其突变导致植株矮化、叶片淡绿以及抽穗期延迟[45]。在拟南芥中，*GLK2*基因的突变体表现为叶片灰绿，而在水稻中过表达*GLK2*的同源基因*OsGLK1*与*OsGLK2*导致愈伤组织转绿时间缩短，加速叶绿体的发育[5]。*OsHAP3A*、*OsHAP3B*和*OsHAP3C*编码CAAAT-box结合复合体HAP3亚基，调控水稻叶绿体生物合成，控制核编码的基因在叶绿体中的表达。反义干扰表达*OsHAP3A/B/C*的转基因植株叶片呈现浅绿色[18]。

染色质重塑因子*OsCHR4*参与水稻近轴叶肉细胞叶绿体早期分化，其功能的丧失阻碍近轴叶肉细胞叶绿体的发育，突变体表现出叶片近轴部白化、矮化、分蘖减少以及穗变短的表型[71]。另一水稻染色质重塑因子*OsCHR729*突变体表现出与*oschr4*类似的表型，如叶片白化、植株矮化、分蘖减少[71]。这些结果表明表观遗传修饰可能在水稻叶绿体发育过程中起着重要的作用。

2.2.6 其他叶绿体发育相关基因 叶绿体蛋白超过3000个，这些蛋白的突变都有可能导致植株叶色异常。近年来水稻中发现了一些叶绿体其他途径的基因突变导致叶色变异（表1）。*OsDG2*编码一个富含甘氨酸的叶绿体蛋白，调控质体分裂，其突变导致植株叶片黄化[27]。*V2*编码一个叶绿体和线粒体双定位的鸟苷酸激酶，参与质体的转录和翻译系统的建立，其突变导致低温下叶片白化[34]。*GRA78*编码一个定位于叶绿体的硫氰酸合成酶，其突变体表现出白条纹、矮化以及抽穗期延迟的表型[17]。*TSV3*编码一个类Obg GTPase蛋白，参与调控叶绿体50S核糖体大亚基的生物合成，其突变导致低温叶片白化[46]。目前，水稻克隆的叶色基因已超过120个，但很多叶色基因调控叶绿体发育的机制尚未完全解析，需要进一步加强相关调控机制的研究。

3 叶色基因在水稻育种中的应用

在水稻育种中，叶色易于观察与鉴定，适宜作为形态标记用于杂交育种和良种繁殖。白条纹与温敏白化转绿突变体如*cbd1*、*ysa*、*tcd9*在植株不同生长时期或一定温度范围内表现出叶色表型，对水稻的主要农艺性状影响较小。这些叶色突变体在水稻育种中已广泛应用，选育出了中紫S、白丰A、玉兔S、全龙A等一批不育系。白化致死突变体不能正常生长，不能用于实际生产。多数黄化、斑马叶以及淡绿突变体如*yl1*、*zebra2*、*fgl*往往伴随着矮化、分蘖减少、粒重降低的表型，表型受环境因素影响较大，严重影响水稻的最终产量。因此，这类突变体一般很难在水稻育种中应用。黄化转绿突变体*ygl1*有较高的光合效率和较强的耐受光抑制能力，获得较高的产量[50]。在水稻中过表达叶绿体基因*D1*生物量提高20.6%~22.9%，大田条件下的转基因水稻增产8.1%~21.0%[89]。Zhang等[72]研究发现过表达叶绿体定位的磷酸核糖胺甘氨酸连接酶*VAL1*可以显著提高转基因水稻的光合作用能力。因此，可以利用常规育种方法或基因工程技术将该类基因导入到常规品种中，提高水稻的生物学与经济产量。

4 展望

叶色突变体是研究植物光合作用和叶绿体发育、次生代谢物合成的理想材料。国内外学者已经克隆鉴定出超过120个叶色基因,利用分子遗传学对这些基因的功能进行了研究。利用白条纹、白化转绿等叶色突变体作为形态标记可以在苗期鉴别出真假杂交种,从而提高杂交种的纯度,进而提高产量。然而,很多适用于水稻育种的叶色基因只是被克隆,还没有真正用于水稻生产中,需要更多的育种家进行尝试应用。

叶绿体是一个具有复杂结构和功能的亚细胞系统,存在许多未知的途径,叶绿体的发育机制及光合作用的调控机制有待进一步研究。目前,生产上应用的叶色标记受环境影响大,不利于杂种的鉴定。因此,需要克隆鉴定出更多的白条纹、白化转绿基因,加强水稻叶色基因的挖掘和调控机理研究,不断完善叶绿体发育调控网络,为基因工程培育高光效作物新品种奠定基础。

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