

转录因子 BES1/BZR1 调控植物生长发育及抗逆性

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摘要: 油菜素内酯(brassinosteroid, BR)是植物特有的甾体激素, 在植物生长发育及逆境应答过程中起重要作用。转录因子 BES1/BZR1(BRI1 EMS SUPPRESSOR 1/BRASSINAZOLE RESISTANT 1)是 BR 信号转导的核心成员, 被 BR 信号激活后, 结合到下游靶基因启动子区的 E 框(CANNTG)或 BRRE 元件(CGTGT/CG), 调节靶基因表达。除介导 BR 信号, BES1/BZR1 还参与脱落酸、赤霉素及光等信号转导途径, 协同调控植物的生长发育。最新研究发现, BES1/BZR1 还参与调控植物的抗逆性。本文对转录因子 BES1/BZR1 通过信号转导调控植物生长发育和抗逆性分子机制的新近研究进展进行了综述, 以期为相关研究提供参考。

关键词: 油菜素内酯; 生长发育; 信号转导; 抗逆性; BES1/BZR1 转录因子

The BES1/BZR1 transcription factors regulate growth, development and stress resistance in plants

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Abstract: Brassinosteroid (BR) is a class of plant-specific steroidal hormone and plays vital roles in plant growth, developmental and stress response. As the core component of BR signaling, the BES1/BZR1 transcription factors are activated by the BR signal, bind to the E-box (CANNTG) or BRRE element (CGTGT/CG) enriched in the promoter of downstream target genes and regulate their expression. Besides BR signal transduction, BES1/BZR1s are also involved in other signaling pathways such as abscisic acid, gibberellin and light to co-regulate plant growth and development. Recently, BES1/BZR1s were found to be related to stress resistance. In this review, we summarize recent advances of molecular mechanism of the BES1/BZR1 transcription factors regulating plant growth, development and stress resistance through signal transduction to provide a reference for related researches.

Keywords: brassinosteroid; growth and development; signal transduction; stress resistance; BES1/BZR1 transcription factors

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油菜素内酯(brassinosteroid, BR)是植物特有的甾体激素,在生长发育及环境胁迫应答中起重要作用,其生理活性远高于生长素(auxin, IAA)、赤霉素(gibberellins, GA)、细胞分裂素(cytokinin, CTK)、脱落酸(abscisic acid, ABA)和乙烯(ethylene, ET)^[1,2]。BR 合成基因过量表达或缺失对植物生长发育及产量、品质等农艺性状均产生严重影响^[3-6]。BR 信号转导被阻断的植物则显现矮化、开花延迟、早衰等缺陷表型^[7,8]。

BR 被细胞膜上 BRASSINOSTEROID INSENSITIVE 1 (BRI1)及 BRI1-ASSOCIATED RECEPTOR KINASE1 (BAK1)等激酶接受后,通过信号转导激活转录因子 BRI1 EMS SUPPRESSOR 1 (BES1)及其同源蛋白 BRASSINAZOLE RESISTANT 1 (BZR1)的活性^[9,10]。BES1 与 BZR1 氨基酸序列相似性达 88%, N 端结构域相似性高达 97%^[11],编码基因以家族形式存在,本课题组在前期研究中将其统一命名为 BES1/BZR1^[12]。被 BR 信号激活后, BES1/BZR1 直接与其他转录因子一起结合到生长发育相关基因启动子的 E 框(CANNTG)或 BRRE 元件(CGTGT/CG),调节这些基因的表达^[13-15]。例如, BES1/BZR1 抑制叶腋分生组织发育基因表达,可促进小穗发育,增加水稻产量^[16]。BES1/BZR1 调节根尖分生组织发育相关基因表达,进而调控根发育^[4,17-19]。除介导 BR 信号, BES1/BZR1 还参与 ABA、GA 及光等信号转导途径,调控植物的生长发育以及抗冻、耐旱、抗病等抗逆性。

本文对转录因子 BES1/BZR1 通过信号转导调控植物生长发育和抗逆性分子机制的新近研究进展进行了综述,以期对相关研究提供参考。

1 BES1/BZR1 介导 BR 信号转导

2002 年, Wang 等^[20]利用 EMS 诱变筛选到一个 BR 合成抑制突变体 *brassinazole-resistant 1-1D* (*bzr1-1D*), 图位克隆获得 *BZR1* 基因, 该基因编码核蛋白且受 BR 诱导。同年, Yin 等^[21]利用 EMS 诱变筛选到 BR 受体抑制因子 BES1, 受 BR 诱导并在细胞核中积累。后经证实 BES1 是一个 BZR1 类蛋白(BZR1-like protein), 二者具有高度的序列相似性, N 端均

有一个核定位信号(NLS), C 端均有 22~24 个丝氨酸或苏氨酸残基(S/TXXXS/T), 该残基是 BIN2、GSK-3 等激酶磷酸化位点, 磷酸化后进入细胞质被 14-3-3 蛋白降解^[16,20,21]。直至 2005 年, Yin 等^[10]进一步证实 BES1/BZR1 是植物中特有的新一类转录因子, 也是 BR 信号转导途径的唯一转录因子。细胞膜上的 BRI1、BAK1 和 BAK1 等激酶接受 BR 信号后, 自身磷酸化并催化 BRASSINOSTEROID-SIGNALLING KINASE1 (BSK)和 CONSTITUTIVE DIFFERENTIAL GROWTH1 (CDG1)磷酸化, BSK 与 CDG1 进一步磷酸化 BRI1-SUPPRESSOR1 (BSU1), BSU1 催化 BRASSINOSTEROID INSENSITIVE2 (BIN2)去磷酸化, 导致其自身被蛋白酶体降解, 削弱 BIN2 对 BES1/BZR1 的磷酸化从而使其活性增加^[9,10,21-23], BES1/BZR1 通过调节下游靶基因的表达, 调控植物的生长发育(图 1A)。

BES1/BZR1 成员 N 端均有一个 bHLH 结构域, 可特异性结合到靶基因启动子区的 E 框或 BRRE 元件^[10,24-26]。此外, 多数 BES1/BZR1 成员均含有能被 BIN2 等激酶磷酸化的丝氨酸(serine, S)富集位点, 个别成员包含一个与蛋白稳定性紧密相关的脯氨酸(proline, P)、谷氨酸(glutamic acid, E)、丝氨酸(serine, S)和苏氨酸(threonine, T)富集区(PEST 基序)^[10]。目前, 拟南芥(*Arabidopsis thaliana*)和水稻(*Oryza sativa*)BES1/BZR1 基因家族已被全部鉴定: 拟南芥 AtBES1/BZR1 基因家族有 6 个成员, 且功能存在部分冗余^[10,20,21]; 水稻 OsBES1/BZR1 基因家族有 4 个成员^[27]。玉米(*Zea mays*)ZmBES1/BZR1 基因家族有 11 个成员^[23,28]。此外, 从白菜(*Brassica rapa* ssp. *pekinensis*)、棉花(*Gossypium*)、油菜(*Brassica napus*)和桉树(*Eucalyptus grandis*)中均鉴定出多个 BES1/BZR1 基因家族成员^[29-33](表 1)。进一步研究证实, BES1/BZR1 基因家族成员通过不同信号途径调控植物生理代谢过程, 进而调控植物生长发育及逆境响应。

2 BES1/BZR1 参与 ABA 信号途径

ABA 是植物体内重要激素之一, 通过其直接受体 PYL (pyrabactin resistance 1-like protein)、第二信

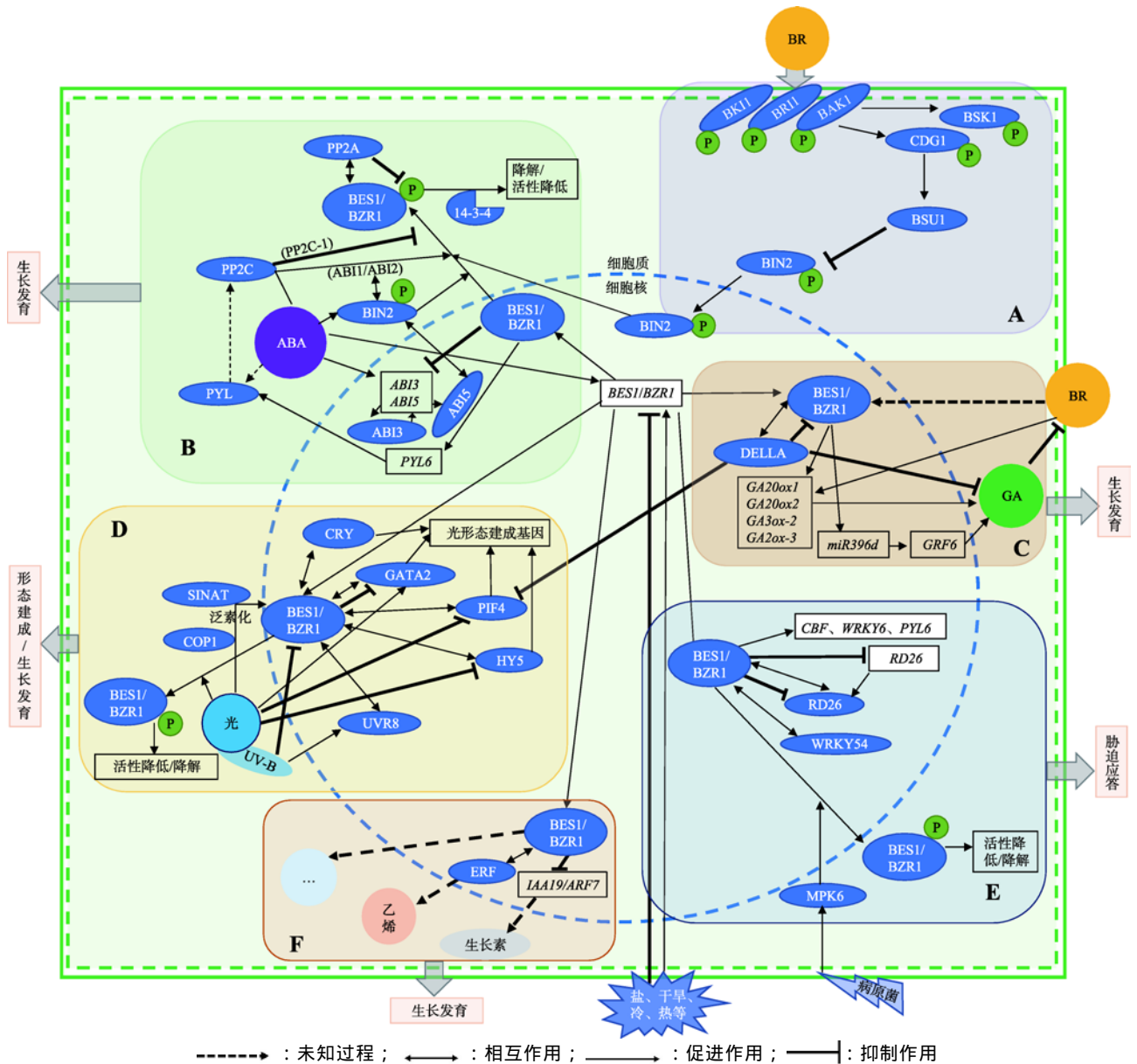


图 1 BES1/BZR1 参与的信号转导网络

Fig. 1 The signal transduction network of BES1/BZR1

A: BES1/BZR1 介导的 BR 信号转导; B: BES1/BZR1 参与的 ABA 信号途径; C: BES1/BZR1 参与的 GA 信号途径; D: BES1/BZR1 参与的光信号途径; E: BES1/BZR1 调控逆境应答途径; F: BES1/BZR1 参与的生长素、乙烯及其他信号途径。BR: 油菜素内酯; BES1/BZR1: 转录因子; BKI1、BRI1、BAK1、BSK1 及 CDG1: 蛋白激酶; BSU1: BRI1 抑制因子; ABA: 脱落酸; GA: 赤霉素; PP2C: 2C 型丝氨酸苏氨酸蛋白激酶; PP2A: 2A 型丝氨酸/苏氨酸蛋白激酶; PYL: ABA 受体; BIN2: 磷酸酶; ABI3 与 ABI5: ABA 响应的 bZIP 转录因子; DELLA: 赤霉素负调控转录因子; SINAT 与 COP1: E3 泛素连接酶; GATA2 与 HY5: 光形态建成相关转录因子; UVR8: 紫外光受体; PIF4: 光敏色素互作因子; CRY: 隐花色素。RD26 与 WRKY26: 干旱相关转录因子; REF: 乙烯应答因子; MEK6: 促细胞分裂原活化蛋白激酶; P: 磷。

使 2C 型蛋白磷酸酶(PP2C)及第三信使蔗糖非酵解型蛋白激酶(SnRK)向下游进行信号传递,在植物生长发育及抗逆过程中扮演重要角色,如衰老、抗旱、耐盐等^[34-36]。研究发现,在突变体 *bzr1-1D* 中,BZR1

结合到 ABA 诱导型转录因子 ABA INSENSITIVE 5 (ABI5)编码基因 *ABI5* 的启动子,抑制其表达,因而抑制突变体 *bzr1-1D* 对 ABA 诱导的应答^[37]。同时,BES1 抑制 ABA 调节的转录因子 ABI3 编码基因的

表 1 已鉴定的不同植物 BES1/BZR1 基因家族成员

Table 1 Identified members of the BES1/BZR1 gene family in different plants

物种	基因家族(数量)	参考文献
拟南芥(<i>Arabidopsis thaliana</i>)	BES1、BZR1 和 BEH1 ~ 4(6)	[10, 20, 21]
水稻(<i>Oryza sativa</i>)	OsBZR1 ~ 4、LOC_Os01g08180.1 和 LOC_Os02g03690.1(6)	[27]
大白菜(<i>Brassica rapa</i> ssp. <i>pekinensis</i>)	BrBEH1 ~ 10、BrBZR1-1 ~ -2 和 BrBES1-1 ~ -3(15)	[29]
陆地棉(<i>Gossypium hirsutum</i>)	GhBES1-1 ~ -21(21)	[30]
雷蒙德氏棉(<i>Gossypium raimondii</i>)	GrBZR1 ~ 7(7)	[31]
亚洲棉(<i>Gossypium arboreum</i>)	GaBZR1 ~ 7(7)	
桉树(<i>Eucalyptus grandis</i>)	EgrBZR1、EgrBEH1、EgrBEH3、EgrBEH4、EgrBAM7 和 EgrBAM8(6)	[32]
玉米(<i>Zea mays</i>)	ZmBES1/BZR1-1 ~ -11(11)	[23, 28]
油菜(<i>Brassica napus</i>)	Bna-BES1-001 ~ -028(28)	[33]

表达,进而抑制 ABI3 对下游 ABI5 转录因子的激活,致使 ABA 信号转导受阻,表现为苗期发育迟缓^[38,39]。

此外,外源 ABA 不仅诱导 BES1/BZR1 基因表达,而且诱导 BES1 蛋白磷酸化,使其稳定性降低,从而抑制 BR 信号转导,此过程依赖于 ABA 第二信使 PP2C 成员 ABI1 和 ABI2^[12,29,40,41]。最新研究表明,ABI1、ABI2 与 BIN2 激酶互作后催化 BIN2 去磷酸化,从而调控 BES1 活性。ABA 还可促进 BIN2 磷酸化并抑制 ABI2 的活性^[42]。在 ABA 存在时,BIN2 磷酸化 ABI5 使其稳定性增强,调控种子发育过程^[43]。在大豆(*Glycine max*)中,PP2C-1 与 GmBZR1 直接互作,催化 GmBZR1 去磷酸化以增强 GmBZR1 活性,促进种子大小相关基因 *SHORT HYPOCOTYL UNDER BLUE1 (SHB1)*、*APETALA2 (AP2)*和 *Auxin response factor 2 (ARF2)*等表达,调控种子的大小与重量^[44,45]。BZR1 也可结合到 ABA 受体 PYL6 编码基因的启动子区,上调 PYL6 表达,从而参与 PYL6 介导的 ABA 信号转导^[46]。研究还发现,BZR1 的 PEST 结构域与蛋白磷酸酶 2A(PP2A)的 B 亚基直接互作,使 BZR1 被 PP2A 去磷酸化,激活 BZR1 介导的 BR 信号途径,调控植物的生长发育^[47](图 1B)。

3 BES1/BZR1 参与 GA 信号途径

作为植物体内重要激素之一,GA 在种子萌发、细胞分裂、胚珠形成等生长发育过程中起关键作用^[48,49]。研究发现,在 BR 缺失的突变体 *bri1-1* 中,GA 合成关键基因 *GA20ox1* 表达显著下调,而

在 *bzr1-1D* 突变体中,*GA20ox1* 基因表达显著上调。同时,在 *bzr1-1D* 和 *bes1-D* 突变体中,*GA20ox1* 基因均受 BR 诱导,表达显著上调。有研究表明,*GA20ox1* 基因启动子区不含 BES1/BZR1 转录因子的结合位点。研究人员通过电泳迁移实验(electrophoretic mobility shift assays, EMSA)和染色质免疫共沉淀(chromatin immunoprecipitation, ChIP)实验证实,BES1/BZR1 可结合 *GA20ox1* 基因启动子区一个非 E-Box 且长度为 12 bp 的基序(Motif)^[50,51]。此外,GA 信号负调控因子 DELLA 家族蛋白(RGA、GAI、RGL1、RGL2 和 RGL3)可以和 BES1/BZR1 结合,阻止 BES1/BZR1 与靶基因的结合^[50,52~55]。这些研究结果证实,DELLA 蛋白降解可促使 BES1/BZR1 活性增强,BES1/BZR1 结合 GA 合成相关基因启动子,使其表达上调,促进 GA 积累。此外,GA 可通过 PP2A 促进 BES1/BZR1 的去磷酸化^[54]。

在水稻中,BR 诱导 GA 合成基因表达,促使 GA 积累。外源 GA 又抑制 BR 合成及其信号转导。进一步研究表明,GA 合成关键基因 *GA20ox-2*、*GA3ox-2*、*GA20ox-3* 和 *D2* 的启动子均包含 CATGTG、BRRE 或 G-box 元件。BES1/BZR1 与这类元件直接结合,调节下游基因的表达,进而影响 GA 合成^[56]。在番茄(*Lycopersicon esculentum*)中过表达 *BZR1* GA 合成关键酶之一的酮戊二酸脱氢酶 2 (2-ODD2)蛋白水平在果实成熟期显著增加,致使 GA 显著积累促进果实成熟^[57]。水稻 OsBZR1 能够促进 miR396d 的积累,调控其靶基因 *GROWTH REGULATING FACTOR 6 (OsGRF6)*的表达,通过 *OsGRF6* 参与的 GA 合成

及信号转导途径,调控水稻株高及叶夹角等形态建成^[58](图 1C)。

4 BES1/BZR1 参与光信号途径

光是植物光合作用的能量之源,在调控植物生长发育中起关键作用,如光信号参与调控种子萌发、光形态建成和开花等^[59]。转录因子 GATA2、HY5 正向调控植物光形态建成并受光诱导积累,黑暗促使其降解。研究发现,被 BR 激活的 BZR1 直接与 GATA2 互作,抑制 GATA2 转录,调控拟南芥幼苗下胚轴伸长^[60,61]。黑暗条件下, HY5 能特异地结合 BZR1,抑制 BZR1 与子叶开闭相关基因的结合能力,调控光形态建成^[61]。光敏色素互作因子(phytochrome interacting factor, PIF)是一类 bHLH 转录因子,在黑暗条件下, PIF 大量积累,促进植物暗形态建成,但在光照条件下, PIF 发生磷酸化后降解,促进植物光形态建成^[62,63]。研究发现, BES1/BZR1 与 PIF 4 相互作用,形成异源二聚体后作用于共同靶基因,其中 80%靶基因受光诱导参与光形态建成^[11]。此外, BZR1 与 PIF4 共同作用的靶基因还受 GA 诱导, GA 促进细胞伸长的过程依赖于 BZR1 和 PIF4。DELLA-BZR1-PIF4 复合体调控下游靶基因 paclobutrazol resistance 家族(PREs)表达,促进细胞伸长,调控光形态建成^[11,53]。在高温条件下, BZR1 和 PIF4 相互作用,调控植物热形态建成^[64]。

最近研究发现,去磷酸化的 BES1 可与紫外光受体 UVR8 (UV RESISTANCE LOCUS 8)互作,二者的复合体受紫外光(UV-B)诱导,并在细胞核大量积累。同时, UV-B 不仅抑制 BES1 靶基因表达,其受体 UVR8 又抑制 BES1 与 DNA 的结合作用,最终控制植物光形态建成过程^[65]。在蓝光条件下,其受体隐花色素(cryptochrome, CRY) CRY1 和 CRY2 特异性与去磷酸化的 BES1 互作,抑制 BES1 与 DNA 结合活性及其靶基因表达,最终抑制下胚轴伸长^[66]。

综上所述, BES1/BZR1 参与光信号途径调控植物的形态建成过程。此外,还有研究发现,植物体内 BES1/BZR1 的磷酸化状态及稳定性也受光信号调控。黑暗条件促进 BES1/BZR1 去磷酸化以增强活性,而光照条件下,大多数 BZR1 被 BIN2 磷酸化以

保持失活状态^[61,67,68]。Kim 等^[68]研究发现,黑暗条件下, E3 泛素连接酶 COP1 催化磷酸化后的 BZR1 降解,去磷酸化的 BZR1 积累。同时,光照条件可诱导 E3 泛素连接酶 SINAT 积累, SINAT 泛素化 BES1 促使其降解。相反,黑暗条件抑制 SINAT 的积累,从而阻止 BES1 降解^[69](图 1D)。

5 BES1/BZR1 调控植物抗逆性

BES1/BZR1 除调控植物生长发育外,在响应生物和非生物逆境胁迫过程中也起重要作用。Guo 等^[70]研究发现, BES1/BZR1 调控硫代糖苷合酶基因的表达,促进硫代糖苷合成,而硫代糖苷在植物与食草动物或与微生物互作中起重要作用。随后, Miyaji 等^[71]发现 BZR1 可能参与茉莉酸信号途径,增强植物抗虫能力。此外,研究表明,病原物相关分子模式(pathogen-associated molecular pattern, PAMP)感知可促进 BES1 磷酸化,在 PAMP 诱导的免疫反应(PAMP-triggered immunity, PTI)过程中, BES1 作为病原菌诱导的 MITOGEN-ACTIVATED PROTEIN KINASE 6 (MPK6)的直接底物被其磷酸化,参与调控植物对病菌的免疫反应^[72]。

Singh 等^[73]研究发现,低磷胁迫促进 BES1/BZR1 由细胞核向细胞质转移,低磷条件下, BES1/BZR1 显著积累,维持根系正常生长,赋予拟南芥对低磷胁迫的耐受性。研究表明, BES1/BZR1 可促进转录因子 CBF (C-repeat binding factor)、WRKY6 以及 ABA 受体 PYL6 等编码基因的表达,并与 WRKY54 转录因子直接互作,正调控拟南芥耐寒性,但负调控其耐旱性^[46,74]。研究还发现, BES1/BZR1 与 NAC 转录因子家族的 RD26 存在拮抗关系, BES1/BZR1 结合到 RD26 基因启动子,抑制 RD26 表达,而 RD26 蛋白又与 BES1/BZR1 蛋白结合,抑制 RD26 干旱应答调节功能^[75]。同时,在干旱和低碳胁迫下, BES1 与泛素受体 DSK2 互作而被降解,参与胁迫诱导的自噬反应过程,调控植物适应逆境^[76]。

此外,在拟南芥、油菜和桉树中, BES1/BZR1 基因的表达受盐、干旱、热和冷等胁迫的诱导或抑制^[29,32,33],表明该基因家族参与这些逆境胁迫响应过程(图 1E)。

6 BES1/BZR1 参与的信号转导网络

BES1/BZR1 是 BR 信号转导途径特异的转录因子, 通过介导 BR 信号调控植物生长发育。但近年来研究发现, BES1/BZR1 在 ABA、GA、光及逆境信号中也发挥着重要作用, 并且还参与 IAA、ET 等信号途径。如 BZR1 直接与生长素诱导基因 *IAA19*、*ARF7* 的启动子结合而抑制其表达, 从而影响生长素的合成, 调控植物生长发育^[77]。BES1/BZR1 通过下调乙烯合成关键酶基因 *ACS7*、*ACS9* 和 *ACS11* 表达, 抑制乙烯合成, 而且与乙烯响应因子 *ERF72* 互作调控其下游基因表达, 最终影响植物生长发育过程^[4,78] (图 1F)。综上所述, BES1/BZR1 参与多种信号途径, 调控植物生长发育及逆境应答, 其功能和作用机制表现出多样性。但是, BES1/BZR1 调控植物响应逆境胁迫方面的研究还不够深入, 除拟南芥外, 在作物及其他植物中 BES1/BZR1 抗逆功能研究尚未见报道。因此, 本文将 BES1/BZR1 参与的信号转导网络进行了归纳总结 (图 1), 以期为后续相关研究提供参考。

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