

REVIEW

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WUSCHEL-related homeobox (WOX) transcription factors: key regulators in combating abiotic stresses in plants

Faiza Shafique Khan^{1,2}, Farhan Goher³, Chun Gen Hu¹ and Jin Zhi Zhang^{1*}

Abstract

The *WUSCHEL*-related homeobox (*WOX*) transcription factors (TFs) belong to the homeodomain (HD) family. *WOX* TFs are involved in various regulatory pathways related to plant growth and development. In addition to their recognized role in various development processes, many reports suggest that they play a key role in abiotic stress perception in plants. However, their underlying molecular mechanisms have rarely been studied in horticultural crops. *WOX*s govern the transcription of the target genes through specific binding to the *cis*-regulatory elements present in their promoters. Additionally, they associate with other factors to form a specific pathway regulating numerous abiotic stress responses. Here, we review the recent advances in the multifaceted functions of *WOX*s in the complex, developmental, and abiotic stress-sensing networks, with particular emphasis on regulating the related genes and other TFs. In addition, we suggest that *WOX*s are essential components of the gene regulatory networks involved in the response of plants to abiotic stress tolerance and aim to provide a reference for future research.

Keywords Abiotic stress, *WOX*, Transcription factors, Gene regulation, Tolerance

Introduction

Plants are sessile and highly sensitive to changing climatic conditions. Owing to climate change and the threat of global warming, it has been estimated that abiotic stresses such as drought, salinity, freezing, and extreme temperature fluctuations will affect commercial agricultural production by up to 50% by the end of this century (FAO 2015). Abiotic stresses can reduce horticultural

crop production and cause yield losses ranging from 50% to 70% (Francini and Sebastiani et al. 2019). Salinity affects almost 20%–30% of arable soils (Thorne et al. 2020). Heat and drought severely impact plant growth and reproductivity due to reactive oxygen species (ROS) imbalance, cell damage, and protein degradation (Devireddy et al. 2021; Wang and Zhu 2022; Khan et al. 2022a). Plants have evolved various adaptive strategies to cope with long-term abiotic stresses through regulatory mechanisms. In this scenario, producing high-yield horticultural crop varieties requires an improved understanding of gene regulatory functions involving development and abiotic stress response.

Stress-tolerant plants display a vast network of regulatory mechanisms, including reprogramming the expression of various genes at the transcriptional and post-transcriptional levels. These regulations are essential for plants to restore cell homeostasis during recovery. Transcription factors (TFs) are prime players at the transcriptional and post-transcriptional levels (Kumar et al.

*Correspondence:

Jin Zhi Zhang
jinzhizhang@mail.hzau.edu.cn

¹ National Key Laboratory for Germplasm Innovation & Utilization of Horticultural Crops, College of Horticulture and Forestry Science, Huazhong Agricultural University, Wuhan 430070, People's Republic of China

² Hainan Yazhou Bay Seed Laboratory/Sanya Research Institute of Chinese Academy of Tropical Agricultural Sciences, Sanya 572000, Hainan, People's Republic of China

³ State Key Laboratory of Crop Stress Biology for Arid Areas, College of Plant Protection, Northwest A&F University, Yangling 712100, Shaanxi, People's Republic of China



2021). Many important TFs, such as *NAC*, *WRKY*, *bZIP*, *NF-Y*, and *ERF*, have been identified through genome-wide studies (Wu et al. 2015; Banerjee and Roychoudhury 2017; Yang et al. 2018; Zhang et al. 2023). These TFs are involved in the responses of plants to abiotic stress and stress-specific transcriptional patterns linked to upstream signaling through TFs. Specific stresses such as drought, cold, and salinity can also induce common transcriptional responses (Ma and Bohnert 2007). For example, the *Arabidopsis thaliana* *NFYA5* (nuclear factor Y) was strongly influenced by drought-induced stress using the abscisic acid (ABA)-dependent pathway. *NFYA5* contains a *miR169* binding site (CCAAT), which targets the translational repression of mRNAs; *miR169* was down-regulated by drought-induced stress in an ABA-dependent manner. *NFYA5* regulated drought-induced stress at the transcriptional and post-transcriptional levels and induced drought tolerance (Li et al. 2008).

WUSCHEL-related homeobox (*WOX*) TFs also play an essential role in the transcriptional and post-transcriptional regulation of genes involved in the developmental processes in plants. In rice, *OsWOX3B* and *OsSPL10* regulated the expression pattern of *HEARY LEAF6* (*HL6*); *OsWOX3B* and *OsSPL10* interact and subsequently impact the transcription of *HL6*, which is essential for developing trichomes (Liao et al. 2023). Trichomes play a positive role in providing resistance against biotic and abiotic stresses (Liao et al. 2023). Additionally, *OsWOX3B* and *HL6* modulated the expression of various genes involved in auxin (indole acetic acid; IAA) biosynthesis and signaling, including *AUXIN RESPONSE FACTOR 4* (*OsARF4*), *PIN-FORMED1a* (*OsPIN1a*), and *Tryptophan aminotransferases 5* (*OsYUCCA5*). *HL6* binds to the promoter of *OsYUCCA5* and the *OsWOX3B*-*HL6* interaction enhances the binding property (Sun et al. 2017). Current research on plant *WOX* TFs has focused on developmental regulation.

WOXs are differentially expressed under abiotic stresses in horticultural crops such as tomato (*Solanum lycopersicum*), citrus (*Citrus sinensis*), apple (*Malus domestica*), and banana (*Musa acuminata*) (Li et al. 2021; Khan et al. 2021; Chaudhary et al. 2022; Lv et al. 2023). For example, tomato *SlWOXs* showed robust, differential expression patterns under cold, NaCl, and drought predicting a significant role in abiotic stress response (Li et al. 2021). Overexpression of *MdWOX13-1* in apple calli increased ROS scavenging and weight (Lv et al. 2023). *MdWOX13-1* directly bound to the promoter of *MdSOD* and enhanced ROS scavenging in response to drought (Lv et al. 2023). Various gene regulatory mechanisms are involved in the fight for survival and play a significant role in the changes in horticultural plants during abiotic stresses.

Previous reviews have illustrated the responses of plants for survival under abiotic stresses (Estravis-Barcala et al. 2020; Saijo and Loo 2020; Khan et al. 2023a, b). Some abiotic stress-responsive families of TFs, such as *WRKY*, *NAC*, *AP2/ERF*, and *MYB*, are ideal candidates for genome editing and genetic improvement to enhance resistance against abiotic stresses (Wang et al. 2016). Thus, understanding the underlying molecular mechanisms in horticultural crop production is essential. The mechanism through which *WOXs* perform their functional roles, including interaction with partners to target promoters, is still not precise. Hence, this review focuses on the regulatory pathways behind the association of the *WOX* family and resistance abiotic stresses and development in horticultural plants. This can further demonstrate the functional identification of gene regulatory mechanisms to customize the genetic improvement in crops, providing a central platform for future research.

Identification and classification of *WOX* TFs

WOXs belong to the homeodomain (HD) family of TFs (Xu et al. 2019). They are divided into 14 subfamilies, including PINTOX, NDX (NODULIN homeobox), KNOX (KNOTTED like homeobox), BELL (BELL like homeodomain), *WOX* (*WUSCHEL* related homeobox), SAWADEE homeodomain, HD-ZIP I-IV (homeodomain leucine zipper), ZF-HD (zinc finger homeodomain), DDT (homeodomain-DDT), LD (luminidependens homeodomain), and PHD (plant homeodomain with a finger domain) (Jain et al. 2008; Mukherjee et al. 2009; Bürglin and Affolter 2016; Xu et al. 2019). HDs bind with DNA as monomers with high affinity mediated *via* interactions through the helix-turn-helix (HTH) structure. The HD in the N-terminal of *WOXs* is conserved in plants (Sun et al. 2023; Zhang et al. 2023; Galibina et al. 2023; Xu et al. 2023; Yang et al. 2023; Tang et al. 2023; Riccucci et al. 2023). The other regions of *WOXs* are highly divergent in their sequences. The C-termini of *WOXs* comprise a distinct WUS box motif “TLXLFP”, where X can be any amino acid that locates the C-terminal to the HDs and ERF-linked amphiphilic repression (EAR)-like motif “SLELRLN” (Park et al. 2005; van der Graaff et al. 2009; Zhang et al. 2010; Chen et al. 2023; Youngstrom et al. 2022). The WUS-box is specific to the WUS clade members and functions as an activator and contains a C-terminal EAR domain that involves transcriptional repression (van der Graaff et al. 2009; Mukherjee et al. 2009; Lin et al. 2013). EAR-motif interacts with TOPLESS (TPL)/TPL-related (TPR) corepressor to repress the transcription of auxin-responsive genes (Szemenyei et al. 2008). This family was identified in various horticultural plants and fruit-bearing trees (Table 1) (Khan et al. 2021; Xu et al. 2022; Chaudhary et al. 2022). Using

Table 1 The number of *WOXs* identified in plants and fruit trees

Common names	Latin names	No. of <i>WOXs</i> identified	References
Sweet orange	<i>Citrus sinensis</i>	11	(Khan et al. 2021)
Pear	<i>Pyrus bretschneideri</i>	9	(Cao et al. 2017)
Walnut	<i>Juglans regia</i> L.	12	(Chang et al. 2019)
Apple	<i>Malus domestica</i> Borkh.	18	(Xu et al. 2022)
Tea plant	<i>Camellia sinensis</i>	18	(Wang et al. 2019)
Loquat	<i>Eriobotrya japonica</i>	18	(Yu et al. 2022)
Grapes	<i>Vitis vinifera</i>	11	(Li et al. 2017)
Peach	<i>Prunus persica</i>	10	(Cao et al. 2017)
Chinese plum	<i>Prunus mume</i>	10	(Cao et al. 2017)
Kiwi	<i>Actinidia chinensis</i>	17	(Feng et al. 2021)
Kiwi	<i>Actinidia eriantha</i>	11	(Feng et al. 2021)
Coffee	<i>Coffea arabica</i> L.	7	(Daude et al. 2020)
Passion flower	<i>Passiflora organensis</i>	19	(da Silva et al. 2018)
Strawberry	<i>Fragaria vesca</i>	16	(Yang et al. 2022)
Banana	<i>Musa acuminata</i>	13	(Chaudhary et al. 2022)
Mulberry	<i>Broussonetia kazinoki</i> × <i>B. papyrifera</i>	10	(Tang et al. 2017)
Pineapple	<i>Ananas comosus</i> L.	10	(Rahman et al. 2017)
Tomato	<i>Solanum lycopersicum</i>	10	(Li et al. 2021)
Blueberry	<i>Vaccinium corymbosum</i> L.	29	(Gao et al. 2021)

phylogenetic analysis and evolutionary relationships, the *WOX* family is grouped into three clades: ancient, WUS/modern, and intermediate (Rahman et al. 2017; Alvarez et al. 2018; Chang et al. 2019; Tang et al. 2020; Daude et al. 2020; Khan et al. 2021; Feng et al. 2021; XU et al. 2022; Galibina et al. 2023; Xu et al. 2023; Yang et al. 2023; Tang et al. 2023; Riccucci et al. 2023) (Fig. 1). The ancient clade represents conserved *WOXs* found in the genomes of algae to angiosperms which includes three genes, *WOX10*, *13*, and *14* in *Arabidopsis*. *WOX8/WOX9* and *WOX11/12* from the intermediate clade are involved in developmental processes such as embryogenesis and regeneration into *Arabidopsis*. The *WOXs* in the modern clade contain HD and WUS motifs, which are essential for normal functioning. They include *WUS*, *WOX5*, and *WOX7*, which contain the EAR-motif domain with specific repressor activity (Feng et al. 2021; Li et al. 2022; Yang et al. 2022; Sun et al. 2023; Zhang et al. 2023).

In *Arabidopsis*, 15 *WOXs* that synergistically participate in the regulatory mechanisms of various developmental processes, such as stem cell proliferation and maintenance, shoot apical meristem (SAM), and root apical meristem (RAM) development, and organ formation (Haecker et al. 2004; van der Graaff et al. 2009). Recently, 127 *WOXs* have been identified in eleven cucurbit crops such as snake gourd (*Trichosanthes anguina*), monk fruit (*Siraitia grosvenorii*), chayote (*Sechium edule*), wax gourd (*Benincasa hispida*), sponge gourd (*Luffa cylindrica*), bottle gourd (*Lagenaria siceraria*), bitter gourd

(*Momordica charantia*), pumpkin (*Cucurbita maxima*), melon (*Cucumis melo*), watermelon (*Citrullus lanatus*), and cucumber (*Cucumis sativus*) (Li et al. 2023). *WOXs* have also been identified in the genomes of other horticultural plants and woody perennials (Table 1). An overview of *WOXs* involved in plant growth and development in model plants is presented in Fig. 2.

***WOX*TFs are crucial for plant development**

Classically, developmental biology studies have mainly focused on *Arabidopsis* as a model plant. However, much progress has been made in analyzing the functions of various *WOXs* in different horticultural plants and woody perennials (Table 2). Generally, the *WOX* family plays a crucial role in shoot apical meristem (SAM) development, floral meristem identity, stem cell maintenance, flower organ formation, lateral root (LR) formation, cell differentiation, somatic embryogenesis, and somatic embryo development (Klimaszewska et al. 2011; Tvorogova et al. 2021; Willoughby and Nimchuk 2021). The *WOX* family regulates developmental processes-related regulatory mechanisms and is well-documented in model plants (Fig. 2). The combined activities of *WOXs* regulated tissue proliferation and embryogenic development in *Arabidopsis* (Wu et al. 2007). *AtWUS* was involved in stem cell and floral meristem identities and regulated SAM maintenance (Laux et al. 1996; Mayer et al. 1998). The *AtWUS* homolog in pineapple (*Ananas comosus* L.) *AcoWUS* is highly conserved functionally and significantly regulates

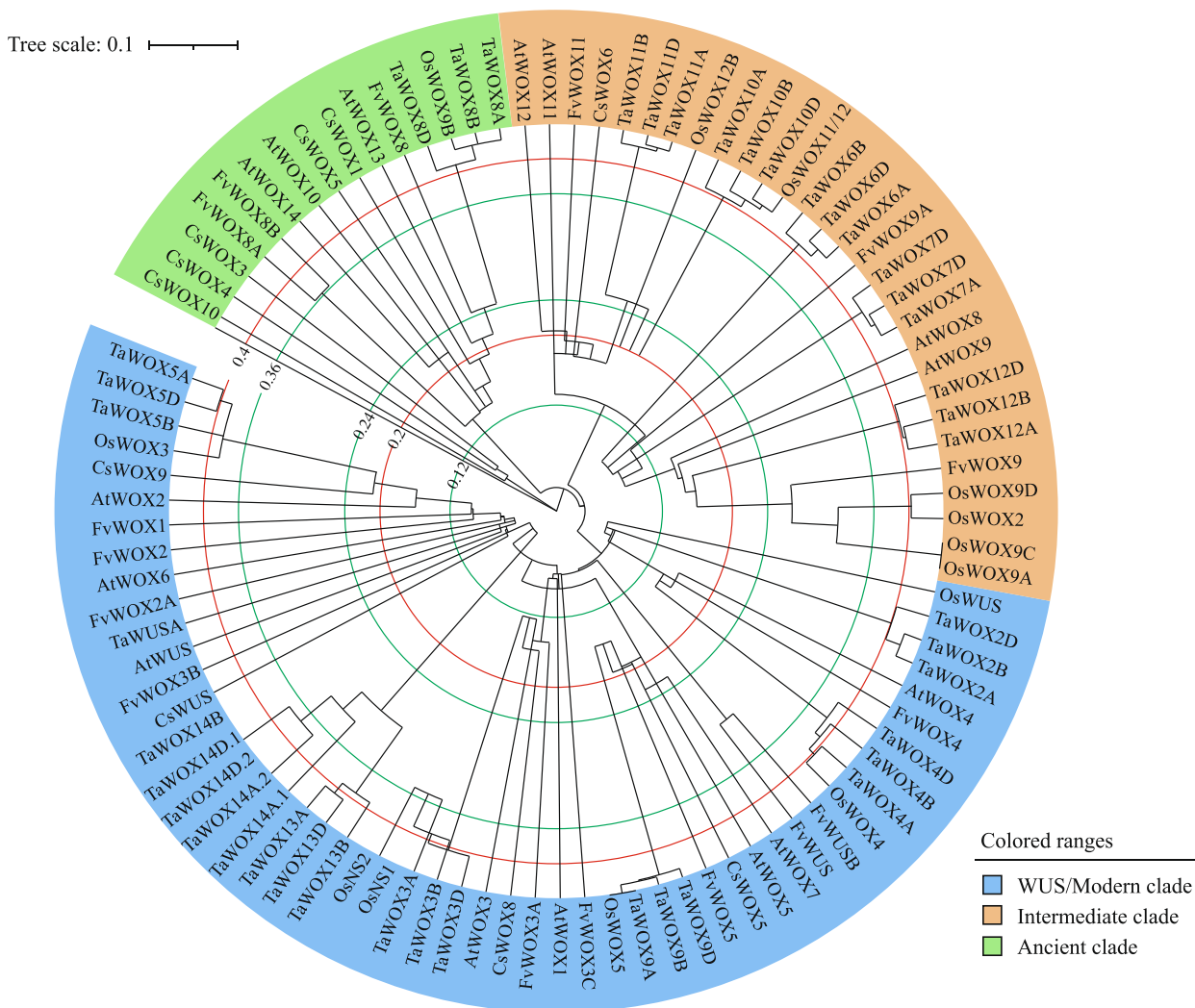


Fig. 1 A midrooted phylogenetic tree of the WUSCHEL-related homeobox (WOX) transcription factor family using various classified plant species such as *Arabidopsis*, strawberry (*Fragaria vesca*), sweet orange (*Citrus sinensis*), rice (*Oryza sativa* L.), and wheat (*Triticum aestivum* L.) (Khan et al. 2021; Yang et al. 2022; Li et al. 2020) was constructed using Clustal Omega (www.ebi.ac.uk/Tools/msa/clustalo/). The tree was drawn using Interactive Tree of Life (IToL) v. 6 (<https://itol.embl.de/>). Scale bars correspond to 0.1 substitutions

female gametophyte development. Moreover, *WUS* positively regulated somatic embryogenesis in coffee (*Coffea canephora*) (Arroyo-Herrera et al. 2008) and dedifferentiation during somatic embryogenesis in coconut (*Cocos nucifera*) (Khan et al. 2023a, b). *C. sinensis* *CsWUS* stimulates stem cell proliferation in *Carrizo citrange*, whereas it regulates floral organ development in tobacco (Zhang et al. 2020; Khan et al. 2021). *CsWUS*-silencing in lemons induced thorn development and upregulated the expression of thorn identity-related genes (Khan et al. 2021). A recent study revealed that radish (*Raphanus sativus*) *RsWUS* plays an important role in shoot development. The *RESPONSE REGULATOR 18-1* (*RsRR18-1*) encoded protein binds to the *RsWUSb* promoter and

activates its expression. *RsRR18-1-WUSb* modulated shoot development in radish through the cytokinin (CK) signaling pathway (Hu et al. 2024). The Loquat (*Eriobotrya japonica*) *EjWUSa* when overexpressed in *Arabidopsis* promoted early flowering (Yu et al. 2022). *AtWOX1* regulated meristem and leaf blade development via the modulation of *CLAVATA3* (*CLV3*) expression (Vandenbussche 2021). Loss of function *wox1* mutation reduced leaf blade in *Petunia* and *Arabidopsis* (Vandenbussche et al. 2009). *PpWOX1* controlled cell division during the early stage of fruit development in pears (*Pyrus pyrifolia*) (Jiang et al. 2018). *CsWOX1* regulated early reproductive development in cucumber and directly interacted with *SPOROCTELESS* (*CsSPL*). *CsWOX1* stimulated

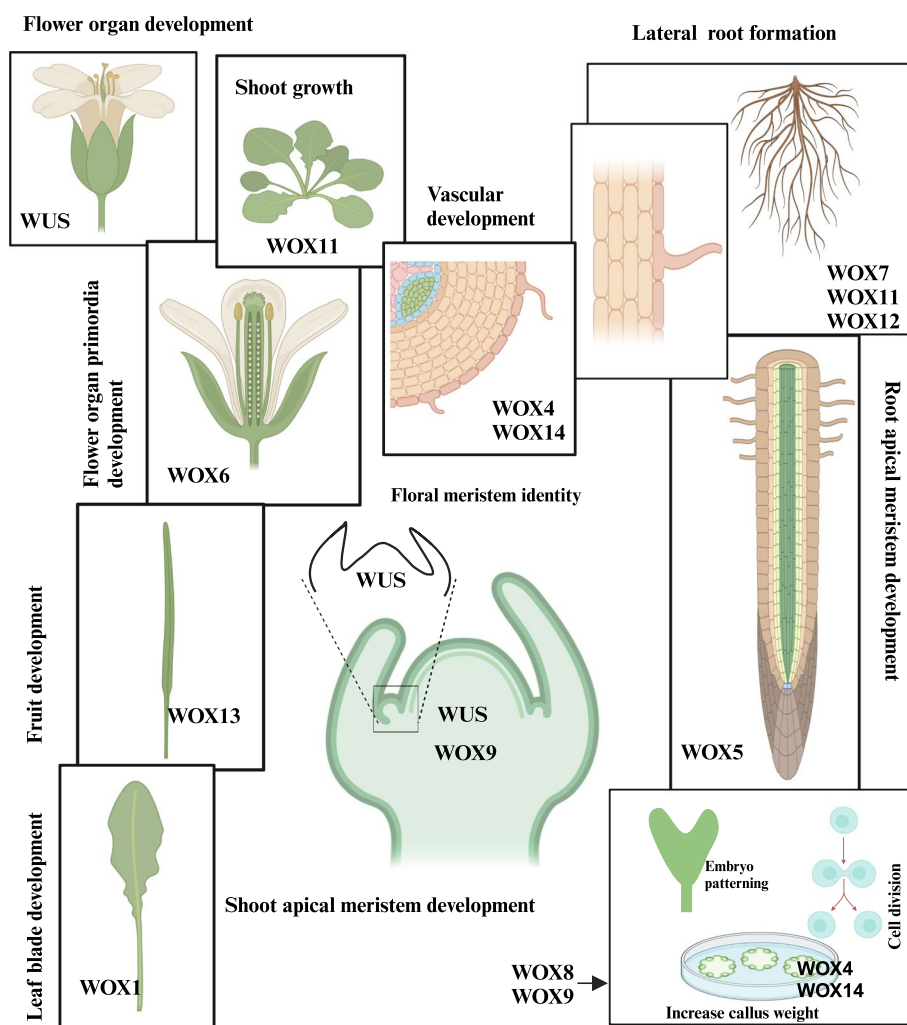


Fig. 2 A graphic representation of the role of the *WUSCHEL*-related homeobox (*WOX*) transcription factor family in plant development

sporogenesis through the *CsSPL*-based signaling pathway and modulated IAA signaling in cucumber (Niu et al. 2018). *AtWOX2* marked the apical cell line during embryo development and is highly expressed in the egg cell and zygote (Haecker et al. 2004). *AtWOX4* regulated cell division in vascular tissues, and *OsWOX4* regulated early leaf development in rice (Etchells et al. 2013; Yasui et al. 2018). In grapevine (*Vitis vinifera*), *VvWOX4* regulated stem cells (Ru et al. 2011). In blueberry (*Vaccinium corymbosum* L.), the expression of *VcWOX4b* was enhanced in the shoots and roots compared to other *VcWOXs*. Further, *VcWOX4b*-overexpression in tobacco inhibited adventitious root formation by modifying vascular cell division and differentiation. *VcWOX4b* regulated CK- and IAA- stimulated primary xylem cell differentiation by inhibiting adventitious root (AR) formation (Gao et al. 2021). *JrWOX5*, 9, and 11 play an essential role in AR formation and determining

root architecture in walnut (*Juglans regia* L.) (Chang et al. 2019; Chang et al. 2022). Apple (*M. domestica*) *MdWOX4* and *MdWOX4-2* are essential for AR and shoot development (Xu et al. 2022; Dong et al. 2022). *AtWOX5* is involved in RAM development; *wox5* mutation is involved in the reduction of LR development, enlargement and differentiation of columella cells, and the quiescent center (QC) (Sarkar et al. 2007). *AtWOX6* regulated the differentiation of megaspore mother cells and proliferation of internal integument and floral primordial cells (Park et al. 2005). *AtWOX7* is involved in initiating LR growth (Kong et al. 2016). *AtWOX8* and 9 are involved in embryonic development and maintain the basal and apical embryo lineages (Wu et al. 2007). Loss of function in *AtWOX8* and 9 causes abnormal cell division in the apical and basal domains of *Arabidopsis* plants (Breuninger et al. 2008). Similarly, grapevine *VvWOX9*, *VvWOX2*, and *VvWUS* are also involved

Table 2 The substantial role of the *WOX* genes in woody perennials and fruiting trees

Common names	Latin names	Genes	Gene functions	References
Citrus	<i>Citrus sinensis</i>	<i>CsWUS</i>	Regulate growth and development in citrus	(Khan et al. 2021)
	<i>Carrizo citrange</i>	<i>CsWUS</i>	Regulate stem cell proliferation	(Zhang et al. 2020)
		<i>CaWOX11-like</i>	May be involved in the embryogenic process	(Daude et al. 2020)
Grapes	<i>Vitis vinifera</i>	<i>VvWOX4</i>	Involved in stem cell regulation	(Ru et al. 2011)
		<i>VvWOX2, VvWOX9, VvWUS</i>	Involved in somatic embryogenesis	(Gambino et al. 2011)
		<i>VvWOX</i>	It may be regulated ovule development	(Li et al. 2017)
Apple	<i>Malus domestica</i>	<i>MdWOX4</i>	Adventitious root development	(Xu et al. 2022)
		<i>MdWOX4-2</i>	Involved in leaf-regenerated adventitious shoots	(Dong et al. 2022)
		<i>MdWOX11</i>	Involved in micro-shoot growth	(Tahir et al. 2022)
		<i>MdWOX11</i>	Regulates adventitious root formation	(Mao et al. 2023)
		<i>MdWOX13-1</i>	Increased callus weight	(Lv et al. 2023)
Pear	<i>Pyrus pyrifolia</i>	<i>MdWOX3, MdWOX13</i>	Involved in floral transition	(Li et al. 2019)
		<i>PpWOX1</i>	May be involved in cell division during the early stage of fruit development	(Jiang et al. 2018)
Pear	<i>Pyrus betulaefolia</i>	<i>PbWoxT1</i>	Involved in long-distance transport via phloem in scions	(Duan et al. 2016)
Pineapple	<i>Ananas comosus</i> L.	<i>AcoWUS</i>	Female gametophyte development	(Rahman et al. 2017)
Walnut	<i>Juglans regia</i> L.	<i>JrWOX5, JrWOX9, JrWOX11</i>	May be related to adventitious root formation	(Chang et al. 2019)
		<i>JrWOX11</i>	Regulate root architecture system	(Chang et al. 2022)
Jasmine	<i>Jasminum sambac</i>	<i>JaWOX1</i>	Involved in root differentiation in callus tissues	(Lu et al. 2019)
Rose	<i>Rosa canina</i>	<i>RcWOX1</i>	Promote lateral root density and rhizoid formation	(Gao et al. 2014)
Coconut	<i>Cocos nucifera</i>	<i>CnWUS</i>	Involved in dedifferentiation during somatic embryogenesis	(Khan et al. 2023a, b)

in somatic embryogenesis (Gambino et al. 2011). The cucumber *CsWOX9* regulated the formation of branches, rosette leaves, and shorter siliques in *Arabidopsis* (Gu et al. 2020). In Lily (*Lilium lancifolium*), overexpression of *LlWOX9* and *11* in stem segments promoted, whereas silencing them inhibited bulbil formation; CK-type B-response regulators bound to the promoters of *LlWOX9* and *11* and upregulated their expression (He et al. 2022). In *MdWOX11*-overexpressing (OE) transgenic plants, AR formation was inhibited; further analysis revealed that the endogenous levels of CK, IAA, and ABA were upregulated in *MdWOX11*-RNAi than in *MdWOX11*-OE transgenic plants (Mao et al. 2022).

In *Arabidopsis*, *AtWOX11* and *12* induced de novo root organogenesis and LR formation (Baesso et al. 2018; Liu et al. 2014), while *AtWOX13* was involved in fruit development and regulated replum (Romera-Branchat et al. 2013). However, *OsWOX13* in rice was involved in abiotic stress tolerance and early flowering (Minh-Thu et al. 2018). *AtWOX14* stimulated the development of conductive tissues and regulated flowering. Loss of function *wox14* mutation led to dwarfism and delayed flowering. *AtWOX14/4* regulated the proliferation of cells in the vascular tissue (Denis et al. 2017), demonstrating that *WOX* TFs had species-specific functional and developmental roles. This reason strongly favors the idea that

plant development biology in common would be beneficial by acting on multimodal approaches.

Regulatory mechanisms of *WOX* TFs in response to abiotic stresses

Abiotic stresses impede the development and growth of plants. As *WOX*s are involved in multiple aspects of plant development and stress responses, an in-depth research is necessary. Moreover, numerous hormones responsive motifs, ABRE abscisic acid-responsive motif, CGTCA-methyl jasmonate responsive motif, ERE-ethylene responsive motif, gibberellic acid responsive motifs (P-box, GARE-motif, and TATC-box) were identified in the promoters of *WOX*s. Auxin-responsive factors (ARFs) and the AUX/IAA-ARF pathway controlled the expression of *WOX*s by binding to Auxin Response Elements (AuxREs) in the *WOX* promoters (Ulmasov et al. 1997; Tiwari et al. 2003; Guan et al. 2017). CK triggered *WUS* expression via binding to the type-B ARABIDOPSIS RESPONSE REGULATORS (B-ARRs) to the B-ARR element in the *WUS* promoters (Wang et al. 2017). *WOX1* is involved in IAA signaling, biosynthesis, and transport. *WOX1* positively regulated *AUX1* and *PIN1*, whereas it negatively regulated *TRYPTOPHAN AMINOTRANSFERASE OF ARABIDOPSIS (TAA)/YUC CAS (YUC5)* and *Tryptophan aminotransferase related*

2 (*TAR2*) (Nakata et al. 2018). B-ARRs (*ARR10*) bound to the B-ARR motif in the promoters of *WOX11* and *12* (Zubo et al. 2017). Abiotic/biotic stress-responsive *cis*-regulatory elements (TC-rich repeats, LTR, and MBS) were also found in the *WOX* promoters (Chaudhary et al. 2022; Wang et al. 2019; Li et al. 2021; Khan et al. 2021; Akbulut et al. 2022). Thus, *WOX*s TFs are active in abiotic stress response in plants.

Expression and regulatory role of *WOX* TFs in response to salinity

The differential expression pattern of *WOX*s in response to abiotic stresses has been reported in many plants (Wang et al. 2019; Li et al. 2020, 2022; Khan et al. 2021; Chaudhary et al. 2022). Banana (*M. acuminata*) is a highly salt-sensitive crop, and *MaWOX*s are essential in the development and abiotic stress response. *MaWOX11* induced tolerance against drought in transgenic rice plants (Cheng et al. 2016). The expression of *MaWOX1*, *3*, and *9a* was markedly enhanced under drought. Furthermore, those of *MaWOX3*, *8a*, and *11b* were higher under 12 h of salinity treatment, while those of *MaWOX* were lower under cold-induced stress (Chaudhary et al. 2022). Expression patterns of *SlWOX3a*, *3b*, *4*, *5*, and *13* significantly changed under 1 h of treatment with NaCl, indicating that they may mediate NaCl-induced stress in tomato plants (Li et al. 2021).

JrWOX11 expression was unexpectedly induced after NaCl, ABA, and PEG treatments, indicating that it was highly responsive to salt- and osmotic-state-related stress. Overexpression of *JrWOX11* enhanced AR formation in walnuts (*J. regia* L.) and abiotic stress tolerance in 84 K poplar (Chang et al. 2022). *OsWOX11* bound to the *cis*-regulatory “TTAATGG/C” motif and directly activated the transcription of *OsLOB16*, *OsASR3*, and *OsFRDL1*. *WOX11* functioned intricately with stress-related genes, such as *OsWRKY24*, *OsTCP21*, *OsMTN3*, *OsERF922*, and *OsPP2C8* (Jiang et al. 2017). Moreover, the AP2/ERF-type gene *ETHYLENE RESPONSE FACTOR 3* (*ERF3*) was expressed during crown root development and interacted with *WOX11*. Both *ERF3* and *WOX11* target the CK signaling-related type *type-A ARABIDOPSIS RESPONSE REGULATORS* (*A-RR2*) gene. CK and IAA regulated *WOX11* expression, and *ERF3* regulated the expression of CK- and auxin-related genes. *ERF3* directly targeted *RR2* through the ERF binding site “GCCGCC” in its promoter and positively regulated its expression during root development (Zhao et al. 2015; Jiang et al. 2017). Moreover, *WOX11* was induced upon exogenous treatment with CK and directly inhibited the expression of *RR2*. The expression of CK-responsive genes elevated in the crown root tips of *wox11* mutants and *WOX11*

played an essential role in modulating the CK-based signaling and stress response (Jiang et al. 2017).

PagWOX11/12a regulated the genes involved in redox processes; *PagWOX11/12a* binds to the promoter of *PagCYP736A12* and regulates its expression (Fig. 3). *PagWOX11/12a*-overexpression lines of poplar showed increased salt tolerance *via* ROS scavenging by directly regulating *PagCYP736A12* (Wang et al. 2021). *SMALL AUXIN UP RNA36* (*SAUR36*) related to the early auxin-inducible gene family encodes an auxin-responsive protein involved in AR formation in poplar *via* auxin signaling under salt stress. Moreover, *PagWOX11/12a* bound to the *WOX*-binding motif “TTAATGG” located in the promoter of *SAUR36*, regulating its transcription, which increased during salt-induced stress (Liu et al. 2022). Overexpression or RNAi of *PagWOX11/12a-PagSAUR36* revealed that this module was essential for AR development during salt-induced stress *via* the IAA pathway (Liu et al. 2022). Further, identifying the regulatory mechanisms and target genes of the abiotic stress-responsive *WOX*s may unravel novel signaling pathways and help better understand the molecular mechanisms involved in response to abiotic stress.

Expression and regulatory role of *WOX* TFs in response to drought

During floral inductive water deficit conditions in sweet orange (*Citrus sinensis*), *CsWUS*, *CsWOX6*, and *CsWOX11* were not expressed; *CsWOX1*, *3*, *4*, and *5* were slightly expressed at the beginning of water deficit (Khan et al. 2021); and *CsWOX13* was upregulated (Khan et al. 2022a). In tomato, *SlWOX1*, *3a*, *3b*, *4*, *5*, and *9* were upregulated under drought treatment for 3 h (Li et al. 2021).

In tea plants, *CsWOX13*, *14*, and *15* were positively upregulated under drought- and cold-induced stress (Wang et al. 2019). The AP2/ERF family member, *CsRAP2.12* (Cs1g16690), encodes a TF that binds to the “GGCGGCC” *cis*-element in the promoter of *CsWUS* to regulate its expression. *CsRAP2.12* was also upregulated in sweet oranges under floral inductive water deficit conditions (Khan et al. 2021). *WOX12*, a close homolog of *WOX11*, is the primary regulator of AR formation in plants (Tvorogova et al. 2021). Very little is known about the identity of the downstream target genes of *WOX* TFs, as only a few studies have addressed the issue. For example, in Poplar, *PagWOX11/12a* was involved in drought tolerance by regulating root development; *PagERF35* bound to the drosophila DNA replication-related element (DRE) motif (TATCGATA) in the promoter of *PagWOX11/12a* and regulated its expression; and drought induced a higher expression of *PagWOX11/12a* and *PagERF35* (Wang et al. 2020). Identifying the

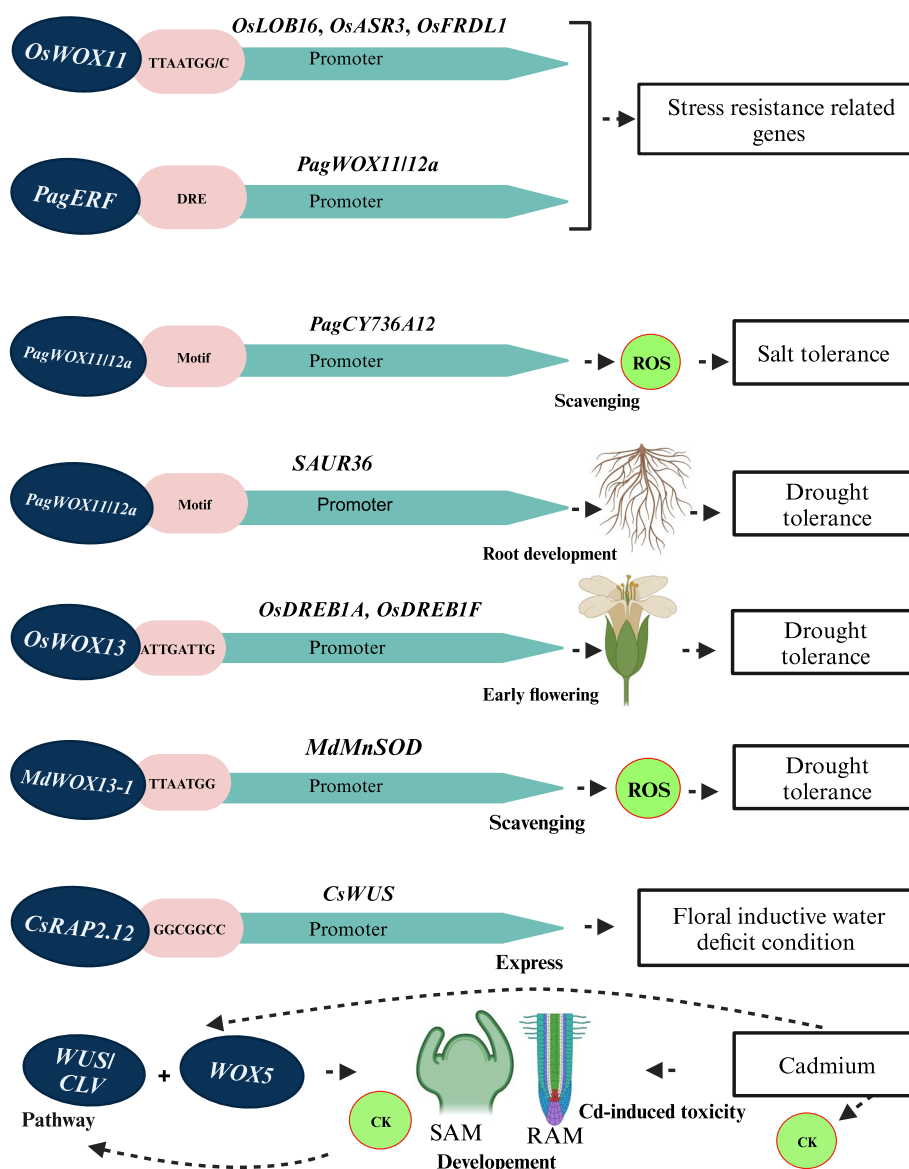


Fig. 3 Effect of *WUSCHEL*-related homeobox (*WOX*) transcription factors in abiotic stress tolerance in trees. *OsWOX11*, *Oryza sativa* L. *WOX*; *PagERF*, *Populus alba* × *P. glandulosa* ETHYLENE RESPONSE FACTOR 3; *MdWOX*, *Malus domestica* *WOX*; *CsRAP2.12* (*Cs1g16690*), *Citrus sinensis* AP2/ERF; *CLV*, *CLAVATA3*; *OsLOB16*, *Os* LATERAL ORGAN BOUNDRY 16; *OsASR3*, abiotic stress responsive rice 3; *OsFRDL1*, *Os* FERRIC REDUCTASE DEFECTIVE LIKE 1; *PagCY736A12*, cytochrome P450 CYP736A12; *SAUR36*, SMALL AUXIN UP RNA 36; *OsDREB1A*, dehydration-responsive element-binding protein 1A; *MdMnSOD*, *Malus domestica* manganese superoxide dismutase; *CsWUS*, *WUSCHEL*; CK, cytokinin

downstream targets of *WOX*s would be highly useful as it would help reveal the specific role of *WOX*s in the gene regulatory mechanism involved in abiotic stress tolerance in plants.

The *WOX*s overlap in abiotic stress responses and plant development markedly. Thus, overexpression in plants may offer various benefits. *MdWOX13-1*-encoded protein directly binds with the “TTAATGG” element in the *MdMnSOD* promoter, increasing drought tolerance by scavenging ROS. The activities of the antioxidant enzymes SOD, POD,

and CAT enhanced in transgenic apple calli than in the wild type (WT). Overexpression of *MdWOX13-1* increased calli weight and promoted ROS scavenging, providing resistance against drought-induced stress (Lv et al. 2023). *OsWOX13* improved drought tolerance and promoted early flowering in rice (Minh-Thu et al. 2018). *OsWOX13* directly bound to the *cis*-regulatory “ATTGATTG” motif. The promoters of drought-responsive-TF encoding genes, such as *OsDREB1A* and *IF*, contained the “ATTGATTG” motif. In rice, the relative expression of *OsDREB1A* and

OsDREB1F was positively upregulated during drought in *OsWOX13*-overexpressing plants, thereby enhancing drought tolerance. *OsWOX13* also promoted early flowering by activating *OsMADS16* and *Hd3a*. The promoters of these genes consisted of the “ATTGATTG” motif, indicating that *OsWOX13* is involved in drought tolerance and floral induction (Minh-Thu et al. 2018).

Expression and regulatory role of *WOX* TFs in response to freezing and heat-induced stress

*WOX*s also regulate the response of plants to temperature fluctuations. *WOX*s were upregulated under heat-induced stress in pineapple (*A. comosus* L.). *AcoWOX13* was highly expressed at 24 h of heat treatment (Rahman et al. 2017). *High expression of osmotically responsive genes 9 (HOS9)* encodes an HD-TF and shares a highly similar motif with *Arabidopsis* *WUS* and *PRESSED FLOWER (PRS)*. *Arabidopsis hos9-1* mutants revealed an improved expression of cold-responsive genes. Cold susceptibility of *hos9-1* mutants revealed a disruption of functions in those genes post-transcriptionally targeted by *HOS9* or other than those targeted by C-repeat dehydration-responsive element binding factor (CBF)-encoding genes. *CBFs* control the *hos9-1* mutation. *HOS9* plays a significant role in cold tolerance by regulating the kind of genes but is not a part of the *CBF* pathway (Zhu et al. 2004). In paper mulberry, the expression of five *WOX*s that may be essential in cambial development was significantly induced after cold exposure (Peng et al. 2015). The *OsWOX11*-target genes and a *NAC-TF*-encoding gene (*OMTN3*) were associated with cold tolerance (Fang et al. 2014). *OsTCP21* and *OsERF922* were negative modulators of cold and salinity response in plants (Liu et al. 2012). Recent studies have proposed *WOX*s as promising candidate genes for manipulating abiotic stress tolerance in plants that can be used for genetic improvement.

The expression patterns and regulatory role of *WOX* TFs in response to heavy metal-induced stress

Cd is a toxic heavy metal that is highly soluble in water.

Cd is absorbed by the roots and translocated to the aerial parts of plants *via* xylem loading, leading to physiological, biochemical, and genetic damage (Song et al. 2017). The *PsnWOX* family plays a crucial role in CdCl₂-induced stress. The expression of *PsnWOX13a* and *PsnWOX13b* in *Populus × xiaohei* T.S. Hwang et Liang was positively regulated during the early stage of CdCl₂ treatment (Li et al. 2022). *WUS*, *CLV3*, and *WOX5* were involved in stem cell maintenance and control of SAM and RAM development in plants. Cd inhibited primary and regulated lateral root growth in *Arabidopsis*. A short treatment with Cd (100–150 μM) for 24 h altered the RAM and SAM. Cd-induced coexpression of *WUS* and *WOX5*

and accumulation of CK played a significant role in SAM and RAM activity (Leonardo et al. 2021). Further, the role of stress-responsive *WOX*s and their regulation must be identified to understand the signaling pathway involved in abiotic stress tolerance.

Conclusions

The response of plants to various abiotic and biotic stresses critically depends on the transcriptional regulation of stress-responsive genes. In the last few years, significant progress has been made in identifying the TFs involved in the expression of genes relevant to stress in horticultural plants. To date, several members of the *WOX* family of TFs have been identified and functionally studied in plants. Increasing genome sequencing in plants and data availability has provided a basis for genome-wide identification, screening, and expression analysis of genes involved in abiotic stresses. *WOX* homologs have species-specific functions in plants. However, the studies regarding the functional characterization of *WOX*s using genetic transformations and *in vitro* regeneration in trees are limited. Previous studies have relied on the coexpression patterns of *WOX*s, which may affect the accurate determination of gene function. *WOX*s are involved in the transcriptional activation of stress-related genes. The regulation of their interactions and the identification of new partners require further investigation. Only a few overexpression and genetic mutation studies of specific genes have explored the variety of *WOX*s in different plant species. Significant evidence indicates the convergence of *WOX*s during abiotic stress tolerance in plants. *WOX*s play crucial roles in abiotic stress responses and are potent targets for modifying abiotic stress tolerance in horticultural plants.

CRISPR/Cas9 technology is a valuable tool for genetic improvement in woody perennials (Khan et al. 2022b), and targeted sequence insertion or deletion can modify the expression patterns of TFs. A functional comparison of the *WOX* orthologs in diverse plant species and its application in constructing *WOX* mutants by CRISPR/Cas9-based genome editing will help achieve sustainable production goals. Notably, gene editing in horticultural crops could encompass abiotic stress resilience and increased yield for food security. Here, we propose that *WOX*s synchronize the link between stress and metabolic regulation; the stresses included in this review involve *WOX*s as significant actors. However, the precise molecular process and equilibrium between defense and growth are mostly unclear. During an abiotic stress response, the *WOX*s and their target genes may lead to identifying novel signaling pathways. Finally, it dissects the functional role of *WOX*s in developing stress-resilient crops that can significantly improve agriculture crop production under the climate change framework.

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Authors' contributions

FSK, concept and writing—original draft preparation; FG and FSK, figures formatting; JZZ, FG and CGH, review and editing.

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