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·综　述·

WRKY 转录因子调控植物逆境胁迫响应的作用机制

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摘　要：WRKYs是植物中特有的一类转录因子(transcription factor, TF)家族，属于典型的多功能调节因子，可参与调控多种信号途径。该类转录因子的显著特征是含有约由60个高度保守的氨基酸构成的WRKY结构域，通常还具有Cys2His2或Cys2His-Cys型锌指结构。WRKYs可与下游靶标基因启动子区域的W-box序列[(T)(T) TGAC (C/T)]相结合，或通过与靶标蛋白相互作用来激活或抑制靶基因的转录，整合脱落酸(abscisic acid, ABA)、活性氧(reactive oxygen species, ROS)等信号通路诱导胁迫相关基因表达，从而调控逆境胁迫应答。本文综述了WRKYs的结构和分类、调控方式及其参与干旱、盐等逆境胁迫响应的分子机制等方面的研究成果，并对其未来研究方向进行展望，以期为农作物抗逆性遗传改良提供理论支持。

关键词：WRKYs；逆境胁迫；靶标基因；蛋白互作；基因表达

Functional mechanisms of WRKY transcription factors in regulating plant response to abiotic stresses

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Abstract: WRKYs is a unique family of transcription factors (TFs) in plants, and belongs to the typical multifunctional regulator. It is involved in the regulation of multiple signaling pathways.

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This type of transcription factor is characterized to contain about 60 highly conservative amino acids as the WRKY domain, and usually also has the Cys2His2 or Cys2His-Cys zinc finger structure. WRKYs can directly bind to the W-box sequence ((T)(T) TGAC (C/T)) in the promoter region of the downstream target gene, and activate or inhibit the transcription of the target genes by interacting with the target protein. They may up-regulate the expression of stress-related genes through integrating signal pathways mediated by abscisic acid (ABA) and reactive oxygen species (ROS), thus playing a vital role in regulating plant response to abiotic stresses. This review summarizes the advances in research on the structure and classification, regulatory approach of WRKYs, and the molecular mechanisms of WRKYs involved in response to drought and salt stresses, and prospects future research directions, with the aim to provide a theoretical support for the genetic improvement of crop in response to abiotic stresses.

Keywords: WRKYs; abiotic stress; target gene; protein interaction; gene expression

干旱、盐分、低温和营养亏缺等是导致植物生长发育受抑制和农作物产量下降的主要环境因素[1-3]。为应对这些非生物胁迫，植物在长期进化过程中从形态、生理、生化、细胞和分子水平上逐渐形成了一系列胁迫应答机制。其中，转录因子在植物的生长发育以及非生物逆境胁迫响应过程中发挥着重要的作用。在逆境胁迫下，一些转录因子被激活，随后大量的防御相关基因被转录调控，这些变化对防御机制的建立至关重要[4]。WRKY、MYB、bZIP 和 NAC 等转录因子家族均与植物的抗逆性有关。其中，WRKY 是植物中最大的转录因子家族之一。该类转录因子不仅可以识别 W-box 序列[(T)(T) TGAC (C/T)]，还可以与靶基因启动子中 DNA 的特定位点结合，进而调控其表达[5]。WRKY 转录因子不仅在植物应对生物胁迫的应答调节过程中发挥着至关重要的作用，而且也参与调控许多非生物逆境胁迫反应，其结构多样性赋予调控网络的复杂性。本文对 WRKYs 转录因子的结构域和分类、调控方式及其参与干旱、盐分等逆境胁迫的调控机制等方面的研究成果加以综述，并对其未来研究方向进行展望，以期为农作物抗逆性遗传改良提供理论支持。

1 WRKYs 转录因子结构域及分类

1.1 WRKYs 的结构域

Ishiguro 等[6]从甘薯(*Ipomoea batatas*)中克隆出 *WRKY* 家族的第一个编码 WRKY 的基因 *SPF1*。随后，人们相继在拟南芥(*Arabidopsis thaliana*)、水稻(*Oryza sativa*)、甜菜(*Beta vulgaris*)等植物中鉴定到了 *WRKY* 家族成员(表 1)。结果表明，不同物种 *WRKY* 家族成员数量有所不同，其中人参(*Panax ginseng*)中最多，有 119 个成员，而银杏(*Ginkgo biloba*)中最少，只有 37 个(表 1)。WRKYs 蛋白结构域包括 DNA 结合域、转录调控域、核定位信号和寡聚化位点这 4 个功能区域[27]。值得注意的是，WRKYs 转录因子最重要的结构特征是其 DNA 结合域中至少含有一个大约由 60 个高度保守的氨基酸构成的 WRKY 结构域。WRKYs 蛋白的 N 端含有 7 个保守的氨基酸残基 WRKYGQK，C 端含有 C_2H_2 ($Cx_{4–5}Cx_{22–23}Hx_1H$)或 C_2HC ($Cx_7Cx_{23}HxC$)型的锌指结构，均为维持 DNA 结合功能不可或缺的元件[28-29]。然而，也有一些植物存在特殊的 WRKY 七肽序列，即 WRKYGQK 被 WRKYGKK、WRKYGEK 所取代，或者“RK”残基被“RR、SK、 KR、VK 或 KK”取代，锌指结构也可能会发生一些变异[30-31]。此外，WRKY 结构域可以与顺式作用元件 W-box 序列[(T)(T) TGAC (C/T)]进行特异性结合，其中 TGAC 是 W-box 序列的核心序列，且该序列是关乎 WRKY 蛋白的结合和功能的重要因素。大量研究表明，与胁迫有关的基因启动子都含有 1 个或若干个 W-box 序列[32]，这也是 WRKYs 能够广泛参与许多植物基因表达调控的原因。

1.2 WRKYs 的分类

根据 WRKYs 结构域的数量和锌指结构的类型可以将 WRKY 家族分为 3 组(表 1)。其中，I 组转录因子含有 2 个 WRKY 结构域和 1 个 C_2H_2 型锌指结构，如小麦(*Triticum aestivum*) TaWRKY133[33]。I 组 WRKY 转录因子又可根据 WRKY 结构域分别命名为 WRKY-N 和 WRKY-C，与 N 端 WRKY 结构域相比，和 W-box 相结合的主要是 C 端 WRKY 结构域[34]。II 组和 III 组 WRKY 转录因子只包含一个结构域，两者的区别在于：II 组的锌指结构类型为 C_2H_2 型，如棉花(*Gossypium hirsutum*) GhWRKY28[35]；III 组结构类型则为 C_2HC 型，如茶(*Camellia sinensis*) CsWRKY70[36]。研究发现，I 组转录因子不仅存在于高等植物中，而且在蕨类植物和一些不能进行光合作用的真核细胞中也存在，说明 I 组转录因子起源是最早的，II 组可能是植物在应对各种胁迫条件下进化而来的[37]。大量研究表明，大多数的 WRKY 转录因子属于 II 组，II 组转录因子又根据结构特征的不同进一步分成 IIa、IIb、IIc、IId 和 IIe 这 5 个亚组。

表 1 不同植物 *WRKYs* 基因

Table 1 The *WRKYs* genes in different plants

Species	Gene name	Total number	Classification			References
			I	II	III	
Arabidopsis thaliana	*AtWRKYs*	62	12	39	11	[7]
Oryza sativa	*OsWRKYs*	99	12	48	39	[8]
Beta vulgaris	*BvWRKYs*	58	11	40	7	[9]
Vigna unguiculata	*VuWRKYs*	92	15	58	16	[10]
Solanum melongena	*SmWRKYs*	58	13	37	6	[11]
Panax ginseng	*PgWRKYs*	118	15	91	12	[12]
Lilium longiflorum	*LlWRKYs*	38	7	22	9	[13]
Liriodendron chinense	*LchiWRKYs*	44	8	28	8	[14]
Kandelia obovata	*KoWRKYs*	64	18	39	7	[15]
Scutellaria baicalensis	*SbWRKYs*	72	15	48	9	[16]
Acer truncatum	*AtruWRKYs*	54	14	11	29	[17]
Xanthoceras sorbifolium	*XsWRKYs*	65	12	45	8	[18]
Daucus carota	*DcsWRKYs*	67	6	53	8	[19]
Ipomoea batatas	*IbWRKYs*	84	15	56	10	[20]
Hordeum vulgare	*HvWRKYs*	86	10	42	34	[21]
Taraxacum kok-saghyz	*TkWRKYs*	72	16	43	12	[22]
Hylocereus undulatus	*HuWRKYs*	70	14	44	11	[23]
Akebia trifoliata	*AktWRKYs*	42	12	23	7	[24]
Petunia hybrida	*PhWRKYs*	79	14	50	15	[25]
Ginkgo biloba	*GbWRKYs*	37	9	26	2	[26]

为探究不同物种 *WRKY* 家族基因的系统发育及进化关系，本研究采用 Clustal W 软件对拟南芥、甜菜和茄子(*Solanum melongena*)的 *WRKY* 编码氨基酸序列进行比对，利用 MEGA 11.0 软件构建系统发育树(图 1)。结果表明，甜菜与茄子的 III 组 WRKY 转录因子中均存在处于同一分支的成员，I 组成员 ***BvWRKY41*** 与 ***SmWRKY8*** 亲缘性最高；IIb 组成员 ***BvWRKY30*** 与 ***SmWRKY14***

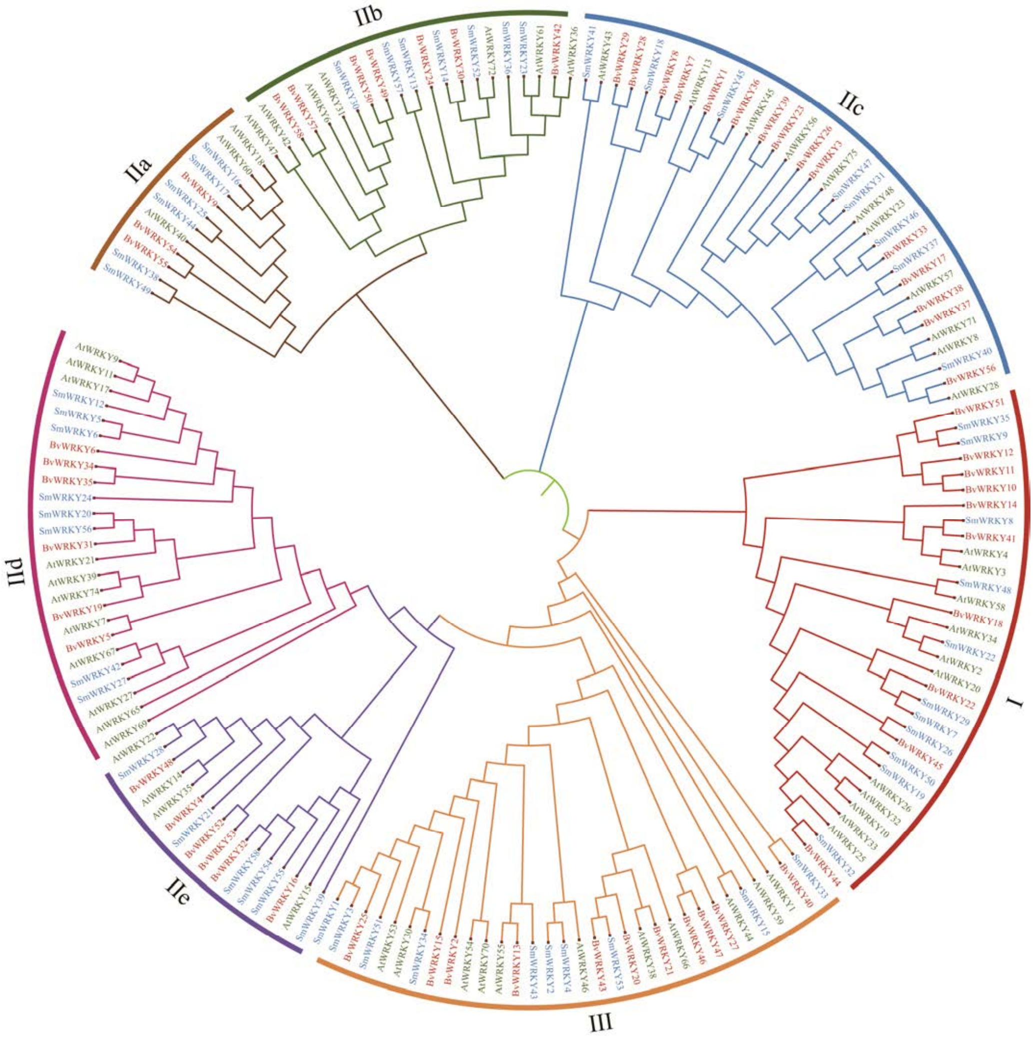

图 1　植物 *WRKYs* 家族基因系统发育树　利用甜菜基因组数据库(https://bvseq.boku.ac.at/)和 NCBI (https://www.ncbi.nlm.nih.gov/)检索甜菜、拟南芥和茄子的 *WRKY* 家族基因序列，通过 Clustal W 进行序列比对，利用 MEGA 11.0 和邻接法(neighbor joining, NJ)构建系统发育树，共进行 1 000 次自助重复. *WRKYs* 基因主要分为 I、II 和 III 组. *AtWRKYs*、*BvWRKYs* 和 *SmWRKYs* 分别用绿色、红色和蓝色表示

Figure 1　Phylogenetic tree of *WRKYs* gene family in plants. The predicted proteins sequences of *Beta vulgaris*, *Arabidopsis thaliana* and *Solanum melongena* were searched through *Beta vulgaris* genomic database (https://bvseq.boku.ac.at/) and NCBI (https://www.ncbi.nlm.nih.gov/). These sequences were aligned by the Clustal W and the phylogenetic tree was constructed using the MEGA 11.0 by the NJ method with 1 000 bootstrap replicates. The *WRKYs* genes were clustered into three major groups: I, II and III. *AtWRKYs*, *BvWRKYs*, and *SmWRKYs* are represented in green, red, and blue, respectively.

亲缘性最高;IIc 组成员 *BvWRKY36* 与 *SmWRKY45* 亲缘性最高；III 组 *BvWRKY43* 与 *SmWRKY53* 亲缘性最高(图 1)。

2 WRKYs 转录因子在逆境胁迫中的调控机制

2.1 WRKYs 的调控方式

干旱等非生物胁迫及虫害等生物胁迫环境因子会刺激植物细胞膜受体蛋白或使膜受体受到丝裂原活化蛋白激酶(mitogen-activated protein kinase, MAPK)级联反应，通过一系列磷酸化反应向细胞内发出信号调控 WRKY 转录因子的表达，引发各种生理生化反应，进而响应逆境胁迫(图 2)。

2.1.1 WRKYs 与自噬

WRKYs 可通过自噬途径减轻植物在生长发育过程中不利环境影响因子的伤害。研究发现，马铃薯(*Solanum tuberosum*) StATG8 与 WKRY 转录因子之间的蛋白相互作用是调控马铃薯生长发育成熟过程中的自噬的机制之一[38]。此外，过表达木薯(*Manihot esculenta*) *MeWRKY20* 可上调 *MeATG8a* 的转录水平，而在感染葡萄孢菌(*Botrytis cinerea*)的拟南芥中突变 *WRKY33* 可下调 *ATG18a* 的转录水平，表明植物在遭受病原体侵害时，可通过正向调控自噬系统在植物抗病性过程中发挥重要作用[39]。这些结果表明，WRKY 转录因子可通过调控自噬相关基因的转录，调节自噬系统，促进植物生长发育及增强逆境胁迫抗性。

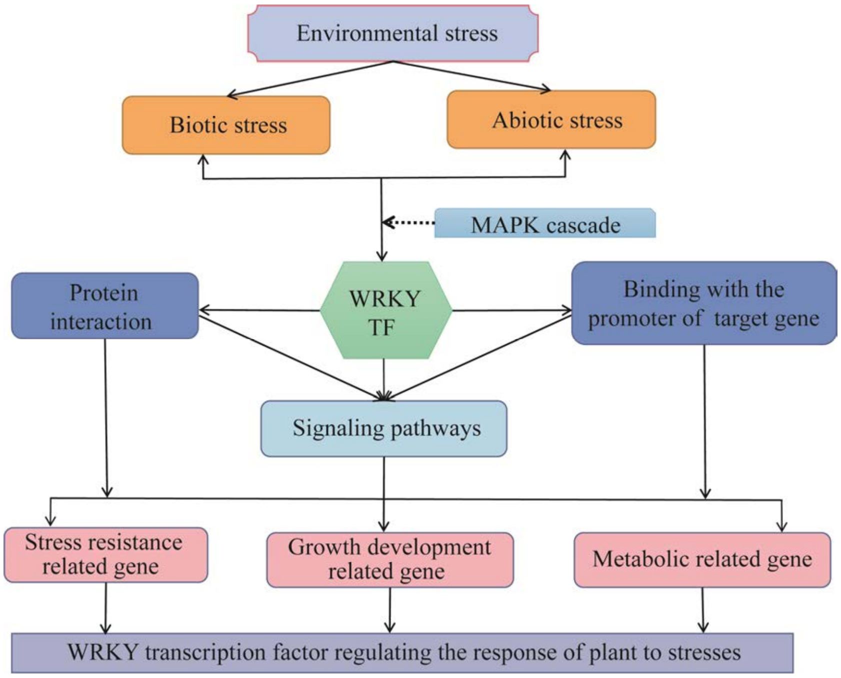

图 2 WRKY 转录因子调控植物逆境胁迫响应示意图 黑色实线箭头表示 WRKYs 调控植物胁迫响应途径；黑色虚线箭头表示 WRKY 转录因子可能会受到 MAPK 级联激活，进而参与调控胁迫应答

Figure 2 The diagram of WRKY transcription factor regulating stress responses in plants. The solid black arrows indicate that WRKYs regulating plant stress response pathway; The dotted black arrow indicates that WRKY transcription factors might be activated by the MAPK cascade and thus participates in the regulation of stress response.

2.1.2 WRKYs 与上下游调控因子

WRKYs 与下游靶基因启动子的结合可能会受到上游其与相关蛋白互作的影响。Tang 等[40]采用酵母双杂交(yeast two-hybrid, Y2H)技术，发现 WRKY33 和 WRKY12 可以相互作用，促进其与下游靶基因 *RAP2.2* 启动子区域 W-box 结合，激活靶基因转录，提高拟南芥由水淹诱导的缺氧胁迫耐受性。此外，WRKY 还可与 MAPK 等蛋白互作，调控下游靶基因表达。黄瓜(*Cucumis sativus*) CsWRKY23 和 27 与 CsMAPK6 互作，增强与靶基因的结合，激活氧化胁迫反应系统[41]。橡胶树(*Hevea brasiliensis*) HbWRKY14 与组蛋白去乙酰化酶 HbHDA3 互作作用于 HbWRKY14 上游，负向调节其对下游橡胶离子蛋白基因 *HbSRPP* 转录的抑制[42]。野生百合(*Lilium henryi*) LhWRKY44 与 LhMYBSPLATTER 互作并和其启动子相结合，增强 LhMYBSPLATTER 和 LhbHLH2 的互作，激活下游靶基因 *DFR*、*UFGT* 和 *GST* 表达，从而促进花色素苷积累[43]。这些结果表明，WRKYs 可以通过与其他蛋白互作，增强其与下游靶基因启动子结合，激活或抑制下游基因的转录，进而调控植物响应逆境胁迫和生长发育。

WRKYs 可直接与下游靶基因启动子相结合，调控其转录。研究表明，烟草(*Nicotiana attenuata*) *NaWRKY3* 和 *NaWRKY6* 与 *NaKTI2* 启动子区域顺式作用元件 W-box 结合，调节植物生长发育[44]。在芭蕉科小果野蕉(*Musa acuminata*)中，*MaWRKY49* 通过直接激活 *MaPL3* 和 *MaPL11* 表达，促进果实成熟[45]。类似地，苹果(*Malus domestica*) *MdWRKY72* 通过与 *MdHY5* 启动子及 *MdMYB1* 启动子中的 W-box 元件结合，促进 *MdMYB1* 转录，提高花青素含量[46]。相反，大麦(*Hordeum vulgare*) *HvWRKY2* 与 *HvCEBiP* 启动子结合，并抑制其转录，负向调控大麦对白粉病菌的抗性[47]。茶树(*Camellia sinensis*) *CsWRKY70* 通过抑制 *CsLAR* 和 *CsUGT84A* 的表达来降低表没食子儿茶酚没食子酸酯(epigallocatechin gallate, EGCG)的生物合成[48]。由此可见，WRKY 转录因子通过激活或抑制下游靶基因转录，进而调控植物生长发育以及响应逆境胁迫。

2.1.3 WRKYs 与信号通路

WRKYs 参与调控激素、MAPK、ABA 等信号通路。苹果(*Malus domestica*) *MdWRKY61* 在水杨酸(salicylic acid, SA)和茉莉酸(jasmonic acid, JA)的作用下被快速诱导表达，并上调 *MdRboh* 基因的表达，进而提高 *MdWRKY61* 过表达苹果对暹罗炭疽病菌的防御反应[49]。脱落酸(abscisic acid, ABA)、SA、乙烯(ethylene, ET)和 JA 处理均可上调橡胶树 *HbWRKY27* 表达，进一步研究发现，*HbWRKY27* 与 *HbFPS1* 启动子结合，并激活其转录，正向调节天然橡胶的生物合成[50]。胰蛋白酶通过 MAPK 级联信号通路途径调节火龙果(*Hylocereus undatus*) *HuWRKY40* 的活性，进一步促进黄酮类化合物的合成，延缓果实的腐败[51]。WRKY33 可直接调控 *PIF4* 的表达，并通过介导 H_2O_2 稳态在调节拟南芥幼苗的生长发育过程中发挥重要作用[52]。此外，康乃馨(*Dianthus caryophyllus*) *DcWRKY33* 可以整合 ET、活性氧(reactive oxygen species, ROS)和 ABA 信号通路，调控相关基因的表达，加速花瓣的衰老[53]。相反，*WRKY72* 通过整合 GA 途径与 *LRK1* 启动子相结合，进而下调 *OsKO2* 的表达水平来抑制水稻的生长[54]。由此可见，WRKY 转录因子可通过参与单个信号通路或整合多个信号通路调控植物响应逆境胁迫和生长发育。

2.2 WRKYs 在植物逆境胁迫响应中的作用机制

植物在长期的进化过程中，形成了独特的逆境适应机制。大量研究表明，WRKYs 在调控植物逆境胁迫响应中发挥着重要功能(表 2)。

表 2　WRKYs 转录因子响应非生物胁迫的调控机制

Table 2　Regulatory mechanisms of WRKYs transcription factors in response to abiotic stresses

Species	Gene	Regulatory mechanism	Target gene	Function	References
Triticum aestivum	*TaWRKY53*	ABA signaling pathway	*AtAREB*	Enhances resistance to drought stress	[55]
Vitis vinifera	*VvWRKY18*	ABA signaling pathway	*AAO2* *CYP707A3*	Reduces resistance to drought stress	[56]
Gossypium hirsutum	*GhWRKY46*	Activating the transcription of downstream genes	*AtRD22* *AtCBL10* *AtCPK3*	Enhances resistance to drought and salt stresses	[57]
Medicago sativa	*MsWRKY11*	Interacting with MsWRKY22 protein	–	Enhances resistance to drought stress	[58]
Solanum lycopersicum	*SlWRKY81*	Inhibiting the transcription of downstream genes	*SlP5CS1*	Reduces resistance to drought stress	[59]
Vitis vinifera	*VvWRKY13*	Inhibiting the transcription of downstream genes	*P5CS1* *BAM1* *BAM4* *SS1*	Reduces resistance to drought stress	[60]
Musa acuminata	*MaWRKY80*	Activating the transcription of downstream genes	*AtNCED2* *AtNCED3* *AtNCED4*	Enhances resistance to drought stress	[61]
Malus domestica	*MdWRKY30*	Interacting with MdWRKY28 protein	–	Enhances resistance to salt and osmosis stresses	[62]
Sorghum bicolor	*SbWRKY30*	Activating the transcription of downstream genes	*SbRD19*	Enhances resistance to drought stress	[63]
Populus trichocarpa	*PtrWRKY75*	Activating the transcription of downstream genes	*PAL1*	Enhances resistance to drought stress	[64]
Capsicum annuum	*CaWRKY27*	ROS signaling pathway	*NtAPX1* *NtSOD* *NtPOX1* *NtPOX2*	Reduces resistance to salt and osmosis stresses	[65]
Populus angustifolia	*PagWRKY75*	ROS signaling pathway	*SODs* *PODs* *P5CS1*	Reduces resistance to salt and osmosis stresses	[66]
Prunus mume	*PmWRKY18*	ABA signaling pathway	*PmLEA10* *PmLEA29*	Enhances resistance to cold stress	[67]
Arabidopsis thaliana	*AtWRKY39*	SA and JA signaling pathway	*AtPR1* *AtMBF1c*	Enhances resistance to heat stress	[68]
Triticum aestivum	*TaWRKY70*	SA and ET signaling pathway	*TaPR1.1* *TaAOS* *TaPIE1*	Enhances resistance to heat stress	[69]
Arabidopsis thaliana	*AtWRKY47*	Activating the transcription of downstream genes	*ELP* XTH_{17}	Enhances aluminum tolerance	[70]
Solanum lycopersicum	*SlWRKY42*	Activating the transcription of downstream genes	*SlAMT9*	Reduces aluminum tolerance	[71]
Arabidopsis thaliana	*AtWRKY13*	Activating the transcription of downstream genes	*PDR8*	Enhances cadmium tolerance	[72]

–: No target gene.

2.2.1 WRKYs 参与调控干旱胁迫响应

干旱是影响植物生长发育和作物产量的主要环境因素之一。研究表明，WRKYs 可通过 ROS 清除系统降低 H_2O_2 含量来提高植物对干旱胁迫的耐受性。例如，在烟草中过表达 *MdWRKY70L* 以及在拟南芥中过表达密罗木(*Myrothamnus flabellifolia*) *MfWRKY40* 或 *MfWRKY7* 均降低 H_2O_2 和 O_2^-的积累，增强转基因植株的抗旱性[73-75]。此外，WRKYs 还可通过 ROS 信号通路调控抗氧化酶相关基因的表达来响应干旱胁迫。过表达三浅裂野牵牛(*Ipomoea trifida*) *ItfWRKY70* 的转基因甘薯及过表达小麦 *TaWRKY1-2D* 的转基因拟南芥中 *SOD*、*POD*、*CAT* 的表达量均被激活上调，增强了转基因植株的耐旱性[76-77]。然而，在水稻和拟南芥中，过表达凤梨(*Ananas comosus*) *AcWRKY31* 则抑制转基因植株 *CAT* 和 *POD* 的表达，进而增强植物对干旱的敏感性[78]。

另外，WRKYs 也可通过 ABA 信号通路调控相关基因的表达来应答干旱胁迫。文冠果(*Xanthoceras sorbifolium*) *XsWRKY20* 通过整合 ROS 稳态和 ABA 信号通路，进而调控抗氧化酶相关基因及与 ABA 信号通路相关基因的表达，来正向调控植物的耐旱性[79]。过表达毛竹(*Phyllostachys edulis*) *PheWRKY86* 的转基因拟南芥和水稻中的 *NCED1* 的转录被激活，过表达红麻(*Hibiscus cannabinus*) *HcWRKY50* 的转基因拟南芥通过促进 *RD29B* 和 *COR47* 表达来调控 ABA 信号通路，均增强了植株的抗旱性[80-81]。相反，*OsWRKY5* 则抑制 *OsLEA3*、*OsRAB16A* 和 *OsDREB2A* 表达，而 *OsWRKY114* 则下调 ABA 信号通路 *OsPYL2* 和 *OsPYL10* 转录水平，负调控水稻对干旱胁迫的耐受性[82-83]。

此外，WRKYs 还可通过调控胁迫相关基因的表达来响应干旱胁迫。过表达马尾松(*Pinus massoniana*) *PmWRKY31* 通过正向调控转基因烟草 *NtAPX*、*NtCBL* 和 *NtCAT* 的表达来提高耐旱性[84]。过表达德国鸢尾(*Iris germanica*) *IgWRKY50* 和 *IgWRKY32* 则使转基因拟南芥促进 *RD29A*、*DREB2A*、*PP2CA* 和 *ABA2* 等胁迫相关基因表达上调，增强植株耐旱性[85]。这些结果表明，WRKY 转录因子通过调控 H_2O_2 的积累，单独参与或整合多信号通路，调节植物对干旱胁迫作出应答响应。

2.2.2 WRKYs 参与调控盐胁迫响应

土壤盐渍化是作物生长所受非生物胁迫因素之一，可破坏细胞结构，对细胞膜渗透性造成影响，限制作物对水分及营养物质的吸收。WRKY 转录因子可与下游靶标基因启动子区域顺式作用元件 W-box 相结合来响应盐胁迫。例如，过表达虎杖(*Polygonum cuspidatum*) *PcWRKY11* 及过表达菊叶薯蓣(*Dioscorea composita*) *DcWRKY12* 的转基因拟南芥中，*PcWRKY11* 及 *DcWRKY12* 可分别与 *LacZ* 及 *AtRCI2A* 启动子区域 W-box 结合，并激活其表达，进而提高转基因植株的耐盐性[86-87]。类似地，过表达玉米和菊叶薯蓣 *WRKYs* 分别调控 *SOD4* 与 *P5CS1* 表达，进而增强转基因植株对盐胁迫的耐受性[88-89]。另外，杜梨(*Pyrus betulaefolia*) *PbWRKY40* 与 *PbVHA-B1* 启动子区域 W-box 元件结合，提高转基因拟南芥植株的耐盐性[90]。在苹果中，MdWRKY55 与 MdNAC17-L 互作并激活 *MdNHX1* 表达来增强苹果耐盐性[91]。相反，玉米(*Zea mays*) ZmWRKY86 能与盐胁迫相关基因 *Zm00001d020840* 和 *Zm00001d046813* 启动子区域直接互作，而 ZmWRKY17 与 *ZmNECD5* 启动子结合并调控其表达，降低玉米对盐胁迫的耐受性[92-93]。

WRKYs 可通过自噬途径响应盐胁迫。盐胁迫可促进水稻幼苗自噬，激活 *WRKY53* 和 *ATG1* 等自噬相关基因的表达，并整合 JA 信号通路提

高其耐盐性[94]。此外，WRKYs 还可通过调控胁迫相关基因的表达量来响应盐胁迫。在拟南芥中，过表达小麦(*Triticum aestivum*) *TaWRKY75-A* 或苦荞麦(*Fagopyrum tataricum*) *FtWRKY46* 后，转基因植株 *PDAT2*、*SSL7*、*AT4G36010*、*NUDT8*、*AtRD29A*、*AtDREB2B*、*AtRAB18*、*AtSOS1* 和 *AtNHX1* 等基因表达上调，耐盐性显著增强[95-96]。类似地，过表达长叶红砂(*Reaumuria trigyna*) *RtWRKY23* 和 *RtWRKY1* 使得转基因拟南芥 *AtP5CS1*、*AtP5CS2* 和 *AtPRODH2* 的表达量显著上调，耐盐性明显增强[97-98]。

WRKYs 也通过调控 ROS、SOS 信号通路相关基因的表达来响应盐胁迫。例如，过表达花生(*Arachis hypogaea*) *AhWRKY75* 上调 *AhCSD1*、*AhCSD2*、*AhPOD* 和 *AhCAT* 表达水平，增强花生的耐盐性[99]。类似地，过表达洋麻(*Hibiscus cannabinus*) *HcWRKY44* 可通过正向调控 *SOS1* 的表达来提高拟南芥的耐盐性[100]。然而，过表达狗牙根草(*Cynodon dactylon*) *CdWRKY50* 和菊花(*Chrysanthemum morifolium*) *CmWRKY17* 使转基因拟南芥 *AtSOS1* 和 *AtSOS3* 的表达受到抑制，对盐胁迫的敏感性增强[101-102]。进一步研究发现，WRKYs 可整合多信号通路参与调控盐胁迫。在楸树(*Catalpa bungei*)中过表达 *CbWRKY27* 使得其整合 ABA 和 ROS 信号通路，增强植株对 ABA 的敏感性，降低抗氧化酶活性，提高 O_2^-和 H_2O_2 含量，负向调控楸树的耐盐性[103]。另外，过表达甜菜 *BvWRKY16* 使得转基因烟草植株的耐盐性显著增强(本课题组未发表数据)。这些结果表明，WRKY 转录因子还可通过蛋白互作或与下游靶基因启动子区域的 W-box 相结合，参与 SOS 信号通路或自噬途径，调控植物对盐胁迫的耐受性。

2.2.3 WRKYs 参与调控极端温度响应

WRKY 在调节植物响应高温或冷害胁迫中发挥重要作用。研究表明，WRKYs 通过调控 ABA 响应相关基因的表达来应答极端温度胁迫。在高温条件下，过表达 *ZmWRKY106* 的转基因拟南芥及过表达 *LlWRKY22* 的麝香百合(*Lilium longiflorum*)中 *DREB* 基因的表达量均上调，植株的耐热性均增强[104-105]。然而，在低温条件下，过表达西瓜(*Citrullus lanatus*) *ClWRKY20* 的转基因拟南芥植株 *ABI5* 表达上调，对低温胁迫的耐受性显著增强[106]。

WRKYs 通过植物激素信号通路或调控胁迫相关基因的表达来应答极端温度胁迫。在高温条件下，拟南芥 *AtWRKY25*、*AtWRKY26* 和 *AtWRKY33* 被乙烯诱导表达，反馈因子 *EIN2* 则受到转录调控，促使乙烯信号转导激活，进而激活氧化胁迫反应，提高拟南芥的耐热性[107]。此外，在低温胁迫下，*WRKY53* 与赤霉素(gibberellin, GA)合成相关基因的启动子结合并抑制其表达，降低水稻的耐寒性[108]。相反，拟南芥中 WRKY42 可与 *RHD6* 启动子结合，并激活其表达，进而提高植株耐寒性[109]。此外，在拟南芥中过表达 *PmWRKY57* 或秋茄(*Kandelia obovata*) *KoWRKY40* 分别提高低温响应基因 *AtCOR6.6* 和 *AtCOR47* 以及抗氧化酶相关基因 *AtMnSOD* 的表达水平，进而增强拟南芥对低温胁迫的耐受性[110-111]。这些结果表明，WRKY 转录因子不仅调控 ABA 及胁迫响应相关基因，还可整合激素信号通路，从而对极端温度作出应答响应。

2.2.4 WRKYs 参与调控营养元素胁迫响应

磷(phosphorus, Pi)元素的缺乏会对植物的生长发育造成严重影响。研究发现，大豆(*Glycine max*) *GmWRKY46* 与 *AtAED1* 启动子区域顺式作用元件 W-box 结合并激活其表达，进而提高转基因拟南芥植株对磷亏缺胁迫的耐受性[112]。此外，低磷胁迫可以提高辣椒(*Capsicum* *annuum*) *CaWRKY58* 转录丰度；进一步研究表明，Ca14-3-3 蛋白与 CaWRKY58 互作，正向调节辣椒对 Pi 饥饿响应[113]。另外，过表达 *OsWRKY108* 的转基因植株通过影响油菜素内酯(brassinosteroid, BR)生物合成及信号转导，进而正向调控水稻在磷亏缺条件下的叶片倾斜程度[114]。相反，在磷亏缺条件下，拟南芥 AtWRKY33 可调控 *AtALMT1* 转录表达，负调控根系结构重建，进一步介导 Fe^{3+}在根尖的积累，使根系生长受到抑制[115]。

此外，在铝(aluminum, Al)胁迫下，过表达 *GmWRKY81* 的转基因大豆中丙二醛(malondialdehyde, MDA)和过氧化氢含量均显著低于野生型(wild type, WT)植株，而过氧化物酶(peroxidase, POD)活性高于 WT 植株；进一步研究表明，过表达 *GmWRKY81* 可调控 Al^{3+}转运和抗氧化酶相关基因的表达来提高大豆对 Al^{3+}胁迫的耐受性[116]。相反，在铝胁迫下，番茄(*Solanum lycopersicum*) *SlALMT3* 受到 WRKY 转录因子 6 个成员(*SlWRKY3*、*SlWRKY6*、*SlWRKY16*、*SlWRKY37*、*SlWRKY39* 和 *SlWRKY71*)的调控，整合 JA 信号通路，从而抑制根系的生长[117]。

WRKYs 还可参与调控植物响应其他营养元素胁迫。例如，在小麦中，WRKY68a 与其他 WRKYs、钙调蛋白结合激活转录因子(calmodulin-binding transcription activator, CAMTA)、MAPK 蛋白激酶、锌指同源结构域(zinc finger-homeodomain, ZF-HD)蛋白和乙烯响应因子互作，从而调节中度和重度氮(nitrogen, N)缺乏条件下小麦幼苗的生长[118]。此外，过表达 *WRKY25* 和 *WRKY33* 通过介导 AGB1 下游锌(zinc, Zn)胁迫基因 *ZIP3* 和 *ZIP4* 转录调控，进而提高转基因拟南芥对锌亏缺的耐受性[119]。土壤发生铁(iron, Fe)毒害会限制作物的产量，铁毒害作用下水稻幼苗中自噬相关(autophagy-related)基因 *OsATGs* 的转录水平明显上调；进一步研究发现，*OsATG* 基因启动子含有 WRKY 靶向的 W-box 顺式作用元件，受 WRKY 转录因子的诱导，增强水稻的抗性[120]。另外，在铁胁迫下，过表达小金海棠(*Malus xiaojinensis*) *MxWRKY64* 的转基因拟南芥可通过提高 ROS 清除能力来调控植株对铁胁迫的应答反应[121]。这些结果表明，WRKYs 不仅可参与多种信号通路，还可能会受到多个 *WRKYs* 的调控作用，进而应答植物对营养元素亏缺的耐受性。

2.2.5 WRKYs 参与调控其他胁迫

WRKY 转录因子除了参与干旱、盐害、极端温度和营养元素胁迫外，还参与其他的非生物胁迫反应。在镉(cadmium, Cd)胁迫下，过表达 *GmWRKY172* 可降低转基因植株中 H_2O_2 的积累，并进一步通过 H_2O_2 信号通路提高过氧化物酶活性，增强大豆对镉的耐受性[122]。类似地，过表达滇杨(*Populus yunnanensis*) *PyWRKY75* 的转基因植株对镉的耐受性也明显增加[123]。此外，Shi 等[124]发现 UV-B/可见光处理可诱导杧果(*Mangifera indica*) *MiWRKY1* 和 *MiWRKY8* 的表达，促进杧果中花青素的合成。相反，拟南芥 *wrky23* 突变体诱导铵态氮转运蛋白 AMT1;2 表达，导致 NH_4^+在根中积累，抑制主根生长[125]。这些结果表明，WRKY 转录因子还可参与调控植物对重金属、紫外线等的胁迫响应。

3 展望

WRKY 转录因子参与植物多种逆境胁迫反应，并且在植物的生长发育过程中发挥着重要的作用。目前，有关 WRKY 调控植物应答非生物胁迫的分子机制研究的报道越来越多，研究技术也日趋成熟。然而，WRKYs 的结构具有多样性，保守结构域和锌指结构域均存在变异体，其参与的调控途径也十分复杂，可能会受到上

游因子的激活，并整合信号通路通过蛋白互作或结合下游靶基因启动子区域 W-box，进一步调控胁迫相关基因的表达，进而调节植物响应不同逆境胁迫。此外，同一 WRKYs 转录因子可调控多种胁迫响应，而同一种胁迫响应又可能会受到多种 WRKYs 的调控，其是否通过目前所报道的信号通路以外的其他途径来调节植物抗逆性，还有待深入探究。

因此，WRKY 转录因子未来研究可从以下 4 个方面着手：(1) 利用已有的技术手段挖掘逆境胁迫下 WRKYs 参与的其他调控途径；(2) 进一步探究 WRKYs 上下游调控因子和靶标基因，解析逆境胁迫响应调控网络；(3) 挖掘更多物种中 WRKYs 结构域新型变异体并深入探索是否会对其参与调控逆境胁迫响应造成影响；(4) 利用过量表达、基因编辑、RNA 干扰等技术，培育抗逆优良作物新品种，促进农业可持续发展。

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