



· 专题论坛 ·

AP2/ERF转录因子调控植物非生物胁迫响应研究进展

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摘要 低温、干旱、高盐和缺氧等多种不良环境影响植物的生长发育, 植物通过长期进化形成复杂的调节机制来适应这些不利条件。AP2/ERF是植物特有的转录因子, 在各种胁迫响应过程中发挥关键调控作用。近年来, 越来越多的研究表明, 植物激素介导的信号级联通路与逆境胁迫响应关系密切, AP2/ERF转录因子可与激素信号转导协同形成交叉调控网络。许多AP2/ERF转录因子通过响应植物激素脱落酸和乙烯, 激活依赖或不依赖于脱落酸和乙烯的胁迫响应基因的表达。此外, AP2/ERF转录因子参与赤霉素、细胞分裂素和油菜素内酯介导的生长发育和胁迫应答。该文简要综述了AP2/ERF转录因子的结构特征、转录调控、翻译后修饰、结合位点、协同互作蛋白及其参与调控依赖或不依赖激素信号转导途径的非生物胁迫响应研究进展, 为解析不同AP2/ERF转录因子在调控激素和胁迫响应网络中的作用提供理论依据。

关键词 AP2/ERF转录因子, 激素, 非生物胁迫, 调控

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植物在生长发育过程中经常受到生物或非生物胁迫的影响, 由此, 植物逐渐形成了复杂的调节机制感知胁迫信号, 对外部环境变化做出快速响应(郭倩倩和周文彬, 2019)。脱落酸(abscisic acid, ABA)、乙烯(ethylene, ET)及赤霉素(gibberellin, GA)等激素作为信号分子能够调节植物的生长发育、形态建成以及抗逆反应等生物学过程。该过程也受转录因子(transcription factor, TF)调控, 即转录因子通过依赖或不依赖于激素介导的信号通路参与调控植物对于干旱、低温、缺氧、高盐和淹水等非生物胁迫的响应, 进而影响植物的逆境耐受能力(Gibbs et al., 2015; Verma et al., 2016; Li et al., 2018)。AP2/ERF (APETALA2/ethylene responsive factor)是植物特有的转录因子家族之一, 已在拟南芥(*Arabidopsis thaliana*)、水稻(*Oryza sativa*)、高粱(*Sorghum bicolor*)、大白菜(*Brassica pekinensis*)、毛竹(*Phyllostachys edulis*)、玉米(*Zea mays*)、大麦(*Hordeum vulgare*)和小麦(*Triticum aestivum*)等物种中被成功分离鉴定(Xu

and Chua, 2011; Chandler, 2018)。通过突变体实验, 科学家发现了许多与AP2/ERF相关的非生物胁迫或激素信号应答基因。目前, AP2/ERF已成为研究非生物胁迫和激素互作的热点候选基因。本文从AP2/ERF转录因子的结构特征、转录调控、翻译后修饰、结合位点、协同互作蛋白以及其参与调控依赖或不依赖激素信号途径的非生物胁迫响应进行综述, 为进一步阐明AP2/ERF转录因子在非生物胁迫调控网络中的作用提供理论依据。

1 AP2/ERF转录因子的结构特征和分类

AP2/ERF转录因子具有独特的结构特征, 其由DNA结合域(DNA-binding domain)、转录调控域(transcription regulation domain)、寡聚化位点(oligomerization site)和核定位信号(nuclear localization signal, NLS) 4个主要功能区组成, 并以高度保守的AP2/ERF结合域而得名(Sakuma et al., 2002)。通常情况下, AP2/ERF转录因子至少含有1个AP2结构域的

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DNA结合区,该结构域包含60–70个氨基酸残基,按照3个 β 折叠和1个 α 螺旋方式形成典型的三维结构(Nakano et al., 2006; Abiri et al., 2017)。根据包含的AP2/ERF结构域数量和结合序列特点,可将AP2/ERF家族分为AP2 (APETALA2)、RAV (related to ABI3/VP1)、脱水反应元件结合蛋白(dehydration-responsive element binding protein, DREB) (A1–A6亚组)、乙烯应答因子(ethylene-responsive factor, ERF) (V–X亚组)和Soloist五个亚族(Nakano et al., 2006; Licausi et al., 2013)。其中,对AP2、DREB和ERF的研究较为广泛和深入,而有关Soloist亚族的研究报道极少,已知其核苷酸序列在多数植物中高度保守(Sun et al., 2016)。

2 AP2/ERF转录因子的结合位点

AP2/ERF转录因子通过特异性结合胁迫应答基因启动子区顺式元件,参与调控植物的逆境防御反应。DREB亚族成员特异性识别并结合启动子区域的DRE/CRT (dehydration responsive element/C-repeat)元件(核心序列A/GCCGAC),诱导干旱、低温和盐胁迫相关应答基因的表达。ERF亚族成员则可通过与乙烯响应元件(ethylene response element, ERE) (核心序列AGCCGCC, 又称GCC-box)结合,从而参与调控乙烯应答和非生物胁迫(Franco-Zorrilla et al., 2014)。此外,研究发现许多AP2/ERF转录因子可同时与DRE/CRT和ERE两种元件结合,如DREB亚族成员TINY、CBF1、ERF53、RAP2.4、TG/RAP2.4a以及ERF亚族成员ERF1、ERF4和ERF71 (Chen et al., 2012; Zhu et al., 2014; Lee et al., 2015),但结合能力有差异。在拟南芥中,DREB2C和DEAR3与类GCC-box元件(GCCGCC)的结合能力远超DRE元件(Franco-Zorrilla et al., 2014)。AP2/ERF转录因子还能与DRE和ERE之外的顺式元件结合,如偶联元件1 (CE1, TGCCACCG)、类偶联元件3 (CE-3like, CGCG)和缺氧响应启动子元件(hypoxia-responsive promoter element, HRPE),以及ATCTA、CAACA、CATGCA、CAA/CA/CTG、ATCGAG和(NC/GT)CGNCCA (Bossi et al., 2009; Zhu et al., 2010; Chen et al., 2016; Gasch et al., 2016; Park et al., 2016)。近年来,科学家通过蛋白质结合微阵列(protein binding microarray, PBM)技术发现结构特征高

度相似的转录因子具有相似的DNA结合位点,同时也具有相似的生物学功能。该研究结果合理地解释了转录因子功能冗余现象,也为预测和挖掘未知AP2/ERF转录因子提供了高效可行的技术方法(Franco-Zorrilla et al., 2014)。

3 AP2/ERFs的转录调控、翻译后修饰及协同互作蛋白

3.1 AP2/ERFs的转录调控

正常环境下,AP2/ERF转录因子表达水平较低,激素或逆境胁迫相关基因与AP2/ERF转录因子保守的顺式作用元件结合,进而调控其表达(Owji et al., 2017)。研究表明,拟南芥*DREB1A/CBF3*、*DREB1C/CBF2*、*DREB2C*、*DREB2G*和*DEAR3*的启动子中包含较多的热激元件(heat shock element, HSE)、低温响应(low temperature responsive, LTR)、脱落酸响应(ABA responsive element, ABRE)等顺式作用元件(Sazegari et al., 2015)。热激因子1 (heat shock factor 1, HSF1)、脱落酸响应结合蛋白(ABA responsive element binding protein/ABRE binding factors, AREB/ABF)可分别与*DREB2A*启动子中的热激应答和ABA响应元件结合,调控其表达,进而改变植物胁迫的耐受性(Kim et al., 2011; Liu et al., 2011)。蛋白磷酸酶2C (type 2C protein phosphatase, PP2C)包含2个以上的ABRE元件,AREB1、AREB2和ABF3协同正调控*AHG1*、*AHG3*、*HAI1*及*HAI2*等PP2Cs基因表达(Yoshida et al., 2010)。此外,越来越多的研究证明ET信号通路参与拟南芥盐胁迫反应。进一步分析表明,ESE1 (ethylene and salt-inducible ERF1)在EIN3/EIL1下游调节ET响应基因。EIN3 (ethylene insensitive 3)可与ESE1启动子结合形成EIN3-ESE1转录复合体,继而调控*RD29A*和*COR15A*等基因的表达(Zhang et al., 2011)。磷酸化、泛素化、甲基化和乙酰化等组蛋白修饰方式通过调控染色质开放或封闭的空间状态,激活或抑制AP2/ERF转录(Pflüger and Wagner, 2007)。组蛋白去乙酰化酶(histone deacetylase, HDAC)和聚乙二醇(PEG)促进*DREB1*基因启动子区乙酰化,增强*DREB1*基因的表达(Zhang et al., 2018)。非生物胁迫下,组蛋白变体和组蛋白修饰状态也可发生改变,并

可遗传到下一代(Asensii-Fabado et al., 2017)。miRNA介导的RNA沉默和翻译抑制在AP2/ERF表达调控中也发挥重要作用。研究发现miRNA172靶向拟南芥AP2mRNA并抑制其翻译,而miRNA156和miRNA838两者也具有类似调节AP2/ERF的功能(Kavas et al., 2015)。此外,在拟南芥、水稻及玉米中还发现通过可变剪切产生的OsDREB2A/2B、ZmDREB2A、WDREB2以及HvDRF1等多种AP2/-ERF功能异构体(Matsukura et al., 2010)。

3.2 AP2/ERFs翻译后修饰

翻译后修饰(post-translational modification, PTM)是蛋白质合成途径的后期加工过程,不同的修饰方式对AP2/ERF蛋白的活性、稳定性和丰度的影响有差异。磷酸化是转录因子的主要修饰途径之一,磷酸化水平与下游靶基因的表达水平关系密切。拟南芥ABA信号通路的正调控因子蔗糖非酵解型蛋白激酶(Snf1-related protein kinases, SnRKs)可磷酸化RAV1,进而抑制RAV1的转录阻遏效应(Feng et al., 2014),而ERF104和ERF6可被后MPK3/6 (mitogen-activated protein kinase 3/6)磷酸化修饰,并在下游级联反应中发挥重要作用,调控植物对病原体的免疫反应(Meng et al., 2013)。DREB2A是拟南芥的关键转录激活因子,在其中央序列存在一个负调控域(negative regulatory domain, NRD)。热胁迫条件下, NRD中的Ser/Thr残基磷酸化水平降低, DREB2A蛋白稳定性提高,敲除NRD后DREB2A呈组成型激活,表明抑制NRD磷酸化可以稳定和激活DREB2A的表达,从而增强植物的耐热性(Mizoi et al., 2019)。泛素介导的蛋白质降解(26S蛋白酶体途径)也参与调节AP2/ERF蛋白的稳定性。非生物胁迫条件下, DREB2A和ERF75/RAP-2.2蛋白分别被RING家族E3泛素连接酶DRIP1/2 (DREB2A-interacting protein1/2)和SIN-AT2 (seven in absentia of *Arabidopsis* 2)直接泛素化(Cheng et al., 2012; Papdi et al., 2015)。研究发现CUL3-E3连接酶适配子BPMs (BTB/POZ and math domain)可与DREB2A蛋白的负调控域NRD在核内发生互作,敲除BPM增加DREB2A蛋白的积累,促进下游靶基因的表达,提高植株的耐热和耐旱能力,这也说明BPM对DREB2A蛋白的稳定性起负调控作用(Morimoto et al., 2017)。此外,研究发现ERF-VII类

蛋白可在质膜上与乙酰辅基A结合蛋白(Acyl-CoA binding protein, ACBP)互作。在缺氧条件下, RAP2.12与ACBP分离后进入细胞核,在脱酰胺基和精氨酰基化的作用下通过氧依赖途径移除ERF72/RAP2.3、ERF74/RAP2.12蛋白的甲硫氨酸N末端,将半胱氨酸氧化成半胱亚磺酸,引发蛋白快速降解并暴露出非稳定N端的氨基酸残基(Gibbs et al., 2015; Abbas et al., 2015)。

3.3 AP2/ERFs的协同互作蛋白

许多研究表明, AP2/ERF转录因子可直接与靶基因启动子结合,激活或抑制下游靶基因的表达,其N端DNA结合域和C端转录激活域在胁迫相关靶基因的转录激活中起重要作用(Nakano et al., 2006)。进一步分析表明, AP2/ERF转录因子中含有EAR基序(LxLxL或DLNxxP)、TLLLFR基序和BRD结构域(B3 repression domain, 保守序列为R/KLFGV)等多个转录抑制结构域(Ikeda and Ohme-Takagi, 2009; Kagale and Rozwadowski, 2011; Deepika et al., 2016)。含EAR基序的转录因子是一种重要的抑制子,在植物非生物胁迫应答基因的诱导表达中起负调控作用。Tiwari等(2012)从拟南芥ERF和AP2亚族中发现了一种转录激活关键元件EDLL, EDLL可与EAR基序(ERF-associated amphiphilic repression)发生互作,拮抗后者介导的转录抑制作用。而不同的AP2/ERF转录因子也可协同招募TPL (topless)和TPR (topless-related)等转录共抑制子(Causier et al., 2012)或组蛋白修饰因子,进而抑制下游靶基因的表达(Song et al., 2005; Song and Galbraith, 2006)。Song等(2005)发现AtERF7特异性地结合GCC-box,与抑制因子ATSIN3及组蛋白去乙酰化酶19 (histone deacetylase 19, HDA19)发生互作并形成转录因子复合物,参与干旱胁迫和ABA响应调控。AtERF7过表达株系保卫细胞对ABA的敏感性减弱,水分散失增加;反之, AtERF7 RNA干扰系对ABA的敏感性增强。类似的, ERF3能与组蛋白去乙酰化酶复合物亚基SAP18 (SIN3 associated polypeptide P18)互作,共同招募HDA19形成复合体,进而抑制相关基因的表达(Song and Galbraith, 2006)。BRD结构域被认为是RAV1和RAV2转录因子行使抑制功能的关键元件,其保守序列中第1位氨基酸残基多为疏水性亮氨酸、

缬氨酸和蛋氨酸残基, 突变导致功能丧失(Ikeda and Ohme-Takagi, 2009)。研究显示, 与AP2/ERFs协同调控的基因同样可被AP2/ERFs靶基因富集, 分析此类基因的同源基序有助于识别转录因子的假定靶基因并预测其生物学功能(Franco-Zorrilla et al., 2014)。

4 AP2/ERF调控非生物胁迫响应

AP2/ERF转录因子在参与调控植物应对冷、干旱、高温、高盐及缺氧等多种非生物胁迫过程中具有重要功能(Licausi et al., 2013)。其中, DREB和ERF亚家族

成员在植物非生物逆境应答中起重要调控作用。研究表明其参与调控的植物环境胁迫应答信号网络比较复杂。胁迫条件下, 部分AP2/ERFs可被快速持续地诱导表达, 而其它进程的响应较为缓慢, 说明可能存在依赖或不依赖于激素信号途径2种胁迫响应模式, 且两者之间存在一定的交叉互作(Van den Broeck et al., 2017)。前人的研究也证明, AP2/ERFs广泛参与调控ABA、ET、GA、细胞分裂素(cytokinin, CTK)和油菜素内酯(brassinolide, BR)等植物激素介导的胁迫响应(Colebrook et al., 2014; Kazan et al., 2015; Tao et al., 2015; Sah et al., 2016; Nolan et al., 2017) (图1)。

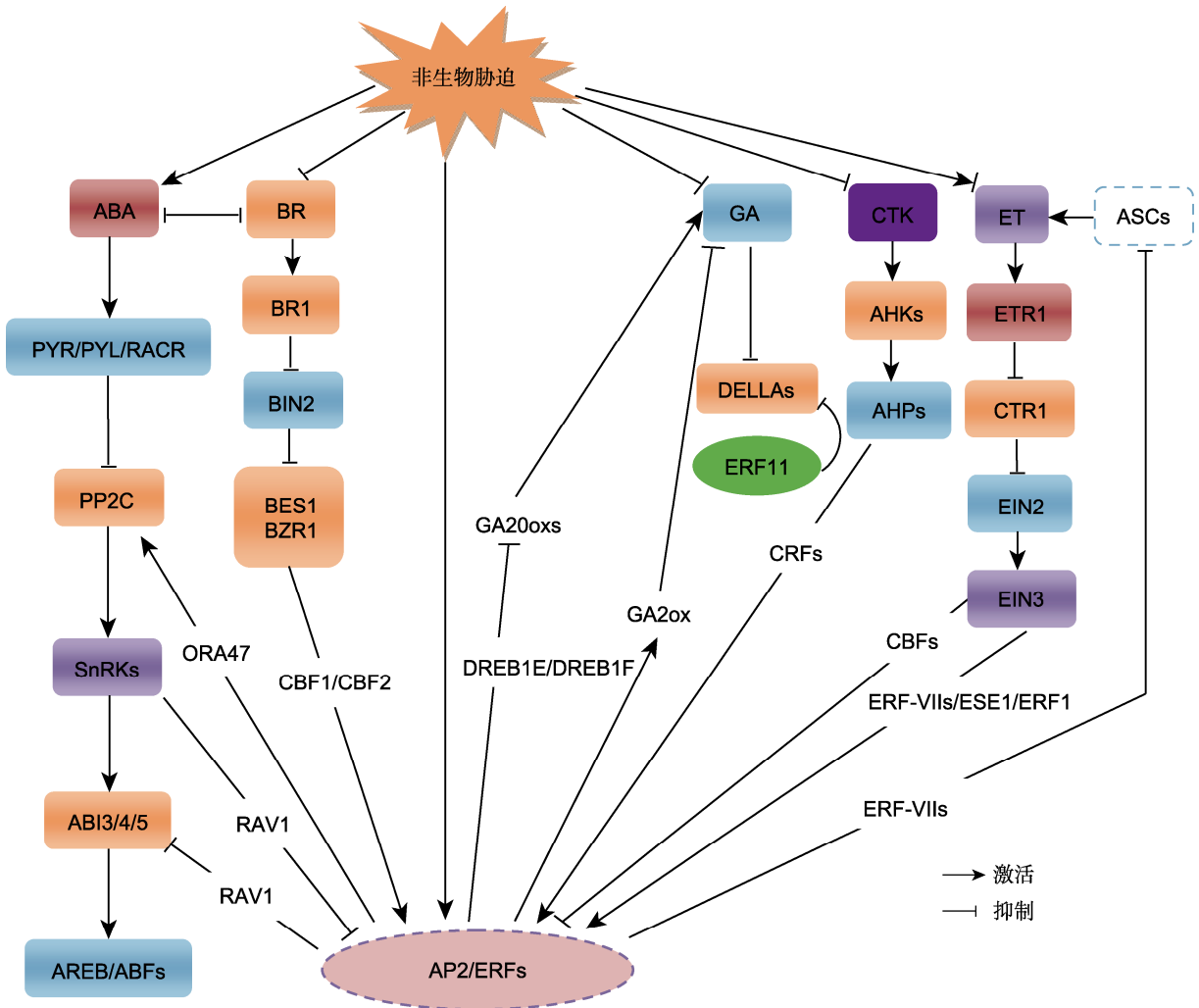


图1 AP2/ERF转录因子参与调控激素介导的非生物胁迫响应网络

ABA: 脱落酸; BR: 油菜素内酯; GA: 赤霉素; CTK: 细胞分裂素; ET: 乙烯

Figure 1 AP2/ERF transcription factors are involved in regulating hormone-mediated response networks during abiotic stress
ABA: Absciscic acid; BR: Brassinolide; GA: Gibberellin; CTK: Cytokinin; ET: Ethylene

4.1 通过不依赖于激素信号的途径调控非生物胁迫响应

4.1.1 DREB亚族参与调控冷、热、干旱和盐胁迫

DREB是AP2/ERF家族的主要亚族之一,参与多种非生物胁迫的协同或拮抗调控,在植物响应冷、热、干旱和高盐等多种胁迫过程中发挥关键作用。

CBFs (C-repeat binding factors)转录因子属于DREB亚族A1亚组成员。近年来,科学家聚焦CBF参与植物冷信号途径的分子调控机制,对其进行了深入系统的研究(Zhou et al., 2011; Yamasaki and Randall, 2016; Shi et al., 2018)。冷胁迫下,植物通过其它通路将冷信号间接传递给CBF基因(Park et al., 2015)。ICE1/2 (inducer of CBF expression 1/2)、CAMTA1/3 (calmodulin-binding transcription activator 1/3)、MYB15 (myeloblastosis 15)、EIN3 (ethylene insensitive 3)、BZR1 (brassica-zole-resistant 1)、SOC1 (suppressor of overexpression of constans 1)、CCA1 (circadian clock associated 1)、LHY (late elongated hypocotyl)及PIF3/4/7 (phytochrome-interacting factor3/4/7)等关键转录调节因子则通过协同或拮抗作用参与CBF基因转录水平的调控(刘静妍等, 2017)。ICE作为CBF冷信号途径中第1个被鉴定的正调控因子,在CBF基因的表达调控网络中发挥重要作用(Park et al., 2015; Jia et al., 2016; Shi et al., 2018)。而ICE1自身也受HOS1 (high osmotic expression 1)介导的泛素化、SIZ1 (SAP and Miz 1)介导的SUMO化和OST1 (open stomata 1)介导的磷酸化修饰,以及MYB15、JAZ (jasmonate ZIM-domain)转录抑制子协同或拮抗作用的精细调控(Chinnusamy et al., 2007; Qin et al., 2011; Zhou et al., 2011)。目前,关于ICE-CBF-COR冷信号途径研究最为深入。低温胁迫下,ICE与CBF共建冷胁迫调控通路,ICE特异性地结合CBF3启动子中的MYC结合位点CANNTG (Agarwal et al., 2006),正调控CBF3基因的表达(Liu et al., 2018a)。而CBF1的表达则受ICE1的同源基因ICE2调控,超量表达ICE2促进CBF1的表达,但CBF2的表达受CBF1和CBF3负调控,其是否受ICE1或ICE2的调控仍未见实验证明(Zhao and Zhu, 2016)。CBFs通过结合COR (cold regulated)、LTI (low-temperature induced)、RD (responsive to dehydration)及DHN (dehydrin)等冷

应答基因启动子区域的DRE/CRT顺式作用元件,激活此类基因的表达,进而增强植物的耐冷性(Zhou et al., 2011; Mizoi et al., 2012; Licausi et al., 2013)。利用RNA-seq技术对cbf突变体进行分析,结果显示CBF突变影响全转录组水平上约10%–25%的COR基因表达(Jia et al., 2016; Zhao et al., 2016)。在拟南芥cbf突变体和过表达株系中,低温均可快速激活CBF1、CBF2和CBF3的转录活性,识别并结合下游基因启动子中的CRT/DRE顺式元件,调控冷诱导相关基因的表达(Park et al., 2015)。与野生型相比,敲除CBF1和CBF3使拟南芥植株的抗冻能力降低60% (Novillo et al., 2007)。

部分A5亚组DREB类转录因子则对上述调控网络具有负反馈调节作用。DEAR1 (DREB and EAR motif protein 1)可能既在CBF上游作用,又与RAP2.1在CBF下游扮演冷胁迫响应的调节子,调节RD29A/COR78、COR15A和KIN1等冷诱导相关基因的表达,负调控植物的耐冷和耐旱性(Fowler and Thomashow, 2002; Tsutsui et al., 2009; Dong and Liu, 2010)。DEAR1过表达抑制冷诱导CBF的表达,进而降低植物的耐冷能力(Tsutsui et al., 2009)。低温胁迫或组成型表达CBF可诱导RAP2.1的表达,CBF2比RAP2.1对低温更为敏感(Dong and Liu, 2010)。在CBF调控通路中,DEAR1和RAP2.1如何整合还需深入研究。RAP2.1是否与其它DEAR转录因子共同调节植物非生物胁迫响应仍不清楚。研究发现DREB-A5亚组有6种含EAR基序的转录抑制子可与DRE元件结合,进而调控非生物胁迫响应基因的表达(Nakano et al., 2006)。

DREB-A2亚组转录因子DREB2主要参与调节植物的抗旱和耐热性(Mizoi et al., 2012)。干旱和高温可诱导DREB2基因的表达,进而正向调控下游干旱或热胁迫响应基因(Maruyama et al., 2009)。研究表明DREB-A4家族成员HRD (hardy)和DREB-A6家族成员(ERF53、RAP2.4和TG/RAP2.4a)也在干旱和耐盐性调控中发挥关键作用(Karaba et al., 2007; Lin et al., 2008; Chen et al., 2012; Zhu et al., 2014)。过表达HRD能显著增强拟南芥和水稻植株的耐旱和耐盐性(Karaba et al., 2007)。同样,过表达TG (translucent green)导致植株叶片玻璃化,叶片细胞含水量增加(Zhu et al., 2014)。TG也参与调控抗坏血酸过氧

化酶基因*APX* (*ascorbate peroxidase*)的表达,抵御活性氧(reactive oxygen species, ROS)引起的光氧化胁迫(Rudnik et al., 2017)。除拟南芥外,人们对水稻、玉米、番茄(*Lycopersicon esculentum*)、葡萄(*Vitis vinifera*)等作物的DREB1和DREB2转录因子也进行了广泛的研究(Xiao et al., 2006; Matsukura et al., 2010; Dou et al., 2014)。

4.1.2 ERF、AP2和RAV亚族调控冷、缺氧和盐胁迫

近年来,有关ERF亚族参与非生物胁迫响应的研究越来越多。在拟南芥中发现多种非生物胁迫可诱导细胞分裂素应答因子(cytokinin response factor, CRF)的表达,CRF是ERF-VI亚族成员之一,具有正向调节植物渗透胁迫耐受性和抗冻性作用(Rashotte et al., 2006)。CRF2和CRF6可与生长素外输载体PIN (PIN-FORMED)基因启动子区的特定元件结合,正向调控PIN基因的表达,这在CRF超表达和缺失突变体研究中得到了验证(Kim, 2016)。CRF2和CRF3均参与调控冷胁迫下拟南芥侧根(lateral root, LR)的发育,crf2、crf3、crf2/crf3突变体在冷胁迫下侧根密度比野生型植株更低,CRF2或CRF3过表达均可促进植株侧根密度的增加(Jeon et al., 2016)。冷胁迫可诱导CRF2的表达,因此CRF2可能通过诱导PIN1和PIN7的表达以弥补冷胁迫对侧根发育的影响;而在缺失突变体crf2中,CRF3超表达可减弱冷胁迫对侧根生长的抑制效应,推测CRF3可能通过其它途径参与侧根的发育调控(Jeon et al., 2016; Kim, 2016)。进一步分析显示,CRF2和CRF3分别通过依赖和不依赖于TCS (two-component signaling)的途径响应冷胁迫(Jeon et al., 2016)。CRF4是少数不受CTK调控的CRF转录因子之一,可促进CORs的表达并正向调控植物的冷/冻耐受性(Zwack et al., 2016a)。多种非生物胁迫会诱导植物积累活性氧(ROS),导致细胞损伤,因此植物维持最低水平的活性氧对其生存至关重要。多种胁迫刺激均可诱导CRF6的表达,CRF6可能通过抑制细胞分裂素相关基因的表达介导细胞分裂素与氧化应激反应之间的联系(Zwack et al., 2016b)。CRF6在H₂O₂诱导的氧化胁迫应答中直接或间接抑制ARR6 (type-A response regulator 6)、ARR9、ARR11、LOG7及ABCG14基因的表达。酵母单杂交实验显示,CRF6直接结合到ARR6启动子区,激活ARR6的表

达,而对ARR9、LOG7的表达调控可能需要其它植物特异因子的参与(Zwack et al., 2016b)。

ERF亚族成员在低氧和淹水胁迫响应过程中也发挥重要作用(Bui et al., 2015; Gibbs et al., 2015)。SUB1A (submergence 1A)是ERF亚族B2亚组成员之一,Sub1A-1超表达的同时促进乙醇脱氢酶基因(*alcohol dehydrogenase 1*, *Adh1*)上调表达,抑制Sub1C的转录水平,说明Sub1A-1是耐淹性的主要调节因子,在淹水胁迫应答调控中起关键作用(Xu et al., 2006)。淹水状态下,低水平海藻糖-6-磷酸合酶(trehalose-6-phosphate, T6P)与CIPK15 (CBL-interacting protein kinase 15)协同激活SnRK1, SnRK1介导SUB1A抑制幼苗胚轴生长和呼吸相关基因的表达,直接或间接调控碳同化过程。而SK1/SK2 (snorkel1/2)激活参与叶柄、茎和导管发育相关基因,促进植株快速生长(Hattori et al., 2009; Locke et al., 2018)。缺氧胁迫下,拟南芥ERF-VIIs可以通过氧依赖的N端规则通路降解(Gibbs et al., 2015)。RING (really interesting gene)类蛋白SINAT2可通过其N端保守的C3H4型RING结构域调控RAP2.12,沉默SINAT1/2可上调RAP2.12的表达水平(Papdi et al., 2015)。此外,ERF71/HRE2、ERF72/RAP2.3、ERF73/HRE1、ERF74/RAP2.12及ERF75/RAP2.2d也受缺氧胁迫诱导,进而正向调控糖代谢和激素信号相关的缺氧响应基因,提高植株的缺氧耐受能力。过表达RAP2.2、RAP2.3和RAP2.12可提高植株在低氧和渗透胁迫下的存活率,而rap2.12-2/rap2.3-1双突变体对淹水和渗透胁迫表现出较高的敏感性(Yao et al., 2017)。

RbohD (respiratory burst oxidase homolog D)是一种NADPH氧化酶,催化活性氧产生(Yao et al., 2017)。ROS是细胞生化反应过程中产生的毒性物质,可作为信号分子触发胁迫响应和信号转导,RAPs通过依赖于RbohD的途径调节非生物胁迫(Qi et al., 2018)。erf74和erf74/erf75突变体中,ROS的产生和RbohD基因的表达均受抑制,ERF74和ERF75通过依赖于RbohD的ROS激活途径协同调控缺氧响应。其中,ERF74可结合RbohD基因的启动子并激活其表达,ERF74过表达促进后期ROS清除酶相关基因的表达,说明在胁迫响应过程中ERF74作为分子开关控制RbohD依赖的ROS迸发(Yao et al., 2017)。研究发

现水稻中也存在类似的调控机制, OsLG3通过诱导活性氧清除相关基因*APX1*、*APX4*、*APX8*、*CATB*和*POD1*的表达进而正调控水稻的耐旱性(Xiong et al., 2018)。

RAVs和AP2s除调节茎与根细胞有丝分裂以及开花等发育过程(Osnato et al., 2012; Horstman et al., 2014)外, 还参与调控非生物胁迫响应。干旱和盐胁迫下, 拟南芥*RAV1*、*RAV1L*和*RAV2*的表达水平下降, 但三者对ABA的敏感性不同。进一步研究发现, 野生型、*rav1*突变体和*RAV1*超表达植株中*RD29A*、*RD29B*以及9-顺式环氧类胡萝卜素双加氧酶基因*NCED9* (*nine-cis-epoxycarotenoid dioxygenase*) 和*NCED3*表现出相同的胁迫响应模式(Fu et al., 2014)。Saito等(2004)发现过表达*RAV1*抑制ABA降解基因(*CYP707A1*和*CYP707A2*)的活性。正常条件下, *RAV1*过表达提高了*NCED9*和*NCED3*基因的表达水平, 而受胁迫后植株体内的ABA水平未发生明显变化(Fu et al., 2014)。以上说明*RAV1*可通过不依赖ABA的途径负调控植物的非生物胁迫响应。此外, 研究发现ANT (*AINTEGUMENTA*)控制发育中的根细胞数量和大小, 同时也可抑制类SOS3钙结合蛋白8 (*sos3-like calcium binding protein 8*, *SCABP8*)转录, 负调控耐盐性, 而ANT功能缺失增强了拟南芥幼苗的耐盐能力, 并维持离子稳态(Meng et al., 2015a)。

4.2 与激素转导途径协同调控非生物胁迫响应

4.2.1 参与脱落酸介导的胁迫应答

植物激素是一类调控植物生长发育以及抵御不良环境影响的重要小分子。脱落酸(ABA)是应答干旱、盐、冷、热等非生物胁迫的关键激素之一。ABA可诱导气孔关闭, 调节根系结构, 促进渗透物质的合成, 进而抵御外部逆境(Sah et al., 2016)。NCED是ABA合成的限速酶, 干旱和渗透胁迫诱导*NCED*基因快速上调表达, 促进ABA的生物合成。ABA与其受体PYR/PLY/RCAR结合, 再与PP2C作用形成复合物, 解除PP2C对SnRK2激酶活性的抑制作用。活性形式的SnRK2磷酸化AREB/ABF、离子通道蛋白和NADPH氧化酶等下游底物, 进而诱导ABA响应基因的表达(Finkelstein, 2013; Sah et al., 2016)。

研究表明, 非生物胁迫下ABA可促进ANT (Meng et al., 2015b)、*ERF53* (Hsieh et al., 2013)、*RAP2.6L*

(Liu et al., 2012)和*RAP2.6* (Zhu et al., 2010)转录, 上述转录因子进而结合胁迫应答顺式作用元件DRE/ABRE, 调控下游相关靶基因的表达, 增强植物对非生物胁迫的耐受能力。在水稻中*ERF71*正向调控ABA信号转导, 过表达*ERF71*可促进根中*ABI5*、*PP2C68*、*RAB16C*及*RAB16D*等基因上调表达。此外, *ERF71*可直接调控木质素生物合成基因*CCR1*、*CCR10*及*C4H*转录, 诱导根系径向生长, 改变根系构型, 提高耐旱能力(Lee et al., 2017; Li et al., 2018)。盐胁迫和ABA双重诱导下, ABA增强*DREB2*的转录活性, 进而促进*Rd29A*协同表达(Lee et al., 2016)。

DREB-A3亚组成员ABI4 (ABA insensitive 4)是ABA信号通路的重要组分。植株受到胁迫后, 体内积累ABA和ROS, ABI4可被ABA、ROS及糖质体等多种信号通路靶向调控。CCAAT结合因子A (CCAAT binding factor A, CBFA)是四吡咯化合物HAP (heme activator protein)三聚体转录复合物的亚基, 当产生过量ROS时, ABI4可与其它转录因子竞争性地结合CCACGT元件, 抑制CBFA的表达, 进而调控质体反向信号通路中相关基因的表达(Zhang et al., 2013)。拟南芥突变体实验表明, ABI4在YL1 (*yellow leaf 1*) (Li et al., 2016)和DPG1 (*delayed pale-greening 1*) (Yi et al., 2019)等基因参与盐胁迫响应的调控网络中也发挥重要作用。逆境胁迫下, ORA47在JA (jasmonate acid)和ABA信号转导途径中靶向调节ABA和JA诱导的下游应答基因, *ERF18*/*ORA-47*识别启动子顺式元件(NC/GT)CGNCCA (O-box), 激活PP2C家族ABI2转录因子的表达。ABI1则在ORA-47上游起作用, 从而形成ABI1-ORA47-ABI2正反馈基因表达回路, 调控ABA信号转导和干旱胁迫响应(Chen et al., 2016)。此外, *RAV1*转录因子在ABA信号转导途径中也发挥关键作用, *RAV1*能与*ABI3*、*ABI4*和*ABI5*启动子结合, 其过表达抑制*ABI3*、*ABI4*和*ABI5*的转录活性, 导致根系生长发育过程中对ABA不敏感。同时, 蔗糖非酵解型蛋白激酶(SnRK2.2、SnRK2.3和SnRK2.6)在核内磷酸化*RAV1*, 降低ABI5对*RAV1*的依赖性, 并负调控*RAV1*对靶基因的转录抑制作用(Feng et al., 2014)。

4.2.2 参与乙烯介导的胁迫应答

乙烯(ET)作为五大植物激素之一, 也在盐、低温和淹

水等多种非生物胁迫响应中发挥作用(Kazan, 2015)。ET生物合成受ACC合酶(ACC synthase, ACS)调控, 当ET被其受体ETR1 (ethylene response 1)识别后, CTR1 (constitutive triple response 1)激酶失活, 解除CTR1对EIN2 (ethylene insensitive 2)的抑制作用。然后, EIN2的C端进入细胞核, 激活EIN3以及乙烯调控的转录级联通路中的应答基因(Qiao et al., 2012; Müller and Munné-Bosch, 2015)。

ERF亚家族转录因子是ET介导的胁迫应答信号通路下游的关键调控因子(Licausi et al., 2013; Gibbs et al., 2015; Kazan, 2015; Müller and Munné-Bosch, 2015)。冷胁迫下, 植物体内的ET主要起负调控作用, 过量ET或1-氨基环丙烷-1-羧酸降低植物的耐冷性, 而ET生物合成抑制剂氨基乙氧基甘氨酸或感知拮抗剂Ag⁺具有相反的作用(Shi et al., 2012)。etr1-1、ein4-1、ein2-5、ein3-1和ein3eil突变体表现出更强的耐冷性, 但组成型ET响应etr1-1和ein3过表达植株表现出耐冷性减弱; 冷胁迫诱导ETR1、EIN4、EBF1及EBF2快速上调表达, 而EIN2和EIL1下调表达。进一步分析表明, EIN3通过与启动子区特定元件结合, 抑制ARR5、ARR7、ARR15和CBF转录, ARR5作为冷信号通路的关键节点基因, 在ET和CTK介导的胁迫响应网络中起着关键作用, 过表达ARRs使植株的耐冷能力增强(Shi et al., 2012)。此外, EIN3可激活ERF1和ESEs, 进而参与调控下游胁迫相关基因, 提高植物的耐盐性(Kazan, 2015; Tao et al., 2015)。35S::AtERF4-GFP转基因植株中ABI2、RD29B和RAP18的表达受抑制, 进一步说明AtERF4是ET和ABA信号途径的负调控因子(Yang et al., 2011)。

此外, ET促进RAP2.3转录因子定位于细胞核内, 通过依赖于RAP2.3的方式激发ORA59介导的ET响应过程(Kim et al., 2018)。而ERF-VIIs通过ET不依赖途径参与调控缺氧响应。在ET不敏感突变体或生物合成抑制剂存在的情况下, 缺氧依然可以诱导ERF73/HRE1的表达, ERF-VIIs也可能通过反馈调节负调控ET信号(Hinz et al., 2010; Yang et al., 2011)。研究发现, ET合酶ACS在RAP2.2过表达植株中表达量降低, 而在rap2.2-2敲除突变体中表达上调(Hinz et al., 2010)。然而, 胁迫条件下ERF-VIIs如何通过负反馈机制调控ET生物合成有待进一步研究。

4.2.3 参与赤霉素介导的胁迫应答

赤霉素(GA)广泛分布在植物中并参与调控叶、芽以及合子发育等多种生物学过程。GA由GA20氧化酶(gibberellin 20-oxidases, GA20ox)和GA3氧化酶(GA3ox)等关键酶合成, 在GA2氧化酶(GA2ox)作用下被分解代谢(Rieu et al., 2008)。DELLA蛋白作为GA信号转导途径中的主要负调控因子, 也是整合生长素、ABA、ET和JA等植物激素或环境信号的枢纽蛋白。植物体接受GA信号后, 通过泛素-蛋白酶体途径降解DELLA蛋白, 解除其对生长的抑制作用(Zhang et al., 2009)。冷、盐和渗透胁迫下, GA含量降低, 导致植物生长减缓(Colebrook et al., 2014)。极低浓度GA下, DELLA蛋白抑制GA介导的应答调控, 外源GA处理促进DELLA蛋白降解(Claeys et al., 2012)。

AP2/ERFs参与调控植物GA生物合成相关基因的转录。盐胁迫下, DREB1E和DREB1F抑制GA20ox的表达, 使GA生物合成减少, 引起植株生长迟缓(Magome et al., 2004)。过表达ERF6抑制GA2ox的表达水平, 诱导赤霉素降解酶(gibberellin 2-oxidase 6, GA2ox6)的合成, 维持DELLA蛋白的稳定性。渗透胁迫下, erf6功能获得突变体植株矮小且对胁迫高度敏感, 而erf5/erf6缺失突变体生长受胁迫影响较小。研究发现ERF6还激活了STZ、MYB51和WRKY33等渗透胁迫响应基因的表达(Dubois et al., 2013)。冷胁迫下, CBF1转录因子激发GA2ox基因的表达而降低GA含量, 组成型表达CBF1抑制GA的积累, 植株表现矮化, 表明DELLA蛋白是CBF1介导的冷胁迫响应的关键组分(Achard et al., 2008)。相反, ERF11作为一种GA生物合成和信号转导的正调控因子, 抑制ET生物合成, 促进植株节间伸长。过表达ERF11上调GA3ox1和GA20ox基因的表达水平, 增加GA的积累量(Zhou et al., 2016)。ERF6作为转录激活因子诱导ERF11的表达, 反之, ERF11抑制GA2-OX6、STZ、MYB51和WRKY33等ERF6相关靶基因的表达。进一步实验表明, 4个靶基因在erf11/erf6过表达植株中也不能被诱导表达, ERF11过表达可消除ERF6过表达导致的极度矮化现象, 说明ERF11可能通过直接竞争目标基因启动子而在分子水平上拮抗ERF6 (Dubois et al., 2015)。

在拟南芥和水稻中, SUB1A、SK1和SK2参与GA

信号转导通路的调控。淹水胁迫下, SUB1A 激活 SLR1 (*slender rice 1*) 和 SLRL1 (*slender rice 1 like 1*) (DELLA 类似蛋白) 转录, 同时 SUB1A 抑制受 GA 诱导的淀粉代谢相关基因的表达, 调控植株节间伸长和呼吸作用 (Fukao and Bailey-Serres, 2008; Locke et al., 2018; Perata, 2018)。SK1 和 SK2 两个转录因子中均含有 EIN3 结合位点, 电泳迁移率测定显示, 类 EIN3 基因 *EIL1b* 可与 SK1 和 SK2 启动子结合, 激活其转录活性。研究发现, 淹水状态下拟南芥中 ET 合成增加, 进而诱导 SK1 和 SK2 表达, 激发 *GA20oxs* 基因上调表达, 促进植株节间伸长, 减轻淹水对其生长的抑制效应 (Hattori et al., 2009; Ayano et al., 2014)。

4.2.4 参与细胞分裂素介导的胁迫应答

细胞分裂素 (CTK) 在植物中具有广泛的生物学效应, 不仅可促进细胞分裂、花芽分化、打破种子休眠及调控营养物质运输, 而且在植物应对逆境胁迫中也起重要作用 (Zwack and Rashotte, 2015)。在拟南芥中, CTK 利用一种类似于细菌双元组分系统的途径传递信号至下游元件, 受体组氨酸激酶 (*Arabidopsis* histidine kinase, AHK) 与 CTK 结合后发生自磷酸化, 并由磷酸转运蛋白 (*Arabidopsis* histidine-phosphotransfer protein, AHP) 介导磷酸基团转移到 A 型和 B 型反应调节因子上, 进而调节下游的细胞分裂素响应基因 (Mähönen et al., 2006)。A 型 RR 是目前发现的受细胞分裂素调控的主要蛋白家族, 且 A 型 ARR 通过抑制 B 型 RR 的活性负调控依赖性 CTK 信号途径。

细胞分裂素应答因子 (cytokinin response factor, CRF) 在植物胚、子叶和叶片发育过程中起关键调控作用 (Rashotte et al., 2006)。拟南芥 *crf1/2/5* 和 *crf2/3/6* 突变体的转录组分析表明 CRF 参与 CTK 介导的调控网络。CRF 基因启动子区含有多个 B 型 ARR 结合位点, 据此推测 CRFs 很可能是 B 型 ARR 的直接靶标, 两者之间存在协同作用, 约 60% 的 CTK 响应基因同时受 CRF 和 B 型 ARR 调控 (Rashotte et al., 2006)。Zwack 等 (2013) 认为 CRF6 是胁迫条件下 AHK3 和 TCS 介导的 CTK 信号通路下游的新组分, CRF6 和 ARR2 可能通过一个部分重叠或相互作用的平行通路负调控胁迫诱导的叶片衰老过程, 这也表明 CRF6 和 CTK 与非生物胁迫之间存在独特的关系 (Zwack et al., 2013)。CRF6 除正向调节 CTK 通路外, 还抑制

CTK 的生物合成、信号转导和胞内转运相关靶基因的表达, 减轻 CTK 对非生物胁迫的负调控作用 (Zwack et al., 2016b)。CRF6 和 CTK 在胁迫响应调控中的作用相反, 但在叶片衰老调控中的作用相似, 推测 CRF6 也可能通过 2 条途径调控 CTK 信号通路。目前有关 CRF 调控的具体机制仍不明确, 鉴定 CRF 靶基因和上游信号分子将有助于更好地理解 CTK 响应非生物胁迫的作用机制。

4.2.5 参与油菜素内酯介导的胁迫应答

油菜素内酯 (BR) 在植物细胞伸长、叶片发育、花粉管生长、木质部分化、衰老、光形态发生以及应激反应过程中起重要作用 (Ye et al., 2017)。BR 信号始于细胞膜上受体激酶 (brassinosteroid insensitive, BRI), BKI1 (BRI kinase inhibitor 1) 是 BRI1 的关键负调控蛋白。无 BR 时, BKI1 和 14-3-3 蛋白分别抑制 BR 的受体 BRI1 和转录因子 BES1 (*bri1-ems-suppressor 1*) (Wang et al., 2011)。而当 BR 被 BRI1 感知后, 即使 BKI1 发生磷酸化, 激活 BRI1 和 BES1 以调控负调节因子 BIN2 (*brassinosteroid insensitive 2*) 的表达, 诱导 BES1 和 BZR1 (*brassinazole-resistant 1*) 积累并与转录因子互作, 影响参与植物生长和胁迫反应的 BR 应答基因的转录水平 (Wang et al., 2011; Guo et al., 2013)。

BZR1 可结合 *CBF1* 和 *CBF2* 的启动子区并促进两者在冷胁迫下的表达。*bin2-3*、*bil1*、*bil2* 缺失突变体在持续的冷胁迫下可以诱导去磷酸化 BZR1 的积累, BZR1 通过调控 *WKRY6*、*PYL6*、*SOC1*、*JMT* 和 *SAG21* 等不依赖 CBF 途径的 *COR* 基因而增强拟南芥的耐冷性 (Li et al., 2017)。研究发现 BR 可与干旱诱导相关转录因子 RD26 互作, 拮抗干旱响应基因的表达, 进而负调控植物的抗旱性 (Ye et al., 2017)。BR 与 ABA 信号途径中的受体、转录因子之间也产生拮抗效应, 进而调节胁迫下植物体的生长平衡 (Nolan et al., 2017)。目前已从 BES1 和 BZR1 靶基因中鉴定出一些 AP2/ERF 类转录因子, 暗示 AP2/ERF 具有整合 BR 信号通路与非生物胁迫响应的潜在功能 (Sun et al., 2010; Yu et al., 2011)。*ERF72* 可能是研究 BR 信号通路与胁迫响应交叉互作的候选基因。在拟南芥中, *ERF72/RAP2.3* 拮抗 BZR1 和 ARF6 (*auxin responsive factor 6*), 抑制下胚轴伸长, 此过程中 BR 信号途

径如何与胁迫响应调控网络协同互作发挥作用尚不清楚(Liu et al., 2018b)。研究表明, SUB1A参与调节GA和BR的交叉网络互作(Schmitz et al., 2013)。GA和BR途径通过DELLA蛋白、BZR1等转录因子协同调控植物的生长(Oh et al., 2012)。在植物淹水过程中SUB1A差异调节BR合成相关基因的表达, 激活BR生物合成和信号转导, 诱导GA降解关键基因GA2ox7的表达, 进而控制水稻植株体内的GA水平, 促进DELLA蛋白的积累(Schmitz et al., 2013)。因此, 推测AP2/ERF可能通过不同的机制参与调控BR信号通路。

5 展望

植物在长期进化过程中建立了一系列复杂而精密的基因表达调控网络或信号通路, 调节植物体内缺氧、高温、干旱、低温、高盐等胁迫下的新陈代谢和生长发育。AP2/ERF转录因子具有十分重要的生物学功能, 其通过依赖或不依赖于激素信号途径在非生物胁迫响应过程中发挥作用。近年来, 关于AP2/ERFs参与调控激素信号介导的胁迫响应的报道较多, 但具体调控机制尚不完善, 需要进一步探索。今后可重点从激素参与AP2/ERFs转录水平调控, AP2/ERFs如何通过协同或拮抗多种激素信号转导组分改变激素敏感性及相关基因的表达, 以及AP2/ERFs如何反馈调节激素生物合成和代谢等方面开展研究。阐明上述问题将有助于系统解释AP2/ERFs对植物发育的影响, 揭示胁迫条件下植物体代谢活动的调控网络, 为后续植物抗逆育种工程提供理论依据。

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Research Advances in AP2/ERF Transcription Factors in Regulating Plant Responses to Abiotic Stress

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Abstract Low temperature, drought, high salt, hypoxia and other adverse environmental changes affect plant growth and development. Plants adapt to these adverse conditions through the development of complex regulatory mechanisms during long-term evolution. APETALA2/ethylene responsive factor (AP2/ERF) is a plant-specific transcription factor that plays a key regulatory role in various stress responses. In recent years, more and more studies have shown that plant hormone-mediated signaling is closely related to stress responses, and AP2/ERF transcription factor and hormone signal transduction form a cross-regulatory network. Many AP2/ERF transcription factors respond to plant hormones abscisic acid (ABA) and ethylene (ET), activating the expression of stress response genes that are dependent on and independent of ABA and ET. In addition, AP2/ERF transcription factors are also involved in gibberellin (GA), cytokinin (CTK) and brassinosteroid (BR) mediated growth and developmental processes and stress responses. This paper briefly reviews the research progress of AP2/ERF transcription factors in term of structure, transcriptional regulation, posttranslational modifications, binding sites and interacting proteins as well as its transduction pathways involved in hormone dependent- or independent- regulation of the abiotic stress responses, which will provide the basis for further understanding the roles of different AP2/ERF transcription factors in the regulation of hormone and stress response network in plants.

Key words AP2/ERF transcription factor, hormone, abiotic stress, regulation

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