

WRKY transcription factors (TFs): Molecular switches to regulate drought, temperature, and salinity stresses in plants

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Abstract

The WRKY transcription factor (TF) belongs to one of the major plant protein superfamilies. The WRKY TF gene family plays an important role in the regulation of transcriptional reprogramming associated with plant stress responses. Change in the expression patterns of WRKY genes or the modifications in their action; participate in the elaboration of numerous signaling pathways and regulatory networks. WRKY proteins contribute to plant growth, for example, gamete formation, seed germination, post- germination growth, stem elongation, root hair growth, leaf senescence, flowering time, and plant height. Moreover, they play a key role in many types of environmental signals, including drought, temperature, salinity, cold, and biotic stresses. This review summarizes the current progress made in unraveling the functions of numerous WRKY TFs under drought, salinity, temperature, and cold stresses as well as their role in plant growth and development.

KEYWORDS

WRKY TFs, drought-stress, salinity-stress, temperature-stress, cold-stress, plant development and growth, plants/crops

Introduction

Structural features and homology of the WRKY TFs

S. No	Name of plant	Number of WRKY TF gene
1	<i>A. thaliana</i>	74
2	<i>B. distachyon</i>	81
3	<i>C. sinensis</i>	51
4	<i>C. clementina</i>	48
5	<i>D. carota</i>	38
6	<i>G. max</i>	179
7	<i>J. curcas</i>	58
8	<i>M. esculenta</i>	117
9	<i>M. domestica</i>	123
10	<i>M. notabilis</i>	54
11	<i>O. sativa Indica</i>	116
12	<i>O. sativa japonica</i>	137
13	<i>P. vulgaris</i>	88
14	<i>P. trichocarpa</i>	119
15	<i>S. lycopersicum</i>	79

16	<i>S. tuberosum</i>	82
17	<i>V. vinifera</i>	98
18	<i>Z. mays</i>	180

Drought stress-related WRKY TFs

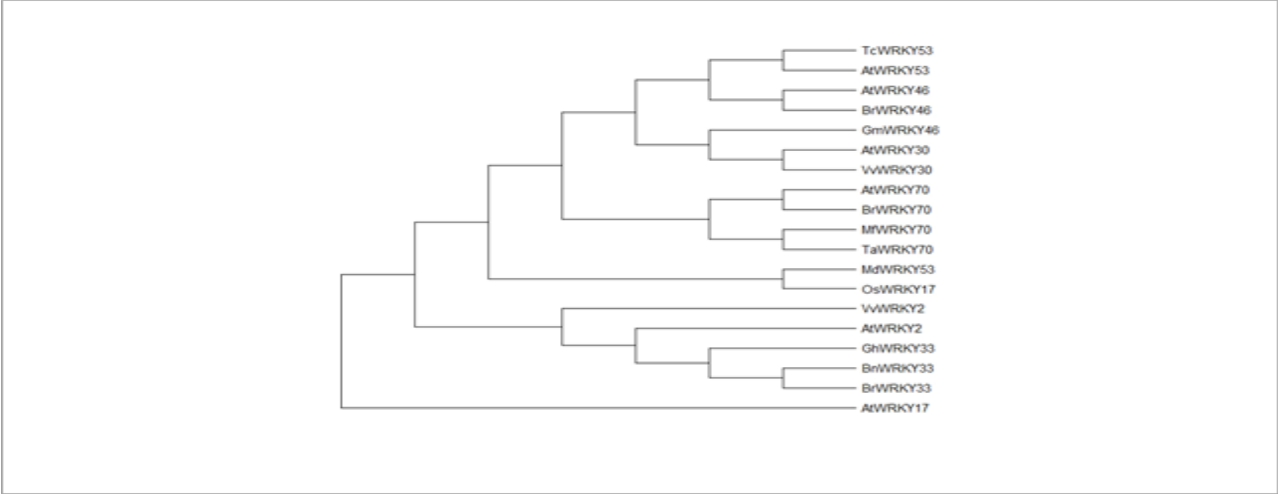


FIGURE 1 Neighbor-joining phylogeny of WRKY-related protein. MEGA X reconstructed the neighbor-joining phylogeny with 1000 bootstrap replicates and used maximum composite likelihood.

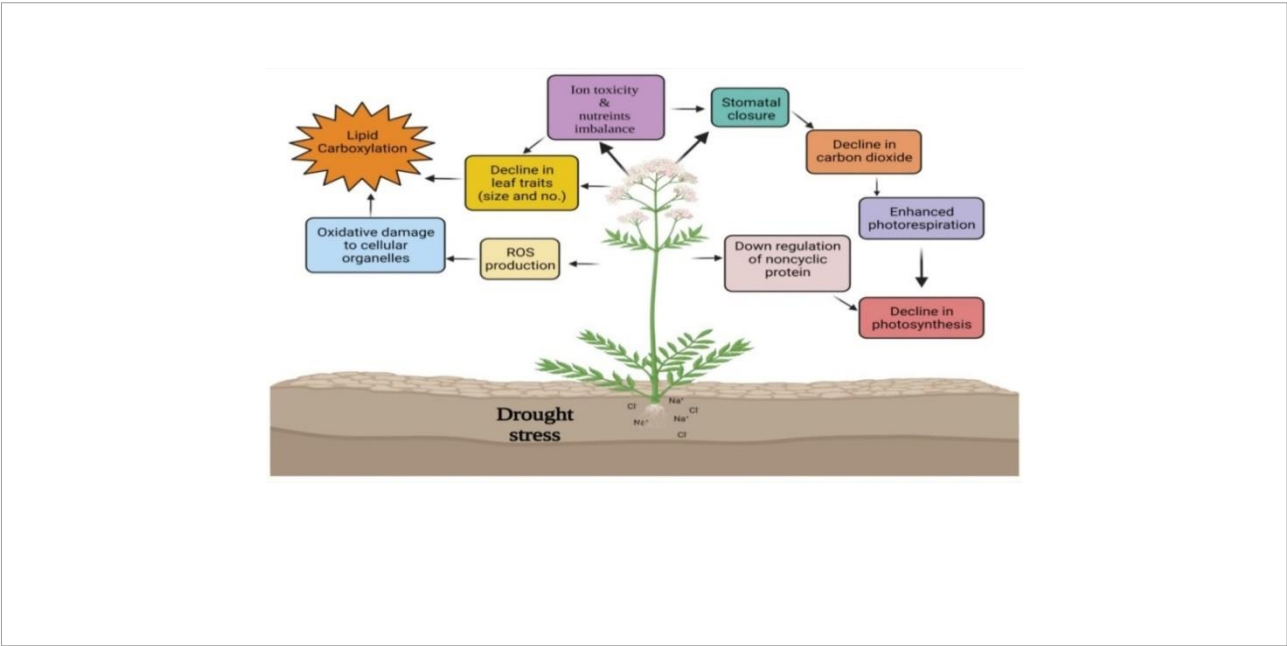


FIGURE 2. Effect of drought stress and the role of WRKY TFs in mitigating drought stress. Drought stress causes ROS production, oxidative damage, ion toxicity, and nutrient imbalance impairing plant growth and development. WRKY TFs regulate the expression of stress response genes and ROS scavenging enzymes. Overexpression of various WRKY TFs reduces ion loss and ROS accumulation, induces leaf stomatal mobility, decreases water loss rate thereby promote water retention, which overall improves phenotypic morphology and plant survival.

TABLE 2 Drought Stress-related WRKY TFs in plants.

S. No.	Gene	Species	Tolerance to stress	Reference
1	<i>AtWRKY53</i>	<i>A. thaliana</i>	drought	(Jiang et al., 2012)
2	<i>SIWRKY81</i>	<i>S. lycopersicum</i>	drought	(Ahmed et al., 2020)
3	<i>GhWRKY33</i>	<i>G. hirsutum</i> L.	drought	(Wang et al., 2019)
4	<i>SIWRKY72</i>	<i>S. lycopersicum</i>	drought	(Karkute et al., 2018)
5	<i>MuWRKY3</i>	<i>M. uniflorum</i> lam.verdc.	drought	(Kiranmai et al., 2018)
6	<i>TaWRKY2</i>	<i>T. aestivum</i> L.	drought	(Gao et al., 2018)
7	<i>TaWRKY1/33</i>	<i>T. aestivum</i> L.	drought	(He et al., 2016)
8	<i>ZmWRKY40</i>	<i>Z. mays</i>	drought	(Wang et al., 2018b)
9	<i>SbWRKY30</i>	<i>S. bicolor</i>	drought	(Yang et al., 2020)
10	<i>AtWRKY30</i>	<i>A. thaliana</i>	drought	(El-Esawi et al., 2019)
11	<i>VIWRKY48</i>	<i>CV.kyoho</i>	drought	(Zhao et al., 2018a)
12	<i>XsWRKY20</i>	<i>X. sorbifolium</i>	drought	(Xiong et al., 2020)
13	<i>GhWRKY41</i>	<i>G. hirsutum</i> L.	drought	(Chu et al., 2015)
14	<i>ZmWRKY106</i>	<i>Z. mays</i>	drought	(Wang et al., 2018a)
15	<i>VfWRKY1/2</i>	<i>V. faba</i> L.	drought	(Abid et al., 2017)
16	<i>AhWRKY</i>	<i>A. hypogaea</i> L.	drought	(Zhao et al., 2020b)
17	<i>VvWRKY13</i>	<i>V. vinifera</i> L.	drought	(Hou et al., 2020)
18	<i>BdWRKY36</i>	<i>B. distachyon</i>	drought	(Sun et al., 2015)
19	<i>GhWRKY27a</i>	<i>G. hirsutum</i>	drought	(Yan et al., 2015)
20	<i>MbWRKY1</i>	<i>M. baccata</i> L.	drought	(Han et al., 2018a)
21	<i>SpWRKY1</i>	<i>Phy. infestans</i>	drought	(Li et al., 2015)
22	<i>EjWRKY17</i>	<i>E. japonica</i>	drought	(Wang et al., 2021a)
23	<i>PheWRKY86</i>	<i>Phy. edulis</i>	drought	(Wu et al., 2022a)
24	<i>BoWRKY10</i>	<i>B. oleracea</i> var. <i>A. DC</i>	drought	(Guo et al., 2021)
25	<i>TaWRKY46</i>	<i>T. aestivum</i> L.	drought	(Yu and Zhang, 2021)
26	<i>OsWRKY5</i>	<i>O. sativa</i>	drought	(Lim et al., 2021)
27	<i>CsWRKY26</i>	<i>C. sinensis</i>	drought	(Chen et al., 2021)

Temperature stress-related WRKY TFs

TABLE 3 Temperature stress-related WRKY TFs.

S. No.	Gene	Species	Tolerance to stress	References
1	<i>AtWRKY30</i>	<i>A. thaliana</i>	temperature	(El-Esawi et al., 2019)
2	<i>AtWRKY46</i>	<i>A. thaliana</i>	temperature	(Suzuki et al., 2005)
3	<i>OsWRKY77</i>	<i>O. Sativa</i>	temperature	(Lan et al., 2013)
4	<i>CaWRKY27</i>	<i>C. annuum</i>	temperature	(Dang et al., 2018)
5	<i>CaWRKY40</i>	<i>C. annuum</i>	temperature	(Dang et al., 2013)
6	<i>AtWRKY41</i>	<i>A. thaliana</i>	temperature	(Ding et al., 2014)
7	<i>TaWRKY70</i>	<i>T. aestivum</i>	temperature	(Wang et al., 2017)
8	<i>AtWRKY54</i>	<i>A. thaliana</i>	temperature	(Li et al., 2020b)
9	<i>PtWRKY13</i>	<i>P. tomentosa</i>	temperature	(Ren et al., 2019)
1	<i>PtWRKY50</i>	<i>P. tomentosa</i>	temperature	(Ren et al., 2019)
0				
1	<i>ZmWRKY106</i>	<i>Z. mays</i>	temperature	(Wang et al., 2018a)
1	<i>AtWRKY39</i>	<i>A. thaliana</i>	temperature	(Li et al., 2010b)
2				
1	<i>AtWRKY72</i>	<i>A. thaliana</i>	temperature	(Cheng et al., 2021)
3				
1	<i>AtWRKY7</i>	<i>A. thaliana</i>	temperature	(Park et al., 2005)
4				
1	<i>AtWRKY8</i>	<i>A. thaliana</i>	temperature	(Han et al., 2015)
5				
1	<i>AtWRKY15</i>	<i>A. thaliana</i>	temperature	(Han et al., 2015)
6				
1	<i>AtWRKY26</i>	<i>A. thaliana</i>	temperature	(Fu and Yu, 2010)
7				
1	<i>AtWRKY33</i>	<i>A. thaliana</i>	temperature	(Fu and Yu, 2010)
8				
1	<i>TaWRKY1</i>	<i>T. aestivum</i>	temperature	(Ren et al., 2019)
9				
2	<i>NtWRKY6</i>	<i>N. tabacum</i>	temperature	(Macková et al., 2013)
0				
2	<i>HaWRKY6</i>	<i>H. annuus</i>	temperature	(Giacomelli et al., 2012)
1				
2	<i>CIWRKY20</i>	<i>C. lanatus</i>	temperature	(Zhu et al., 2022)
2				

Cold stress-related WRKY TFs**TABLE 4 Cold stress-related WRKY TFs**

S. No.	Gene	Plant species	Factors	Responses	Reference
	<i>AtWRKY3</i> 4	<i>A. thaliana</i>	Cold	Play a role as a negative regulator in cold stress	(Zou et al., 2010)
	<i>VvWRKY24</i>	<i>V. vinifera</i>	Cold	Up-regulate regulation of hypothermia	(Wang et al., 2014b)
	<i>OsWRKY76</i>	<i>O. sativa</i>	Cold	Tolerance to cold	(Yokotani et al., 2013)
	<i>BcWRKY46</i>	<i>B. campestris</i>	Cold and Salt	Drought and salt tolerance	(Wang et al., 2012)
	<i>VbWRKY32</i>	<i>V. bonariensis</i>	Cold	Tolerance to cold stress	(Wang et al., 2020)
	<i>GmWRKY2</i> 1	<i>G. max</i>	Cold, Drought,	Tolerance to cold stress	(Zhou et al., 2008)
	<i>VpWRKY2</i>	<i>V. pseudoreticulata</i>	Cold, ABA, and Salt	Tolerance to cold and salt stress	(Li et al., 2010a)
	<i>TcWRKY53</i>	<i>T. caerulea</i>	Cold, NaCl, and PEG	Play a role as a negative regulator in osmotic stress	(Wei et al., 2008)
	<i>JrWRKY2</i>	<i>J. regia</i>	Cold and Drought	Cold and drought tolerance	(Yang et al., 2017)
	<i>JrWRKY7</i>	<i>J. regia</i>	Cold and Drought	Tolerance to cold and drought stress	(Yang et al., 2017)
	<i>LchiWRKY</i> 33	<i>L. chinense</i> (<i>Lchi</i>)	Cold	Tolerance to cold stress	(Wu et al., 2022b)

Salinity stress-related WRKY TFs**Table 5 Salinity stress-related WRKY TFs**

S. No.	Gene	Plant species	Tolerance to stress	Reference
	<i>FcWRKY7</i> 0	<i>F. crassifolia</i>	Salt	(Wang et al., 2007)
	<i>GmWRKY</i> 17	<i>G. max</i>	Salt	(Yan et al., 2014)
	<i>ZmWRKY</i> 17	<i>Z. mays</i>	Salt	(Cai et al., 2017)
	<i>SbWRKY3</i> 0	<i>S. bicolor</i>	Salt	(Yang et al., 2020)
	<i>GbWRKY1</i>	<i>G. barbadense</i>	Salt	(Luo et al., 2020)
	<i>IbWRKY4</i>	<i>I. batatas</i>	Salt	(Qin et al., 2020)

	7			
	<i>PgWRKY3</i>	<i>P. glaucum</i>	Salt	(Chanwala et al., 2020)
	3/62			
	<i>SbWRKY5</i>	<i>S. bicolor</i>	Salt	(Song et al., 2020b)
	0			
	<i>VpWRKY</i>	<i>V. pseudoreticulata</i>	Salt	(Li et al., 2010a)
	1			
	<i>VpWRKY</i>	<i>V. pseudoreticulata</i>	Salt	(Li et al., 2010a)
(	2			
	<i>MbWRKY</i>	<i>M. baccata</i>	Salt	(Han et al., 2018b)
1	5			
	<i>CmWRKY</i>	<i>C. pepo</i>	Salt	(Bankaji et al., 2019)
2				
	<i>PbWRKY4</i>	<i>P. betulaefolia</i>	Salt	(Lin et al., 2022)
3	0			
	<i>ClWRKY2</i>	<i>C. Lanatus</i>	Salt	(Zhu et al., 2022)
4	0			
	<i>MxWRKY</i>	<i>M. xiaojinensis</i>	Salt	(Han et al., 2021b)
5	53			
	<i>MxWRKY</i>	<i>M. xiaojinensis</i>	Salt	(Han et al., 2021a)
6	64			
	<i>AhWRKY7</i>	<i>A. hypogaea L.</i>	Salt	(Zhu et al., 2021)
7	5			
	<i>MfWRKY7</i>	<i>M. Flabellifolia</i>	Salt	(Xiang et al., 2021)
8	0			

WRKY TFs as key regulators in plant growth and development

TABLE 6 Role of WRKY TFs in plant growth and development.

Name	Plant	Function	References
<i>VvWRKY30</i>	<i>V. vinifera</i>	Increasing salt stress resistance by ROS and accumulation of osmoticum.	(Zhu et al., 2019)
<i>GmWRKY12</i>	<i>G. max</i>	Drought and salinity tolerance	(Shi et al., 2018; Zhang et al., 2020)
<i>MdWRKY40</i>	<i>M. domestica</i>	Important regulators of wound-induced anthocyanin biosynthesis	(An et al., 2019)
<i>TaWRKY51</i>	<i>T. aestivum L.</i>	Promotes lateral root formation due to negative regulation of ethylene biosynthesis	(Hu et al., 2018)

<i>GhWRKY</i> 59	<i>G. hirsutum</i>	Drought responses	(Li et al., 2017a)
<i>HbWRKY</i> 82	<i>H. brasiliensis</i>	Abiotic resistance and leaf aging	(Kang et al., 2021)
<i>MjWRKY</i> 70	<i>M. Flabellifolia</i>	Drought and salinity tolerance	(Xiang et al., 2021)
<i>HmoWR</i> KY40	<i>H. monacanthus</i>	Betalain biosynthesis	(Zhang et al., 2021b)
<i>MxWRK</i> Y64	<i>M. xiaojinensis</i>	It plays an important role in response to Fe and salt stress	(Han et al., 2021a)
<i>AhWRKY</i> 75	<i>A. hypogaea L</i>	Conferred salt tolerance in transgenic peanut lines	(Zhu et al., 2021)
<i>BoWRKY</i> 10	<i>B. oleracea</i> var.acephalaDC	Regulation of drought stress tolerance	(Guo et al., 2021)
<i>AtWRKY</i> 28	<i>A. thaliana</i>	Oocyte development	(Zhao et al., 2018b)
<i>AtWRKY</i> 2	<i>A. thaliana</i>	Seed germination, growth after germination	(Jiang and Yu, 2009)
<i>AtWRKY</i> 10	<i>A. thaliana</i>	The size of the seed	(Luo et al., 2005)
<i>AtWRKY</i> 34	<i>A. thaliana</i>	Seed germination, growth after germination	(Guan et al., 2014)
<i>AtWRKY</i> 41	<i>A. thaliana</i>	The dormancy of seed	(Ding et al., 2014)
<i>AtWRKY</i> 44	<i>A. thaliana</i>	In the proanthocyan seed coat of tannins	(Gonzalez et al., 2016)
<i>OsWRKY</i> 78	<i>O. sativa</i>	The development of seed and stem elongation	(Zhang et al., 2011a)
<i>OsWRKY</i> 24	<i>O. sativa</i>	Increased lamina inclination and grain size through cell elongation.	(Jang and Li, 2018)
<i>GhWRKY</i> 42	<i>G. hirsutum</i>	Premature leaf senescence and stem development	(Gu et al., 2018)
<i>AtWRKY</i> 23	<i>A. thaliana</i>	Root growth and biosynthesis of flavanols	(Grunewald et al., 2012)
<i>GhWRKY</i> 91	<i>G. hirsutum</i>	Leaf senescence and stress response	(Gu et al., 2019b)
<i>OsWRKY</i> 93	<i>O. sativa</i>	Leaf senescence and in response to fungi attack	(Li et al., 2021)
<i>BrWRKY</i> 6	<i>B. rapa ssp.pekinensis</i>	Leaf senescence	(Fan et al., 2018)
<i>GhWRKY</i> 27	<i>G. hirsutum</i>	Leaf senescence	(Gu et al., 2019a)

<i>PyMYB1</i> 14	<i>Red-Skinned</i> <i>pears</i>	Regulate anthocyanin biosynthesis and transport	(Li et al., 2020a)
<i>WRKY6</i>	<i>A. thaliana</i>	Improve FA accumulation and seed yield	(Song et al., 2020a)
<i>T</i> <i>aWRK</i> <i>Y40-D</i>	<i>T. aestivum L.</i>	Association to the promotion of leaf senescence with jasmonic acid and abscisic acid	(Zhao et al., 2020a)
<i>WRKY46</i> /6	<i>A. thaliana</i>	PBZ/SA-mediated leaf senescence	(Zhang et al., 2021a)
<i>WRKY45</i>	<i>A. thaliana</i>	Positive regulator of age-triggered leaf senescence	(Chen et al., 2017)
<i>VvWRK</i> Y2	<i>V. vinifera</i>	Vigor, yield, and tuber quality	(Chiab, 2021)
<i>AtWRKY</i> 26	<i>A. thaliana</i>	Leaf senescence	(Li et al., 2017b)
<i>WRKY12</i> /13	<i>A. thaliana</i>	Regulate flowering time	(Li et al., 2016b)
<i>WRKY42</i>	<i>A. thaliana</i>	Root hair growth and development	(Moison et al., 2021)
<i>OsWRKY</i> 11	<i>O. sativa</i>	Flowering time and plant height	(Cai et al., 2014)
<i>AtWRKY</i> 45	<i>A. thaliana</i>	Play a key role in Phosphate uptake	(Wang et al., 2014a)
<i>AtWRKY</i> 42	<i>A. thaliana</i>	Play a great role in phosphate uptake	(Su et al., 2015)
<i>AtWRKY</i> 71	<i>A. thaliana</i>	Flowering time	(Yu et al., 2016)
<i>MxWRK</i> Y55	<i>M. xiaojinensis</i>	Tolerance to salt, low-iron and high-iron stress	(Han et al., 2020)

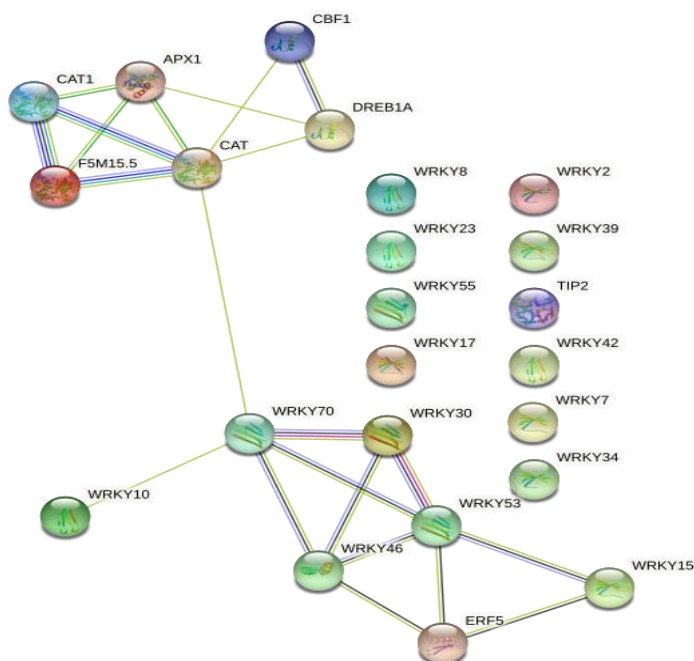


Figure 3. Interaction network analysis of WRKY genes identified in *Arabidopsis* by using STRING.

Conclusion and Future Perspective

Plants are considered as sessile organisms; they cannot avoid adverse abiotic stresses such as, drought, salinity, temperature, cold as well as other major environmental stresses and developed complex signaling networks, that are composed of several pathways. As one of the largest TF families, WRKY TFs act as molecular switches and regulate expression of stress responsive genes. The stress-inducible expression of WRKY TFs in order is regulated via complex transcriptional regulatory network that allows plants to continue a reasonable balance among growth and stress response. This review about the WRKY TFs discussed recent studies above shows that plenty of WRKY TFs play significant roles in abiotic stress tolerance, whose applications are likely to make a great improvement in crop breeding (**Figure 4**). Now days the sequencing of plant genomes has increased largely, especially in economically important crops. It has been indicated that (related to functional genes in plants), the genome wide identification of WRKY genes will facilitate screening, furthermore former studies identified that WRKY genes were mostly reliant on transcriptomics as well as functional predications. In addition, genetic confirmations joint to latest technologies are increasing the WRKY genes novel roles, whereas representation of the down-stream genes regulated via WRKY TFs or Self-regulation of WRKY TFs will assist to simplify the regulatory network of abiotic stress responses. In future studies, noncoding RNAs as well as epigenetic modifications needs to be explored, because these are involved in the regulation of WRKY TFs. At present, studies on the role of WRKY TFs in the regulation of plant responses to abiotic stress specifically related to drought, salinity and temperature stress is not satisfactorily detailed specially on transcriptional level. Finally, in context to aggravated climate change via using WRKY TFs screen for plant stress-resistance will significantly benefit agricultural crop yield as well as quality.

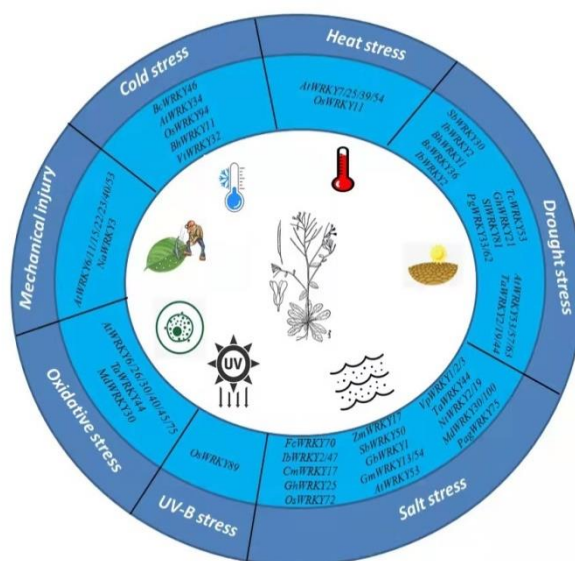


Figure 4. Response of WRKY transcription factors to abiotic stresses

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