

GA 信号途径及其调控果树生长发育的研究进展

王 弋,董 晨,魏永赞,郑雪文,李伟才*

(中国热带农业科学院南亚热带作物研究所·农业部热带果树生物学重点实验室,广东湛江 524091)

摘 要: 赤霉素(gibberellins, GAs)是一类重要的植物激素,参与调控植物生长发育的各个阶段,如种子的萌发、幼苗的生长、茎和根的生长及开花等过程。随着分子生物学及遗传学的发展,科学家已经逐步解析了GA在植物体内的信号转导过程及调控植物生长发育的机制。2017年以来,科学家在GA受体GID1的降解机制、DELLA新互作蛋白的鉴定以及O-fucosyltransferase修饰对GA信号的影响等多个方面均有重要发现,这些新成果大大扩展了人们对GA信号调控机制的认知。GA在果树育种中也发挥着重要作用,早在16世纪育种家就在葡萄中成功利用GA信号途径阻遏蛋白DELLA的功能获得型突变实现矮化育种,提高产量。近年来,又在多种果树中发现了GA途径基因突变造成的矮化材料。GA突变体在果树育种中的利用已证明,人为调控GA信号是实现果树高产稳产的有效方法。鉴于GA在植物生长发育及果树生产中的重要作用,笔者将对GA信号途径的最新研究进展及其在果树生产中的应用进行系统介绍,为将来在果树中更高效、更广泛地利用GA途径基因、提高果树产量及品质提供参考。

关键词: 果树;赤霉素;信号转导;DELLA蛋白;转录因子

中图分类号: S66 文献标志码: A 文章编号: 1009-9980(2018)04-0500-12

Research progress on GA signaling pathway and its function in regulating fruit trees growth and development

WANG Yi, DONG Chen, WEI Yongzan, ZHENG Xuewen, LI Weicai*

(South Subtropical Crop Research Institute, Chinese Academy of Tropical Agricultural Sciences·Key Laboratory of Tropical Fruit Biology, Ministry of Agriculture, Zhanjiang 524091, Guangdong, China)

Abstract: GAs are geranylgeranyl diphosphate (GGDP)-derived phytohormones, control diverse aspects of plant growth and development, such as seed germination, flowering, root development and fruit development. At least 136 GAs have been identified, but only a few GAs such as GA₁, GA₃, GA₄ and GA₇ exhibit biological activity. In the past decades, great progress has been made in the understanding of GA signaling transduction and a functional GA-GID1-DELLA-SCF^{GID2/SLY1/SNE}-plant development repression regulatory model has been established. GID1 was identified from rice in 2005, the loss-of-function *gid1* mutant exhibit a severely dwarfed phenotype which was insensitive to exogenous GA. Recombinant glutathione S-transferase (GST)-GID1 showed high affinity only for biologically active GAs, whereas mutated GID1 had no GA-binding affinity. The *Arabidopsis* genome encodes three *GID1* homologous, *AtGID1a*, *AtGID1b* and *AtGID1c*. GA-binding activities of *AtGID1a/AtGID1b/AtGID1c* were confirmed by biochemical analyses *in vitro*. With the uncovering of *OsGID1* crystal structure, scientists found *OsGID1* showed an alpha/beta-hydrolase fold characteristic. GID1s interact with N-terminal domain of DELLA proteins directly in a bioactive GA-dependent manner and promote the degradation of DELLA proteins via the 26S proteasome pathway. The DELLA proteins are members of the

收稿日期:2017-11-01 接受日期:2018-02-12

基金项目:海南省自然科学基金(317241);中央级公益性科研院所基本科研业务费专项(1630062018013);国家现代农业(荔枝龙眼)产业技术体系(CARS-032-20)

作者简介:王弋,男,助理研究员,研究方向为荔枝花穗发育调控。Tel:0759-2859112, E-mail:wangyi30626@163.com

*通信作者 Author for correspondence. Tel:0759-2859112, E-mail:lwc-619@163.com

plant-specific GRAS gene family, acting as negative regulators of GA signaling. They include the conserved N-terminal DELLA and TVHYNP motifs which are responsible for the interaction with GID1 and the conserved C-terminal GRAS domain which mediates the secondary interactions with the GID1 and F-box proteins. DELLA proteins function as transcriptional repressors by blocking the activity of transcription factors such as PIFs, NACs, JAZ, SCL3, IDD3, SPLs etc. GID2 (GIBBERELLIN INSENSITIVE DWARF2), SLY1 (SLEEY1) and SNE (SNEEZY) all belong to E3 ubiquitin ligase F-box protein. SLY1/GID2/SNE positive regulate GA signaling through mediating the degradation of DELLA proteins via the 26S proteasome system. The binding of bioactive GAs to GID1 induce the formation of GA-GID1-DELLA protein complex, and then enhances the interaction between DELLA proteins and SCF^{SLY1/GID2/SNE} complex. GAs have long been associated with dwarfism in plant and beneficial mutations in GA pathway had been used in fruit trees breeding. A semi-dominant *Vvgai* allele that contains a gain of function mutation in the DELLA domain had been used in grape dwarfing breeding in the 1500s, long before the wheat “green revolution” in 1950s. The peach GID1c act as the GA receptor and regulate vegetative growth, a nonsense mutation within *Ppegid1c* result in dwarf phenotype while fruit development was not impaired. Besides GA perception and signaling genes, GA biosynthesis and inactivation genes also play important role in fruit trees dwarfing breeding. For example, suppression of *GA20-oxidase* in apple reduced the levels of bioactive GAs, resulting in significant reduction in plant height. The dwarfing phenotype of scion was not affected when grafting on to normally rootstocks. In plum, high expression level of GA inactivation gene *PsIGA2ox* associated with low accumulation of bioactive GA₁ and GA₄, and resulting in smaller leaves, shorter stems, late flowering. Therefore, both GA perceptions, signal transduction, synthesis and inactivation genes are all applicable in fruit trees dwarfing breeding. GAs also play an important role in coordinating fruit development processes, application of GAs could significantly improve fruit size, weight and many other characteristics. Pollination significantly increases GAs content by inducing gibberellin biosynthesis in fruit trees such as apple and grape. In addition, GAs involve in the induction of parthenocarpy in fruit trees. Wittwer firstly demonstrated that exogenous GAs were able to induce tomato parthenocarpy in 1957, thereafter GAs were used to induce parthenocarpy in many fruit trees, such as apple, grape and pear. Plant dormancy refers to the slow growth or temporary cessation of whole plant or some organ growth. GAs are widely used in bud dormancy breaking to improve fruit yield and quality in fruit trees, such as citrus, peach and cherry. GAs are also important signaling substances that relieve seed dormancy. GAs are synthesized in embryo and then transport to aleurone cells to induce a series of hydrolases, such as alpha-amylase, protease and beta-glucanase. Up to now, only a few fruit trees have obtained dwarfing genetic resources, thus GA synthesis inhibitors are widely used in fruit trees to inhibit vegetative growth, including dwarfing fruit trees, shortening internodes, promoting rhizogenesis etc. In 2017, a series of breakthroughs in GA signal transduction have been discovered, such as the degradation mechanism of GA receptor GID1s, the identification of new DELLA interaction proteins and the function of O-fucosyltransferase in GA signaling pathway. These new discoveries enhance the understanding of GA signaling pathway. The application of GA mutants in fruit trees breeding and the application of GA-related growth regulators in fruit trees cultivation have proved that artificial control of GA signal could significantly enhance the yield of fruit trees. In view of the important roles of GAs in plant growth, this review will introduce the latest research progress in GA signaling pathway and its function in regulating fruit trees growth and development.

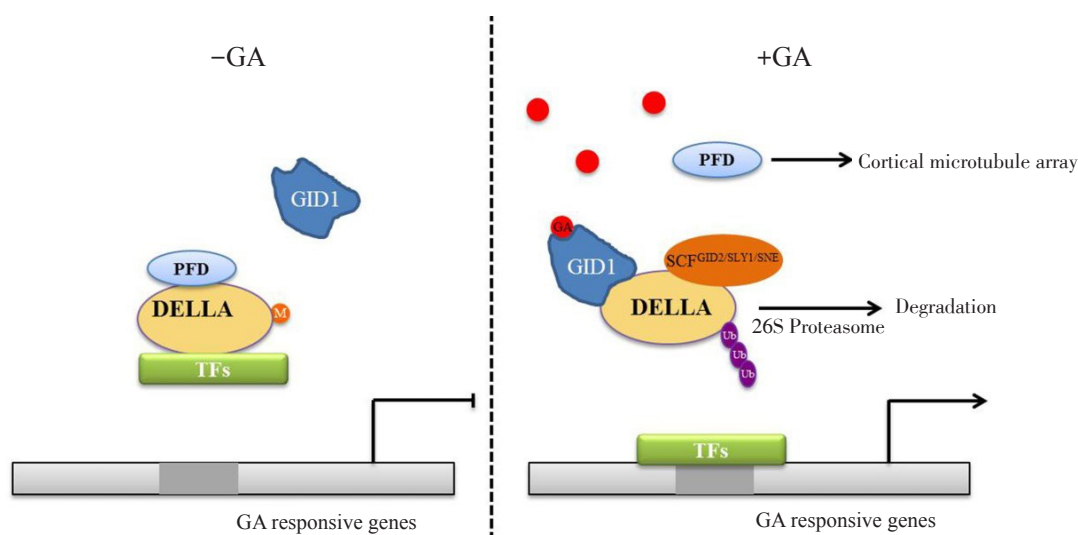
Key words: Fruit trees; Gibberellin; Signal transduction; DELLA; Transcription factor

赤霉素(gibberellins, GAs)是一大类萜类化合物家族,目前已发现至少 136 个成员,但只有少数成员具有生物学活性,如 GA₁、GA₃、GA₄及 GA₇等^[1-2]。GA 参与调控植物生命周期几乎所有的生长发育阶段,包括种子的萌发、幼苗的生长、茎和根的生长、开花、花器官发育及果实成熟等过程^[3]。在果树生产中,GA 在调控株高、果实发育、花穗发育、打破休眠等方面均有重要作用^[4-6]。利用模式植物 GA 不敏感的矮化突变体,科学家已揭示了高等植物 GA 信号转导途径的主要组分。笔者将通过对这些组分的介绍,阐述 GA 信号转导的过程,同时结合 GA 在生产中的应用,介绍 GA 调控果树生长发育的机

制。

1 GA 信号途径

近 20 a(年),随着遗传学、分子生物学及生物化学的发展,科学家已经逐步解析了 GA 信号的转导过程,GA 信号转导的基本框架为 GA-GID1-DELLA-SCF^{GID2/SLY1/SNE}-植物生长发育^[7-8]。其中 GID1(GIBBERELLIN INSENSITIVE DWARF1)为 GA 受体蛋白,DELLA 为 GA 信号途径阻遏蛋白;而 GID2(GIBBERELLIN INSENSITIVE DWARF2)、SLY1(SLEZY1)和 SNE(SNEZY)均为 F-box 蛋白,参与介导 DELLA 蛋白的降解^[8](图 1)。



无 GA 时,受体 GID1 与 DELLA 蛋白不存在互作,DELLA 蛋白处于稳定状态,并抑制其互作蛋白功能,GA 响应基因被抑制。施加 GA 后,GID1 与 DELLA 发生互作,并激活由 SCF^{GID2/SLY1/SNE} 介导的 DELLA 降解,互作蛋白被释放,GA 信号被激活。

In the absence of GA, the receptor GID1 and the DELLA protein do not interact with each other. The DELLA protein is in a stable state and inhibits the function of its interaction proteins, and the GA response genes are suppressed. when GA was applied, GID1 interacts with DELLA and activation the degradation of DELLA mediated by SCF^{GID2/SLY1/SNE}, then the interacting proteins are released and the GA signal is activated.

图 1 GA 信号的去阻遏模型^[8-10]

Fig. 1 The de-repression regulatory model of GA^[8-10]

1.1 GA 受体蛋白——GID1

GA 参与调控植物的生长发育,但 GA 如何被细胞感知的问题一直困扰着科学家。2005 年,名古屋大学的研究人员通过对水稻 GA 不敏感矮化突变体 *gid1* 的研究,首先发现了 GA 受体蛋白 GID1^[9]。生化实验表明,体外表达的 GST-GID1 融合蛋白与具有生物学活性的 GA 具有高亲和性^[9]。拟南芥基因组中含有 3 个 *GID1* 的同源基因,分别为 *AtGID1a*、*AtGID1b* 及 *AtGID1c*,研究已证实 3 者均具有 GA 亲和性^[10-11]。GID1 受体蛋白研究的另一个突破来自于晶

体结构的解析,2008 年拟南芥和水稻 GID1 蛋白的晶体结构分别被解析^[1,12]。晶体结构表明 GID1 属于 α/β -hydrolase 超家族中的羧酸酯酶家族,当具有生物学活性的 GA 被 GID1 感知并占据口袋结构时,GID1 的构象迅速发生改变,N 端的延伸结构在 C 端的口袋结构上形成一个盖子,而盖子的外表面则与 DELLA 蛋白互作,形成 GA-GID1-DELLA 蛋白复合体,促进 DELLA 蛋白的降解^[13]。2017 年来自日本的课题组发现并揭示了 GID1 蛋白稳定性受泛素化负调控、磷酸化正调控的分子机制^[14]。该研究利用小

麦无细胞体系鉴定了一个GID1蛋白特异的E3连接酶GARU(GA receptor RING E3 ubiquitin ligase)以及GARU的蛋白激酶TAGK2/CRK2。研究发现,E3连接酶GARU通过诱导GID1s的泛素化促进其降解,负调控GA信号;而Tyr-激酶TAGK2通过磷酸化GARU第321位的酪氨酸减弱其对GID1a的亲性和,进而正调控GA信号途径^[14]。

1.2 GA途径阻遏因子——DELLA蛋白

1.2.1 DELLA蛋白的稳定性及活性调控 DELLA属于GRAS蛋白家族,是GA信号途径的负调控因子,其功能是阻遏植物的生长发育。拟南芥基因组中含有5个DELLA蛋白成员,分别是GA-INSENSITIVE(GAI)、REPRESSOR-of-gal-3(RGA)、RGA-LIKE1(RGL1)、RGL2和RGL3,水稻中只有1个DELLA成员,即SLENDER RICE1(SLR1)^[8]。DELLA蛋白的C端与其他GRAS家族成员高度同源,而N端含有2个保守区,即DELLA结构域与VHYNP结构域。当DELLA蛋白的C端发生突变时,其阻遏功能消失,植株表现出株高增加、开花提前等GA信号增强的表型,水稻的*slr1*和大麦的*sln1*突变均属于这一类型。而当DELLA蛋白N端发生突变时,形成不被降解的稳定形式,阻遏功能增强,植株表现出矮小、叶色暗绿、开花延迟等表型,拟南芥的*gai*突变体即属于此类型^[2]。

Fu^[15]首先证明DELLA蛋白的降解过程由蛋白酶体介导。随后,在拟南芥和水稻中分别发现了DELLA蛋白特异的泛素E3连接酶SLY1(SLEEPY1)与GID2(GIBBERELLIN INSENSITIVE DWARF2)。这2个突变体均表现出植株矮小、叶色深绿、育性降低以及DELLA蛋白大量积累的性状。生化实验表明,SLY1和GID2均能与DELLA发生直接的蛋白互作,并介导DELLA蛋白的降解^[2,10]。

DELLA蛋白不仅稳定性受到泛素修饰调控,其蛋白活性还受到O-岩藻糖基化(O-fucosylation)、O-葡萄糖胺乙酰化(O-GlcNAcylation)、SUMO化及磷酸化(phosphorylation)等蛋白翻译后修饰的调控。SPINDLY(SPY)具有岩藻糖基转移酶活性,能够在DELLA特定丝氨酸和苏氨酸残基上进行单海藻糖修饰,增强DELLA蛋白活性^[16]。SECRET AGENT(SEC)蛋白所催化的O-GlcNAc修饰对于DELLA蛋白与PIF3/4、BZR1等转录因子的结合也有重要作用^[17]。

*ELI*基因编码酪蛋白激酶,其通过磷酸化水稻DELLA蛋白SLR1增强其稳定性,负调控GA信号^[18];而Type-One型磷酸酶TOPP4蛋白通过互作将DELLA去磷酸化,引起GA介导的DELLA蛋白降解,正调控GA信号^[19]。DELLA蛋白的SUMO化修饰对于提高植物在逆境条件下的适应性也具有重要作用^[20]。转录后修饰影响GA信号途径机制的发现,大大拓展了人们对GA信号途径的认识。

1.2.2 DELLA抑制转录因子功能 DELLA蛋白积累抑制植物的生长发育,那么从DELLA蛋白积累到抑制植物生长之间的信号如何传递?研究表明DELLA蛋白具有转录抑制功能,但是该蛋白本身并无结合启动子的结构域,因此必须依赖于转录因子才能实现对下游基因的调控。利用酵母双杂、BiFC和Co-IP等生化方法,科学家已在拟南芥和水稻中鉴定了至少28个DELLA调控的互作蛋白。这些互作蛋白大部分为转录因子,DELLA蛋白通过与这些转录因子的互作,抑制其调控下游基因的能力(如PIFs、ERF11、IDDs、ABI3/5、SPLs及ARF6等),影响GA响应。笔者已将DELLA调控的互作蛋白信息列于表1。

GA还通过与转录因子的互作参与不同激素调控植物生长发育的过程。GA和BR均促进拟南芥下胚轴伸长,但当缺失BR信号时,GA对下胚轴伸长几乎没有影响^[21],这表明GA调控下胚轴伸长依赖BR。进一步的研究发现,存在外源GA时,DELLA蛋白被降解,进而释放出被其失活的BZR1转录因子,激活下游响应基因表达。GA和乙烯能够协同调控顶点钩的弯曲,An等^[22]的研究发现,DELLA蛋白与乙烯信号途径组分EIN3/EIL1蛋白的DNA结合结构域互作,抑制其调控下游*HOOKLESS1(HLS1)*基因的表达,并影响顶点钩的发育。最近的研究发现,乙烯途径基因*AtERF11*能够参与GA信号途径,一方面通过阻碍乙烯合成抑制乙烯信号,另一方面通过蛋白互作抑制DELLA蛋白功能,进而促进GA应答反应,并促进下胚轴的伸长^[23]。

2 GA调控果树生长发育的机制

2.1 GA与树体矮化

GA在作物矮化育种中具有极为重要的作用,上世纪50年代的“绿色革命”中,水稻和小麦分别利用了GA20ox2和DELLA蛋白的有益突变^[24],实现

表 1 与 DELLA 蛋白互作的下游信号组分

Table 1 The downstream signal components interact with DELLA protein

DELLA 蛋白 DELLA proteins	互作蛋白 Interaction proteins	物种 Species	生物学过程 Biological process	参考文献 Reference
GAI/RGA	Ethylene-insensitive3 (EIN3)	拟南芥 <i>Arabidopsis</i>	乙烯信号途径 Ethylene signaling pathway	[22]
RGA	Jasmonate ZIM-domain (JAZ)	拟南芥 <i>Arabidopsis</i>	茉莉酸信号途径 Jasmonic acid signaling pathway	[25]
GAI	RELATED TO APETALA2.3 (RAP2.3)	拟南芥 <i>Arabidopsis</i>	顶点钩发育 Apical hook development	[26]
RGA	CONSTANS (CO)	拟南芥 <i>Arabidopsis</i>	开花时间 Flowering time	[27]
RGA	BRASSINAZOLE-RESISTANT1 (BZR1)	拟南芥 <i>Arabidopsis</i>	油菜素内酯信号途径 Brassinosteroid signaling pathway	[21]
RGA/RGL2	WD-repeat/bHLH/MYB	拟南芥 <i>Arabidopsis</i>	表皮毛发育 Trichome development	[28]
GAI/RGA/RGL2	ALCATRAZ (ALC)	拟南芥 <i>Arabidopsis</i>	果实发育 Fruit development	[29]
RGA/RGL2	SPATULA (SPT)	拟南芥 <i>Arabidopsis</i>	果实发育 Fruit development	[30]
GAI/RGA	PICKLE (PKL)	拟南芥 <i>Arabidopsis</i>	光信号途径 Light signaling pathway	[31]
SLR1	NAC transcription factor 29/31 (NAC29/31)	水稻 Rice	纤维素合成 Cellulose synthesis	[32]
SLR1	Culm easily fragile1 (CEF1)	水稻 Rice	纤维素合成 Cellulose synthesis	[33]
GAI	PREFOLDIN3/5 (PFD3/5)	拟南芥 <i>Arabidopsis</i>	微管形成 Microtubule formation	[34]
RGA	SQUAMOSA PROMOTER BINDING PROTEIN-LIKEs (SPLs)	拟南芥 <i>Arabidopsis</i>	成花诱导 Floral induction	[35]
GAI/RGA/RGL1/ RGL2/RGL3	INDETERMINATE DOMAINS (IDDs)	拟南芥 <i>Arabidopsis</i>	根发育 Root development	[36]
RGA	SCARECROW-LIKE 3 (SCL3)	拟南芥 <i>Arabidopsis</i>	根发育 Root development	[37]
RGA	Auxin response factor 6 (ARF6)	拟南芥 <i>Arabidopsis</i>	下胚轴伸长 Hypocotyl elongation	[38]
GAI/RGA/RGL1/ RGL2/RGL3	Phytochrome interacting factors (PIFs)	拟南芥 <i>Arabidopsis</i>	下胚轴伸长 Hypocotyl elongation	[21]
RGA/GAI	Ethylene response factor 11 (ERF11)	拟南芥 <i>Arabidopsis</i>	下胚轴伸长 Hypocotyl elongation	[23]
GAI/RGA/RGL1/ RGL2/RGL3	BOTRYTIS SUSCEPTIBLE1 INTERACTORS (BOIs)	拟南芥 <i>Arabidopsis</i>	种子萌发 开花 Germination and flowering	[39]
RGL2/RGL3	SWITCH/SUCROSE NONFERMENTING 3C (SWI3C)	拟南芥 <i>Arabidopsis</i>	种子萌发 叶片发育 Germination and leaf development	[40]
SLR1	Dwarf14 (D14)	水稻 Rice	独脚金内酯信号途径 Strigolactone signaling pathway	[41]
RGL1	WRKY DNA-binding protein 45 (WRKY45)	拟南芥 <i>Arabidopsis</i>	叶片衰老 Leaf senescence	[42]
RGL1	Basic helix-loop-helix48/60 (bHLH48/60)	拟南芥 <i>Arabidopsis</i>	开花 Flowering	[43]
RGL2	DNA-BINDING ONE ZINC FINGER6 (DOF6)	拟南芥 <i>Arabidopsis</i>	种子休眠 Seed dormancy	[44]
GAI/RGA/RGL1/ RGL2/RGL3	GAI-ASSOCIATED FACTOR1 (GAF1)	拟南芥 <i>Arabidopsis</i>	GA 合成 GA biosynthesis pathway	[45]
RGA	ABA-insensitive3/5 (ABI3/5)	拟南芥 <i>Arabidopsis</i>	种子萌发 Germination	[46]
GAI/RGA	Type-B ARABIDOPSIS RESPONSE REGULATORS1 (ARR1)	拟南芥 <i>Arabidopsis</i>	根发育 Root development	[47]
RGA	MUT9p-LIKE PROTEIN1/2 (MLK1/2)	拟南芥 <i>Arabidopsis</i>	节律钟 Circadian clock	[48]

了半矮化育种,解决了发展中国家的粮食自给问题。矮化也是果树育种的一个重要目标,一方面,矮化的树体和紧凑的树冠适宜密植,提高了土壤及光能的利用效率;另一方面,矮化果树将有限的光合产物更多地用于生殖生长而非营养生长,因此矮化育种是果树实现增产增效的必经之路。早在16世纪,葡萄中就已利用GA途径基因的有益突变实现了矮化育种,这比粮食作物的矮化育种早了300多年^[49]。

‘莫尼耶皮诺’(‘Pinot Meunier’)是一个古老的葡萄品种,在16世纪育成,与‘黑比诺’(‘Pinot noir’)和‘霞多丽’(‘Chardonnay’)并称为酿造香槟的3大葡萄品种。目前认为,‘莫尼耶皮诺’由‘黑比诺’突变而来,与‘黑比诺’相比,‘莫尼耶皮诺’具有半矮化及多花序的表型,但长期以来对其矮化机制并不清楚。Boss等^[49]研究发现,相比‘黑比诺’,‘莫尼耶皮诺’L1层细胞的DELLA蛋白发生了变异,其L1层细胞的DELLA蛋白-VvGAI1编码基因发生了1个单碱基突变,该突变造成DELLA结构域的第2个亮氨酸(Leu)突变为组氨酸(His),引起功能获得型的半显性突变,造成矮化表型。此外,由‘莫尼耶皮诺’L1层细胞分化而来的再生植株对GA不敏感,且GA₁和GA₄的含量较野生型分别升高4倍和12倍,这进一步表明‘莫尼耶皮诺’是由于GA信号缺失导致的矮化^[49]。

桃树中也发现一系列具有矮化表型的遗传材料,根据表型这些矮化材料可分为*dw*、*dw2*和*dw3*3种类型。其中*dw*矮化类型受1个隐性基因控制,携带该基因纯合位点的材料表现出节间缩短、树干粗壮、高阶分枝减少,同时该材料果实发育并不受影响^[50]。2016年Hollender等^[50]利用基于测序技术的图位克隆对该基因进行精细定位,发现目的基因编码GA受体*PpeGID1c*,*dw*材料中*PpeGID1c*基因在编码区发生1个TGG至TAG的单碱基突变,导致翻译提前终止,形成无义突变。在李子中沉默*PpeGID1c*基因会导致类似*dw*材料的矮化表型,这进一步证明*dw*类型矮化材料

的表型是由*PpeGID1c*基因位点的突变所致。

随着分子生物学的发展,在部分果树中已可通过转基因的方法调控DELLA蛋白的表达水平,并实现果树矮化。Zhu等^[51]在苹果中过表达拟南芥突变型的DELLA蛋白*Atgai*,结果表明过表达该蛋白能够显著矮化苹果树,转基因植株的茎秆长度、节间长度及节数相比野生型均显著下降。随后日本的研究组发现,在韧皮部表达突变型*Atgai*的砧木能够诱导野生型接穗的矮化。嫁接试验证明,在此过程中*Atgai*基因转录形成的mRNA可通过韧皮部进行长距离的运输,最终影响接穗的生长^[52-53]。

除了GA信号途径组分,GA合成和代谢途径在果树矮化育种中同样起到重要作用。DGO24是一个矮化的李树(*Prunus salicina* L.)材料,外源施加GA₃可恢复矮化表型。El-Sharkawy等^[54]研究发现,该材料中的*PsIGA2ox*表达水平异常高。*PsIGA2ox*酶是将有活性的GA₁和GA₄转化为无活性的GA₈和GA₃₄,GA含量检测结果表明,该材料中GA₁和GA₄的含量分别为野生型的1/6和1/8。嫁接试验表明,DGO24作为砧木能够降低接穗的生长活力,并导致接穗具有紧凑的株型,因此DGO24可作为优良的矮化砧木使用,实现李树的矮化栽培。通过抑制GA合成基因的表达同样可以起到矮化树体的作用,Bulley等^[55]发现利用RNAi技术下调GA合成基因*GA20ox*的表达能显著降低苹果茎秆高度,而外源施加GA₃能够恢复转基因材料表型。这些RNAi接穗嫁接到正常的砧木后,依然能够保持矮化表型,这表明该矮化接穗表型不受正常砧木的影响,矮化接穗的利用有利于减少化学生长调解剂的使用,降低人工成本和对环境的影响。以上可以看出,GA合成代谢途径的GA20ox、GA2ox和信号途径的DELLA蛋白以及受体蛋白GID1在果树的矮化育种中均有应用,显示了GA在果树生产中的重要性。现将GA途径基因在果树矮化中的利用列于表2。

表2 GA途径基因资源在果树矮化中的利用

Table 2 GA pathway gene resources used in dwarfing of fruit trees

物种 Species	基因 Gene	矮化材料来源 Dwarfing material sources	显隐性 Dominance/Recessive	参与途径 Pathway	参考文献 Reference
葡萄 <i>Vitis vinifera</i> L.	<i>VvGAI1</i>	自然突变 Natural variation	半显性 Semi-dominant	GA信号途径 GA signaling pathway	[49]
桃 <i>Amygdalus persica</i> L.	<i>PpeGID1c</i>	自然突变 Natural variation	隐性 Recessive	GA信号途径 GA signaling pathway	[50]
苹果 <i>Malus pumila</i>	<i>Atgai</i>	过表达 Over expression	显性 Dominance	GA信号途径 GA signaling pathway	[51]
李 <i>Prunus salicina</i> Lindl.	<i>PsIGA2ox</i>	自然突变 Natural variation	显性 Dominance	GA失活途径 GA inactivation pathway	[54]
苹果 <i>Malus pumila</i>	<i>MpGA20ox1</i>	转录抑制 RNAi	显性 Dominance	GA合成途径 GA biosynthesis pathway	[56]

2.2 GA与果实发育

果实发育是果树生殖生长的重要阶段,决定着果实的大小和品质,GA在该过程中发挥着重要作用。受精后,子房中的GA合成酶基因 *GA20ox1*、*GA20ox2*、*GA20ox1/2*、*GA20ox3* 和 *CPS* 表达水平急剧升高,GA大量产生^[56]。此后,在果实发育过程中,GA含量也一直维持在较高水平。例如,在龙眼果实发育过程中,GA含量在花后14、44和92 d存在3个高峰^[57]。苹果授粉后,GA含量在第70、98和154 d均出现不同程度的上升^[58]。在葡萄中,果肉中的GA含量在花后30 d,即果实缓慢生长期前达到高峰^[59]。

GA诱导 α -淀粉酶、总淀粉酶和蔗糖转化酶的活性,促进淀粉的降解,提高细胞质中可溶性糖浓度和渗透压,渗透压的提高有利于外界水分进入细胞,促进细胞伸长^[4]。苹果盛花期或花后果实发育早期施用GA,可以显著促进果实膨大,增加果实质量,并使果实纵径延长^[60]。葡萄中的研究发现,100 mg·L⁻¹ GA能有效拉长‘丽红宝’葡萄果穗,增加‘丽红宝’葡萄果粒质量^[61]。王涛等^[62]的研究表明,GA对‘翠冠’梨果实的生长发育具有良好的促进作用,可增大果实、提早成熟期,但不影响果实内在品质和果形指数。

GA不仅参与调控果实的正常发育,外源施加GA还能够诱导单性结实。1957年Wittwer等^[63]首先发现外源施加GA能够诱导番茄单性结实,此后GA还被发现可诱导多种果树的单性结实。Yuda等^[4]发现GA₄₅、GA₄₊₇、GA₁₅和GA₂₄均可诱导去胚的梨幼果正常发育。Weaver等^[64]发现葡萄中利用GA诱导无籽果实的正常发育,目前利用GA诱导葡萄单性结实已是常规的栽培方法。Looney等^[65]发现GA₄和GA₇均可诱导苹果单性结实,且明显提高苹果的果形指数。盛宝龙等^[66]发现,GA可诱导‘霸王’枇杷单性结实,且在花前处理效果最好。此外,GA还可诱导枣、无花果、杏、樱桃、猕猴桃等果实的单性结实^[67]。Liu等^[68]对GA₄₊₇诱导梨单性结实过程中激素水平及基因表达变化进行检测,结果显示,GA₄₊₇处理后ABA合成基因的表达和ABA积累被显著抑制,而IAA转运基因、细胞分裂和细胞伸长基因均上调表达。

近十几年来,随着GA合成代谢及信号途径的解析,科学家通过编辑GA通路关键基因,已获得具有稳定表型的单性结实转基因材料。例如过表达柑橘 *CcGA20ox1* 基因可提高番茄GA₄含量,并诱导单

性结实^[69],而在番茄中抑制GA失活基因 *GA2ox* 也能够诱导单性结实^[70]。此外,在番茄和拟南芥中抑制GA信号途径阻遏因子 DELLA 蛋白编码基因的表达水平也能够诱导单性结实,转基因材料的果实相比野生型较小,细胞学观察表明,GA促进果实增大主要通过增强细胞伸长水平而非细胞分裂水平^[71]。番茄中通过人为调控GA途径实现单性结实,为果树的遗传改良提供了良好的研究思路。

2.3 GA与休眠的解除

植物休眠是指植物整体或某些器官生长缓慢或暂时停止的现象,是植物对低温和干旱等不良环境的一种适应。植物休眠主要分为芽休眠和种子休眠。GA对芽休眠的作用因物种的不同而不同,例如在豌豆、拟南芥和杨树中,GA促进芽休眠,而在柑橘、桃、樱桃等果树中则促进休眠的解除^[72]。Choubane等^[73]发现,在月季芽萌发过程中,GA合成基因 *GA20ox* 和 *GA3ox* 表达水平显著提高,而GA代谢基因 *GA2ox* 的表达水平则被抑制。

利用GA打破芽休眠在果树生产中已被广泛应用,以提高水果产量和品质^[74]。早在上世纪50年代就已发现GA₃可以替代低温诱导,促进桃树开花^[74]。Zhuang等^[75]发现,外源施加GA₄能够诱导果梅提前结束休眠。段成国等^[76]比较了GA₃、6-BA和IAA对解除大樱桃花芽休眠的效果,发现早期剥鳞时GA₃打破休眠的效果最好。高东升等^[77]对桃树枝条的研究发现,外源GA能显著破除芽休眠并促进芽萌发。姚丽萍等^[78]研究表明,GA处理能够促进桑芽的萌发,且20和50 mg·L⁻¹ GA的效果较好。徐红艳等^[79]发现GA₃能够替代低温,打破黑莓和树莓的芽休眠。

GA不仅能解除芽休眠,还是解除种子休眠的重要信号物质,施加GA能够提高种子萌发率及萌芽开花的一致性。GA促进种子萌发大致经历3个阶段,分别是种子休眠的打破、胚乳降解及胚细胞扩张,在这个过程中由木葡聚糖内糖基转移酶(endo-transglycosylase/hydrolase)和扩张蛋白(expansins)所介导的细胞壁修饰起到重要作用^[80]。种子中GA于胚中合成,随后移动至糊粉层细胞,并诱导分泌一系列水解酶,如 α -淀粉酶、蛋白酶和 β -葡聚糖酶,最终促进种子萌发。对模式植物拟南芥的研究表明,DELLA蛋白在调控种子萌发过程中具有重要作用。DELLA蛋白与种子萌发的负调控因子ABI3/5

存在直接的蛋白互作,并促进下游 *SOMNUS* 基因的表达,调控种子萌发;此外,DELLA 还通过 RING-H2 类锌指蛋白 XERICICO 调控种子萌发^[46]。

科研人员对 GA 与果树种子萌发的关系进行了大量研究,以指导果树生产。陈红等^[81]研究发现,GA 可以替代低温沉积并促进果梅种子萌发,且 50 mg·L⁻¹ GA 效果最好,发芽率为 32%。Wani 等^[82]研究表明,GA₃ 能够显著改善苹果种子的萌发,其中以 500 mg·L⁻¹ 处理 40 h 的效果最好,该研究还发现 GA₃ 不仅促进种子萌发,还能够改善小苗的生长情况以及树苗的存活率。Chen 等^[83]在杨梅中的研究发现,5.2 mmol·L⁻¹ GA₃ 足以打破种子休眠,萌发率超过 70%。毛桃是核果类果树最重要的砧木,但种子休眠常出现烂种和隔年发芽问题,张义等^[84]发现 GA 浸种可打破毛桃的种子休眠,增强种子活力,促进种子萌发。对猕猴桃种子的研究发现,GA 能够显著提高种子的发芽势和发芽率,播种后 20 d 的发芽数比对照高 38.3%~80.1%,同时缩短了萌发时间,相比对照早 2~4 d^[85]。除了以上提到的果树,GA 还能够促进大果蔷薇^[80]、无花果、橄榄、黑桑^[86-87]等果树种子的萌发。

3 展 望

GA 在果树种子萌发、营养生长至生殖生长的不同生长阶段中均具有重要作用,生产中 GA 相关的生长调节剂也已被广泛应用,用以提高果实品质、产量和果农的经济效益。但是利用生长调节剂调控果树的生长依然需要大量的人工,在目前人工费用逐年提高的新形势下,创制具有矮化、短枝表型的品种是减少人工成本、提高经济效益的有效方法。但是目前 GA 途径有益突变在果树育种中的应用依然落后,目前仅在葡萄、桃等极少数果树中利用了 GA 矮化突变基因资源,利用范围十分狭窄,因此如何在更多的果树中创制、发掘 GA 相关的矮化突变材料是摆在果树科研工作者面前的重要课题。此外,在生产中果树在不同生长阶段对 GA 有不同的需求,在营养生长阶段需要减弱 GA 信号以控制株高及抑制秋梢的生长,而在生殖生长阶段需要增强 GA 信号以提高坐果、促进果实发育。开发有效的栽培手段,以协调果树矮化与果实正常坐果与发育是另一个需要解决的生产问题。

目前 CRISPR/Cas 基因编辑技术方兴未艾,在动

植物中均有重要的应用,该方法具有效率高、特异性强、无外源片段插入等优点,是制备矮化材料的良好方法。因此,在果树中也应该加以推广利用,例如,可针对 GA 信号途径的不同组分进行特异的基因编辑,分别获得 GA 信号缺失或增强的遗传材料,以实现果树的矮化或单性结实,最终提高果树育种的目的是性及效率。

尽管近年来关于 GA 信号转导分子机制研究取得了很大的进展,但是仍然有一些问题未得到解决。例如,是否存在细胞膜定位的 GA 受体;DELLA 如何响应不同的外界信息,并选择性地与某个蛋白复合体互作等。此外,过表达 *GID1* 能在不影响 DELLA 蛋白稳定性的前提下部分恢复 *slY1/gid2* 植株矮小,且具雄性不育的表型^[88-89],表明在植物体内存在一条不依赖 DELLA 蛋白的 GA 信号途径,但是目前对该途径知之甚少。除了调控株高、果实发育、打破休眠等方面,GA 在调控植物花性别方面也有重要作用。在热带果树荔枝中,GA 合成抑制剂烯效唑可显著诱导雌花分化,提高坐果率,增加产量,且已在生产中广泛应用^[6],但是目前对 GA 调控花性别分化的分子机制依然不清楚^[6]。以上这些理论上或生产中的重要问题均是科学家将来需要研究的课题。前人的研究已经证明,在果树生产中人为调控 GA 途径是实现高产稳产的有效途径,随着 GA 信号通路的解析及基因编辑技术的成熟,GA 途径基因将会在果树育种中成为重要的基因资源。

参考文献 References:

- [1] MURASE K, HIRANO Y, SUN T P, HAKOSHIMA T. Gibberellin-induced DELLA recognition by the gibberellin receptor *GID1* [J]. *Nature*, 2008, 456(7221): 459-463.
- [2] LI J Y, LI C Y, SMITH S M. Hormone metabolism and signaling in plants[M]. Salt Lake: Academic Press, 2017: 107-160.
- [3] RICHARDS D E, KING K E, AIT-ALI T, HARBERD N P. How gibberellin regulates plant growth and development: a molecular genetic analysis of gibberellin signaling[J]. *Annual Review of Plant Physiology and Plant Molecular Biology*, 2001, 52(1): 67-88.
- [4] YUDA E, MATSUI H, YUKIMOTO M, NAKAGAWA S. Effect of 15 β -OH gibberellins on the fruit set and development of three pear species[J]. *Engei Gakkai Zasshi*, 1984, 53(3): 235-241.
- [5] 周宇, 佟兆国, 张开春, 闫国华. 赤霉素在落叶果树生产中的应用[J]. *中国农业科技导报*, 2006, 8(2): 27-31.
ZHOU Yu, TONG Zhaoguo, ZHANG Kaichun, YAN Guohua. Application of gibberellin to production of deciduous fruit crops

- [J]. Review of China Agricultural Science and Technology, 2006, 8(2): 27-31.
- [6] WEI Y, DONG C, ZHANG H, ZHENG X, SHU B, SHI S, LI W. Transcriptional changes in litchi (*Litchi chinensis* Sonn.) inflorescences treated with uniconazole[J]. PLoS One, 2017, 12(4): e0176053.
- [7] OLSZEWSKI N, SUN T P, GUBLER F. Gibberellin signaling: biosynthesis, catabolism, and response pathways[J]. Plant Cell, 2002, 14(Suppl.): 61-80.
- [8] XU H, LIU Q, YAO T, FU X. Shedding light on integrative GA signaling[J]. Current Opinion in Plant Biology, 2014, 21: 89-95.
- [9] UEGUCHI-TANAKA M, ASHIKARI M, NAKAJIMA M, ITOH H, KATOH E, KOBAYASHI M, CHOW T Y, HSING Y I, KITANO H, YAMAGUCHI I, MATSUOKA M. Gibberellin insensitive dwarf1 encodes a soluble receptor for gibberellin[J]. Nature, 2005, 437(7059): 693-698.
- [10] GRIFFITHS J, MURASE K, RIEU I, ZENTELLA R, ZHANG Z L, POWERS S J, GONG F, PHILLIPS A L, HEDDEN P, SUN T P, THOMAS S G. Genetic characterization and functional analysis of the GID1 gibberellin receptors in *Arabidopsis*[J]. Plant Cell, 2006, 18(12): 3399-3414.
- [11] NAKAJIMA M, SHIMADA A, TAKASHI Y, KIM Y C, PARK S H, UEGUCHI-TANAKA M, SUZUKI H, KATOH E, IUCHI S, KOBAYASHI M, MAEDA T, MATSUOKA M, YAMAGUCHI I. Identification and characterization of *Arabidopsis* gibberellin receptors[J]. Plant Journal, 2006, 46(5): 880-889.
- [12] SHIMADA A, UEGUCHI-TANAKA M, NAKATSU T, NAKAJIMA M, NAOE Y, OHMIYA H, KATO H, MATSUOKA M. Structural basis for gibberellin recognition by its receptor GID1[J]. Nature, 2008, 456(7221): 520-523.
- [13] HARBERD N P, BELFIELD E, YASUMURA Y. The angiosperm gibberellin-GID1-DELLA growth regulatory mechanism: how an "inhibitor of an inhibitor" enables flexible response to fluctuating environments[J]. Plant Cell, 2009, 21(5): 1328-1339.
- [14] NEMOTO K, RAMADAN A, ARIMURA G I, IMAI K, TOMII K, SHINOZAKI K, SAWASAKI T. Tyrosine phosphorylation of the GARU E3 ubiquitin ligase promotes gibberellin signalling by preventing GID1 degradation[J]. Nature Communications, 2017, 8(1): 1004.
- [15] FU X. Gibberellin-mediated proteasome-dependent degradation of the barley DELLA protein SLN1 repressor[J]. Plant Cell, 2002, 14(12): 3191-3200.
- [16] ZENTELLA R, SUI N, BARNHILL B, HSIEH W P, HU J, SHABANOWITZ J, BOYCE M, OLSZEWSKI N E, ZHOU P, HUNT D F, SUN T P. The *Arabidopsis* O-fucosyl transferase SPINDLY activates nuclear growth repressor DELLA[J]. Nature Chemical Biology, 2017, 13(5): 479-485.
- [17] ZENTELLA R, HU J, HSIEH W P, MATSUMOTO P A, DAWDY A, BARNHILL B, OLDENHOF H, HARTWECK L M, MAITRA S, THOMAS S G, COCKRELL S, BOYCE M, SHABANOWITZ J, HUNT D F, OLSZEWSKI N E, SUN T P. O-GlcNAcylation of master growth repressor DELLA by SE-CRET AGENT modulates multiple signaling pathways in *Arabidopsis*[J]. Genes & Development, 2016, 30(2): 164-176.
- [18] DAI C, XUE H W. Rice early flowering1, a CKI, phosphorylates DELLA protein SLR1 to negatively regulate gibberellin signaling[J]. The EMBO Journal, 2010, 29(11): 1916-1927.
- [19] QIN Q, WANG W, GUO X, YUE J, HUANG Y, XU X, LI J, HOU S. *Arabidopsis* DELLA protein degradation is controlled by a type-one protein phosphatase, TOPP4[J]. PLoS Genetics, 2014, 10(7): e1004464.
- [20] CONTI L, NELIS S, ZHANG C, WOODCOCK A, SWARUP R, GALBIATI M, TONELLI C, NAPIER R, HEDDEN P, BENNETT M, SADANANDOM A. Small ubiquitin-like modifier protein SUMO enables plants to control growth independently of the phytohormone gibberellin[J]. Developmental Cell, 2014, 28(1): 102-110.
- [21] BAI M Y, SHANG J X, OH E, FAN M, BAI Y, ZENTELLA R, SUN T P, WANG Z Y. Brassinosteroid, gibberellin and phytochrome impinge on a common transcription module in *Arabidopsis*[J]. Nature Cell Biology, 2012, 14(8): 810-878.
- [22] AN F, ZHANG X, ZHU Z, JI Y, HE W, JIANG Z, LI M, GUO H. Coordinated regulation of apical hook development by gibberellins and ethylene in etiolated *Arabidopsis* seedlings[J]. Cell Research, 2012, 22(5): 915-927.
- [23] ZHOU X, ZHANG Z L, PARK J, TYLER L, YUSUKE J, QIU K, NAM E A, LUMBA S, DESVEAUX D, MCCOURT P, KAMIYA Y, SUN T P. ERF11 promotes internode elongation by activating gibberellin biosynthesis and signaling pathways in *Arabidopsis*[J]. Plant Physiology, 2016, 171(4): 2760-2770.
- [24] PENG J, RICHARDS D E, HARTLEY N M, MURPHY G P, DEVOS K M, FLINTHAM J E, BEALES J, FISH L J, WORLAND A J, PELICA F, SUDHAKAR D, CHRISTOU P, SNAPE J W, GALE M D, HARBERD N P. 'Green revolution' genes encode mutant gibberellin response modulators[J]. Nature, 1999, 400(6741): 256-261.
- [25] HOU X, LEE L Y, XIA K, YAN Y, YU H. DELLA modulate jasmonate signaling via competitive binding to JAZs[J]. Developmental Cell, 2010, 19(6): 884-894.
- [26] MARÍN-DE L A, ROSA N, SOTILLO B, MISKOLCZI P, GIBBS D J, VICENTE J, CARBONERO P, OÑATE-SÁNCHEZ L, HOLDSWORTH M J, BHALERAO R, ALABADÍ D, BLÁZQUEZ M A. Large-scale identification of gibberellin-related transcription factors defines group VII ETHYLENE RESPONSE FACTORS as functional DELLA partners[J]. Plant Physiology, 2014, 166(2): 1022-1032.
- [27] XU F, LI T, XU P B, LI L, DU S S, LIAN H L, YANG H Q. DELLA proteins physically interact with CONSTANS to regulate flowering under long days in *Arabidopsis*[J]. FEBS Letters, 2016, 590(4): 541-549.
- [28] QI T, HUANG H, WU D, YAN J, QI Y, SONG S, XIE D. *Arabidopsis* DELLA and JAZ proteins bind the WD-repeat/BHLH/MYB complex to modulate gibberellin and jasmonate signaling synergy[J]. Plant Cell, 2014, 26(3): 1118-1133.

- [29] ARNAUD N, GIRIN T, SOREFAN K, FUENTES S, WOOD T A, LAWRENSON T, SABLowski R, OSTERGAARD L. Gibberellins control fruit patterning in *Arabidopsis thaliana*[J]. *Genes & Development*, 2010, 24(19): 2127-2132.
- [30] JOSSE E M, GAN Y, BOU-TORRENT J, STEWART K L, GILDAY A D, JEFFREE C E, VAISTIJ F E, MARTÍNEZ-GARCÍA J F, NAGY F, GRAHAM I A, HALLIDAY K J. ADELLA in disguise: SPATULA restrains the growth of the developing *Arabidopsis* seedling[J]. *Plant Cell*, 2011, 23(4): 1337-1351.
- [31] ZHANG D, JING Y, JIANG Z, LIN R. The chromatin-remodeling factor PICKLE integrates brassinosteroid and gibberellin signaling during skotomorphogenic growth in *Arabidopsis*[J]. *Plant Cell*, 2014, 26(6): 2472-2485.
- [32] HUANG D, WANG S, ZHANG B, SHANG-GUAN K, SHI Y, ZHANG D, LIU X, WU K, XU Z, FU X, ZHOU Y. A gibberellin-mediated DELLA-NAC signaling cascade regulates cellulose synthesis in rice[J]. *Plant Cell*, 2015, 27(6): 1681-1696.
- [33] YE Y, LIU B, ZHAO M, WU K, CHENG W, CHEN X, LIU Q, LIU Z, FU X, WU Y. CEF1/OsMYB103L is involved in GA-mediated regulation of secondary wall biosynthesis in rice[J]. *Plant Molecular Biology*, 2015, 89(4/5): 385-401.
- [34] LOCASCIO A, BLAZQUEZ M A, ALABADI D. Dynamic regulation of cortical microtubule organization through pre-foldin-DELLA interaction[J]. *Current Biology*, 2013, 23(9): 804-809.
- [35] YAMAGUCHI N, WINTER C M, WU M F, KANNO Y, YAMAGUCHI A, SEO M, WAGNER D. Gibberellin acts positively then negatively to control onset of flower formation in *Arabidopsis*[J]. *Science*, 2014, 344(6184): 638-641.
- [36] YOSHIDA H, HIRANO K, SATO T, MITSUDA N, NOMOTO M, MAEO K, KOKETSU E, MITANI R, KAWAMURA M, ISHIGURO S, TADA Y, OHME-TAKAGI M, MATSUOKA M, UEGUCHI-TANAKA M. DELLA protein functions as a transcriptional activator through the DNA binding of the indeterminate domain family proteins [J]. *Proceedings of the National Academy of Sciences of the United States of America*, 2014, 111(21): 7861-7866.
- [37] ZHANG Z L, OGAWA M, FLEET C M, ZENTELLA R, HU J, HEO J O, LIM J, KAMIYA Y, YAMAGUCHI S, SUN T P. Scarecrow-like 3 promotes gibberellin signaling by antagonizing master growth repressor DELLA in *Arabidopsis*[J]. *Proceedings of the National Academy of Sciences of the United States of America*, 2011, 108(5): 2160-2165.
- [38] OH E, ZHU J Y, BAI M Y, ARENHART R A, SUN Y, WANG Z Y. Cell elongation is regulated through a central circuit of interacting transcription factors in the *Arabidopsis* hypocotyl[J]. *Elife*, 2014(3): e03031.
- [39] PARK J, NGUYEN K T, PARK E, JEON J S, CHOI G. DELLA proteins and their interacting RING Finger proteins repress gibberellin responses by binding to the promoters of a subset of gibberellin-responsive genes in *Arabidopsis*[J]. *Plant Cell*, 2013, 25(3): 927-943.
- [40] SARNOWSKA E A, ROLICKA A T, BUCIOR E, CWIEK P, TOHGE T, FERNIE A R, JIKUMARU Y, KAMIYA Y, FRANZEN R, SCHMELZER E, PORRI A, SACHAROWSKI S, GRATKOWSKA D M, ZUGAJ D L, TAFF A, ZALEWSKA A, ARCHACKI R, DAVIS S J, COUPLAND G, KONCZ C, JERZMANOWSKI A, SARNOWSKI T J. DELLA-interacting SWI3C core subunit of SWI/SNF chromatin remodeling complex modulates gibberellin responses and hormonal crosstalk in *Arabidopsis*[J]. *Plant Physiology*, 2013, 163(1): 305-317.
- [41] LI J Y, LI C Y, SMITH S M. Hormone metabolism and signaling in plants[M]. Salt Lake: Academic Press, 2017: 327-359.
- [42] CHEN L, XIANG S, CHEN Y, LI D, YU D. *Arabidopsis* WRKY45 interacts with the DELLA protein RGL1 to positively regulate age-triggered leaf senescence[J]. *Molecular Plant*, 2017, 10(9): 1174-1189.
- [43] LI Y, WANG H, LI X, LIANG G, YU D. Two DELLA-interacting proteins bHLH48 and bHLH60 regulate flowering under long-day conditions in *Arabidopsis thaliana*[J]. *Journal of Experimental Botany*, 2017, 68(11): 2757-2767.
- [44] RAVINDRAN P, VERMA V, STAMM P, KUMARP P. Anovel RGL2-DOF6 complex contributes to primary seed dormancy in *Arabidopsis thaliana* by regulating a GATA transcription factor [J]. *Molecular Plant*, 2017, 10(10): 1307-1320.
- [45] FUKAZAWA J, TERAMURA H, MURAKOSHI S, NASUNO K, NISHIDA N, ITO T, YOSHIDA M, KAMIYA Y, YAMAGUCHI S, TAKAHASHI Y. DELLAs function as coactivators of GAI-ASSOCIATED FACTOR 1 in regulation of gibberellin homeostasis and signaling in *Arabidopsis*[J]. *Plant Cell*, 2014, 26(7): 2920-2938.
- [46] LIM S, PARK J, LEE N, JEONG J, TOH S, WATANABE A, KIM J, KANG H, KIM D H, KAWAKAMI N, CHOI G. ABA-insensitive 3, ABA-insensitive 5, and DELLAs interact to activate the expression of SOMNUS and other high-temperature-inducible genes in imbibed seeds in *Arabidopsis*[J]. *Plant Cell*, 2013, 25(12): 4863-4878.
- [47] MARÍN-DE L R N, PFEIFFER A, HILL K, LOCASCIO A, BHALERAO R P, MISKOLCZI P, GRÖNLUND A L, WANCHOO-KOHLI A, THOMAS G, BENNETT M J, LOHMANN J U, BLÁZQUEZ M A, ALABADI D. Genome wide binding site analysis reveals transcriptional coactivation of cytokinin responsive genes by DELLA proteins[J]. *PLoS Genetics*, 2015, 11(7): e1005337.
- [48] ZHENG H, ZHANG F, WANG S, SU Y, JIANG P, CHENG R, JI X, HOU S, DING Y. MLK1 and MLK2 coordinate RGA and CCA1 activity to regulate hypocotyl elongation in *Arabidopsis thaliana*[J]. *Plant Cell*, 2018, 30(1): 67-82.
- [49] BOSS P K, THOMAS M R. Association of dwarfism and floral induction with a grape 'green revolution' mutation[J]. *Nature*, 2002, 416(6883): 847-850.
- [50] HOLLENDER C A, HADIARTO T, SRINIVASAN C, SCORZA R, DARDICK C. A brachytic dwarfism trait (dw) in peach trees is caused by a nonsense mutation within the gibberellin acid receptor PpGID1c [J]. *New Phytologist*, 2016, 210(1): 227-

- 239.
- [51] ZHU L H, LI X Y, WELANDER M. Overexpression of the *Ara-bidopsis* gai gene in apple significantly reduces plantsize [J]. *Plant Cell Reports*, 2008, 27(2): 289-296.
- [52] XU H, IWASHIRO R, LI T, HARADA T. Long- distancetransport of gibberellic acid insensitive mRNA in *Nicotiana ben-thamiana*[J]. *BMC Plant Biology*, 2013, 13(1): 165.
- [53] 张抗萍, 李荣飞, 常耀栋, 梁国鲁, 陆智明, 易佑文, 胡涛, 鲁振华, 郭启高. 果树树形的形成机制与调控技术研究进展[J]. *果树学报*, 2017, 34(4): 495-506.
- ZHANG Kangping, LI Rongfei, CHANG Yaodong, LIANG Guolu, LU Zhiming, YI Youwen, HU Tao, LU Zhenhua, GUO Qigao. A review of the canopy architectureformation mechanism and regulation technology in fruit trees[J]. *Journal of Fruit Science*, 2017, 34(4): 495-506.
- [54] EL-SHARKAWY I, EL KAYAL W, PRASATH D, FERNANDEZ H, BOUZAYEN M, SVIRCEV A M, SANKAR S. Identification and genetic characterization of a gibberellin 2- oxidase gene that controls tree stature and reproductive growth in plum [J]. *Journal of Experimental Botany*, 2012, 63(3): 1225-1239.
- [55] BULLEY S M, WILSON F M, HEDDEN P, PHILLIPS L, CROKER S J, JAMES D J. Modification of gibberellin biosynthesis in the grafted apple scion allows control of tree height independent of the rootstock[J]. *Plant Biotechnology Journal*, 2005, 3(2): 215-223.
- [56] SERRANI J C, SANJUAN R, RUIZ-RIVERO O, FOS M, GARCIA-MARTINEZ J L. Gibberellin regulation of fruit set and growth in tomato[J]. *Plant Physiology*, 2007, 145(1): 246-257.
- [57] 周碧燕, 李建国, 黄旭明, 周贤军. 龙眼果实发育过程中 ZRs、GA 和 IAA 含量的变化[J]. *华南农业大学学报*, 1999, 20(3): 50-53.
- ZHOU Biyan, LI Jianguo, HUANG Xuming, ZHOU Xianjun. Changes of ZRs, GA and IAA content during fruitdevelopments of longan[J]. *Journal of South ChinaAgricultural University*, 1999, 20(3): 50-53.
- [58] 徐臣善. 不同授粉品种对苹果果实生长及内源激素含量影响 [J]. *植物生理学报*, 2013, 49(3): 277-284.
- XU Chenshan. Effects of different POLLINATION varietieson fruit growth and endogenous hormones content in *Malus domestica* Borkh.[J]. *Plant Physiology Journal*, 2013, 49(3): 277-284.
- [59] 张国海, 李学强, 李秀珍, 史国安, 夏仁学. 葡萄浆果发育期果皮、果肉和叶中内源激素含量的变化[J]. *四川农业大学学报*, 2010, 28(4): 449-453.
- ZHANG Guohai, LI Xueqiang, LI Xiuzhen, SHI Guoan, XIA Renxue. Changes in content of endogenous hormonesin fruit peel, fruit flesh and leaf during fruit growth and development of grape[J]. *Journal of Sichuan Agricultural University*, 2010, 28(4): 449-453.
- [60] 闫国华, 甘立军, 孙瑞红, 张利华, 周燮. 赤霉素和细胞分裂素调控苹果果实早期生长发育机理的研究[J]. *园艺学报*, 2000, 27(1): 11-16.
- YAN Guohua, GAN Lijun, SUN Ruihong, ZHANG Lihua, ZHOU Xie. A study on the mechanisms of exo-gibberellins and cytokininsin in the growth regulation of young apple fruit[J]. *Acta Horticulturae Sinica*, 2000, 27(1):11-16.
- [61] 赵荣华, 白世践, 李超, 陈光, 蔡军社. 赤霉素处理对‘丽红宝’葡萄果实品质及着色的影响[J]. *北方园艺*, 2016(19): 35-39.
- ZHAO Ronghua, BAI Shijian, LI Chao, CHEN Guang, CAI Junshe. Effects of exogenous gibberellic acid on fruit qualityand coloring of ‘Libaohong’ grape[J]. *Northern Horticulture*, 2016(19): 35-39.
- [62] 王涛, 陈伟立, 黄雪燕, 陈丹霞, 金伟. 几种赤霉素产品对翠冠梨果实生长发育的影响[J]. *中国南方果树*, 2006, 35(5): 59-60.
- WANG Tao, CHEN Weili, HUANG Xueyan, CHEN Danxia, JIN Wei. Effects of several gibberellic acids on fruit development of ‘Cuiguan’ pear[J]. *South China Fruits*, 2006, 35(5): 59-60.
- [63] WITTWER S H, BUKOVAC M J, SELL H M, WELLERL E. Some effects of gibberellin on flowering and fruit setting[J]. *Plant Physiology*, 1957, 32(1): 39-41.
- [64] WEAVER R J, MCCUNE S B. Further studies with gibberellin on *Vitis vinifera* grapes[J]. *Botanical Gazette*, 1960, 121(3): 155-162.
- [65] LOONEY N E, GRANGER R L, CHU C L, MANDER L N, PHARIS R P. Influences of gibberellins A4, A4+7 and A4+iso-A7 on apple fruit quality and tree productivity. II. Other effects on fruit quality and importance of fruit position within the tree canopy[J]. *Journal of Pomology & Horticultural Science*, 1992, 67(5): 841-847.
- [66] 盛宝龙, 吴伟民. 无核枇杷生产技术研究[J]. *中国南方果树*, 1998, 27(5): 3-6.
- SHENG Baolong, WU Weimin. Study on the productiontechnology of seedless loquat[J]. *South China Fruits*, 1998, 27(5): 3-6.
- [67] 邓英毅. GA₃ 诱导枇杷无核机理研究[D]. 重庆: 西南大学, 2009.
- DENG Yingyi. Study on the mechanism of seedlessness of loquat induced by GA₃[D]. Chongqing: Southwest University, 2009.
- [68] LIU L, WANG Z, LIU J, LIU F, ZHAI R, ZHU C, WANG H, MA F, XU L. Histological, hormonal and transcriptomicreveal the changes upon gibberellin-induced parthenocarpy in pear fruit [J]. *Horticulture Research*, 2018, 5(1): 1.
- [69] GARCÍA- HURTADO N, CARRERA E, RUIZ- RIVERO O, LÓPEZ- GRESA M P, HEDDEN P, GONG F, GARCÍA-MARTÍNEZ J L. The characterization oftransgenic tomato overexpressing gibberellin 20-oxidasereveals induction of parthenocarpic fruit growth, higher yield, and alteration of the gibberellin biosynthetic pathway[J]. *Journal of Experimental Botany*, 2012, 63(16): 5803-5813.
- [70] MARTÍNEZBELLO L, MORITZ T, LÓPEZDÍAZ I. Silencing C19-GA 2-oxidases induces parthenocarpic development and inhibits lateral branching in tomato plants[J]. *Journal of Experimental Botany*, 2015, 66(19): 5897-5910.
- [71] MARTÍ C, ORZÁEZ D, ELLUL P, MORENO V, CARBONELL

- J, GRANELL A. Silencing of DELLA induces facultative parthenocarpic tomato fruits[J]. *Plant Journal for Cell & Molecular Biology*, 2007, 52(5): 865-876.
- [72] NI J, GAO C, CHEN M S, PAN B Z, YE K, XU Z F. Gibberellin promotes shoot branching in the perennial woody plant *Jatropha curcas*[J]. *Plant and Cell Physiology*, 2015, 56(8): 1655-1666.
- [73] CHOUBANE D, RABOT A, MORTREAU E, LEGOURRIERE J, PÉRON T, FOUCHER F, AHCÈNE Y, PELLESCHITRAVIER S, LEDUC N, HAMAMA L, SAKR S. Photocontrol of bud burst involves gibberellin biosynthesis in *Rosa* sp.[J]. *Journal of Plant Physiology*, 2012, 169(13): 1271-1280.
- [74] 蔡斌华, 庄维兵, 高志红, 章镇. 赤霉素解除木本植物季节性休眠机制的研究进展[J]. *西北植物学报*, 2014, 34(10): 2145-2152.
- CAI Binhua, ZHUANG Weibing, GAO Zhihong, ZHANG Zhen. Research advances on the mechanism of gibberellins releasing seasonal dormancy in woody plants[J]. *Acta Botanica Boreali-Occidentalia Sinica*, 2014, 34(10): 2145-2152.
- [75] ZHUANG W, GAO Z, WANG L, ZHONG W, NI Z, ZHANG Z. Comparative proteomic and transcriptomic approaches to address the active role of GA_i in Japanese apricot flower bud dormancy release[J]. *Journal of Experimental Botany*, 2013, 64(16): 4953-4966.
- [76] 段成国, 李宪利, 高东升, 刘焕芳, 李萌. 剥鳞和激素处理对大樱桃花芽休眠解除及内源激素变化的影响[J]. *西北植物学报*, 2004, 24(4): 615-620.
- DUAN Chengguo, LI Xianli, GAO Dongsheng, LIU Huanfang, LI Meng. Effect of removing scales and exogenous hormone treatments on changes of endogenous hormone in sweet cherry flower buds and dormancy release during dormancy[J]. *Acta Botanica Boreali-Occidentalia Sinica*, 2004, 24(4): 615-620.
- [77] 高东升, 夏宁, 王兴安. 休眠桃树枝条中碳水化合物的含量变化和外界生长调节剂对破除休眠的效应[J]. *植物生理学报*, 1999, 35(1): 10-12.
- GAO Dongsheng, XIA Ning, WANG Xing'an. Changes of carbohydrate content and effect of exogenous growth regulators on dormancy-breaking during dormant period of peach shoots[J]. *Plant Physiology Communications*, 1999, 35(1): 10-12.
- [78] 姚丽萍, 刘明鲁, 杜伟. 低温和赤霉素处理对桑芽萌发的影响[J]. *北方蚕业*, 2014, 35(4): 21-23.
- YAO Liping, LIU Minglu, DU Wei. The effect of low temperature and gibberellin treatment on germination of mulberry[J]. *North Sericulture*, 2014, 35(4): 21-23.
- [79] 徐红艳, 徐迎春, 董凤祥, 张清华, 王彦辉. 夏果型树莓和黑莓品种需冷量及药剂打破休眠效果的研究[J]. *中国农学通报*, 2013, 29(16): 119-124.
- XU Hongyan, XU Yingchun, DONG Fengxiang, ZHANG Qinghua, WANG Yanhui. Study on chilling requirement of floricane raspberry and blackberry cultivars and artificial methods of breaking dormancy[J]. *Chinese Agricultural Science Bulletin*, 2013, 29(16): 119-124.
- [80] MIRANSARI M, SMITH D L. Plant hormones and seedgermination[J]. *Environmental and Experimental Botany*, 2014, 99(3): 110-121.
- [81] 陈红, 李焕, 谭志刚. 不同处理对果梅种子萌发的影响[J]. *北方园艺*, 2011(17): 50-51.
- CHEN Hong, LI Huan, TAN Zhigang. Effects of different treatments on seed germination of *Prunus mume*[J]. *Northern Horticulture*, 2011(17): 50-51.
- [82] WANI R A, MALIK H, MALIK A, BABA J A, DAR N. Studies on apple seed germination and survival of seedlings as affected by gibberellic acid under cold arid conditions[J]. *International Journal of Scientific & Technology Research*, 2014, 3(3): 2010-2016.
- [83] CHEN S Y, KUO S R, CHIEN C T. Roles of gibberellins and abscisic acid in dormancy and germination of red bayberry (*Myrica rubra*) seeds[J]. *Tree Physiology*, 2008, 28(9): 1431-1439.
- [84] 张义, 夏冰. 毛桃种子层积处理前浸泡赤霉素对其萌发的影响[J]. *中国南方果树*, 2002, 31(4): 70.
- ZHANG Yi, XIA Bing. Effects of gibberellin on seed germination of peach seed[J]. *South China Fruit*, 2002, 31(4): 70.
- [85] 向世明. 赤霉素对猕猴桃种子萌发的影响[J]. *现代园艺*, 2013(4): 13.
- XIANG Shiming. Effects of gibberellin on seed germination of *Actinidia*[J]. *Modern Horticulture*, 2013(4): 13.
- [86] 朱小虎, 盛方. 大果蔷薇种子的休眠与萌发初探[J]. *种子*, 2009, 28(3): 77-80.
- ZHU Xiaohu, SHENG Fang. Preliminary on dormancy and germination of *Rosa webbiana* Wall[J]. *Seeds*, 2009, 28(3): 77-80.
- [87] CAVUSOGLU A, SULUSOGLU M. The effects of exogenous gibberellin on seed germination of the fruit species[J]. *Derleme*, 2015, 8(1): 6-9.
- [88] ARIIZUMI T, LAWRENCE P K, STEBER C M. The role of two F-box proteins, SLEEPY1 and SNEEZY, in *Arabidopsis* gibberellin signaling[J]. *Plant Physiology*, 2011, 155(2): 765-775.
- [89] DE VLEESSCHAUWER D, SEIFI H S, FILIPE O, HAECK A, HUU S N, DEMEESTERE K, HÖFTE M. The DELLA protein SLR1 integrates and amplifies salicylic acid- and jasmonic acid-dependent innate immunity in rice[J]. *Plant Physiology*, 2016, 170(3): 1831-1847.