

GATA转录因子对植物发育和胁迫响应调控的研究进展

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摘要: 植物转录因子GATA能与靶基因启动子上的WGATAR区域结合, 激活或抑制下游靶基因的转录, 从而调控植物的发育。目前已从拟南芥、水稻(*Oryza sativa*)、大豆(*Glycine max*)等物种中分离和鉴定出多种GATA转录因子。拟南芥基因中共发现29个GATA转录因子, 根据其氨基酸保守结构域和外显子-内含子特征可将其分为A、B、C、D四个亚族, 分别含有14、10、3、2个GATA成员。GATA转录因子具有多种生物学功能, 能够参与植物种子、根、花、叶绿体等的生长发育, 并响应干旱、高温、冷害等环境胁迫, 是一类调控植物各种生理反应的关键因子。本文对GATA转录因子的结构特点、生物学功能及其表达调控等方面在植物中的研究现状进行了阐述, 以期为相关研究提供理论参考。

关键词: GATA转录因子; 结构特征; 生物学功能; 表达调控

植物转录因子(transcription factors)可通过识别靶基因启动子上的顺式作用元件并结合特殊序列来调节基因的表达(Franco-Zorrilla等2014), 从而调控包括细胞分化、组织和器官发育、响应植物激素和环境因子、代谢网络、植物抗病性等功能(Hong 2016)。目前, 研究较多的植物转录因子家族包括: WRKY、NAC (NAM、ATAF1/2和CUC1/2)、MYB、DREB (dehydration-responsive element-binding protein)、bZIP (basic leucine zipper, 碱性亮氨酸拉链)、bHLH (basic helix loop helix, 碱性螺旋环螺旋)、MADS-box等。植物GATA转录因子因其特异性结合WGATAR序列(W为T或A, R为G或A)而得名, 其DNA结合域具有典型的锌指结构模体C-X₂-C-X₁₇₋₂₀-C-X₂-C (IVb型)。近年来的研究表明, 植物GATA转录因子在光形态建成、种子萌发、植物激素应答、花发育以及碳、氮代谢等生物学过程中都发挥重要作用。由于植物GATA转录因子的重要功能及其有限报道的现状, 本文对植物GATA转录因子的重要生物学功能及其分子调控机制等方面取得的进展进行综述, 以期为相关研究提供参考。

1 GATA转录因子的结构和分类

20世纪90年代, Terzaghi等(1995)和Arguello-Astorga等(1998)先后证实了光和生物钟响应基因的调控区含有GATA基序。随后的凝胶迁移率和DNase I足迹实验进一步证实GATA蛋白因子可结合这些GATA元件并参与光和昼夜节律的调控(Jeong和Shih 2003; Manfield等2006)。此外, Teakle等(2002)利用酵母双杂实验证实了拟南芥中4个高

度同源的GATA转录因子(AtGATA1~AtGATA4)能够结合到细胞核内靶基因的GATA元件上。烟草*NtGATA1*基因是植物中克隆的首个GATA转录因子基因(Daniel-Vedele和Caboche 1993)。

Reyes等(2004)从拟南芥和水稻(*Oryza sativa*)基因组中分别鉴定了29和28个GATA转录因子, 根据系统进化关系、DNA结合域及内含子-外显子构成, 将拟南芥和水稻GATA家族成员分成了A、B、C、D四个亚家族。对拟南芥、水稻和大豆(*Glycine max*)主要GATA转录因子进行系统进化、保守结构域及内含子和外显子组成分析(图1), 结果显示, A亚族包括14个GATA转录因子, 所有蛋白都存在一个C-X₂-C-X₁₈-C-X₂-C锌指环(其中C代表半胱氨酸), 每个GATA基因都含有2个外显子, 在靠近3'端的外显子处编码一个完整的锌指结构; B亚族包括16个GATAs, 也含有上述锌指环结构, 其中AtGATA29在第一和第二半胱氨酸之间存在另外4个氨基酸残基(CTNMMC), 每个GATA基因包含2或3个外显子; C亚族包括3个GATAs, 编码一个C-X₂-C-X₂₀-C-X₂-C锌指环, 对应基因含有7个外显子, 锌指结构位于第五个外显子上, 在这3个蛋白的中间区域还含有一个保守结构域CCT [CONSTANS, CO-like protein, TOC1 (timing of cab expression 1)]以及TIFY (TIFYXG)保守结构域, 与植物生物钟调节和响应植物激素信号相关(Gendron等2012; Ye等

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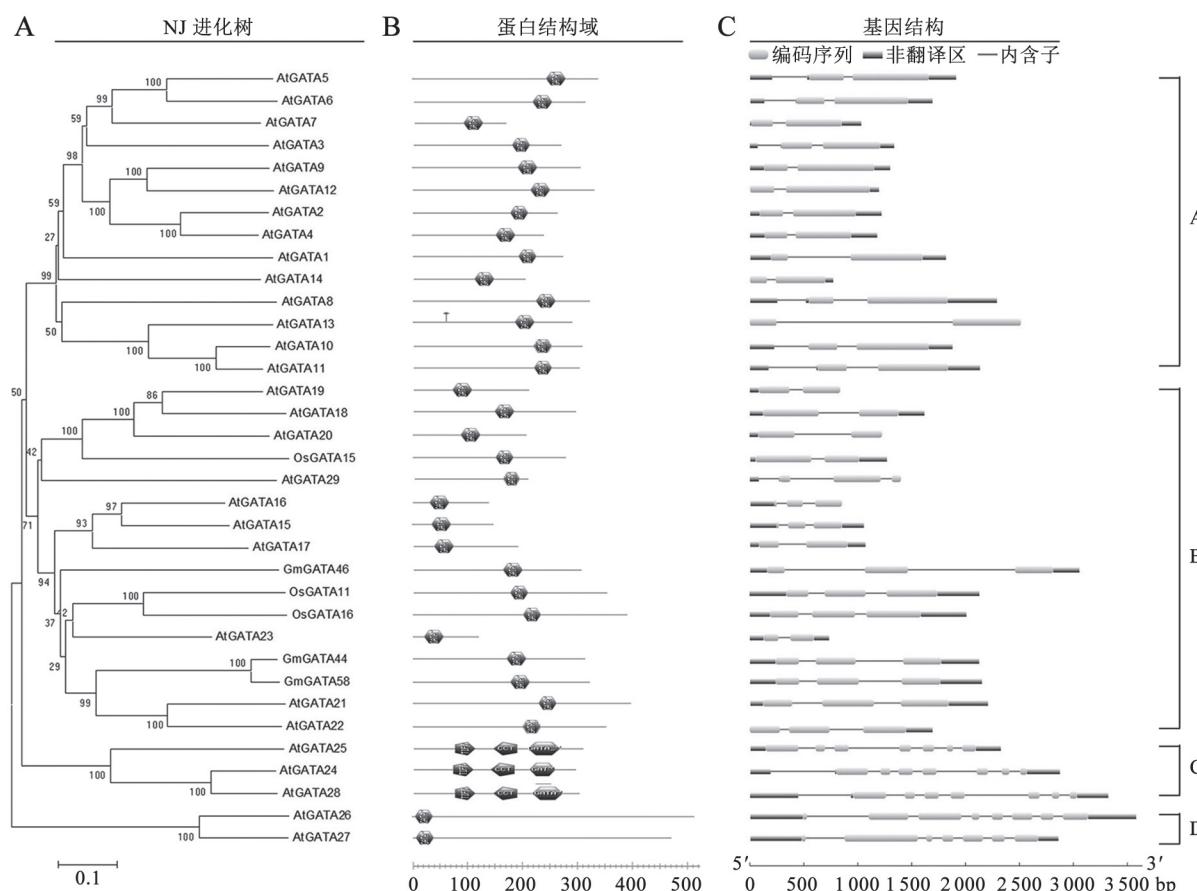


图1 拟南芥、水稻及大豆GATA转录因子的遗传进化关系

Fig.1 Phylogenetic analysis of *Arabidopsis*, rice and soybean GATA transcription factors

A: GATA转录因子氨基酸序列的系统进化树; B: 蛋白保守结构域; C: 外显子-内含子结构特征。利用MEGA 6.06中neighbor-joining法构建系统进化树，并通过1000-bootstrapping进行检验。利用PROSITE (<http://prosite.expasy.org>)和GSGD 2.0 (<http://gsds.cbi.pku.edu.cn>)分别对GATA转录因子的蛋白和基因序列进行保守结构域和基因结构分析，GATA蛋白和基因序列表来自The Plant Genomics Resource中Phytozome 11 (<https://phytozome.jgi.doe.gov/pz/portal.html#>)。

2009); D亚族GATAs包含2个GATAs，在N端具有一个C-X₂-C-X₁₈-C-X₂-C锌指环, GATA26含有7个外显子, 而GATA27含有6个外显子。

对GATA转录因子的氨基酸序列进行保守模体分析发现(图2), 除了具有一个典型的锌指结构C-X₂-C-X₁₈-C-X₂-C (motif 1和3), 大多数GATA转录因子还存在不同的可变区。A亚族GATA转录因子含有另外4个模体(motif 2、5、7、8), 推测这些模体可能参与植物光和激素调节(Luo等2010)。目前, 研究最多的是B亚族GATA转录因子, 大多数B亚族GATA转录因子根据其保守结构域可将其分为两个功能亚类, 一种是N端具有HAN [VDCTLSQLGT-PS(T/S)R(L/R)(C/D/A)]结构域(Zhang等2013; Zhao等2004), 另一种是其C端具有亮氨酸-亮氨酸-甲硫

氨酸(LLM)结构域(motif 4) (Behringer和Schwechheimer 2015; Behringer等2014)。研究表明, 拟南芥、番茄(*Solanum lycopersicum*)、大麦(*Hordeum vulgare*)及短柄草(*Brachypodium distachyon*)中含有HAN或LLM结构域的B-GATA转录因子具有不同的生物及生化活性(Ranftl等2016; Whipple等2010), 而B亚族GATA的其他模体(如motif 9和10)在植物生长发育过程中可能发挥的作用还有待进一步阐明。C亚族GATA的motif 6为CCT保守结构域, 主要与开花时间相关(Cockram等2012)。目前关于D亚族GATA的功能研究还未见报道, 但对其氨基酸序列分析显示其含有一个与A亚族GATA相同的保守模体(motif 8), 这可能为其今后的功能研究提供一个方向。

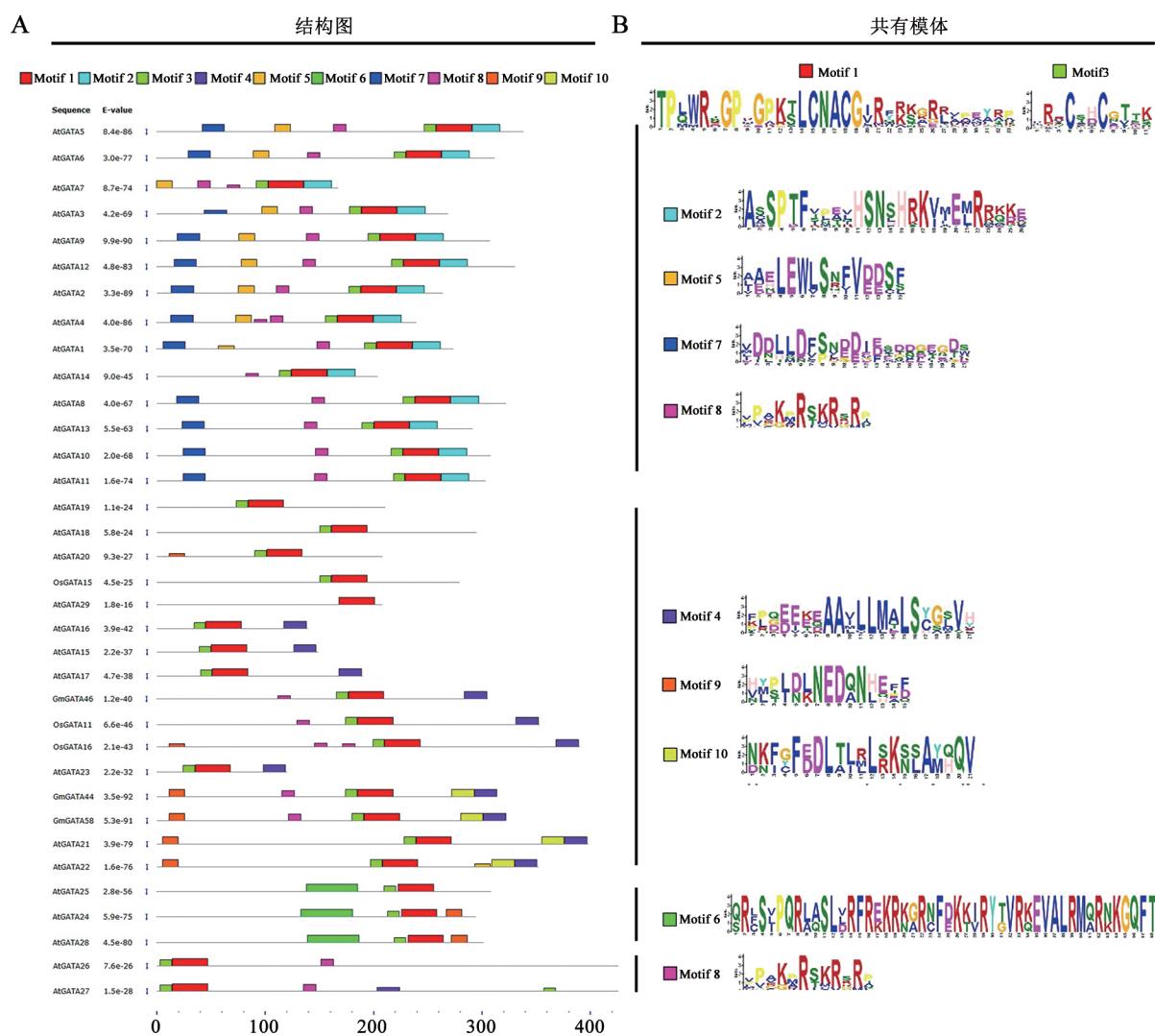


图2 GATA转录因子保守模体分析
Fig.2 Motif analysis of GATA transcription factors

A: 35个GATA转录因子蛋白保守模体结构图; B: 10个保守模体的一致序列。利用MEME Suite 4.11.2 (<http://meme-suite.org/tools/meme>)对拟南芥、水稻、大豆GATA转录因子进行蛋白保守模体扫描分析, bits(纵轴值)表示该位点氨基酸残基出现的概率。

2 GATA转录因子对植物发育及成花的分子调控机制

2.1 对种子萌发和幼苗生长的影响

赤霉素(gibberellin, GA)对种子萌发有显著促进作用, 它作为信号分子通过调节基因的表达控制种子的萌发过程(Neff 2012)。DELLA蛋白作为GA信号传导途径中的负调控因子起作用, 同时, DELLA蛋白也是其他植物激素或环境信号的枢纽蛋白(Wang等2009), 如DELLA蛋白能够干扰转录因子PHYTOCHROME INTERACTING FACTORS (PIFs)的活性(Richter等2010), 而PIF3可与GATA转录因子GNL/CGA1 (*GNC-LIKE/CYtokinin-RE-*

SPONSIVE GATA FACTOR1, GATA22)的启动子直接结合; PIF1可能通过调节*GNC (NITRATE-INDUCIBLE, CARBONMETABOLISM INVOLVED, GATA21)*和*GNL*的表达影响种子萌发(Naito等2007; Richter等2010)。在GA抑制剂多效唑(paclobutrazol, PAC)处理下, 过表达*GNC*和*GNL*株系的种子萌发率显著低于野生型拟南芥, 而*gnc gnl*双突变体则促进种子萌发(Behringer等2014), 表明*GNC*和*GNL*在种子萌发过程中起负调控作用。此外, 在冷层积过程中, 拟南芥GATA转录因子*BME3 (Blue Micropylar End 3, GATA8)*在种子中大量积累, 而在敲

除BME3基因突变体中, 种子深度休眠, 表现对冷层积不敏感; 外源GA3可以恢复突变体的种子萌发, 表明2个突变体中存在正常的GA信号转导途径, 而且BME3对拟南芥种子萌发起正调控作用(Liu等2005)。

光和油菜素内酯(brassinosteroid, BR)是调节幼苗发育的关键信号分子。BR在光形态建成过程中起重要作用, 植物接收BR信号后, BRZ1 (BR-activated transcription factor 1)受体能与GATA2的启动子结合, 并抑制GATA2的表达; 而光能抑制光形态建成相关因子COP1 (CONSTITUTIVE PHOTOMORPHOGENESIS 1)的水解, 由此激活GATA2, 使其直接与光响应基因的启动子元件结合, 调控光和BR响应基因的表达, 从而影响植物幼苗生长。由此显示GATA2是光与BR信号途径的连接点并在光形态建成过程中起正调节因子的作用(Luo等2010)。

2.2 对植物形态建成的调控

2.2.1 促进植物绿化、叶绿体发育及叶绿素合成

细胞分裂素(cytokinin, CK)在调节植物发育及促进叶绿体功能中起重要作用(Cortleven和Schmülling 2015)。GATA转录因子GNC和GNL在绿色组织中高度表达, 并介导了细胞分裂素对质体发育的调控(Naito等2007), 二者在光反应和暗反应中的表达有显著差异(Manfield等2006)。当CK存在时, GNL在CK受体AHK2/AHK3作用下在茎和根中被迅速诱导表达, 而GNC的积累则较少, 表明CK对GNC的表达影响较小(Chiang等2012; Naito等2007)。CK处理的光敏色素突变体 $phyA\ phyB$ 中GNL显著上调表达, 研究表明细胞分裂素可通过光响应基因HY5 (*elongated hypocotyl 5*)和HYH (*HY5 homologue*)共同调节GNL的表达(Monte等2004)。 gnl 和 gnc 单突变体均不能使植物正常绿化, 而 gnc 单突变体或 $gnc\ gnl$ 双突变体根中的叶绿素含量显著减少, 因此, 在调节植物叶绿素合成过程中GNC起更加主要的作用(Chiang等2012)。在黑暗条件下, 过表达GNC和GNL促进原质体到黄化质体的分化; 而在光下, 则促进叶绿体的发育(Chiang等2012)并在根中异源产生叶绿素(Kollmer等2011; Richter等2010)。以上结果可能与谷氨酸合酶(GLUTAMATE SYNTHASE)、HEMA、GUN4 (GENOMES UNCOUPLED4)、叶绿素氧化还原酶(PROTOCHLOROPHYLLIDE OXYDOREDUCTASE)、PDV2

(PLASTID DIVISION 2)等基因表达升高相关(Hudson等2011)。GNC和GNL还可直接抑制花发育调节因子APETALA3和PISTILLATA的活性, 阻止拟南芥花瓣变绿(Mara和Irish 2008), 但具体调节机制还不清楚。B型ARR (ARABIDOPSIS RESPONSE REGULATOR)在植物响应CK过程中起关键作用(Hill等2013)。在 $arr1$ 和 $arr12$ 突变体中, CK诱导的GNL表达量显著降低, 叶绿体分裂受到抑制, 从而影响了拟南芥的正常变绿过程(Argyros等2008)。综上所述, GNC和GNL介导了光和细胞分裂素对叶绿体发育及叶绿素合成的调控作用。

GATA转录因子GNC和GNL同时也在GA和生长素(auxin)信号途径中起作用, 与细胞分裂素和其他植物激素形成汇聚点, 在植物生长发育过程中发挥类似的功能(Weiss和Ori 2007)。在细胞水平上, 生长素响应受ARF (AUXIN RESPONSE FACTOR)和AUX/IAA (AUXIN/INDOLE-3-ACETIC ACID INDUCIBLE)蛋白因子调控(Korasick等2014), 而AUX/IAA因子经E3泛素连接酶靶向降解后能够抑制ARF活性(Kepinski和Leyser 2005; Dharmasiri等2005)。研究发现, $arf2$ 突变体表型与过表达GNC或GNL植株表型相似, 能加速叶绿素的积累; 而 $gnc\ gnl\ arf2$ 三突变体的叶绿素含量显著减少, 暗示GNC和GNL是ARF2下游的重要调节因子。 $arf7$ 和 $arf19$ 突变体的叶绿素含量及叶绿体数目与 $arf2$ 突变体、过表达GNC或GNL株系相似, 但需要AUX/IAA SLR1 (SOLITARY ROOT1)因子的介导作用。以上结果暗示, GNC和GNL的表达受生长素和ARFs的调控(Richter等2013b)。GA能够促进ARF2的富集, 而生长素则通过ARF2抑制GATA转录因子GNC和GNL的表达, 因此, GNC和GNL的表达受两种激素在转录水平上的交叉调控(Richter等2013b), 进而影响叶绿体发育和叶绿素合成(Richter等2010)。

GATA转录因子ZML1 (ZINC FINGER PROTEIN EXPRESSED IN INFLORESCENCE MERISTEM LIKE1, GATA24)和ZML2 (GATA28)可与隐花色素1 ($Cry1$)的顺式作用元件结合, 导致在充足光照下, $zml1$ 和 $zml2$ 拟南芥突变体的子叶黄化速度比野生型显著减慢, 表现对高辐照度不敏感性, 并对光合系统II有显著的光钝化作用, 由此暗示ZML2和ZML1是 $Cry1$ 介导的光保护响应途径中的必要组分(Shaikhali等2012)。

2.2.2 影响分生组织细胞分化和叶片的发育

光照条件下, 过表达GATA转录因子基因 $At\text{-}GNC$ 、 $At\text{-}GNL$ 和 $Os\text{-}CGA1$ (*CYTOKININ-RESPONSIVE GATA FACTOR1*)可以促进拟南芥和水稻下胚轴延伸(Hudson等2013; Klermund等2016)、增加主花序和侧花序之间的开度(Behringer等2014)。过表达另一个GATA转录因子ZIM (zinc-finger protein expressed in inflorescence meristem, GATA25)基因能够影响光受体介导的光信号转导途径, 使转基因株系的下胚轴显著伸长且叶片向上延展, 并促进细胞壁延伸相关基因 $XTH33$ 的上调表达(Shikata等2004)。 $At\text{-}GATA23$ 的C端含有部分降解的LLM结构域, 受到生长素响应因子ARF7和ARF19的调节在木质部中柱鞘细胞第一次非对称分裂前特异表达, 并影响侧根起始细胞分化及根分支模式(Rybel等2010), 这是AUX/IAA28信号途径中的IAA28在抑制ARF7和ARF19活性的同时激活了GATA23转录因子, 从而促使与侧根发育相关的下游基因表达, 最终影响根的发育。

此外, 在胚胎发生期, AN3/GIF1 (ANGUSTI-FOLIA3/GRF INTERACTING FACTOR1)和GATA转录因子HANABA TARANU (HAN, GATA18)通过调节 $PLT1$ (*PLETHORA1*)的表达影响子叶的形状(Kanei等2012)。过表达 $At\text{-}GNC$ 和 $At\text{-}GNL$ 能够促进下胚轴和子叶的气孔形成, 而 gnl 和 gnc 突变体则正相反。研究显示 $At\text{-}GATAs$ 可与下游的气孔形成调节因子SPEECHLESS (*SPCH*)、MUTE以及SCREAM/SCREAM2相结合, 促进气孔的形成(Klermund等2016)。黄瓜(*Cucumis sativus*) GATA转录因子 $Cs\text{-}HANI$ 可能通过调节 WUS (*WUSCHEL*)和STM (*SHOOT MERISTEMLESS*)代谢途径影响茎尖分生组织的发育, 并通过复杂的基因调控网络引导叶片的发育(Ding等2015a)。

2.3 对成花的调控

2.3.1 调节植物花器官的发育

植物花序和花分生组织具有特殊的边界域, 从而使花器官正确分离和分化(Zhang等2013)。 HAN 编码一个GATA3家族转录因子, 可调节拟南芥花器官发育, 主要在发育的花原基间、不同的花轮间以及茎尖分生组织和茎之间表达(Zhao等2004)。 han 突变体具有融合萼片、花器官数减少以及小而平的茎尖分生组织表型(Zhao等2004)。研究

表明, HAN与HANL2 (HANABA TARANU LIKE 2, GATA19)、GNC和GNL能形成一个负反馈环调节花器官的发育(Zhang等2013)。黄瓜 $Cs\text{-}HANI$ 基因主要在茎尖分生组织和茎连接处表达, 并能改善拟南芥 han 突变体的花器官表型(Ding等2015a)。进一步研究发现, 在花发育期, HAN能决定花瓣数量并在转录水平与分生组织调节因子 PNH (*PIN-HEAD*)相互作用, 共同调节分生组织的活性; 还能与花原基 JAG (*JAGGED*)基因相互作用, 并与花瓣相关基因 $BOP2$ (*BLADE-ON-PETIOLE 2*)共同调控花器官的发育(Ding等2015b)。

对野生型拟南芥花中GNC和GNL表达模式分析发现, 从第三阶段花芽开始, 随后在花萼、花瓣、雄蕊和心皮中均检测到两个基因的显著表达(Mara和Irish 2008)。拟南芥 $gata17$ 突变体植株花器官的表型(5~6个花瓣和花萼)与野生型(4个花瓣和花萼)相比有显著差异(Ranftl等2016), 暗示GATA转录因子GNC和GNL具有调节花发育的功能。

2.3.2 调节植物开花时间

植物的开花时间对其完成正常生活史十分关键(Weng等2016)。早期研究发现, 拟南芥GATA锌指蛋白CONSTANS (CO) (Putterill等1995)与水稻(Song等1998)、小麦(*Triticum aestivum*) (Nemoto等2003)和多年生黑麦草(*Lolium perenne*) (Martin等2004)中的同源蛋白均能影响植物的开花时间。 gnc 或 gnl 单突变体和 $gnc gnl$ 双突变体的开花时间均早于野生型拟南芥(Richter等2013a, b)。研究发现开花相关转录因子SOC1 (SUPPRESSOR OF OVEREXPRESSION OF CONSTANS 1)参与植物开花时间的调节(Lee和Lee 2010), 而过表达GNC或GNL株系中SOC1表达受到显著抑制, 导致开花时间延迟; 在 $gnc gnl$ 双突变体及 $gal gnc gnl$ 三突变体中SOC1表达量升高, 且开花时间明显提前, 暗示GATA转录因子GNC和GNL与MADS转录因子SOC1互作共同调控拟南芥的开花时间(Richter等2013a)。此外, HAN及其同源蛋白也具有调控开花时间的功能, 如玉米(*Zea mays*) *TSH1* (*TASSEL SHEATH1*)、水稻 $NL1$ (*NECK LEAF 1*)、大麦 TRD (*THIRD OUTER GLUME*)均能抑制苞片生长、推迟开花时间, 并与下游 $PLASTOCHRON1$ (*PLA1*)基因相互作用, 影响花器官发育(Wang等2009)。

综上所述, 植物GATA转录因子能够响应多种

激素信号分子以及光照等的刺激,从而调节植物的生长和发育。图3总结了GATA转录因子参与的各种调控途径。

3 GATA转录因子对胁迫的响应

在低温处理下,拟南芥GNC和GNL的表达量显著增加,过表达GNC或GNL株系的幼苗存活率较高,推测两个GATA转录因子可能响应冷胁迫;此外,SOC1能够介导冷胁迫(Lee和Lee 2010),Richter等(2013a)发现gnc gnl双突变体和soc1 gnc gnl三突变体的存活率低于soc1单突变体,同时下游与冷胁迫相关基因CBF2的表达迅速累积,表明GNC和GNL能与SOC1相互作用共同提高拟南芥的耐冷性。此外,植物GATA转录因子还能响应氮胁迫,在低浓度氮($0.5 \text{ mmol} \cdot \text{L}^{-1}$)处理下拟南芥GNC表达量比高浓度氮($3 \text{ mmol} \cdot \text{L}^{-1}$)增加了约1.5倍(Bi等2005)。当不同浓度氮处理水稻时,过表达Cga1(CYTOKININ-RESPONSIVE GATA FACTOR1)株系在氮含量减少条件下仍能维持叶绿素含量的增加,

而cga1突变体则相反(Hudson等2013)。此外,在低氮胁迫下,大豆幼苗GATA44和GATA58的表达量比对照分别降低了81%和79% (Zhang等2015),表明GATA转录因子对氮胁迫敏感。

随着大规模测序技术的发展,利用不同组学技术研究发现,低温胁迫处理班巴拉花生(*Vigna subterranea*)后,GATA9的表达量下调,并能激活下游相关基因的表达,从而响应低温胁迫(Bonthala等2016)。此外,在构树(*Broussonetia papyrifera*)中也鉴定出与冷胁迫相关的GATA转录因子(Peng等2015)。Bhardwaj等(2015)利用RNA-Seq技术筛选芥菜型油菜(*Brassica juncea*)在高温和干旱胁迫下的抗逆相关基因,鉴定出29个GATA转录因子,其中5个在干旱胁迫下下调表达,2个在高温胁迫上调表达。以上结果显示GATA转录因子可能参与冷、高温和干旱胁迫响应。

在烟草(*Nicotiana tabacum*)中,AGP1 GATA锌指蛋白可与 $NtMyb2$ 启动子的特异基序AGATCCAA

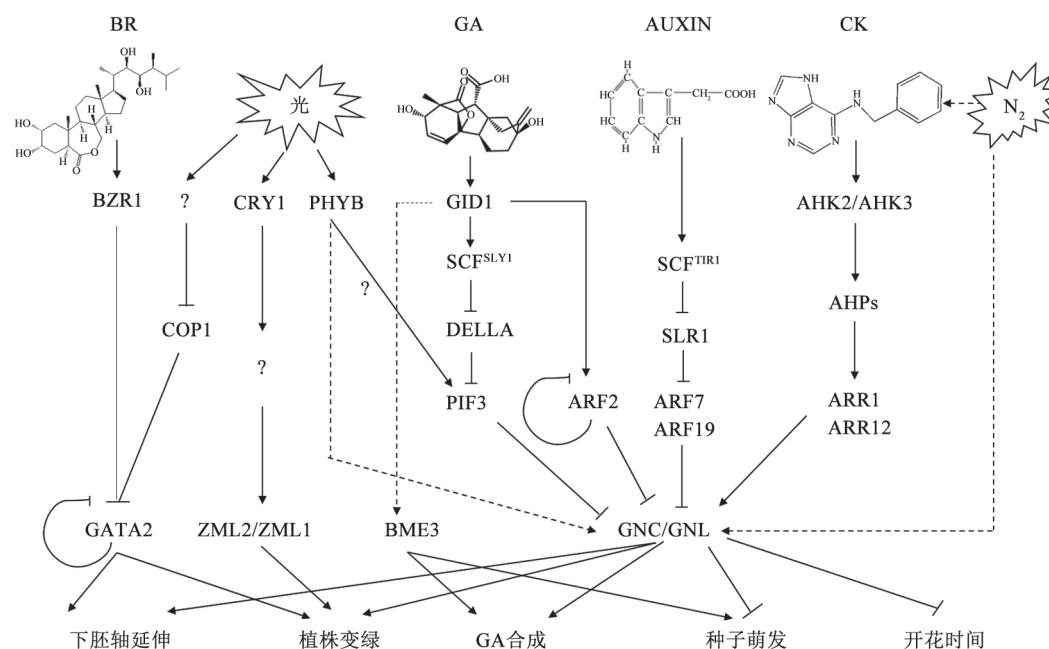


图3 拟南芥中GATA转录因子参与不同信号调控途径的模式图

Fig.3 Schematic diagram of different signal pathways in which GATA transcription factors are involved in *Arabidopsis*

AHK: cytokinin receptors, 细胞分裂素受体; AHP: *Arabidopsis* histidine phosphotransfer proteins, 拟南芥组氨酸磷酸转移蛋白; ARF: auxin response factor, 生长素响应因子; ARR: *Arabidopsis* response regulator, 拟南芥响应调节子; BR: brassinosteroid, 油菜素内酯; BZR1: brassinazole resistant 1; CK: cytokinin, 细胞分裂素; COP1: constitutive photomorphogenesis protein 1, 组成型光形态建成蛋白1; CRY1: cryptochrome 1, 隐花色素1; GA: gibberellin, 赤霉素; GID1: gibberellin insensitive dwarf 1; PHYB: phytochrome B, 光敏色素B; PIF: phytochrome interacting factor, 光敏色素作用因子; SCF^{SLY1}: skp1-cullin-F-BOX protein type E3 ubiquitin ligase with the F-box protein SLY1 (Sleepy 1); SLR1: solitary root 1 (AUX/IAA protein)。实线表示直接和已证实的途径,虚线表示间接调节,问号表示预测的调节模式。

结合, 调节苯丙氨酸氨裂解酶基因(*PAL*)的表达, 从而应答生物胁迫(Sugimoto等2003)。此外, 植物GATA转录因子还参与脂肪酸积累、花青素代谢、叶片衰老等过程。表1总结了不同物种GATA转录因子所涉及的生物学功能。

4 展望

植物GATA转录因子在生长发育和胁迫响应中发挥着重要的调控作用, 但对GATA转录因子靶基因的鉴定相对滞后。A-GATA (GATA2、GATA3和GATA8)、C-GATA (ZML1和ZML2)及含有LLM结构域的B-GATA转录因子的研究目前主要集中在植物激素信号和光调节及其相关生理过程, 如变绿和开花时间调节, 而HAN结构域的B-GATA的研究则聚焦在控制成花过程。植物B-GATA不同亚族成员HAN、GNC和GNL蛋白之间可以形成同源或异源二聚体, 并作为激活因子

或阻遏物参与植物的调控过程。目前对此方面的研究很有限。

GATA与植物生长发育特别对花器官的调控具有重要作用, 目前对花器官生长发育的研究已成为新的热点(Sablowski 2015), 因此, 可以利用转录因子GATA对植物花器官的发育调控进行深入研究, 从而探索花器官发育相关基因的表达调控及代谢途径。其次, 叶片衰老是细胞程序性死亡的一个重要阶段, 而GATA转录因子近年来被发现与叶片衰老有关, 并在叶片衰老过程中上调表达(Richter等2013b), 因此, 可以进一步研究GATA转录因子在叶片衰老过程的调控机制。

综上所述, GATA转录因子在植物生长发育、响应植物激素信号及叶片衰老等方面有重要作用, 对其调控机制及功能开展深入系统的研究将对植物生长发育及响应逆境领域做出贡献。

表1 植物GATA转录因子的结构特征及功能

Table 1 Structure and function of plant GATA transcription factors

物种	GATA名称	GATA类型	功能	参考文献
拟南芥	BME3 (GATA8)	A	种子萌发	Liu等2005
	GATA2	A	光形态建成	Luo等2010
	HANABA TARANU	B	花发育	Ding等2015b; Hang等2013; Zhao等2004
	GNC (GATA21)	B	碳代谢、氮代谢; 叶绿素合成; 糖代谢; 下胚轴延伸、气孔发育	Bi等2005; Klermund等2016
	GNL (GATA22、CGA1)	B	氮代谢; 叶绿体发育、生长和分化; 碳代谢	Chiang等2012; Hudson等2011; Li等2014; Richter等2010
	GATA23	B	侧根延伸	Rybel等2010
	ZML1 (GATA24)、ZML2 (GATA28)	C	下胚轴和叶柄延伸、光形态建成	Shaikhali等2012; Shikata等2004
	GATA		脂肪酸合成和积累	Peng和Weselake 2011
	NECK LEAF 1	B	器官形成	Wang等2009
	Cga1	B	叶绿素合成和叶绿体发育	Hudson等2013
烟草	NTL1		氮代谢	Daniel-Vedele和Caboche 1993
大豆	GATA44、GATA58	B	氮代谢、叶绿素合成	Zhang等2015
	Glyma13g00200.1 (GATA44)、Glyma14g10830.1 (GATA46)	B	种子萌发	Meyer等2012
	GATA 7、GATA 33、HANABA TARANU	B	顶端分生组织生长和发育	Takacs等2012; Zhan等2015
玉米	GATA-like transcription factor	B	细胞延伸、叶绿素合成、叶绿体发育	Wen等2013
	HANABA TARANU	B	顶端分生组织生长和发育、叶片发育	Ding等2015a
小麦 黄瓜 胡黄连 (<i>Picrorhiza kurrooa</i>)	GATA		光响应	Kawoosa等2014
	GATA		冷胁迫	Peng等2015
	GATA26		花青素代谢	Cho等2016
(马铃薯 <i>Solanum tuberosum</i>)				

参考文献

- Argüello-Astorga G, Herrera-Estrella L (1998). Evolution of light-regulated plant promoters. *Annu Rev Plant Physiol Plant Mol Biol*, 49 (4): 525–555
- Argyros RD, Mathews DE, Chiang YH, Palmer CM, Thibault DM, Etheridge N, Argyros DA, Mason MG, Kieber JJ, Schaller GE (2008). Type B response regulators of *Arabidopsis* play key roles in cytokinin signaling and plant development. *Plant Cell*, 20 (8): 2102–2116
- Behringer C, Bastakis E, Ranftl Q, Mayer KFX, Schwechheimer C (2014). Functional diversification within the family of B-GATA transcription factors through the LLM-domain. *Plant Physiol.* 166 (1): 293–305
- Behringer C, Schwechheimer C (2015). B-GATA transcription factors – insights into their structure, regulation, and role in plant development. *Front Plant Sci*, 6 (2): 90
- Bhardwaj AR, Joshi G, Kukreja B, Malik V, Arora P, Pandey R, Shukla RN, Bankar KG, Katiyar-Agarwal S, Goel S, et al (2015). Global insights into high temperature and drought stress regulated genes by RNA-Seq in economically important oilseed crop *Brassica juncea*. *BMC Plant Biol*, 15 (1): 9
- Bi YM, Zhang Y, Signorelli T, Zhao R, Zhu T, Rothstein S (2005). Genetic analysis of *Arabidopsis* GATA transcription factor gene family reveals a nitrate-inducible member important for chlorophyll synthesis and glucose sensitivity. *Plant J*, 44 (4): 680–692
- Bonthala VS, Mayes K, Moreton J, Blythe M, Wright V, May ST, Massawe F, Mayes S, Twycross J (2016). Identification of gene modules associated with low temperatures response in bamba- ra groundnut by network-based analysis. *PLoS ONE*, 11 (2): e0148771
- Chiang YH, Zubo YO, Tapken W, Kim HJ, Lavanway AM, Howard L, Pilon M, Kieber JJ, Schaller G (2012). Functional characterization of the GATA transcription factors GNC and CGA1 reveals their key role in chloroplast development, growth, and division in *Arabidopsis*. *Plant Physiol*, 160 (1): 332–348
- Cho K, Cho K, Sohn H, Ha IJ, Hong S, Lee H, Kim YM, Nam MH (2016). Network analysis of the metabolome and transcriptome reveals novel regulation of potato pigmentation. *J Exp Bot*, 67 (5): 1519–1533
- Cockram J, Thiel T, Steuernagel B, Stein N, Taudien S, Bailey PC, O'Sullivan DM (2012). Genome dynamics explain the evolution of flowering time CCT domain gene families in the Poaceae. *PLoS ONE*, 7 (9): e45307
- Cortleven A, Schmülling T (2015). Regulation of chloroplast development and function by cytokinin. *J Exp Bot*, 66 (16): 4999–5013
- Daniel-Vedele F, Caboche M (1993). A tobacco cDNA clone encoding a GATA-1 zinc finger protein homologous to regulators of nitrogen metabolism in fungi. *Mol Genet*, 240 (3): 365–373
- De Rybel B, Vassileva V, Parizot B, Demeulenaere M, Grunewald W, Audenaert D, Van Campenhout J, Overvoorde P, Jansen L, Vanneste S, et al (2010). A novel aux/IAA28 signaling cascade activates GATA23-dependent specification of lateral root founder cell identity. *Curr Biol*, 20 (19): 1697–1706
- Dharmasiri N, Dharmasiri S, Weijers D, Lechner E, Yamada M, Hobbe L, Ehrismann JS, Jürgens G, Estelle M (2005). Plant development is regulated by a family of auxin receptor F-box proteins. *Dev Cell*, 9 (1): 109–119
- Ding L, Yan S, Jiang L, Liu M, Zhang J, Zhao J, Zhao W, Han YY, Wang Q, Zhang X (2015a). *HANABA TARANU* regulates the shoot apical meristem and leaf development in cucumber (*Cucumis sativus* L.). *J Exp Bot*, 66 (22): 7075–7087
- Ding L, Yan S, Jiang L, Zhao W, Ning K, Zhao J, Liu X, Zhang J, Wang Q, Zhang X (2015b). *HANABA TARANU* (*HAN*) bridges meristem and organ primordia boundaries through *PINHEAD*, *JAGGED*, *BLADE-ON-PETIOLE2* and *CYTOKININ OXIDASE 3* during flower development in *Arabidopsis*. *PLoS Genet*, 11 (9): e1005479
- Franco-Zorrilla JM, López-Vidriero I, Carrasco JL, Godoy M, Vera P, Solano R (2014). DNA-binding specificities of plant transcription factors and their potential to define target genes. *Proc Natl Acad Sci USA*, 111 (6): 2367–2372
- Gendron JM, Pruneda-Paz JL, Doherty CJ, Gross AM, Kang SE, Kay SA (2012). *Arabidopsis* circadian clock protein, TOC1, is a DNA-binding transcription factor. *Proc Natl Acad Sci USA*, 109 (8): 3167–3172
- Hill K, Mathews DE, Kim HJ, Street IH, Wildes SL, Chiang YH, Mason MG, Alonso JM, Ecker JR, Kieber JJ, et al (2013). Functional characterization of type-B response regulators in the *Arabidopsis* cytokinin response. *Plant Physiol*, 162 (1): 212–224
- Hong JC (2016). General aspects of plant transcription factor families. In: Gonzalez DH (ed). *Plant Transcription Factors: Evolutionary, Structural and Functional Aspects*. London: Academic Press, 35–56
- Hudson D, Guevara D, Yaish MW, Hannam C, Long N, Clarke JD, Bi YM, Rothstein SJ (2011). *GNC* and *CGA1* modulate chlorophyll biosynthesis and glutamate synthase (*GLU1/FD-GOGAT*) expression in *Arabidopsis*. *PLoS ONE*, 6 (11): e26765
- Hudson D, Guevara DR, Hand AJ, Xu Z, Hao L, Chen X, Zhu T, Bi YM, Rothstein SJ (2013). Rice cytokinin GATA transcription Factor1 regulates chloroplast development and plant architecture. *Plant Physiol*, 162 (1): 132–144
- Jeong MJ, Shih MC (2003). Interaction of a GATA factor with *cis*-acting elements involved in light regulation of nuclear genes encoding chloroplast glyceraldehyde-3-phosphate dehydrogenase in *Arabidopsis*. *Biochem Biophys Res Commun*, 300 (2): 555–562
- Kane, M, Horiguchi, G, Tsukaya H (2012). Stable establishment of cotyledon identity during embryogenesis in *Arabidopsis* by *ANGUSTIFOLIA3* and *HANABA TARANU*. *Development*, 139 (13): 2436–2446
- Kawoosa T, Gahlan P, Devi AS, Kumar S (2014). The GATA and SORLIP motifs in the 3-hydroxy-3-methylglutaryl-CoA reductase promoter of *Picrorhiza kurrooa* for the control of light-mediated expression. *Funct Integr Genomics*, 14 (1): 191–203
- Kepinski S, Leyser O (2005). The *Arabidopsis* F-box protein TIR1 is an auxin receptor. *Nature*, 435 (7041): 446–451
- Klermund C, Ranftl QL, Diener J, Bastakis E, Richter R, Schwechheimer C (2016). LLM-domain B-GATA transcription factors

- promote stomatal development downstream of light signaling pathways in *Arabidopsis thaliana* hypocotyls. *Plant Cell*, 28 (3): 646–660
- Köllmer I, Werner T, Schmülling T (2011). Ectopic expression of different cytokinin-regulated transcription factor genes of *Arabidopsis thaliana* alters plant growth and development. *J Plant Physiol*, 168 (12): 1320–1327
- Korasick DA, Westfall CS, Lee SG, Nanao MH, Dumas R, Hagen G, Guilfoyle TJ, Jez JM, Strader LC (2014). Molecular basis for AUXIN RESPONSE FACTOR protein interaction and the control of auxin response repression. *Proc Natl Acad Sci USA*, 111 (14): 5427–5432
- Lee J, Lee I (2010). Regulation and function of SOC1, a flowering pathway integrator. *J Exp Bot*, 61 (9): 2247–2254
- Li Y, Xu J, Haq NU, Zhang H, Zhu XG (2014). Was low CO₂ a driving force of C₄ evolution: *Arabidopsis* responses to long-term low CO₂ stress. *J Exp Bot*, 65 (13): 3657–3667
- Liu PP, Koizuka N, Martin RC, Nonogaki H (2005). The BME3 (*Blue Micropylar End 3*) GATA zinc finger transcription factor is a positive regulator of *Arabidopsis* seed germination. *Plant J*, 44 (6): 960–971
- Luo XM, Lin WH, Zhu S, Zhu JY, Sun Y, Fan XY, Cheng M, Hao Y, Oh E, Tian M, et al (2010). Integration of light- and brassinosteroid-signaling pathways by a GATA transcription factor in *Arabidopsis*. *Dev Cell*, 19 (6): 872–883
- Manfield IW, Devlin PF, Jen C, Westhead DR, Gilman PM (2007). Conservation, convergence, and divergence of light-responsive, circadian-regulated, and tissue-specific expression patterns during evolution of the *Arabidopsis* GATA gene family. *Plant Physiol*, 143 (2): 941–958
- Mara CD, Irish VF (2008). Two GATA transcription factors are downstream effectors of floral homeotic gene action in *Arabidopsis*. *Plant Physiol*, 147 (2): 707–718
- Martin J, Storgaard M, Andersen CH, Nielsen KK (2004). Photoperiodic regulation of flowering in perennial ryegrass involving a CONSTANS-like homolog. *Plant Mol Biol*, 56 (2): 159–169
- Meyer LJ, Gao J, Xu D, Thelen JJ (2012). Phosphoproteomic analysis of seed maturation in *Arabidopsis*, rapeseed, and soybean. *Plant Physiol*, 159 (1): 517–528
- Monte E, Tepperman JM, Al-Sady B, Kaczorowski KA, Alonso JM, Ecker JR, Li X, Zhang Y, Quail PH (2004). The phytochrome-interacting transcription factor, PIF3, acts early, selectively, and positively in light-induced chloroplast development. *Proc Natl Acad Sci USA*, 101 (46): 16091–16098
- Naito T, Kiba T, Koizumi N, Yamashino T, Mizuno T (2007). Characterization of a unique GATA family gene that responds to both light and cytokinin in *Arabidopsis thaliana*. *Biosci Biotechnol Biochem*, 71 (6): 1557–1560
- Neff MM (2012). Light-mediated seed germination: connecting phytochrome B to gibberellin acid. *Dev Cell*, 22 (4): 687–688
- Nemoto Y, Kisaka M, Fuse T, Yano M, Ogiwara Y (2003). Characterization and functional analysis of three wheat genes with homology to the CONSTANS flowering time gene in transgenic rice. *Plant J*, 36 (1): 82–93
- Peng FY, Weselake RJ (2011). Gene coexpression clusters and putative regulatory elements underlying seed storage reserve accumulation in *Arabidopsis*. *BMC Genom*, 12: 286
- Peng X, Wu Q, Teng L, Tang F, Pi Z, Shen S (2015). Transcriptional regulation of the paper mulberry under cold stress as revealed by a comprehensive analysis of transcription factors. *BMC Plant Biol*, 15: 108
- Putterill J, Robson F, Lee K, Simon R, Coupland G (1995). The CONSTANS gene of *arabidopsis* promotes flowering and encodes a protein showing similarities to zinc finger transcription factors. *Cell*, 80 (6): 847–857
- Ranftl QL, Bastakis E, Klermund C, Schwechheimer C (2016). LLM-domain containing B-GATA factors control different aspects of cytokinin-regulated development in *Arabidopsis thaliana*. *Plant Physiol*, 170 (4): 2295–2311
- Reyes JC, Muro-Pastor MI, Florencio FJ (2004). The GATA family of transcription factors in *Arabidopsis* and rice. *Plant Physiol*, 134 (4): 1718–1732
- Richter R, Bastakis E, Schwechheimer C (2013a). Cross-repressive interactions between SOC1 and the GATAs GNC and GNL/CGA1 in the control of greening, cold tolerance, and flowering time in *Arabidopsis*. *Plant Physiol*, 162 (4): 1992–2004
- Richter R, Behringer C, Müller IK, Schwechheimer C (2010). The GATA-type transcription factors GNC and GNL/CGA1 repress gibberellin signaling downstream from DELLA proteins and PHYTOCHROME-INTERACTING FACTORS. *Genes Dev*, 24 (18): 2093–2104
- Richter R, Behringer C, Zourelidou M, Schwechheimer C (2013b). Convergence of auxin and gibberellin signaling on the regulation of the GATA transcription factors GNC and GNL in *Arabidopsis thaliana*. *Proc Natl Acad Sci USA*, 110 (32): 13192–13197
- Sablowski R (2015). Control of patterning, growth, and differentiation by floral organ identity genes. *J Exp Bot*, 66 (4): 1065–1073
- Shaikhali J, de Dios Barajas-López J, Ötvös K, Kremnev D, Garcia AS, Srivastava V, Wingsle G, Bako L, Strand Å (2012). The CRYPTOCHROME1-dependent response to excess light is mediated through the transcriptional activators ZINC FINGER PROTEIN EXPRESSED IN INFLORESCENCE MERISTEM LIKE1 and ZML2 in *Arabidopsis*. *Plant Cell*, 24 (7): 3009–3025
- Shikata M, Matsuda Y, Ando K, Nishii A, Takemura M, Yokota A, Kohchi T (2004). Characterization of *Arabidopsis ZIM*, a member of a novel plant-specific GATA factor gene family. *J Exp Bot*, 55 (397): 631–639
- Song J, Yamamoto K, Shomura A, Itadani H, Zhong HS, Yano M, Sasaki T (1998). Isolation and mapping of a family of putative zinc-finger protein cDNAs from rice. *DNA Res*, 5 (2): 95–101
- Sugimoto K, Takeda S, Hirochika H (2003). Transcriptional activation mediated by binding of a plant GATA-type zinc finger protein AGP1 to the AG-motif (AGATCCAA) of the wound-inducible *Myb* gene *NtMyb2*. *Plant J*, 36 (4): 550–564
- Takacs EM, Li J, Du C, Ponnala L, Janick-Buckner D, Yu J, Muehlbauer GJ, Schnable PS, Timmermans MCP, Sun Q, et al (2012). Ontogeny of the maize shoot apical meristem. *Plant Cell*, 24 (8): 3219–3234

- Teakle GR, Manfield IW, Graham JF, Gilmartin PM (2002). *Arabidopsis thaliana* GATA factors: organisation, expression and DNA-binding characteristics. *Plant Mol Biol*, 50 (1): 43–57
- Terzaghi WB, Cashmore AR (1995). Light-regulated transcription. *Annu Rev Plant Physiol*, 46 (4): 445–474
- Wang F, Zhu D, Huang X, Li S, Gong Y, Yao Q, Fu X, Fan LM, Deng XW (2009). Biochemical insights on degradation of *Arabidopsis* DELLA proteins gained from a cell-free assay system. *Plant Cell*, 21 (8): 2378–2390
- Wang L, Yin H, Qian Q, Yang J, Huang C, Hu X, Luo D (2009). NECK LEAF 1, a GATA type transcription factor, modulates organogenesis by regulating the expression of multiple regulatory genes during reproductive development in rice. *Cell Res*, 19 (5): 598–611
- Weiss D, Ori N (2007). Mechanisms of cross talk between gibberellin and other hormones. *Plant Physiol*, 144 (3): 1240–1246
- Wen W, Deng Q, Jia H, Wei L, Wei J, Wan H, Yang L, Cao W, Ma Z (2013). Sequence variations of the partially dominant della gene *Rht-B1c* in wheat and their functional impacts. *J Exp Bot*, 64 (11): 3299–3312
- Weng L, Bai X, Zhao F, Li R, Xiao H (2016). Manipulation of flowering time and branching by overexpression of the tomato transcription factor *SIZFP2*. *Plant Biotechnol J*, doi: 10.1111/pbi.12584
- Whipple CJ, Hall DH, DeBlasio S, Taguchi-Shiobara F, Schmidt RJ, Jackson DP (2010). A conserved mechanism of bract suppression in the grass family. *Plant Cell*, 22 (3): 565–578
- Ye H, Du H, Tang N, Li X, Xiong L (2009). Identification and expression profiling analysis of *TIFY* family genes involved in stress and phytohormone responses in rice. *Plant Mol Biol*, 71 (3): 291–305
- Zhan J, Thakare D, Ma C, Lloyd A, Nixon NM, Arakaki AM, Burnett WJ, Logan KO, Wang D, Wang X, et al (2015). RNA sequencing of laser-capture microdissected compartments of the maize kernel identifies regulatory modules associated with endosperm cell differentiation. *Plant Cell*, 27 (3): 513–531
- Zhang C, Hou Y, Hao Q, Chen H, Chen L, Yuan S, Shan Z, Zhang X, Yang Z, Qiu D, et al (2015). Genome-wide survey of the soybean GATA transcription factor gene family and expression analysis under low nitrogen stress. *PLoS ONE*, 10 (4): e0125174
- Zhang X, Zhou Y, Ding L, Wu Z, Liu R, Meyerowitz EM (2013). Transcription repressor HANABA TARANU controls flower development by integrating the actions of multiple hormones, floral organ specification genes, and GATA3 family genes in *Arabidopsis*. *Plant Cell*, 25 (1): 83–101
- Zhao Y, Medrano L, Ohashi K, Fletcher JC, Yu H, Sakai H, Meyerowitz EM (2004). HANABA TARANU is a GATA transcription factor that regulates shoot apical meristem and flower development in *Arabidopsis*. *Plant Cell*, 16 (10): 2586–2600

Advances in regulation of GATA transcription factor to plant development and stress responses

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Abstract: Plant GATA transcription factors (TFs) can activate or inhibit downstream target genes normally by recognizing the consensus sequence of WGATAR in the promoter region, which then contributes to regulation of plant development. So far, a variety of GATA TFs have been identified and characterized from *Arabidopsis*, rice, soybean, etc. Twenty-nine GATA TFs from *Arabidopsis* are classified into four subfamilies (A, B, C and D) based on their sequence similarity and exon-intron structures, which consists of fourteen, ten, three or two GATA TF members, respectively. GATA TFs play vital functions in regulating various physiological processes in seed, root, floral and chloroplast development, and also response to different stresses, e.g. drought, high temperature and cold. In this review, we summarized the structure, function and regulation of GATA TFs in plant development, which may provide insight for further study in this field.

Key words: GATA transcription factors; structural characteristic; biological functions; expression and regulation

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