

植物中 Gibberellin 2-oxidases 基因研究进展

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摘要: 赤霉素 2-氧化酶 (Gibberellin 2-oxidases, GA2oxs) 是赤霉素代谢过程中的关键酶, 根据底物特异性可分为 C₂₀-GA2oxs 和 C₁₉-GA2oxs 两类, 其中 C₂₀-GA2oxs 直接作用于 GA 合成前体 (GA₁₂, GA₅₃), C₁₉-GA2oxs 负责分解活性 GA (GA₁, GA₄) 及其前体 (GA₂₀, GA₉)。GA2oxs 由多基因编码, 参与维持植物生长发育多个过程, 受外源环境与内源因素严格而精密调控。研究表明 GA2oxs 通过调节植物体内赤霉素水平影响植物的生长发育, 如株高、种子萌发、开花和结实等。主要综述了 GA2oxs 基因时空表达模式, 生理功能, 转录调控等方面的研究进展, 为了解其对植物生长发育的调控机制提供参考, 同时也有助于在生产实践中更好地利用其开展基因工程研究, 定向培育植物新品种。

关键词: 赤霉素 2-氧化酶基因; 表达模式; 生理功能; 环境因素; 植物激素; 转录因子

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Advances on Gibberellin 2-oxidases Gene in Higher Plants

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Abstract: Gibberellin 2-oxidases (GA2oxs) are a kind of key enzymes in the metabolism of GA. According to the substrate specificity, GA2oxs can be divided into two types: C₁₉-GA2oxs and C₂₀-GA2oxs, in which C₂₀-GA2oxs acts on GA synthesis precursors (GA₁₂, GA₅₃), and C₁₉-GA2oxs is responsible for metabolizing active GA (GA₁, GA₄) and precursors (GA₂₀, GA₉). GA2oxs are encoded by multiple genes, involved in regulating plant growth and development and strictly regulated by environment and endogenous factors. Studies have shown that GA2oxs affect the growth and development of plants, for example, plant height, seed germination, flowering and fruiting by regulating the gibberellin level. Here, we summarized the research progress in the expression patterns, physiological functions and transcriptional regulation of GA2oxs, aiming to provide reference for understanding the regulatory mechanisms of GA2oxs genes on plant growth and development. It is also helpful to make better use of GA2oxs genes in genetic engineering research for crop improvement.

Keywords: GA2oxs; expression pattern; physiological function; environmental factor; plant hormone; transcription factor

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赤霉素 (Gibberellin, GA) 属于四环二萜类化合物, 在植物生长旺盛部位, 如茎端、嫩叶、根尖和果实种子中合成。目前已发现 136 种天然 GA, 但在植物体内只有少数 GA, 如 GA₁、GA₃、GA₄ 和 GA₇ 具有生物活性 (MacMillan & Takahashi, 1968; Hedden & Thomas, 2012), 最近也有研究认为 GA₆ 具有生物活性 (Graeber et al., 2014)。在植物生命周期中主要是具有生物活性的 GA 起着关键调控作用 (Ogas et al., 1997), 如种子萌发 (Groot & Karssen, 1987; Ogawa et al., 2003; Yamauchi et al., 2004; Sun et al., 2017)、茎伸长 (Peng et al., 1999)、开花 (Wilson et al., 1992; Blázquez et al., 1998; Mutasagottgens & Hedden, 2009)、花粉发育 (Phatak et al., 1966; Singh et al., 2002; Sakata et al., 2014)、坐果 (Serrani et al., 2007) 以及侧生器官的启动及形态建成 (Fleet & Sun, 2005) 等。其中 GA₁ 和 GA₄ 是主要的活性 GA, 不同植物中两种活性 GA 所占比例不同, GA₁ 是水稻、玉米、高粱中主要的活性 GA, GA₄ 是拟南芥、番茄、黄瓜中主要的活性 GA (陈申, 2016)。

高等植物中活性 GA 的浓度由合成和代谢速率平衡来调节, 活性 GA 的钝化对调节植物体内 GA 的平衡起着至关重要的作用, 其钝化主要是通过赤霉素 2-氧化酶 (Gibberellin 2-oxidases, GA2oxs) 催化完成, 将活性 GA 及其前体不可逆地转变成无活性形式。本文简要介绍植物中 GA2oxs 基因的分类、时空表达、生理功能, 综述环境因素、植物激素以及转录因子对其表达的调控, 为揭示 GA2oxs 在植物中的生理功能提供重要参考。

1 赤霉素的生物合成与代谢

如图 1 所示, 植物中活性赤霉素的合成首先是质体内牻牛儿牻牛儿基焦磷酸 (geranylgeranyl diphosphate, GGPP) 在内根-古巴焦磷酸合成酶 (ent-copalyl diphosphate synthase, CPS) 和内根-

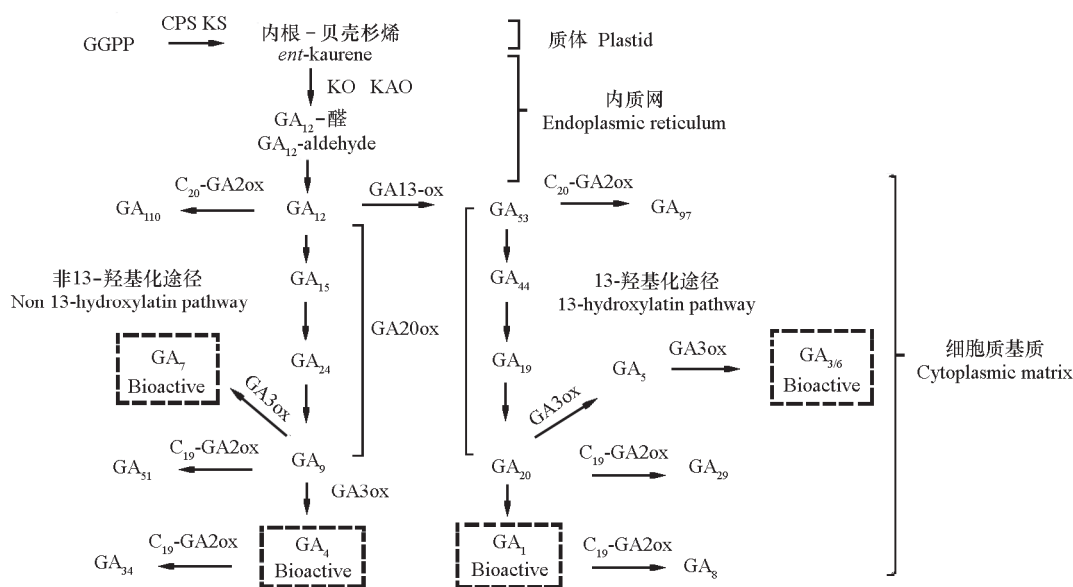


图 1 赤霉素合成与代谢途径 (Martinezbello et al., 2015; Urbanova et al., 2013; Graeber et al., 2014; 黄桃鹏 等, 2015)
GGDP: 牻牛儿牻牛儿基焦磷酸; CPS: 内根-古巴焦磷酸合成酶; KS: 内根-贝壳杉烯合成酶; KO: 内根-贝壳杉烯氧化酶; KAO: 内根-贝壳杉烯酸氧化酶; GA13ox: GA13-氧化酶; GA20ox: 赤霉素20-氧化酶; GA3ox: 赤霉素3-氧化酶; GA2ox: 赤霉素2-氧化酶。
Fig. 1 GA biosynthesis and metabolic pathway (Martinezbello et al., 2015; Urbanova et al., 2013; Graeber et al., 2014; Hang et al., 2015)
GGDP: geranylgeranyl diphosphate; CPS: ent-copalyl diphosphate synthase; KS: ent-kaurene synthase; KO: entkaurene oxidase; KAO: ent-kaurenic acid oxidase; GA13ox: GA 13-oxidase; GA20ox: GA 20-oxidase; GA3ox: GA 3-oxidase; GA2ox: GA 2-oxidase.

贝壳杉烯合成酶 (ent-kaurene synthase, KS) 催化下环化为赤霉素的合成前体内根 - 贝壳杉烯 (ent-kaurene) (Sun & Kamiya, 1997)。随后在内质网中内根 - 贝壳杉烯经内根 - 贝壳杉烯氧化酶 (ent-kaurene oxidase, KO) 和内根 - 贝壳杉烯酸氧化酶 (ent-kaurenoic acid oxidase, KAO) 氧化形成 GA₁₂ - 醛, 再分别经非羟基化和羟基化两种途径形成 GA₁₂ 与 GA₅₃ (Helliwell et al., 2001), 最后, GA₁₂ 与 GA₅₃ 在细胞质基质中经 GA20oxs, GA3oxs 和 GA2oxs 氧化分别形成不同的 GA (Hirano et al., 2008; Hedden & Thomas, 2012)。GA2oxs 编码一种依赖 2 - 酮戊二酸和氧分子作为辅底物、Fe²⁺ 和抗坏血酸为辅因子的双加氧酶 (石海燕和张玉星, 2011), 定位在细胞核和细胞质中行使功能 (Huang et al., 2010)。GA2oxs 是赤霉素代谢的关键酶, 将活性 GA 及其前体不可逆地转变成无活性形式, 根据底物特异性 GA2oxs 可分为 C₂₀-GA2oxs 和 C₁₉-GA2oxs 两类, 其中 C₂₀-GA2oxs 直接作用于 GA 合成前体 GA₁₂、GA₅₃, C₁₉-GA2oxs 负责分解活性 GA₁, GA₄ 及其前体 GA₂₀、GA₉ (Schomburg et al., 2003; Martinezbello et al., 2015)。

2 GA2oxs 基因分类与时空表达模式

1999 年, 首次从红花菜豆 (*Phaseolus coccineus*) 子叶 cDNA 文库中分离克隆得到 GA2oxs 基因, 验证其具有分解赤霉素的功能 (Thomas et al., 1999; Hedden & Phillips, 2000)。GA2oxs 由多基因编码, 对其分类与时空表达已有大量研究, 特别是在拟南芥 (Schomburg et al., 2003; Rieu et al., 2008)、水稻 (Lo et al., 2008)、番茄 (Serrani et al., 2007; Chen et al., 2016)、黄瓜 (王增辉, 2014)、甘蓝型油菜 (廖晓英, 2015) 和矮牵牛 (郭余龙 等, 2013) 等植物中。GA2oxs 基因组织表达模式多样, 受时空等多种因素调控, 不同生长发育阶段、不同组织表达水平不同 (表 1)。

拟南芥中 7 个基因编码 GA2oxs, 其中 5 个 C₁₉-GA2oxs (*AtGA2ox1* ~ *AtGA2ox4* 和 *AtGA2ox6*), 2 个 C₂₀-GA2oxs (*AtGA2ox7*, *AtGA2ox8*) (Schomburg et al., 2003; Rieu et al., 2008)。水稻中包含 10 个 GA2oxs 基因, *OsGA2ox1* ~ *OsGA2ox4*, *OsGA2ox7*, *OsGA2ox8* 和 *OsGA2ox10* 属于 C₁₉-GA2oxs, *OsGA2ox5*, *OsGA2ox6* 和 *OsGA2ox9* 与拟南芥 *AtGA2ox7* 和 *AtGA2ox8* 聚为一类, 包含独特且保守的结构域, 属于 C₂₀-GA2oxs (Lo et al., 2008)。番茄中 GA2oxs 基因系统发育分析表明, *SIGA2ox1* ~ *SIGA2ox5* 属于 C₁₉-GA2oxs (Serrani et al., 2007)。Chen 等 (2016) 鉴定出 6 个 *SIGA2oxs*, *SIGA2ox6* ~ *SIGA2ox11*, 属于 C₂₀-GA2oxs (Chen et al., 2016)。黄瓜中预测包含 8 个 GA2oxs, 聚类分析发现 *CsGA2ox1* ~ *CsGA2ox4* 和 *CsGA2ox6* 属于 C₁₉-GA2oxs, *CsGA2ox5*, *CsGA2ox7*, *CsGA2ox8* 属于 C₂₀-GA2oxs (王增辉, 2014)。甘蓝型油菜克隆到 7 个 GA2oxs 基因, 聚类分析表明 *BnGA2ox1-2*, *BnGA2ox1-5*, *BnGA2ox2*, *BnGA2ox4*, *BnGA2ox6-1*, *BnGA2ox6-2* 属于 C₁₉-GA2oxs, *BnGA2ox8* 属于 C₂₀-GA2oxs, *BnGA2oxs* 在各个组织均有表达, 在子叶和果荚中表达较高 (廖晓英, 2015)。矮牵牛中克隆到 3 个 GA2oxs 基因 *PhGA2ox1* ~ *PhGA2ox3*, 系统进化分析显示这 3 个基因都属于 C₁₉-GA2oxs (郭余龙 等, 2013)。菠菜 (*Spinacia oleracea*) *SoGA2ox3* 属于 C₂₀-GA2oxs, 主要在茎尖表达, 高于叶片和叶柄 (Lee & Zeevaart, 2005)。

其他植物中 GA2oxs 基因表达模式也有报道。豌豆 (*Pisum sativum*) 中 GA2oxs 基因主要在根、花、果以及外种皮中表达 (Martin et al., 1999)。原位杂交显示毒麦草 (*Lolium temulentum*) *LtGA2ox1* 在茎尖表达 (King et al., 2008)。山茶属 (*Camellia*) 荔枝连蕊茶 *CIGA2ox1* 在各器官中均有表达, 在茎中最高, 嫩叶和根中次之 (肖政 等, 2016)。花生 (*Arachis hypogaea*) *AhGA2oxs* 空间表达模式分析发现所检测的 10 种组织中均有表达, 其中叶片中表达最丰富, 根次之 (王成祥 等, 2013)。另外, 不同品种间 GA2oxs 基因表达也存在差异, 芹菜 (*Apium graveolens*) *AgGA2oxs* 在根、叶柄

和叶片中表达量有明显差异, 叶柄中表达量明显高于根和叶片中, 其中‘文图拉’芹菜中 *AgGA2oxs* 基因在组织间的表达差异显著, 相对表达量从高到低依次为叶柄、叶片和根, 而‘六合黄心芹’芹菜中 *AgGA2oxs* 在根和叶中相对表达量差异不显著, 叶柄中极显著高于根和叶片中(冯凯等, 2016)。

上述研究表明, *GA2oxs* 基因广泛分布于各个组织器官, 茎尖、种子、茎、花、果实、叶片和根中均有表达, 但在各组织中表达差异很大, 这与不同组织、器官的生理功能以及 *GA2oxs* 基因分类的不同有关。

3 *GA2oxs* 基因的功能

GA2oxs 家族包含多个成员, 通过调节植物体内赤霉素水平影响植物的生长发育, 如株高、种子萌发、开花和结实等(表1)。

株高是一个重要的农艺性状, 植株过高容易引起倒伏, 半矮化品种是现代育种的重要方向。因此, 发掘和鉴定控制植物株高的基因并对其进行定向改良具有重要意义。对 *GA2oxs* 基因与植物株高的关系已有大量研究。拟南芥 *AtGA2ox7* 和 *AtGA2ox8* (Schomburg et al., 2003)、水稻 *OsGA2ox1* (Sakamoto et al., 2003)、*OsGA2ox5* (Shan et al., 2014)、*OsGA2ox6* (Huang et al., 2010)、菠菜 *SoGA2ox3* (Lee & Zeevaart, 2005) 和矮牵牛 *PhGA2ox1* (郭余龙等, 2013) 过量表达植株均表现出矮化表型。赤霉素一个重要的作用就是调节节间伸长, 以上对多个物种的研究证实无论是 *C₁₉-GA2oxs* 基因还是 *C₂₀-GA2oxs* 基因都可以通过调节植物体内 GA 水平进而调节节间长度。

GA2oxs 基因与种子、叶、花、果以及根发育的关系等方面已有大量研究。拟南芥敲除 5 个 *C₁₉-GA2oxs* 基因能够促进种子萌发以及营养生长向生殖生长转换, 花数量减少, 雌蕊伸长受到抑制, 导致提前受精(Rieu et al., 2008)。*C₂₀-GA2oxs* 功能缺失 *Atga2ox7Atga2ox8* 双突变体植株中活性 GA 含量增加 2~4 倍, 表现出提早抽薹(Schomburg et al., 2003)。草地早熟禾(*Poa pratensis*) *PpGA2oxs* 在拟南芥中过表达使植株矮化、延迟开花、叶绿素含量增加(Tan et al., 2018)。在甘蓝型油菜中过表达拟南芥 *AtGA2ox8* 后, 表现出萌发延迟, 生长发育迟缓, 叶片浓绿, 开花延迟, 植株矮化等特征(朱登峰, 2010)。过表达菠菜 *SoGA2ox3* 植株种子萌发率降低, 下胚轴和茎变短, 叶色变深绿, 开花延迟(Lee & Zeevaart, 2005)。矮牵牛中过表达 *PhGA2ox1* 能够导致植株节间长度明显变短、叶色变深(郭余龙等, 2013)。对以上多个物种的研究结果表明, *GA2oxs* 基因在抑制节间伸长、抑制种子萌发、延迟开花, 影响叶绿素含量和叶片颜色加深等方面的功能是保守的。

GA2oxs 基因在调节结实、侧枝发育、根长以及植物纤维等方面也有研究。小麦(*Triticum aestivum*) 中异位表达红花菜豆 *PcGA2ox1* 降低活性 GA 含量, 导致穗长度、结实率与谷粒大小降低(Appleford et al., 2007)。用果实特异启动子 TFM7 启动番茄 *SIGA2ox1* 表达, 转基因番茄植株营养生长没有变化, 但种子数量、萌发率和果实质量降低(Chen et al., 2016)。沉默番茄中 5 个 *C₁₉-GA2oxs* 基因, 转基因植株子房和腋芽中 GA₄ 含量显著增加, 未受精的子房大小是野生型的 30 倍左右, 导致单性结实, 抑制侧枝发育(Martinezbello et al., 2015)。水稻中过表达 *C₂₀-GA2oxs* 基因, 在调节植株生长中表现出多效性作用, 如矮化, 但分蘖数和根数增多(Lo et al., 2008)。拟南芥过表达 *AtGA2ox2* 植株根分生组织中 GA 水平降低, 主根根长变短(Li et al., 2017)。烟草(*Nicotiana rustica*) *NrGA2oxs* 沉默植株的木质部纤维细胞数量增加, 烟草长势以及纤维素产量增加(Dayan et al., 2010)。以上结果说明, *GA2oxs* 基因的高水平表达可以降低结实率、种子数量、果实质量, 能够抑制侧枝发育、降低纤维产量以及稳定根发育系统等。

表 1 *GA2oxs*基因分类、组织表达及功能
Table 1 Classification, tissue expression and function of *GA2oxs*

分类 Classification	基因 Gene	表达组织 Expression in tissue	功能 Function	参考文献 Reference
<i>C₁₉-GA2oxs</i>	<i>AtGA2ox1</i>	幼苗、茎尖、根、莲座叶、叶、茎、花序、长角果 shoot, root, rosette, leaf, stem, inflorescence, silique	Seedling,	Rieu et al., 2008
	<i>AtGA2ox2</i>	种子、幼苗、茎尖、根、莲座叶、叶、茎、花序、 长角果 Seed, seedling, shoot, root, rosette, leaf, stem, inflorescence, silique	控制根细胞数量, 限制根长 Regulate the number of root cells and limit root length	Jasinski et al., 2005; Rieu et al., 2008; Li et al., 2017 Rieu et al., 2008
	<i>AtGA2ox3</i>	种子、幼苗、茎尖、根、莲座叶、叶、茎、花序、 长角果 Seed, seedling, shoot, root, rosette, leaf, stem, inflorescence, silique		Rieu et al., 2008
	<i>AtGA2ox4</i>	幼苗、茎尖、根、莲座叶、花序、长角果 Seedling, shoot, root, rosette, inflorescence, silique		Jasinski et al., 2005; Rieu et al., 2008
	<i>AtGA2ox6</i>	种子、幼苗、茎尖、根、莲座叶、叶、茎、花序、 长角果 Seed, seedling, shoot, root, rosette, leaf, stem, inflorescence, silique		Rieu et al., 2008
	<i>OsGA2ox1</i>	茎尖、根、叶原基 Shoot, root, leaf primordia	内源GA ₁ 缺陷, 抑制生殖生长, 矮化, 结实失败 Deficient in endogenous GA ₁ , later development of reproductive organs, dwarfism, fail to set grain	Sakamoto et al., 2001, 2003
	<i>SIGA2ox1</i>	花、子房、果实 Flower, ovary, fruit	种子数减少, 萌发率降低, 果实质 量减少 Decrease seed number, germination rate and fruit weight	Serrani et al., 2007; Chen et al., 2016
	<i>SIGA2ox2</i>	花、叶、节间、萼片, 花瓣、雄蕊、子房、果实 Flower, leaf, internode, sepal, petal, stamen, ovary, fruit		Serrani et al., 2007; Chen et al., 2016
	<i>SIGA2ox3</i>	根、花、叶、节间、萼片、花瓣、子房、Root, flower, leaf, internode, sepal, petal, ovary		Serrani et al., 2007; Chen et al., 2016
	<i>SIGA2ox4</i>	根、花、叶、节间、萼片、花瓣、子房、果实 Root, flower, leaf, internode, sepal, petal, ovary, fruit		Serrani et al., 2007; Chen et al., 2016
	<i>SIGA2ox5</i>	根、花、叶、节间、子房、果实 Root, flower, leaf, internode, ovary, fruit		Serrani et al., 2007; Chen et al., 2016
	<i>CsGA2ox1</i>	根、茎、叶、花、果实、卷须 Root, stem, leaf, flower, fruit, tendril		王增辉, 2014
	<i>CsGA2ox2</i>	根、花 Root, flowers		王增辉, 2014
	<i>CsGA2ox3</i>	根、茎、叶、花、果实、卷须 Root, stem, leaf, flower, fruit, tendril		王增辉, 2014
	<i>CsGA2ox4</i>	根、茎、花、果实 Root, stem, flower, fruit		王增辉, 2014
	<i>CsGA2ox6</i>	根、花、果实 Root, flower, fruit		王增辉, 2014
	<i>BnGA2ox1-2</i>	子叶、下胚轴、胚根、茎、叶片、花、长角果 Cotyledon, hypocotyl, radicle, stem, leaf, flower, silique		廖晓英, 2015
	<i>BnGA2ox2</i>	子叶、下胚轴、胚根、根、茎、叶片、花、长角果 Cotyledon, hypocotyl, radicle, root, stem, leaf, flower, silique		廖晓英, 2015
	<i>BnGA2ox4</i>	子叶、下胚轴、胚根、根、茎、叶片、花、长角果 Cotyledon, hypocotyl, radicle, root, stem, leaf, flower, silique		廖晓英, 2015
	<i>BnGA2ox6-1</i>	子叶、下胚轴、胚根、根、茎、叶片、花、长角果 Cotyledon, hypocotyl, radicle, root, stem, leaf, flower, silique		廖晓英, 2015
<i>C₂₀-GA2oxs</i>	<i>PhGA2ox1</i>	茎、叶、雄蕊、心皮、花瓣 Stem, leaf, stamen, carpels, petal	矮化, 叶色变深 Dwarfism, dark-green leaf,	Guo et al., 2013
	<i>PhGA2ox2</i>	茎、叶、花芽、雄蕊、心皮、花瓣 Stem, leaf, flower bud, stamen, carpels, petal		Guo et al., 2013
	<i>PhGA2ox3</i>	根、茎、叶、花芽、雄蕊、心皮、花瓣 Root, stem, leaf, flower bud, stamen, carpels, petal		Guo et al., 2013
	<i>OsGA2ox5</i>	根、茎、叶、鞘, 圆锥花序 Root, culm, leaf, sheaths, panicles	矮化, 生殖器官发育延缓 Dwarfism, later development of reproductive organs	Shan et al., 2014
	<i>SIGA2ox6</i>	根、茎、叶、花、果实 Root, stem, leaf, flower, fruit		Chen et al., 2016
	<i>SIGA2ox7</i>	根、茎、果实 Root, stem, fruit		Chen et al., 2016
	<i>SIGA2ox8</i>	根、花 Root, flower		Chen et al., 2016
<i>SIGA2ox9</i>	茎、叶、花、果实 Stem, leaf, flower, fruit		Chen et al., 2016	

续表1

分类	基因	表达组织	功能	参考文献
Classification	Gene	Expression in tissue	Function	Reference
	<i>SlGA2ox10</i>	根、茎、叶、花、果	Root, stem, leaf, flower, fruit	Chen et al., 2016
	<i>CsGA2ox5</i>	根、茎、叶、花、果实、卷须	Root, stem, leaf, flower, fruit, tendril	王增辉, 2014
	<i>CsGA2ox7</i>	根、茎、叶、花、果实、卷须	Root, stem, leaf, flower, fruit, tendril	王增辉, 2014
	<i>CsGA2ox8</i>	茎、叶、花、卷须	Stem, leaf, flower, tendril	王增辉, 2014
	<i>BnGA2ox8</i>	根、叶片、花、长角果	Root, leaf, flower, silique	廖晓英, 2015
	<i>SoGA2ox3</i>	茎尖、叶柄	Shoot, petiole	Lee & Zeevaart, 2005
			萌发率低, 叶色变深, 延迟开花 Reduced germination, dark-green leaf, and delayed flowering	

4 环境因素对 *GA2oxs* 基因表达的调控

4.1 光照对 *GA2oxs* 基因表达的调控

研究表明光照对 *GA2oxs* 表达调控至少部分由光敏色素介导。拟南芥种子吸水膨胀过程中, 依赖 PHYA 和 PHYB 的光敏色素互作蛋白 PIL5 调节赤霉素的合成, 远红光信号可以刺激 PIL5 蛋白通过 26S 蛋白酶体降解, 促进 GA 生物合成基因 (*GA3ox1* 和 *GA3ox2*) 的表达, 并抑制 GA 分解基因 (*GA2ox*) 的表达, 使 GA 含量升高, *pil5* 突变体中 GA₄ 含量升高, 而 *PIL5* 过表达植株中 GA₄ 含量降低, 表明 PIL5 可以通过调控 GA 合成和代谢来调节种子萌发 (Oh et al., 2006)。莴苣 (*Lactuca sativa*) 萌发过程中 *LsGA2ox2* 在红光条件下显著下调, 导致红光诱导下莴苣种子内 GA₁ 水平增加 (Nakaminami et al., 2003)。功能缺失 *ga2ox2* 突变体植株中活性 GA₄ 水平增加, 远红光脉冲照射后置于黑暗吸涨 48 h 的突变体种子萌发率远远高于野生型, 且 *AtGA2ox2* 在胚轴皮层积累, 这在一定程度上解释了种子萌发过程中光敏色素介导的赤霉素敏感度的改变 (Yamauchi et al., 2007)。红光, 蓝光或远红光下照射 4 h, *PsGA2ox2* 表达上调, GA₁ 含量急剧下降, 节间缩短, 解释了光照会抑制节间伸长 (Reid et al., 2002)。以上研究证明光照对 *GA2oxs* 基因表达的调控具有组织特异性, 种子萌发过程中, 光照可以通过抑制 *GA2oxs* 表达, 提高 GA 水平, 促进种子萌发。而在调控节间伸长的过程中, 光照则促进 *GA2oxs* 表达, 分解 GA, 抑制节间伸长。

蓝光调控下胚轴伸长过程中可以通过诱导锌指蛋白家族 Double B-box 1a (DBB1a) 抑制 *GA2ox1* 和 *GA2ox8* 表达, 诱导 *GA3ox1* 和 *GA20ox1* 表达来提高活性 GA 水平, 促进下胚轴伸长 (Wang et al., 2011)。也可以由隐花色素介导, 促进 *AtGA2oxs* 表达, GA 水平下调, 抑制下胚轴伸长 (Zhao et al., 2007)。

4.2 低温对 *GA2oxs* 基因表达的调控

CBF1/DREB1B 转录因子是低温响应通路中的一个重要调控因子, 冷驯化过程可以诱导 *CBF* 表达 (Cook et al., 2004; Fowler et al., 2005)。过表达 *CBF* 植株具有较强的抗寒性并伴有生长迟缓的现象。这种生长延滞现象可以通过外源施用 GA₃ 恢复, 证明低温条件下, *CBF* 至少部分通过赤霉素代谢调节植物生长发育 (Zhang et al., 2012)。DELLA 蛋白是 *CBF1* 介导响应冷胁迫的重要组成部分, 拟南芥冷诱导以及过表达 *CBF1* 可以通过促进 *AtGA2ox3* 和 *AtGA2ox6* 表达降低 GA 含量进而促进 DELLA 蛋白积累, 抑制植株生长发育, 提高抗寒性 (Achard et al., 2008)。Zhou 等 (2017) 研究表明拟南芥 *CBF3* 与 *CBF1*、*CBF2* 在胁迫中抑制赤霉素的机制类似, 体内、体外结合试验验证发现 *AtGA2ox7* 作为 *CBF3* 新的调节者响应低温, 促进 DELLA 蛋白积累, *CBFs* 与 DELLA 协同在低温条件下延缓植株生长 (Zhou et al., 2017)。种子萌发过程中, 低温诱导 *DELAY OF GERMINATION1* (*DOG1*) 表达, 而 *DOG1* 通过正向调控 *AtGA2ox6* 表达, 分解 GA 延缓种子萌发 (Kendall et al., 2011)。

HY5 属于 bZIP 类转录因子, 在光信号和低温信号通路中都具有重要的作用。HY5 可能通过调控一系列胁迫应答基因的表达来增强植物的耐寒性 (Catala et al., 2011)。拟南芥中, HY5 介导 10% 以上与低温胁迫相关基因的表达, 其中包括花青素合成相关的一些基因, 来确保低温驯化的顺利进行 (Catala et al., 2011; Zhang et al., 2011)。此外, 赤霉素可以降低低温下花青素的积累, 相反, 多效唑 (赤霉素合成抑制剂) 可以增加低温下花青素的积累, 暗示赤霉素可能参与这一过程, 研究发现低温胁迫以依赖 HY5/HYH 方式上调 *AtGA2ox1* 表达诱导花青素积累 (Zhang et al., 2014)。

4.3 干旱对 *GA2oxs* 基因表达的调控

GA2oxs 基因参与响应干旱胁迫, 过表达 *GA2oxs* 植株抗旱能力显著提高 (Zawaski & Busov, 2014)。转录组分析发现小麦根部在干旱处理后赤霉素、脱落酸和生长素的合成和信号响应相关基因变化显著 (Krugman et al., 2011)。*SPINDLY (SPY)* 在植物非生物胁迫中起负调控作用, 受干旱胁迫强烈诱导, 轻微响应盐胁迫, 通过调节赤霉素和细胞分裂素代谢基因 *GA2oxs* 和 *CKTOKININ OXIDASE 3 (CKX3)* 的表达, 整合环境信号调节植物生长发育 (Qin et al., 2011)。拟南芥干旱胁迫处理能快速诱导叶片中 *ETHYLENE RESPONSE FACTOR5 (ERF5)* 和 *ERF6* 的表达, 导致 *GA2ox6* 表达上调, 活性 GA 水平降低, 细胞增殖减慢进而叶片发育延缓 (Dubois et al., 2013)。干旱胁迫下, 过表达马铃薯 (*Solanum tuberosum*) *StGA2ox1* 转基因株系较对照具有相对较高的叶绿素含量、游离脯氨酸含量和相对叶片含水量 (石建斌, 2016)。

4.4 盐胁迫对 *GA2oxs* 基因表达的调控

GA2oxs 基因参与响应盐胁迫, 过表达 *OsGA2ox5* 植株抗盐胁迫能力显著提高 (Shan et al., 2014)。盐响应因子 *DWARF AND DELAYED FLOWERING 1 (DDF1)* 编码 DREB1/CBF 亚家族 AP2 转录因子, 是拟南芥 CBFs 的同系物, 参与胁迫响应。*ddf1* 突变体表现出矮化, 延迟开花, 外源施用 GA_3 可以缓解此表型 (Magome et al., 2004)。盐胁迫下, 拟南芥中包括 *AtGA2ox7* 在内的 6 个 *AtGA2oxs* 上调, 而且 *DDF1* 过表达植株中 *AtGA2ox7* 显著上调, *DDF1* 蛋白可以直接结合到 *GA2ox7* 启动子 DRE-like 基序 (GCCGAC 和 ATCGAC) 激活其转录, 表现出矮化, 延迟开花和提高抗盐性的表型 (Magome et al., 2008)。因此, 鉴于 *AtGA2ox7* 在低温胁迫中作为 CBF/DREB1 信号通路中协调 GA 和 DELLAs 的关键组成部分 (Zhou et al., 2017), 在应对非生物胁迫的功能相对保守, 因此, *AtGA2ox7* 可在基因工程编辑以及抗胁迫分子育种中作为一个很好的候选基因。

5 植物激素对 *GA2oxs* 基因表达的调控

5.1 赤霉素对 *GA2oxs* 基因表达的调控

GA2oxs 基因表达受植物内源赤霉素的反馈调节, 且不同 *GA2oxs* 基因对赤霉素的响应存在差异。烟草中过表达豌豆 *PsGA3ox1* 后活性 GA 水平升高, 此时 *NtGA2ox* 家族成员 *NtGA2ox3*、*NtGA2ox5* 表现为上调表达, 而 *NtGA2ox1* 表达无明显变化。研究证明该现象与 *NtGA2ox* 家族成员对赤霉素敏感程度不同有关, *NtGA2ox3* 和 *NtGA2ox5* 属于赤霉素敏感型, 较低浓度的活性 GA 即可对其产生正反馈调节, 而 *NtGA2ox1* 对赤霉素不敏感, 只受高浓度的 GA 调节 (Gallegogiraldó et al., 2008)。通常, 外源施用 GA_3 可促使 *GA2oxs* 基因上调表达, 如拟南芥 (Thomas et al., 1999) 和早熟禾 (Tan et al., 2018) 等。水稻 *GA2oxs* 基因在响应赤霉素的过程中表达情况有所差异, 仅 *OsGA2ox3* 表现为

上调表达, *OsGA2ox1* 无明显响应 (Sakai et al., 2003), 而 *OsGA2ox6* 表现为轻微下调 (Huang et al., 2010)。推测可能由于 *OsGA2ox6* 属于 *C₂₀-GA2oxs*, 分解非活性 GA₁₂ 和 GA₅₃, 所以外源施用活性 GA₃, *OsGA2ox6* 表达变化不显著。

5.2 细胞分裂素、生长素和乙烯对 *GA2oxs* 基因表达的调控

赤霉素与细胞分裂素通过拮抗作用调节植物顶端分生组织发育, 至少部分通过 *GA2oxs* 基因实现的 (Jasinski et al., 2005)。拟南芥外源施用细胞分裂素, 显著提高了 *AtGA2ox2* 的表达, 同时过表达细胞分裂素合成基因 (*phosphate-isopentenyl transferase, IPT*) 提高内源细胞分裂素含量, 进而提高了转基因植株 *AtGA2ox2* 转录水平 (Jasinski et al., 2005)。证明细胞分裂素可以促进 *GA2oxs* 基因表达, 进而降低活性 GA 水平。

生长素对赤霉素的调控至少部分由 *GA2oxs* 基因介导。对拟南芥生长素合成突变体 *yucca* 以及外源施用生长素研究表明 *GA2oxs* 基因响应生长素, 6 d 大小的拟南芥幼苗外源施用 50 $\mu\text{mol} \cdot \text{L}^{-1}$ 1-Naphthaleneacetic acid (NAA), 7 个 *AtGA2oxs* 基因除了 *AtGA2ox7* 外都表现出上调表达, 尤其 *AtGA2ox3* 和 *AtGA2ox8* 显著上调 (Frigerio et al., 2006)。豌豆去除顶端后生长素合成受阻, *PsGA2ox1* 表达上调 (Ross et al., 2000)。O'Neill 等 (2010) 研究发现豌豆生长素缺失, *PsGA2ox1* 以依赖 DELLA 的方式上调, 而 50 $\mu\text{mol} \cdot \text{L}^{-1}$ NAA 处理后, *PsGA2ox2* 则以独立于 DELLA 的方式上调 (O'Neill et al., 2010)。以上研究证明 *GA2oxs* 基因对生长素不同的响应可能是由 DELLA 蛋白介导。此外, 信号转导也会影响 *GA2oxs* 基因的表达, 沉默番茄生长素信号响应因子 *AUXIN RESPONSE FACTOR 7 (SIARF7)* 后, *SIGA2ox2* 和 *SIGA2ox4* 表达下调 (de Jong et al., 2011)

外源施用乙烯前体 ACC 后, *AtGA2ox1* 和 *AtGA2ox7* 表达显著下调, *AtGA2ox2* 表达轻微下调, 导致 GA 水平增加诱导下胚轴伸长 (Vriezen et al., 2004; Vandenbussche et al., 2007)。对乙烯突变体 *Sletr1-1* 研究发现番茄坐果过程中 *SIGA2ox3* 表达上调, 而 *SIGA2ox4* 和 *SIGA2ox5* 表达下调, GA 含量增加, 提高了坐果率 (Shinozaki et al., 2015)。证明 *GA2oxs* 基因响应乙烯调控具有组织特异性。

6 转录因子对 *GA2oxs* 基因表达的调控

AGL15 (Agamous-Like 15) 是一类具有 MADS 功能域的 DNA 结合调控因子, 在发育的胚中大量表达, ChIP 试验表明, 在发育的胚中 AGL15 可以直接结合到 *AtGA2ox6* DNA 片段 CarG 序列 (CCAATTTAATGG), 通过激活其表达来调节植物体内 GA 含量, 进而调控体细胞胚胎发育和种子萌发 (Wang et al., 2004)。APETALA2 (AP2) 家族成员 ABA-INSENSITIVE 4 (ABI4), 直接结合到 ABA 合成基因 *NCED6* 以及 *GA2ox7* 启动子激活其表达, 且 ABA 可诱导 *GA2ox7* 表达, GA 抑制 *NCED6* 表达依赖 *ABI4*, 证明 *ABI4* 可正调控 ABA 与 GA 间的拮抗作用 (Shu et al., 2016)。拟南芥 C2H2 锌指蛋白 INDETERMINATE DOMAIN1 (IDD1) /ENHYDROUS (ENY) 通过调节 *GA2ox1* 和 *GA2ox6* 的表达介导 GA 和 ABA 对种子发育的调控 (Feurtado et al., 2011)。

DREB (DRE binding factor) 属于 AP2/ERF 家族一员。菊花中鉴定出 13 个 *DREB1*, 系统进化将其分为 3 组, *DgDREB1A*、*DgDREB1B* 和 *DgDREB1C*。过表达 *DgDREB1A* 植株由于与胁迫相关的 *DREB1* 下游基因 *COR47*、*COR15A* 和 *RD29A* 的表达被强烈诱导, 两个光周期响应开花基因 *CO* 和 *FT* 被抑制, 表现出延迟开花但是并不矮化; 而过表达 *DgDREB1B* 植株中 *GA2ox7* 显著上调, 表现出矮化但并不延迟开花。上述结果表明, 不同 *DgDREB1* 组成员可能对植物发育影响不同: *DgDREB1A* 可能参与光周期相关开花时间调控, 而 *DgDREB1B* 参与 GA 介导的植物发育过程 (Tong et al., 2009)。

KNOTTED1(KN1)-like homeobox I (KNOXI)负责维持顶端分生组织分化,其与 *GA2ox1*mRNAs 在顶端分生组织以及新启动叶片基部表达重叠, KNOXI 可以直接结合 *GA2ox* 基因内含子含有两个 TGAC 结构域的元件促进 *GA2oxs* 表达, 维持顶端分生组织正常活动 (Bolduc & Hake, 2009)。拟南芥中 *AtGA2ox2* 和 *AtGA2ox4* 响应 STM(KNOXI 家族成员)诱导,在分生组织基部存在 KNOXI-GA2oxs 途径控制叶片向顶端分生组织运输活性 GA, 维持顶端分生组织正常发育 (Jasinski et al., 2005)。A20/AN1 ZFPs (zinc-finger proteins) 是植物胁迫响应过程中一类重要蛋白, *Oryza sativa dwarf rice with overexpression of gibberellin-induced gene (OsDOG)* 属于赤霉素诱导的 A20/AN1 ZFP, 研究表明此蛋白可通过降低 *OsGA3ox2* 的表达、促进 *OsGA2ox1* 和 *OsGA2ox3* 表达, 进而负调节 GA 介导的茎细胞伸长 (Liu et al., 2011)。番茄 CIN - TC 转录因子 LANCEOLATE (LA) 促进早期叶分化, 研究表明 LA 是通过负调控 *SIG2ox4* 的表达来调节活性 GA 含量以调控早期叶分化 (Yanai et al., 2011)。

7 小结与展望

GA2oxs 在赤霉素代谢途径中的作用已经明确, 根据底物不同分为 C₂₀-GA2oxs 和 C₁₉-GA2oxs 两类。目前拟南芥、水稻、番茄和黄瓜中两类成员构成已经探明, 而其他物种中分类尚不明确, 亟待拓宽研究。GA2oxs 基因位于调控网络的中心位置, 参与赤霉素自身反馈调节以及对细胞分裂素、生长素和乙烯的响应, 并通过赤霉素代谢调节种子萌发、株高、开花和果实发育等生长发育过程, 同时参与温度、光照、干旱和盐胁迫等应答过程 (图 2)。虽然已经初步明确 GA2oxs 作为枢纽联通外界环境与内源因素参与植物生长发育及胁迫响应, 但其发挥作用的具体分子机制尚不清楚, 有待进一步研究。

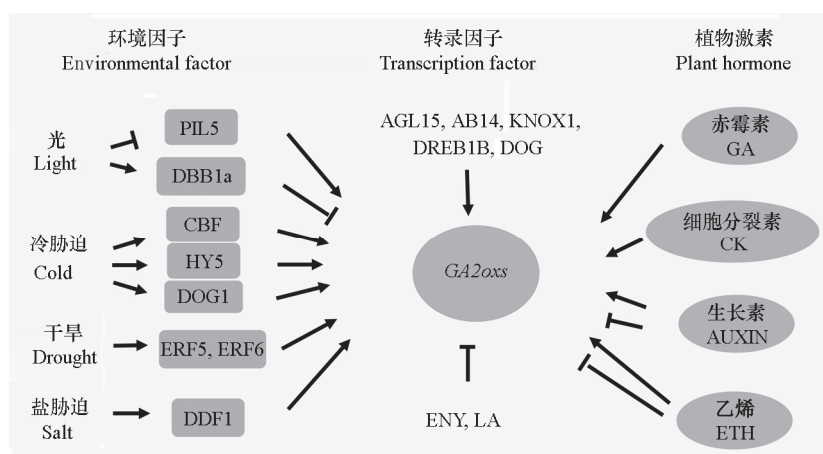


图 2 植物体内 Gibberellin 2-oxidases 表达调控

箭头表示促进作用, T 型箭头表示抑制作用。

Fig. 2 Regulation of Gibberellin 2-oxidases expression in plants

Promotion is shown by arrows and inhibition is shown by T-arrow.

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