

# WRKY 转录因子家族调控植物逆境胁迫响应

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**摘要:** WRKY 转录因子是一组含有保守的 WRKYGQK 结构域的蛋白质家族, 广泛参与植物的营养体生长、器官发育、物质代谢和对各种生物、非生物胁迫的响应过程。目前, 对 WRKY 家族转录因子的研究主要集中在不同物种中 WRKYs 对逆境胁迫响应的信号转导机制的解释。以近年来发表的关于 WRKYs 的研究成果为基础, 综述了 WRKY 家族成员的不同功能, 讨论了 WRKYs 的不同成员在植物正常生长发育的重要作用。模式植物之外其他的植物物种中 WRKY 家族成员的作用报道相对较少, 且缺少全面的研究和分析; WRKYs 参与的很多信号通路还没有完全清晰, 这些问题有待深入研究。

**关键词:** WRKYs; 生物胁迫响应; 非生物胁迫响应; 植物激素

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## WRKY Transcription Factors in Regulation of Stress Response in Plant

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**Abstract:** WRKY transcription factor families are characterized by a highly conserved WRKYGQK domain and involved in plant development, metabolism, answering to comprehensive biotic or abiotic stress. Recently, the research of WRKY transcription factors concentrate on stress response signaling network in different species. It reviewed progress of WRKYs members, and indicated that WRKY transcription factors play a heavy role in plant growth and regulating stress response. At the same time, there is less reported of WRKYs function in plant species besides model plant *Arabidopsis thaliana* and most of them focus on systematic research and analysis. In addition, numerous networks of WRKY transcription factors are still unclear.

**Key words:** WRKYs; biotic stress response; abiotic stress response; phytohormone

植物时刻暴露在各种环境条件下, 恶劣的环境条件阻碍着植物的生理性生长过程, 这些恶劣的环境条件被称为非生物胁迫/生物逆境, 包括干旱、土壤盐浓度、重金属、低温、放射性物质和不同类型的氧化还原反应病虫害等<sup>[1]</sup>。植物体通过分子、细胞、形态建成各个层次产生对环境的适应性响应<sup>[2]</sup>, 这些复杂的调控网络操纵着细胞和植物个体对环境的响应、对气候的适应性<sup>[3]</sup>。病原体的入侵引起植物内源信号分子, 如植物激素水杨酸 (salicylic acid, SA) 和茉莉酸 (jasmonic acid, JA) 以及他们

的衍生物含量的迅速升高, 这对下游防御基因的表达有着重要的调控作用<sup>[4]</sup>。其中 SA 触发植物体对于活营养体寄生病原体的防御反应, JA 则是参与对死营养体病原菌的抗性<sup>[5]</sup>。ABA (abscisic acid) 和乙烯 (ethylene) 对 JA 调控起协同作用, 但他们都拮抗 SA。生长素 (auxin)、赤霉素 (gibberellins) 和细胞分裂素 (cytokinins) 则是优先促进植物的生长过程, 抑制胁迫响应基因的表达; 但是这个过程可以被 SA 和 JA 所抑制, 以牺牲植物生长的代价来进行逆境防御和抵抗<sup>[4]</sup>。

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在过去的20年中,人们对WRKY转录因子(TF)家族参与植物对生物和非生物逆境响应的调控有了很多研究和认识<sup>[6]</sup>,其在高等植物中是最大的转录因子家族之一,并且存在于所有绿色植物基因组中<sup>[7]</sup>,也被称为非生物胁迫响应的“中心调控因子”<sup>[8]</sup>。关于WRKY家族转录因子参与SA、JA逆境胁迫响应信号转导过程的报道逐年增多。WRKYs调节植物对多种非生物胁迫响应,例如盐胁迫<sup>[9]</sup>、干旱胁迫<sup>[10]</sup>、冷胁迫<sup>[11]</sup>、伤口反应<sup>[12]</sup>;且不仅仅局限于模式植物拟南芥,还包括很多其他的物种<sup>[13]</sup>。WRKY蛋白在产生生物胁迫的病原体防御<sup>[14, 15]</sup>和昆虫防御<sup>[16, 17]</sup>中起重要作用。本文主要总结了近年来报道的WRKYs参与植物胁迫响应的的作用,希望对WRKY家族在植物逆境响应中的角色,有一个全面的认识。

## 1 WRKY 转录因子的结构特点、分类和分布

WRKY家族转录因子具有相同的结构特征,N端都有包含WRKYGQK七肽序列的WRKY结构域,C端则含有C<sub>2</sub>H<sub>2</sub>-或C<sub>2</sub>HC-类型的锌指结构<sup>[15]</sup>。根据这些特点,WRKYs可以分成三个家族:第I家族含两个WRKY结构域和两个C<sub>2</sub>H<sub>2</sub>锌指结构,第II家族含一个WRKY结构域和一个C<sub>2</sub>H<sub>2</sub>锌指结构,第III家族含一个WRKY结构域和一个C<sub>2</sub>HC锌指结构。第II家族又被分成a, b, c, d和e五个小亚族。第II家族的WRKY蛋白参与调控植物的生长发育,例如衰老、种子休眠和萌发等;还参与植物对干旱、盐胁迫和冷害响应过程<sup>[18]</sup>。WRKYs如果没有LZ(leucine zipper)基序,则不能形成同源或者异源二聚体<sup>[19]</sup>。

不同物种中WRKY家族基因数量也是不同的,黄瓜(*Cucumis sativus*)中57个,麻风树(*Jatropha curcas*)中58个,葡萄藤(*Vitis vinifera*)中9个,白梨(*Pyrus bretschneideri*)中103个,谷子(*Setaria italica*)中105个,蓖麻子(*Ricinus communis* L.)中58个,拟南芥(*Arabidopsis thaliana*)中74个,水稻(rice)中102个,杨树(*poplar*)中104个,二穗短柄草(*Brachypodium distachyon*)中86个成员,182个成员在大豆中,116和102个WRKY基因在两个不同的棉花种。油菜(*Brassica napus*)中有

287个WRKY家族基因,桑树(*Morus notabilis*)中有54个WRKY家族基因,甜木薯(*Manihot esculenta*)中被鉴定出来85个WRKY家族基因<sup>[20-29]</sup>。

## 2 WRKY 转录因子参与调控植物逆境胁迫响应

### 2.1 WRKY转录因子响应生物逆境胁迫

*AtWRKY50*和*AtWRKY51*促进SA的生物合成<sup>[30]</sup>。*AtWRKY17*和*AtWRKY33*在JA处理过后被诱导表达<sup>[31]</sup>。过表达*AtWRKY28*和*AtWRKY46*经由SA信号通路可以诱导*ICS1*和*PBS3*<sup>[32]</sup>。此外,从长春花中分离到的12个WRKY基因都可以响应JA信号<sup>[33]</sup>,丹参(*Salvia miltiorrhiza*)中的49个WRKY基因可以显著被JA上调或者下调表达<sup>[34]</sup>。从杨树(*Populus trichocarpa*)中分离的WRKY第III家族成员*PtrWRKY89*可以被SA快速诱导<sup>[35]</sup>。*PtrWRKY89*的过表达转基因株系中检测到PR基因持续表达,且该株系对*P. syringae*和*B. cinerea*更敏感。*PtrWRKY89*参与SA与JA的协同信号转导过程<sup>[36]</sup>。在烟草中,WRKY 3/4基因可以被TMV、SA和SA类似物所快速诱导,且表达量足够启动PR蛋白合成,增强抵抗力<sup>[37]</sup>。我们的研究结果证实*AtWRKY8*通过直接调控*ABI4*、*ACS6*和*ERF104*的表达参与植物对TMV的防御响应过程中,并且介导了TMV和拟南芥之间ABA和乙烯的信号交叉传递<sup>[38]</sup>。香蕉VQ基因通过抑制冷害响应转录因子*MaWRKY26*参与到JA生物合成基因的调节<sup>[39]</sup>。人参中WRKY转录因子对于胁迫的响应有6个PgWRKY基因(*PgWRKY2*、*PgWRKY3*、*PgWRKY4*、*PgWRKY5*、*PgWRKY6*、*PgWRKY7*)参与。SA处理后3个WRKY基因(*PgWRKY3*、*PgWRKY5*、*PgWRKY9*)明显表达量下调。ABA处理后5个PgWRKYs(*PgWRKY2*、*PgWRKY4*、*PgWRKY5*、*PgWRKY8*、*PgWRKY9*)一直明显的上调表达<sup>[40]</sup>。

在水稻中,*OsWRKY71*<sup>[41]</sup>、*OsWRKY31*<sup>[42]</sup>、*OsWRKY45-1*、*OsWRKY45-2*<sup>[43]</sup>都被报道在细菌病原菌侵染过程中被诱导。相似的,在拟南芥中,*AtWRKY8*<sup>[44]</sup>、*AtWRKY33*<sup>[45]</sup>、*AtWRKY25*<sup>[46]</sup>、*AtWRKY11*和*AtWRKY17*<sup>[31]</sup>在细菌病原体侵染时候基因下调表达。WRKY参与菜豆对于SCN大豆胞囊线

虫病 (Soybean Cyst Nematode) 的侵染胁迫响应<sup>[47]</sup>。*CmWRKY15* 通过调控 ABA 信号途径可以促进细极链格孢 (*Alternaria tenuissima*) 对于植物体的感染作用<sup>[48]</sup>。但是, *CmWRKY48* 过表达的转基因菊花却可以抑制蚜虫的群体数量<sup>[49]</sup>。

油菜在响应核盘菌侵染 24 h 内快速诱导的关键病原体响应基因, 包括葡聚糖酶、几丁质酶、过氧化物酶和 WRKY 转录因子等, 这些都是参与宿主早期病原体响应的基因。其中, *WRKY11* 在 24 hpi 被诱导 (3 倍) 但是在 48 hpi 被抑制 (-2 倍)<sup>[50]</sup>; *WRKY33* 之前被报道过正调控植物对于营养体坏死型真菌的抗性<sup>[51]</sup>; 而且在甘蓝型油菜中过表达 *WRKY33* 导致抗性响应基因的持续表达, 包括 *PR1*、*PDF1.2*, 增加了植株的抵抗力<sup>[52]</sup>。*WRKY11*、18、53 则表现出了负调控或者是对病原菌侵染的延迟响应。在之前的报道中 *BnWRKY11* 在侵染早期 6 hpi 的时候, 表达水平同时被 JA 和 ET 所抑制<sup>[53]</sup>。

在拟南芥中过表达 *AtWRKY28* 和 *AtWRKY75* 都能增强植株对病菌的抗性反应<sup>[54]</sup>。实验结果证明, 13 个 *BnWRKYs* 都明显地被 *S. sclerotiorum* 诱导; 包括 *WRKY6*、8、11、15、28、33、40、69 和 75, 在所有烟草株系中都能够检测到表达量的变化; 其中 6 个被大幅上调, 分别是 *BnaA08g12420D* (*WRKY11*)、*BnaC04g35770D* (*WRKY15*)、*BnaC06g-19560D* (*WRKY40*)、*BnaC06g40170D* (*WRKY40*)、*BnaA08g180-40D* (*WRKY65*) 和 *BnaA09g55250D* (*WRKY69*), 同时 5 个 *WRKYs* 被下调<sup>[55]</sup>。

*WRKY40* 和铜离子转运蛋白是调节棉花对于橘黄粉虱侵袭防御的中心调控基因<sup>[56]</sup>。*OsWRKY53* 可以被咀嚼食草动物高粱条螟 (SSB) 啃食所诱导, 负调控转录调节子 *OsMPK3/OsMPK6* 导致 JA、JA-Ile 和乙烯水平下降从而诱发水稻对 SSB 的抗性。褐飞虱 (BPH) 侵袭的 8 h 之内 *OsWRKY53* 转录水平上调, 在水稻对于啃食性昆虫 BPH 的抵抗起到重要作用。实验发现, BPH 可以导致水稻中  $H_2O_2$  的显著减少, 而在 *oe-wrky* 植物体中 BPH 诱导的  $H_2O_2$  含量明显低于 WT; 说明 *OsWRKY53* 通过调节  $H_2O_2$  的水平来正调控水稻对啃食性昆虫的防御方应<sup>[57]</sup>。

## 2.2 WRKY 转录因子调控非生物胁迫响应

干旱是所有非生物胁迫类型中对植物体伤害

最大的, 缺水使植株生长缓慢且矮小。WRKY 家族转录因子在植物对干旱的耐受起到至关重要的作用<sup>[58]</sup>。*CmWRKY10* 通过 ABA 途径来调控菊花的干旱耐受性; 在其高表达植株中 *DREB1A*、*DREB2A*、*CuZnSOD*、*NCED3A*、*NCED3B* 等基因转录活跃, 说明该株系的干旱耐受机制与 ABA 信号途径有关联。另外, 在高表达株系中 ROS 的积累明显低于野生型, 过氧化物酶、超氧歧化酶、过氧化氢酶的酶活性则是高于野生型, 这些高酶活都对提高缺水耐受性有帮助<sup>[59]</sup>。*CmWRKY1* 是从菊花重克隆出来的 WRKY II b 亚家族的转录因子, 它和拟南芥 *AtWRKY6* 高度同源, 外施 ABA 下调内源 *CmWRKY1*, 但是湿润条件可以明显的诱导 *CmWRKY1* 的表达<sup>[60]</sup>。*CmWRKY1* 通过调节 ABA 相关基因表达增强杭菊的脱水耐受性。*AtWRKY6* 调控有正调控和负调控两种调控方式, 而 *CmWRKY1* 经过证实同样如此<sup>[61]</sup>。相反, 过表达 *CmWRKY17* 则增加了菊花对于盐胁迫的敏感性<sup>[62]</sup>。

*AtWRKY46* 可以明显地被干旱、 $H_2O_2$ 、盐胁迫等所诱导, 它的突变体相比野生型来说对渗透胁迫更敏感<sup>[63]</sup>。*TaWRKY44* 在烟草中表达可以提高其对干旱、盐胁迫、渗透胁迫的抗性<sup>[64]</sup>。研究结果显示, *OsWRKY11*<sup>[65]</sup>、*HvWRKY38*<sup>[66]</sup>、*TaWRKY2* 和 *TaWRKY19*<sup>[67]</sup> 都能提高植物对于干旱胁迫的抵抗能力。被 *HSP101* 调控的 *OsWRKY11* 可以增强水稻对高温和干旱的耐受性<sup>[65]</sup>。相似的, 在大豆中过表达 *GmWRKY54* 使得植物体对干旱的耐受性有明显的提高<sup>[68]</sup>。WRKY 基因还参与到大豆干旱和洪涝胁迫的响应过程中<sup>[69]</sup>。

从羊草 (*Leymus chinensis*) 中分离的 *LcWRKY5*, 在拟南芥中过表达 *LcWRKY5* 可以强烈地增强植物体的耐受性<sup>[70]</sup>。从短柄草 (*Brachypodium distachyon*) 中克隆到的 *BdWRKY36* 有增强干旱期间植株的适应性的功能。此外, 过表达 *BdWRKY36* 蛋白的转基因烟草对干旱的抵抗力显著提高, 这种增强作用是通过减少活性氧 ROS 的积累, 激活抗性相关基因 *NtLEA5*、ABA 生物合成相关基因 *NtNCED1* 和调节基因 *NtDREB3* 等途径来实现的<sup>[71]</sup>。与 *AtWRKY60* 同源的 *BhWRKY1*, 可以被缺水和 ABA 短暂而快速的诱导表达。*BhWRKY1* 与 *BhGolS1* 互作, 依赖 ABA 途径来增加转基因烟草对于水分缺失的耐受性<sup>[72]</sup>。



大豆遭受水分胁迫时, *GmWRKY17* 和 *GmWRKY67* 的转录激活作用增强。*GmWRKY161* 在叶片中可被快速短暂诱导表达, 在诱导 3 h 后达到峰值 71 倍。*GmWRKY112* 在叶片中短暂上调, 在处理 2 h 后达到最大值 21 倍。*GmWRKY17* 和 *GmWRKY67* 转入大豆根系中, 干旱处理后分别有 12.7 倍和 4.8 倍的表达量。之前的研究已经表明 *GmWRKY53* 和 *GmWRKY112* 启动子正响应外施用盐和 PEG<sup>[73]</sup>。烟草的转录因子 *NtWRKY69* 能够直接被水分胁迫所诱导<sup>[74]</sup>。*WRKY70* 还参与落花生的低温胁迫响应<sup>[75]</sup>。互花米草冷胁迫响应中, *WRKY* 起始了 PR 蛋白和 AFP 蛋白 (anti-freezing protein) 的表达<sup>[76]</sup>。*WRKY44* 在烟草对多种非生物胁迫的耐受性起到重要作用<sup>[77]</sup>。

最近的一个研究显示, 来自于棉花 (*G. hirsutum* L.) 的 *GhWRKY68*, 在烟草中过表达该蛋白, 可以通过 ABA 信号途径来提高转基因植物体对干旱和盐胁迫的敏感性<sup>[78]</sup>。人参用 NaCl 处理时除了 *PgWRKY5* 之外所有的 *PgWRKYs* 转录水平都明显的上调或者下调表达<sup>[79]</sup>。遏蓝菜 (*Thlaspi caerulescens*) 的 *WRKY53*<sup>[80]</sup> 和拟南芥中 *AtMYB4*<sup>[81]</sup> 有可能参与到植物对于重金属镉 (Cd) 的胁迫响应过程中。怪柳 (*Tamarix hispida*) 的 *ThWRKY7* 可以特异性的结合到 *ThVHAc1* 启动子的 W-box 上并且具有转录激活活性, 而且在 Cd 处理条件下 *ThWRKY7* 与 *ThVHAc1* 具有相同的表达模式, 表明 *ThWRKY7* 能够提高植物对 Cd 的耐受性<sup>[82]</sup>。低氧浓度诱导属于 AUX/IAA、WRKY、HB、锌指家族的转录因子的高表达, 属于 WRKYs 第 I 家族的 *WRKY23* 和 *WRKY33* 在 0.4 kPa 时被诱导<sup>[83]</sup>, 他们可能与 VQ 蛋白协同作用<sup>[84]</sup>。在马樱丹 (*V. lantana*) 中 *WRKY* 蛋白对于 O<sub>3</sub> 胁迫在转录水平的响应, 诱导一个参与 O<sub>3</sub> 胁迫感受/信号转导途径的基因表达并且参与氧化还原反应<sup>[85]</sup>。*WRKY* 基因可能参与两个杨树杂交克隆受到 O<sub>3</sub> 间断式胁迫条件下的氧化还原反应调控<sup>[86]</sup>。同样的在 Col-0 拟南芥 *WRKY* 转录因子可以被 O<sub>3</sub> (350 ppb, 2 h) 处理高度诱导, 该现象也能在番茄被 *B. cinerea* 侵染和被 *P. syringae* 感染<sup>[87]</sup>、O<sub>3</sub> 处理过后观察到<sup>[88]</sup>。*WRKY* 蛋白还参与毛竹 (*Phyllostachys edulis*) 对强光照的响应调控中<sup>[89]</sup>。

### 3 WRKY 转录因子的其他功能

*WRKY* 蛋白已经被证明参与植物的生长发育过程的调节, 例如毛状体形态发生<sup>[90]</sup>, 开花<sup>[91]</sup>, 种子发育<sup>[92]</sup>、休眠和萌发<sup>[93]</sup>, 衰老<sup>[94]</sup>。拟南芥 *WRKY13* 通过直接结合于 *NST2* 的启动子上正调控茎中木质素的生物合成<sup>[95]</sup>。在木髓部细胞中 *AtWRKY12* 直接抑制 *NST2* 的表达来负调控次级细胞壁 (SCW) 的形成, 次级细胞壁相关的 NAC 结构域蛋白 *SND1/NST3* 和它的功能同源基因 *NST1* 和 *NST2*、维管特异性 *VND6* 和 *VND7* 是一个关键的调控节点, 对于下游 SCW 生物合成基因 *SND3*、*MYB46*、*MYB83*、*MYB103* 等次级转录因子的转录具有开关作用<sup>[96, 97]</sup>。*PtrWRKY19* 与 *AtWRKY12* 具有高度同源性, 都负调控木质部髓细胞的 SCW 发育<sup>[98]</sup>。*WRKY* 还参与苜蓿 (*Medicago truncatula*) 的次级细胞壁形成以及表皮转移细胞发育<sup>[99]</sup> 的调控, 调节小麦的抽穗期<sup>[100]</sup>。*GsWRKY20* 正调控开花反应, 通过调控开花相关基因和花分生组织基因的表达来促进植物开花过程<sup>[101]</sup>。同样, 芒草 (*Miscanthus*) 的 *MIWRKY12* 转录因子也被报道控制开花<sup>[102]</sup>。*WRKY* 还参与到了大豆叶片脱落的器官极性和细胞命运的转录调控中<sup>[103]</sup>。

我们研究发现, *AtWRKY25* 很有可能对 ABA 调控种子萌发和萌发后生长有拮抗作用<sup>[104]</sup>。*WRKY40* 通过直接抑制 ABA 敏感基因例如 *ABI5* 的转录, 作为 ABA 响应途径的中心转录抑制子来起作用<sup>[106]</sup>。*AtWRKY41* 通过直接调控 *ABI3* 在成熟种子中的表达来控制早期的种子休眠和热抑制<sup>[107]</sup>, *CaWRKY6* 可以激活 *CaWRKY40*, 使其作为一个正调控因子调节 *Ralstonia solanacearum* 抗性和对热的耐受性<sup>[108]</sup>。*WRKY* 参与到水稻叶片早衰和种子休眠中, 通过对 *WRKY* 的上调表达来激活信号转导<sup>[109]</sup>。在 *P. trichocarpa* 中约有 100 个 *WRKY* 基因, 他们中的大部分都可以被 JA、SA、冷胁迫、干旱胁迫、盐胁迫或者伤口胁迫所诱导<sup>[110]</sup>。

*AtWRKY6*、*AtWRKY22*、*AtWRKY53* 参与到植物衰老过程调控中<sup>[111-113]</sup>。*WRKY53* 被报道加快了叶片的衰老过程<sup>[114]</sup>。*AtWRKY54*、*AtWRKY57* 和 *AtWRKY70* 同样在叶片衰老中起调控作用<sup>[115]</sup>。我们

的研究结果显示 *AtWRKY57* 在 JA 诱导的衰老过程中, 作为一个关节点来调控生长素和 JA 的信号转导过程<sup>[116]</sup>。在水稻中过表达 *OsWRKY42* 导致叶片早衰<sup>[117]</sup>。之前报道过 SA 和  $H_2O_2$  可以刺激 WRKY 基因的表达, 包括 (*WRKY-6*、*-42*、*-53*、*-71*、*-72*、*-77*、*-79* 和 *-97*) 在叶片衰老中起到重要作用, 并且这些 WRKY 转录因子在 *ospls1* 中的表达量明显高于野生型<sup>[118,119]</sup>。在小麦基因组中, 共有 116 个 WRKY 基因, 其中 30 个确定为衰老相关 WRKY 基因, *TaWRKY7*、*16*、*24*、*36*、*39*、*68*、*71*、*74*、*89*、*96*、*114*、*115* 和 *116* 很可能是调节衰老的 SAGs。在拟南芥中异位过表达 *TaWRKY7*, 在黑暗处理条件下观察到叶片衰老过程的明显加快; 它还可以被 ABA 诱导, 同时阻止了叶片的水分流失提高植株对干旱的忍耐性<sup>[120]</sup>。*AtWRKY6* 可以直接结合到 W-box 上从而调控衰老诱导的类受体激酶基因的转录活性, *atwrky6* 突变体和过表达 *AtWRKY6* 转基因植株分别表现出早衰和延迟衰老的表型<sup>[121]</sup>。此外, 在铁缺失的条件下 *WRKY46* 转录因子通过调节液泡 Fe 转运基因的表达, 来调控 Fe 元素在植物体内从根到茎叶的转运<sup>[122]</sup>。

WRKYs 转录因子例如 *GaWRKY1*、*AaWRKY1*、*WRKY3*、*WRKY6* 和 *WRKY33* 都参与控制多种生物合成过程的调节中, 包括棉子酚、青蒿素和植物抗毒素的生物合成调控<sup>[123-125]</sup>。在紫杉醇的生物合成过程中, 从红豆杉 (*Taxus chinensis*) 中分离的 MeJA 响应转录因子 *TcWRKYA1*, 在体外可以特异性地与两个 DBAT 基因启动子上 W-box 元件结合, 而 DBAT 编码紫杉醇生物合成过程中的关键酶<sup>[126]</sup>。*CjWRKY1* 属于 IIc 亚家族且响应 JA 信号, 在生物碱异喹啉的生物合成过程中, 过表达 *CjWRKY1* 能够增强多种黄连素生物合成基因的转录激活<sup>[127]</sup>。雌性蛇麻草 (*Humulus lupulus* L.) 中的 *HWKY1* 调控蛇麻素生物合成的最后步骤, 通过激活黄腐酚和苦酸生物合成的关键基因, 例如查耳酮合酶 H1, 己酰苯合酶, 异戊烯转移酶 1、1L 和 2, O- 甲基转移酶的转录来完成调控过程<sup>[128]</sup>。

## 4 WRKY 转录因子的转录后调控

### 4.1 可变剪接

在病原体防御反应中, 水稻 *WRKY62* 和

*WRKY76* 转录因子的基因存在可变剪接。短的可变剪接 *OsWRKY62.2* 和 *OsWRKY76.2* 亚型可以彼此互作, 也可以和全长的蛋白互作。*OsWRKY62.2* 在植物中转录抑制作用减弱, *OsWRKY62.2* 和 *OsWRKY76.2* 的剪接使得其对 W-box 的结合能力有所下降<sup>[129]</sup>。

### 4.2 磷酸化

量光谱测定显示, 体外 *WRKY46* 能够被 *MPK3* 磷酸化 S168 和 S250 位点。磷酸化位点的突变减慢了 PAMP 诱导的 *WRKY46* 降解的过程。在原生质体中过表达 *WRKY46* 可以增加 PAMP 响应提高植物基础抗性<sup>[130]</sup>。*WRKY8* 和 *WRKY48* 作为植物对丁香假单胞菌 (*P. syringae*) 基础防御的负调控因子又作为 ETI 的正调控因子, 他们的生物突变体表现出抗性减弱和防御基因表达量的减少<sup>[131]</sup>。*WRKY8*、*WRKY28* 和 *WRKY48* 的 WRKY 结构域可以直接被 CPKs 磷酸化, 增强 HR 反应中 *WRKY46* 对细胞程序性死亡相关的标记基因启动子区 W-box 元件的结合能力<sup>[132]</sup>。*WRKY53* 可以直接被 MAPK 信号途径的 MEKK1 蛋白磷酸化从而参与到植物的基础防御反应的信号转导过程中<sup>[133]</sup>, *WRKY53* 的磷酸化状态可以加强靶基因的启动和转录能力<sup>[134]</sup>。在响应 *B. cinerea* 侵染的过程中, *WRKY33* 可以被两个明显受病原菌诱导的 MAPKs 所磷酸化, 启动植物抗菌剂-植保素的生物合成<sup>[135]</sup>。在本生烟中 MAPK 介导 *NbWRKY8* 的磷酸化, *NbWRKY8* 与 *AtWRKY33* 同源, 参与 PTI 和 ETI 可以激活 NADPH 氧化酶的表达<sup>[136]</sup>。*OsWRKY70* 可以被 MAPK3 和 MAPK6 磷酸化参与 GA 的生物合成, 并且对植物生长和发育的动态平衡起重要作用。目前的报道显示, 在不同物种间 MAPK 是作为通用磷酸酶来磷酸化 WRKY 家族的蛋白质, 并且最终作用到他们的靶基因上<sup>[137]</sup>。

## 5 总结与展望

WRKYs 参与到植物生命周期的多个方面, 在植物正常的生命活动中有着重要的不可或缺的作用。通过调控植物细胞壁的合成、开花时间、种子储藏物质代谢、种子萌发和休眠和植物衰老等过程参与植物的生长发育的各个阶段。WRKYs 和 SA、JA 等植物激素之间存在复杂的信号转导调控网络, 并且在植物受到环境中的各种胁迫因素, 例如干旱、盐、

缺氧、低温、强光照等非生物胁迫的威胁和病原体、昆虫、食草性或杂食性动物的入侵等生物胁迫的影响时, WRKY 家族的转录调控蛋白通过激活或者抑制相关胁迫响应基因的转录激活, 来增加植物对于环境的适应性和耐受性。WRKYs 转录因子家族广泛存在于绿色植物中, 已经有关于不同物种中 WRKYs 相关作用的报道, 但是大部分的调控网络还不清晰, 仍然还有很多内容需要进一步的研究证实和完善。

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