

植物类胡萝卜素和花青苷代谢响应光信号的转录调控机制

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摘要 类胡萝卜素和花青苷是抗氧化代谢物,对于植物抵抗光氧化胁迫有重要作用。类胡萝卜素和花青苷同时赋予叶片、花朵和果实丰富多彩的色泽,果实富含的色泽代谢物对人体健康有益。本文总结了光信号对植物类胡萝卜素和花青苷生物合成代谢途径的影响,重点归纳了参与光信号途径的重要转录因子对类胡萝卜素和花青苷合成基因的调控机制,明晰了转录调控在光信号调控类胡萝卜素和花青苷合成代谢中的重要作用,有助于探索光调控果实品质的有效途径和靶基因,为利用基因工程和环境调控增加类胡萝卜素和花青素的积累提供理论依据。

关键词 光信号;类胡萝卜素;花青苷;转录调控;抗氧化;合成代谢;果实品质;非生物胁迫

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光调控植物类胡萝卜素和花青苷的生物合成和代谢贯穿植物整个生命过程,从幼苗破土而出受光诱导开始光形态建成到果实发育成熟,光能从多个层面对类胡萝卜素和花青苷的生物合成进行调控。类胡萝卜素是一类经异戊二烯途径合成的脂溶性萜类化合物,在质体中合成^[1];花青苷是一类经苯丙酸途径合成的水溶性黄酮类化合物,主要以糖苷的形式存在于植物液泡中^[2]。类胡萝卜素和花青苷对于植物的生长发育具有重要作用,如能保护植物免受光氧化伤害^[3];类胡萝卜素和花青苷也是果实和花卉呈色的重要色素,丰富的色彩能吸引昆虫帮助传播花粉和种子,利于植物的繁衍^[4-5]。近年来,有关光调控类胡萝卜素和花青苷代谢的研究已经在拟南芥、番茄、苹果、梨、柑橘和葡萄等植物中取得较好进展。

1 光信号及其受体参与类胡萝卜素和花青苷调控

植物主要通过光受体蛋白来接收不同波长的光,已知有4种光受体蛋白:吸收红光和远红光(600~750 nm)的光敏色素(PHYA~PHYE)、吸收UVA和蓝光(315~500 nm)的隐花色素(CRY1~CRY3)和向光素(PHOT1和PHOT2)以及吸收UV-B(280~315 nm)的紫外光受体

(UVR8)。光信号被光受体接收后,以调控一系列转录因子表达的形式参与植物花青苷生物合成与代谢调控^[6],研究表明,光受体蛋白和光信号转导因子响应相偶联,协同参与植物适应光环境过程。在拟南芥 *phyA* 突变体和 *uvr8* 突变体中,光不能诱导花青苷合成关键酶基因 *CHS* 的表达,导致花青苷的含量显著降低^[7];而 *CRY1* 能激活花青苷合成基因的表达促进花青苷的合成^[8];拟南芥 *UVR8* 在 UV-B 光下,与 *COP1* 互作,释放 *HY5*,从而开启 UVB 信号转导通路^[9]; *UVR8* 还能通过抑制 *WRKY36* 转录因子来促进 *HY5* 表达^[10]。在光敏型茄子中, *CRY1* 和 *CRY2* 能与 *COP1* 互作,为 *HY5* 和 *MYB1* 与下游花青苷合成基因如 *CHS* 和 *DFR* 的结合创造条件,从而促进花青苷的合成^[11]。番茄中 *CRY1a* 能介导蓝光诱导番茄花青苷的合成调控过程^[12]。苹果中 *CRY2* 能与 *COP1* 直接互作,从而减少 *COP1* 对 *MYB1* 蛋白的降解,促进花青苷的积累;超表达 *MdCRY2* 的拟南芥植株中内源基因 *HY5*、*CHS* 以及 *DFR* 的表达均受到诱导^[13]。梨中蓝光转导模块 *CRY-COP1-HY5* 参与蓝光诱导红梨果皮花青苷的积累^[14]。研究表明 *UVR8* 在 UV-B 促进苹果果皮着色中起关键作用, *UVR8* 与 *COP1* 形成复合体,使得下游 *HY5* 和 *MYB* 等正调控因子的

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表达激活,促进苹果果皮花青苷的积累^[15]。

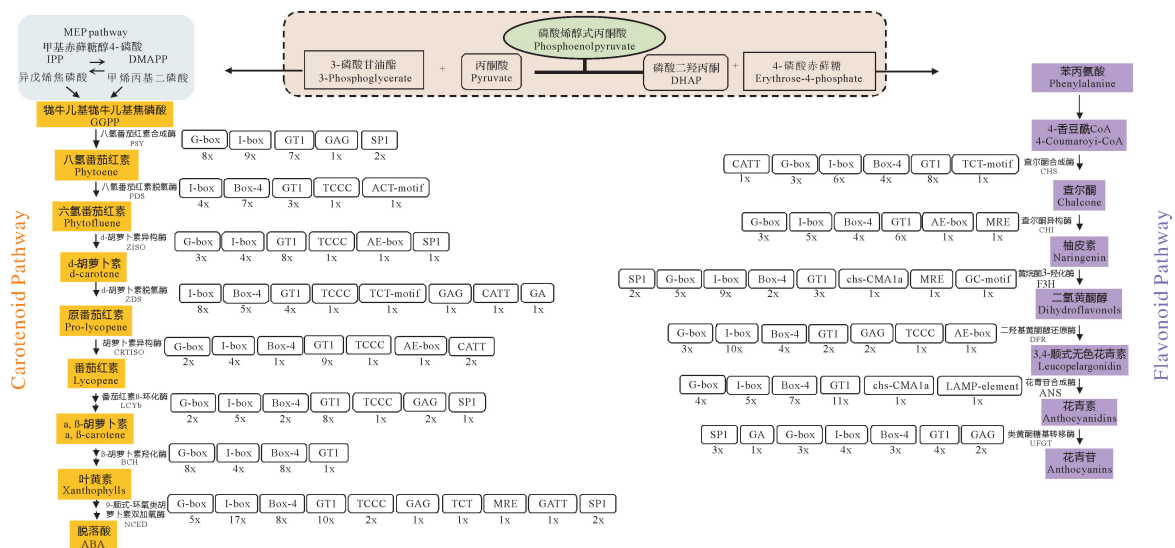
光受体参与植物类胡萝卜素合成调控的分子机制也取得了新的进展。如缺乏光敏色素的突变体番茄果实因不能积累类胡萝卜素而呈白色,这与黑暗中生长的番茄一样^[16],而在番茄中超表达 CRY2 能增加果实中类胡萝卜素的含量^[17];桃 CRY2 能参与蓝光促进桃果实中类胡萝卜素合成和积累^[18]。

2 类胡萝卜素和花青苷合成基因启动子的光响应元件

不同物种中直接调控类胡萝卜素和花青苷生物合成基因的转录调控因子、靶基因、靶基因启动子上

的结合位点以及类胡萝卜素和花青苷含量的变化等归纳于表 1 和表 2。光信号转录因子调控类胡萝卜素和花青苷生物合成代谢模式,与靶基因启动子上的光响应元件结合(如 G-box、I-box、GT1-box、Box 4 等),通过转录激活或抑制下游基因,从而调控类胡萝卜素和花青苷的代谢。

利用 PlantCARE 和 PLACE 在线网站对甜橙类胡萝卜素和花青苷生物合成通路基因启动子进行元件分析,结果显示,这些通路基因的启动子上均包含多个光响应元件(图 1),表明植物类胡萝卜和花青苷的生物合成受到光信号的调控。



1)水平的白色框代表基因启动子区域中含有的光响应原件,“x”表示基因启动子上该元件的数量。这些元件的核苷酸序列如下: ACE(GA-CACGTATG /CTAACGTATT); AT 1-motif (AATATTTTTTTATT); ATC-motif (AGTAATCT); ATCT-motif (AATCTAATCC); Box 4(AT-TAAT); chs-CMA1a (TTACTTAA); GAG (AGAGAGT); GATA-motif (AAGATAAGATT /AAGGATAAGG); G-box (HACGTG/CACGTH/CACGAC/TCCACATGGCA); GC-motif (CCCCCG); GT1 (GGTTAA /TTTTTC/GAAAAA/TTAACC); I-box (TTATC /GATAA); LAMP-element (CTTTATCA); MRE (AACCTAA); Sp1 (GGGCGG); TCCC (AGGGAGA/TCTCCCT); TCT-motif (TCTTAC); 2)MEP; 甲基赤藓糖醇 4-磷酸; DMAPP; 烯丙基二磷酸; IPP; 异戊烯焦磷酸; DHAP; 磷酸二羟丙酮。 1)The horizontally listed white boxes represent the promoter regions containing the light binding sites. The number of binding elements on each promoter region is indicated by 'x'. The nucleotide sequences of the putative binding sites are listed. ACE(GACACGTATG /CTAACGTATT); AT 1-motif (AATATTTTTTTATT); ATC-motif (AGTAATCT); ATCT-motif (AATCTAATCC); Box 4(ATTAAT); chs-CMA1a (TTACTTAA); GAG (AGAGAGT); GATA-motif (AAGATAAGATT /AAGGATAAGG); G-box (HACGTG/CACGTH/CACGAC/TCCACATGGCA); GC-motif (CCCCCG); GT1 (GGTTAA /TTTTTC/GAAAAA/TTAACC); I-box (TTATC /GATAA); LAMP-element (CTTTATCA); MRE (AACCTAA); Sp1 (GGGCGG); TCCC (AGGGAGA/TCTCCCT); TCT-motif (TCTTAC); 2) MEP; Methylerythritol phosphate; DMAPP; Dimethylallyl diphosphate; IPP; Isopentenyl diphosphate; DHAP; Dihydroxyacetone phosphate.

图 1 甜橙类胡萝卜素(左边)和花青苷(右边)代谢途径及光调控元件

Fig.1 Carotenoids (left) and flavonoid (right) biosynthetic pathways and their light regulatory elements in *Citrus sinensis*

3 参与光信号调控类胡萝卜素和花青苷合成的转录因子

3.1 HY5

HY5 是 bZIP 家族转录因子^[54],是光形态建成

的正调控因子, HY5 可以直接结合光响应基因启动子上的 T/G-box(CACGTT)、E-box(CANNTG)、GATAbbox(GATGATA)、ACE 元件(ACGT)、Z-box(ATACGGT)和 C-box(GTCANN)来参与各种信号通路,可结合的基因超 9 000 个^[55-56]。在黑暗

表 1 植物中报道的对类胡萝卜素直接调控的转录因子
Table 1 Transcription factors that directly regulating carotenoid biosynthesis in plants

转录因子 Transcription factor	家族 Class	靶基因 Target gene	启动子结合位点 Binding sites in promoter	总类胡萝卜素含量变化 Change of total carotenoids	物种 Species	参考文献 Reference
AtHY5	bZIP	PSY	G-box	↑	<i>Arabidopsis</i>	[19]
AtPIF1	bHLH	PSY	G-box	↓	<i>Arabidopsis</i>	[20]
AtRAP2.2	AP2/ERF	PSY, PDS	ATCTA	↓	<i>Arabidopsis</i>	[21]
CsMADS6	MADS	LCYb1, PSY, PDS, CCD1	CArG element	↑	<i>Citrus</i>	[22]
CrMYB68	MYB	BCH, NCED5	ACCAAC, ACCAAA	↓	<i>Citrus</i>	[23]
AdMYB7	MYB	PSY, PDS, ZDS, LCYB, LCYE	AACCATCC	↑	Kiwifruit	[24]
ZmPBF	P-box	BCH2	P-box	↑	Maize	[25]
GAMYB	MYB	BCH2	AACA motif	↑	Maize	[25]
MtWPI	MYB	LCYe, LCYb	MYB-core, AC-rich element	↑	<i>Medicago</i>	[26]
ofWRKY	WRKY	CCD4	W-box	↑	<i>Osmanthus</i>	[27]
CpEIN3a	EIN3/EIL	PDS4, BCH	PERE	↑	Papaya	[28]
CpNAC2	NAC	PDS2, PDS4, ZDS, LCYE, BCH	NACBS	↑	Papaya	[28]
CpbHLH1	bHLH	CYCB, LCYB	bHLH element	↓	Papaya	[29]
CpbHLH2	bHLH	CYCB, LCYB	bHLH element	↑	Papaya	[29]
CpNAC1	NAC	PDS2/4	NACBS	↑	Papaya	[30]
SlPIF1a	bHLH	PSY1	G-box, PBE-box	↓	Tomato	[31]
SIFUL1	MADS-box	PSY1, Z-ISO, CRTISO, BCH, LCYB, ZEP	—	↑	Tomato	[32]
SIFUL2	MADS-box	Z-ISO, CRTISO, BCHLCYB, ZEP	—	↓	Tomato	[32]
SINAC1	NAC	PSY1	C/TACG	↑	Tomato	[33]
SIBX20	B-box	PSY1, VDE	G-box	↑	Tomato	[34]
SlMYB72	MYB	PSY, ZISO, LCYB	R2R3-MYB-binding motif	↑	Tomato	[35]

注:“↑”表示总类胡萝卜素含量上调;“↓”表示总类胡萝卜素含量下调 Note:“↑” indicates that total carotenoids are increased; “↓” indicates that total carotenoids are decreased.

表 2 植物中报道的对花青苷直接调控的转录因子
Table 2 Transcription factors that directly regulating anthocyanin biosynthesis in plants

转录因子 Transcription factor	家族 Class	靶基因 Target gene	启动子结合位点 Binding sites in promoter	总花青苷含量变化 Change of total anthocyanins	物种 Species	参考文献 Reference
MdbHLH3	bHLH	<i>DFR, UFGT</i>	MYC, LTR, E-box	↑	Apple	[36]
MdWRKY11	WRKY	<i>UFGT</i>	W-box	↑	Apple	[37]
AtPIF3	bHLH	<i>CHS, CHI, F3H, F3'H, DFR, LDOX</i>	G-box	↑	<i>Arabidopsis</i>	[38]
AtHY5	bZIP	<i>CHS, CHI, F3H, F3'H, DFR, LDOX</i>	ACE, G-box	↑	<i>Arabidopsis</i>	[38-39]
AtMYB75	MYB	<i>CHS, DFR, LDOX, UFGT</i>	ACE-box	↑	<i>Arabidopsis</i>	[39]
AtPIF5	bHLH	<i>DFR</i>	G-box	↓	<i>Arabidopsis</i>	[40]
CmbHLH2	bHLH	<i>DFR</i>	E-box	↑	<i>Chrysanthemum</i>	[41]
CsPH4	MYB	<i>DFR</i>	MRE	↑	<i>Citrus</i>	[42]
CsRuby1	MYB	<i>F3H, DFR</i>	MRE	↑	<i>Citrus</i>	[43]
SmHY5	bZIP	<i>CHS, DFR</i>	G-box	↑	Eggplant	[11]
SmMYB1	MYB	<i>CHS, DFR</i>	MBS	↑	Eggplant	[11]
VlmvA	MYB	<i>UFGT</i>	—	↑	Grape	[44]
ZmC1	MYB	<i>CHS, DFR, UFGT</i>	—	↑	Maize	[45]
MtWP1	MYB	<i>CHS, ANS</i>	MYB-core element	↑	<i>Medicago</i>	[26]
PpMYB10.1	MYB	<i>UFGT, DFR</i>	ACE-box	↑	Peach	[46]
PpbHLH64	bHLH	<i>UFGT</i>	G-box	↑	Pear	[47]
PpHY5	bZIP	<i>CHS, DFR, ANS</i>	G-box	↑	Pear	[14]
PbMYB9	MYB	<i>UFGT1</i>	MYB CORE-like element	↑	Pear	[48]
PbMYB10	MYB	<i>UFGT1</i>	MYB CORE-like element	↑	Pear	[48]
PbMYB12b	MYB	<i>CHS, FLS</i>	ACE-box	↑	Pear	[49]
PcMYB10	MYB	<i>UFGT</i>	MBS	↑	Pear	[50]
StMYB44-1	MYB	<i>DFR</i>	MBS	↓	Potato	[51]
FvMYB10	MYB	<i>DFR, UFGT</i>	ACE-box	↑	Strawberry	[52]
FvbHLH33	bHLH	<i>DFR, UFGT</i>	ACE-box	↑	Strawberry	[52]
FvHY5	bZIP	<i>CHS, DFR</i>	—	↑	Strawberry	[53]
FvbHLH9	bHLH	<i>CHS, DFR</i>	—	↑	Strawberry	[53]
SlMYB72	bZIP	<i>CHS</i>	ACE-box	↑	Tomato	[35]

注：“↑”表示总花青苷含量上调；“↓”表示总花青苷含量下调。Note：“↑” indicates that total anthocyanins are increased；“↓” indicates that total anthocyanins are decreased.

中,E3 泛素连接酶 COP1 会靶向结合并通过 26S 蛋白酶体泛素化降解 HY5^[57]。

HY5 在光诱导花青苷的积累过程中发挥重要作用,在拟南芥^[39]、茄子^[11]、梨^[58]、苹果^[59]、柑橘^[59]中均有报道。总结发现,HY5 调控花青苷的合成代谢主要通过 2 条途径,一是直接结合结构基因的启动子,激活其表达;另一种是通过调控 MYB 类转录因子来间接调控结构基因的表达。大多数情况下,在光通过 HY5 调控植物花青苷的合成途径中,2 条途径都同时存在。HY5 能招募花青苷合成代谢的正调控因子 MdMYBDL1 共同促进花青苷的积累^[37];番茄中,HY5 能通过激活 AN1 和 AN2-like 的表达,促进花青苷的积累,而敲除 HY5 后,该番茄品种不能积累花青苷,说明 HY5 对于番茄积累花青苷起决定性作用^[60]。这一现象与光敏型茄子及柑橘品种血橙和紫皮柚的果皮在套袋情况下完全不积累花青苷的情况(图 2)一致,说明 HY5 是介导光调控果实花青苷积累的核心^[11,59]。此外,在拟南芥中还报道了 HY5 能转录及转录后水平调控花青苷积累的现象^[61]。由此可见,HY5 能通过多种方式参与光介导植物类胡萝卜素和花青苷合成的调控。



左图为血橙,黄色果实为套袋果实,红色果实为正常光照果实;右图为紫皮柚,黄色果实为套袋果实,红色果实为套袋后摘袋处理果实。Left is the blood orange,the yellow fruit is bagged and red fruit is under light exposure.Right is the purple pummelo tree,the yellow fruit is bagged all the time and the red fruit is from bag removal treatment.

图 2 同一棵树上柑橘果实受不同光照造成着色差异

Fig.2 Effect of different degree of light exposure on fruit color from the same tree

HY5 直接参与类胡萝卜素调控的报道较少。Toledo-Ortiz 等^[19]报道,HY5 通过直接与 PSY 启动子上的 G-box 结合,能促进 PSY 的表达,增加类胡萝卜素和叶绿素的积累。抑制高色素积累的 DDB1 缺失突变体 *hp-1* 番茄中 HY5 的表达,会抑制类囊体的形成以及类胡萝卜素的积累^[62]。

3.2 BBXs

B-box 家族蛋白是一类有 1 个或者 2 个 N 端的锌指结合 BBX 结构域的蛋白,在拟南芥中有 32 个家族成员^[63],在水稻中有 30 个家族成员^[64],在苹果中有 64 个家族成员^[65],在梨中有 39 个家族成员^[66]。在已报道的 BBX 家族蛋白中,可以分为促进光形态建成和抑制光形态建成 2 类^[67]。近年来,越来越多的 BBX 蛋白被报道参与光调控类胡萝卜素和花青苷合成代谢。

梨 BBX16 能促进梨愈伤中花青苷的积累,其要是与 HY5 形成复合体,两者协同调控梨花青苷的积累^[66];梨 BBX18 能诱导梨花青苷合成的正调控因子 bHLH64 的表达,两者协同调控光诱导梨果实着色^[47];Ou 等^[68]还报道 BBX24 的序列变异是造成“红早酥”梨果实积累花青苷差异的关键。苹果 BBX22 是 UV-B 诱导苹果花青苷合成的正调控因子,但 BBX22 促进花青苷积累的功能部分依赖于 HY5 的协同作用^[69];苹果 BBX20 也能与 HY5 形成复合体,直接与 MYB1、DFR 以及 ANS 启动子结合,促进花青苷的合成^[70];此外,Fang 等^[71]还报道了 MdCOL(BBX24)作为负调控因子参与果实花青苷合成调控过程。

在番茄中,超表达番茄 BBX20 使番茄质体变大、类胡萝卜素和叶绿素含量增加。互作实验表明,BBX20 通过结合 PSY1 启动子上的 G-box 元件,激活 PSY 的表达^[34]。

3.3 COP1

COP1 基因编码一个 RING-finger 类型 E3 泛素连接酶^[72],COP1 能整合多种光受体信号以及调控下游光响应因子,是光信号调控网络的核心^[73]。

COP1 在黑暗中通过降解 HY5 和其他光建成促进因子负调控光介导的植物类胡萝卜素及花青苷合成。在番茄中沉默 COP1-LIKE 基因表达,会增加花青苷和类胡萝卜素的含量^[62]。拟南芥中,COP1/SPA 复合体通过泛素化降解 MYB10 蛋白,抑制花青苷的积累^[74]。苹果中,COP1 抑制果皮花青苷的积累,黑暗下苹果 COP1 诱导 MYB1 蛋白降解,从而下调花青苷结构基因表达^[13]。套袋处理下,血橙花青苷积累显著降低,且 Ruby1 蛋白水平急剧下降,其原因可能是 COP1 介导了 CsRuby1 蛋白的降解过程^[59]。光照下,光受体能与 COP1 结合,抑制其对下游因子的降解作用^[7]。与上述机制有所不同的是,在非光依赖型葡萄中,COP1 无论在

光下还是黑暗中均定位于细胞质中,因此,不能介导 HY5 在黑暗中的降解,所以即使套袋情况下,该类型葡萄仍然积累花青苷^[75]。研究表明,COP1 的核定位受到 COP/DET/FUS 的调控^[9],因此有关非光依赖型葡萄中花青苷的积累在光信号转导传递层面的机制还有待完善。综上,COP1 参与植物类胡萝卜素和花青苷的调控主要有 2 条途径,一是通过互作降解 HY5 蛋白,另一方面,COP1 也可以直接介导花青苷合成重要调控因子的降解。

3.4 PIFs

PIFs 是一类 bHLH 家族转录因子,主要包括 PIF1 及 PIF3~8。PIFs 主要通过直接结合靶基因启动子上的 G-box 元件(CACGTG),参与抑制种子萌发、抑制幼苗光形态建成以及促进避荫响应等过程^[76]。PIFs 的蛋白水平还受到 COP/SPA 蛋白复合体的调控^[77]。

Toledo-Ortiz 等^[19]报道了 PIF1 通过直接与 *PSY* 启动子上的 G-Box 元件结合,抑制 *PSY* 的转录,降低类胡萝卜素的含量。DELLA-PIF 能形成复合体调控暗培养下子叶中叶绿素和类胡萝卜素的合成前体 POR 的水平^[78]。

PIFs 能通过抑制 *PSY1* 的表达以及类胡萝卜素的合成来响应避荫信号^[79]。除 HY5 外,PAR1 也负调控 PIF1,阻止遮阴下 PIF1 对 *PSY1* 表达的抑制,从而诱导类胡萝卜素的积累^[79]。PIF1 除了结合 *PSY1* 启动子上的 G-box 元件外,在番茄果实成熟过程中,PIF1 能结合 *PSY1* 启动子上的 PBE-box (CACATG),抑制 *PSY1* 的表达,从而负调控类胡萝卜素代谢^[31]。PIFs 对 *PSY1* 表达的抑制存在组织特异性,如在拟南芥根中,PIF 家族蛋白对 *PSY1* 的表达没有影响^[80]。

PIFs 还参与果实中花青苷的合成调控。通常情况下,PIFs 与 HY5 在很多调控过程中都是互相拮抗,但在远红光条件下,PIF3 需要 HY5 的协同作用才能结合花青苷合成基因的启动子,促进合成基因表达^[38]。在红光下,PIF4 和 PIF5 则表现为抑制花青苷合成基因及调控基因如 *CHS*、*F3H*、*DFR*、*LDOX*、*PAP1* 和 *TT8* 等的表达,从而抑制拟南芥幼苗花青苷的积累^[40]。

4 转录因子复合体对植物类胡萝卜素和花青苷的调控

纵观参与光调控植物类胡萝卜素和花青苷生物

合成的转录因子,发现 HY5 通常是直接作用于下游基因,参与类胡萝卜素和花青苷的生物合成调控,而 COP1、PIFs 和 BBXs 通常是通过调控 HY5 或者其他转录因子,间接调控下游基因,参与类胡萝卜素和花青苷的生物合成调控。同时,也有一些研究表明,HY5 能结合下游基因启动子但是不能激活下游基因的表达,这意味着 HY5 行使功能需要一些协作蛋白^[81]。近几年,关于以 HY5 为核心,与 COP1、PIFs 和 BBXs 等形成复合体调控下游基因表达的研究报道不断涌现,主要模型有 HY5-BBXs^[82]、HY5-PIFs^[83]、HY5-PIFs-BBXs^[63]、HY5-COP1-BBXs^[84]。

PIFs 与 HY5 之间有协同作用也有拮抗作用,如 PIF3 需要 HY5 的协同作用才能促进下游花青苷合成基因的表达^[38];而 PIF1 与 HY5 作为拮抗因子响应光照和温度,调控类胡萝卜素基因的表达^[20],但在红光/远红光下,PIF1 和 PIF3 结合 HY5 启动子,促进 HY5 的表达^[84]。相似地,BBXs 中也分为正调控和负调控 HY5 表达两类。拟南芥中,BBX20/BBX21 能调控 HY5 转录后水平,BBX20/BBX21 与 HY5 蛋白互作形成复合体促进光形态建成,包括促进花青苷合成基因的表达^[85];而 BBX24 的作用与 BBX21 相反,抑制 HY5 结合下游基因的启动子^[77]。最新研究表明,BBX20、BBX21 和 BBX22 是 HY5 介导下胚轴伸长、花青苷积累以及转录调控的重要协同蛋白^[86]。

COP1 作为光形态建成的核心负调控因子,也调控 HY5、BBXs、PIFs 的转录后水平,共同调控光形态建成、避荫响应和色素积累等过程。AtBBX21 和 COP1 相互作用,BBX24 能与 DELLA 蛋白互作响应避荫反应^[87]。COP1 通过与下游 HY5、BBX22、BBX24 互作,抑制这些基因的蛋白水平^[83]。Delker 等^[88]报道 DET1-COP1-HY5 复合体能响应光和温度,调控 PIF4 介导幼苗光形态建成;这进一步说明了该过程的具体调控机制是 DET 促进 PIF4 表达,HY5 与 PIF4 拮抗调控;在高温下,DET1/COP1 促进 PIF4 蛋白的稳定,调控光形态建成中下胚轴伸长^[89]。在梨中,BBX16-HY5 复合体,直接结合 MYB10 的启动子或者直接与 *CHS*、*CHI* 结构基因的启动子互作,从而促进光诱导花青苷的合成^[66]。在苹果中 BBX20-HY5 形成复合体,直接与 MYB1、*DFR* 以及 *ANS* 启动子结合,促进花青苷的合成^[64];Fang 等^[71]还报道了苹果中 MdCOL4

(AtBBX24 的同源基因)能同时响应 UV-B 和高温调控苹果果实的着色,与 BBX20 功能相反,MdCOL4 与 HY5 形成复合体会抑制 MYB1、ANS 和 UFGT 的表达,从而抑制苹果果实花青苷的积累;苹果中 BBX22 与 HY5 也能形成复合体,增强 HY5 与 MYB10 和 CHS 启动子的结合,从而促进花青苷的合成^[69]。在番茄中,BBX20 能激活 PSY1 的表达,超表达番茄 BBX20 使得番茄果实类胡萝卜素含量增加^[34]。BBXs 之间还能形成竞争抑制,梨 BBX21 能分别与 HY5、BBX18 互作,抑制 HY5-BBX18 复合体的形成,从而抑制 HY5-BBX18 复合体对 MYB10 的激活作用,导致花青苷的积累减少^[90]。

5 展 望

光作为植物生长发育最重要的环境因子之一,不仅是植物光合作用的能源,还作为信号因子参与植物生长发育的许多过程。解析光信号调控植物生长发育的分子机制始于 COP1 的鉴定,在过去的 30 年里,又有 PIFs、HY5、BBXs 等基因不断被挖掘,有关这些转录因子参与光信号调控的分子机制在模式植物拟南芥中得到了深入的解析。近年来,在苹果、柑橘、梨、葡萄、番茄等园艺作物中,光信号参与果实色素积累的调控机制不断被解析。光照条件是栽培中影响园艺作物生长水平的重要因素,且色泽是园艺作物果实的重要品质指标,因此,解析光信号对果实色泽(叶绿素、类胡萝卜素、花青苷)的调控分子机制,能为生产上对园艺植物的光环境进行合理调控,为改善果实色泽品质提供一定的理论依据。

光信号调控植物类胡萝卜素和花青苷生物合成的分子机制研究已取得了很多进展,然而还有一些问题值得深入挖掘和解析:(1)目前对光信号调控植物类胡萝卜素和花青苷的分子机制的解析仅限于单一调控,未能发掘到同时调控 2 种色素的关键调控因子或调控复合体;(2)目前光信号对花青苷的调控分子机制解析较多,但光信号调控类胡萝卜素的研究多停留在生理层面,有待进一步挖掘新的调控转录因子和转录因子复合体,以及进一步解析这些转录因子调控类胡萝卜素代谢的具体机制;(3)有关表观遗传修饰在光信号调控植物类胡萝卜素和花青苷生物合成过程的报道较少,可以进一步挖掘是否有 DNA 甲基化、组蛋白乙酰化和染色质重塑等参与该过程的调控;(4)在苹果中发现 *IncRNAs* 参与白光和蓝光诱导花青苷的积累^[91],但尚未有研究报道小

RNA 是否参与光对类胡萝卜素生物合成的调控过程;(5)植物类胡萝卜素和花青苷的积累受到光照、温度、激素等多种环境因素的协同调控,目前仅在苹果中发现 MdBT2 能够整合多种环境信号和激素调控花青苷积累^[92],而有关光信号、温度信号、激素信号等协同调控植物类胡萝卜素的分子机制还有待阐明。以上几方面的深入研究能更全面地解析光调控类胡萝卜素和花青苷代谢的分子机制,这能为利用基因工程和环境调控等手段定向调控植物类胡萝卜素和花青苷代谢提供一定的理论基础。

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Transcription regulation of plant carotenoids and anthocyanin metabolism in response to light signals

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Abstract Carotenoids and anthocyanins are antioxidant metabolites, which play an important role in the resistance of plants to photooxidative stress and contribute to the color of leaves, flowers, and fruits at the same time. The rich color metabolites of fruits are beneficial to human health. This article summarizes the effects of light signals on the biosynthetic metabolic pathways of plant carotenoids and anthocyanins, focusing on the regulatory mechanisms of important transcription factors involved in the light signal pathways of genes for synthesizing carotenoid and anthocyanin, and clarifies a significant role for light signals and photoreceptors in mediating the regulation of carotenoids and anthocyanins biosynthesis. Using sweet orange (*Citrus sinensis*) as an example, the light response elements of carotenoid and anthocyanin biosynthetic genes were analyzed. The major transcription factors including HY5 (elongated hypocotyl 5), BBXs (B-BOX containing proteins), COP1 (constitutively photomorphogenic 1), PIFs (phytochrome-interacting factors), and HY5-BBXs complexes, HY5-PIFs complexes, HY5-PIFs-BBXs complexes, HY5-COP1-BBXs complexes that participate in these pathways are summarized. It provides an insight into the regulatory mechanism underlying of HY5, BBXs, COP1, PIFs-mediated carotenoids and anthocyanins accumulation. Understanding the crucial role of the transcription regulation of carotenoid and anthocyanin mediated by light may help us to explore effective pathways and target genes for improving fruit quality and increasing the accumulation of carotenoid and anthocyanin via genetic engineering and environmental treatments.

Keywords light signals; carotenoids; anthocyanins; transcription regulation; antioxidation; anabolism; fruit quality; abiotic stress

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