

Article

Genome-Wide Characterization Identifies *SIWUS*, *SIWOX4* and *SIWOX13* as Key Regulators in Plant Development and Stress Signaling in Tomato (*Solanum lycopersicum* L.)

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Abstract

Tomatoes are globally significant crops worldwide. Understanding the molecular mechanisms underlying their growth, development, and stress responses is crucial to enhance crop productivity and resilience. The WUSCHEL-related homeobox (WOX) gene family is implicated in developmental processes and stress responses, yet its regulatory complexity in tomato remains underexplored. This study presents an integrative genome-wide analysis approach to characterize the WOX family in tomato. Ten *SIWOX* genes were identified and phylogenetically classified into three clades, WUS, intermediate and ancient, underscoring their evolutionary relationships. Structural analysis revealed significant variability in gene structure even within the same clade, indicating potential diversity in functional roles. Conserved domains' screening enables the detection of conserved motifs, including the homeodomain and WUS box. *Cis*-element analysis showed diverse regulatory elements across the *SIWOX*s, with a strong emphasis on elements involved in growth and development and stress response. Expression profiling across different organs and growth conditions including abiotic and biotic stresses revealed variability in *SIWOX*s' expression patterns. Furthermore, several miRNAs were predicted to target the *SIWOX*s, emphasizing the existence of post-transcriptional regulation. Functional annotation and interactome analysis further revealed the key role of some *SIWOX*s, mainly *SIWUS*, *SIWOX4* and *SIWOX13*, as central regulatory hubs. Collectively, these findings uncover the structural diversity, regulatory mechanisms and functional flexibility of the *SIWOX* gene family. It also highlights potential targets for improving tomato crop resilience and productivity, making it a significant contribution to plant biology and agriculture.

Keywords: WOX transcription factor; plant development; stress response; functional diversification; tomato



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1. Introduction

Tomato (*Solanum lycopersicum* L.) is one of the most extensively cultivated and economically important horticultural crops worldwide [1]. This crop species constitutes not only a major source of human nutrition but a broadly recognized model plant for the Solanaceae family and more importantly for the study of fleshy fruit development [2]. With the growing increase in the global population, maintaining a continuous and stable productivity under increasing environmental constraints is a major challenge for modern agriculture [3,4]. Plant growth, development and response to external stimuli is highly governed by complex regulatory mechanisms [5,6]. Establishing a comprehensive structural and regulatory framework of these gene families is therefore important to identify candidate targets for the development of new cultivars with stable productivity and enhanced resilience to adverse environmental stresses.

Transcription factors play a pivotal role in the coordination of plant developmental processes and the set of adaptive responses to environmental constraints [7,8]. Among them, the WUSCHEL-related homeobox (WOX) gene family encodes for transcriptional regulators that are uniquely found in the plant kingdom. This family of transcription factors is distinguished by the presence of a conserved domain, known for its DNA-binding activity [9–11]. WOX proteins' function has been broadly related with the control of several plant developmental processes, mainly embryogenesis, stem cell maintenance, organ patterning and floral development [12–19]. Aside from their pleiotropic roles, emerging evidence has suggested their involvement in the set of adaptive responses to external stimuli [19–22].

Diversification of the transcription factors gene family usually occurs as a result of cumulative changes in the exon–intron structure, conserved motifs composition and promoter architecture, thereby leading to functional divergence among members [23,24]. This complexity goes beyond the transcriptional regulation to englobe the post-transcriptional modulation through microRNA to help plants adjusting gene activity during development and in response to external cues [25,26].

Genome-wide identification analysis of WOXs has been reported in numerous plant species [10,20–22,27]. Despite the acknowledged significance of WOX genes in plants, there are significant gaps regarding their biological function, particularly those linked to stress responsive regulatory and interactome networks, duplication events, and key regulatory systems involved in the regulation of WOX activities in tomato. Earlier reports such as Li et al. [28] provided a genome-wide identification and basic expression analysis under abiotic stress. However, increasing interest has emerged on unveiling their specific roles. For instance, SIWOX13 has been identified as a key regulator of fruit ripening while SIWOX4 was found to be negatively correlated with drought tolerance [29,30]. However, a multi-level study focusing on how this family operates as a coordinated regulatory unit is still lacking. More importantly, the post-transcriptional regulation and the protein–protein interactome networks remain unexplored. Thus, this study fills the gaps by providing a holistic study that integrates to enhance our understanding on how tomato WOX family members coordinate plant development and environmental stress responses.

The present study delivers an integrative genome-wide mining and characterization of the WOX gene family in tomato, with the objective to uncover the complex regulatory networks associated with WOX gene family members' function. By combining phylogenetic classification, gene structural organization, regulatory features and expression patterns, this study delivers a deeper and more oriented perspective regarding the putative functions of SIWOX gene family members while providing a robust framework to complement and extend prior functional studies.

2. Results

2.1. Genome-Wide Identification and Characterization of SIWOX Proteins

The genome-wide screening enabled the identification of ten non-redundant *SIWOX* genes in tomato genome. These genes were designated as *SIWUS*, *SIWOX1*, *SIWOX2*, *SIWOX3a*, *SIWOX3b*, *SIWOX4*, *SIWOX5*, *SIWOX9*, *SIWOX11* and *SIWOX13* based on their sequence homology with already known *WOX* members that have earlier been in other plant species, notably *Arabidopsis thaliana*, *Nicotiana tabacum*, *Cucumis melo*, *Cucumis sativus* and *Triticum aestivum* (Table 1). The ten identified genes comprised a conserved homeobox domain, typically found in the *WOX* gene family, which confirms their classification and the accuracy of the genome-wide identification approach. The CDSs of the identified genes are listed in Supplementary File S1.

The physico-chemical properties of the *SIWOX* genes, which comprise diverse numbers of introns and exons, are encoding proteins with sizes ranging from 18.66 KDa (*SIWOX5*) to 44.05 KDa (*SIWOX1*) (Figure 1). *SIWOX1* displayed the longest amino acids sequence (393 amino acids) whereas *SIWOX5* exhibited the shortest. The theoretical isoelectric points were between 5.38 and 9.40, with 50% of *SIWOX* proteins showing a $pI > 7$, indicating the presence of a great proportion of basic amino acids. Regarding the stability, *SIWOX3b* showed the lowest instability index of 42.16 while the highest values 80.80 and 69.00 were also recorded in *SIWOX11* and *SIWOX5*, respectively. Grand average of hydropathicity (GRAVY) ((−0.128)–(−0.967)) and Aliphatic index values (40.30–80.80) established that all the ten identified *SIWOX* proteins were hydrophobic. Subcellular localization was determined and nine of the ten *SIWOX*s showed a nuclear localization while the remaining protein (*SIWOX3a*) is predicted to be found in the cytoplasm (Table 1).

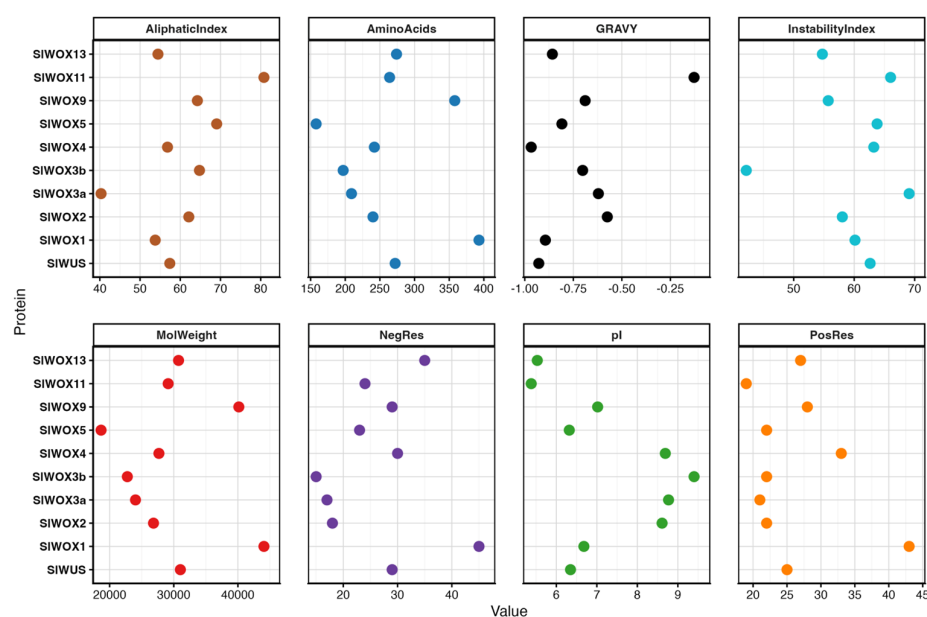


Figure 1. Physico-chemical characterization of *SIWOX* proteins. The different analyzed parameters were represented in dot plot with each dot corresponding to an individual protein.

Table 1. Basic characteristics of the ten identified *SIWOX* gene family in tomato.

Gene Name	Gene ID	Gene Length (kb)	Peptide Length (aa)	Subcellular Localization
<i>SIWUS</i>	Solyc02g083950.2	1.42	273	Nucleus
<i>SIWOX1</i>	Solyc03g118770.2	2.36	394	Nucleus
<i>SIWOX2</i>	Solyc06g076000.1	1.41	241	Nucleus
<i>SIWOX3a</i>	Solyc11g072790.1	1.19	210	Cytoplasm

Table 1. Cont.

Gene Name	Gene ID	Gene Length (kb)	Peptide Length (aa)	Subcellular Localization
<i>SIWOX3b</i>	Solyc11g072770.1	1.60	198	Nucleus
<i>SIWOX4</i>	Solyc04g078650.2	1.42	243	Nucleus
<i>SIWOX5</i>	Solyc03g096300.2	0.57	159	Nucleus
<i>SIWOX9</i>	Solyc02g077390.1	1.93	359	Nucleus
<i>SIWOX11</i>	Solyc06g072890.1	1.45	265	Nucleus
<i>SIWOX13</i>	Solyc02g082670.2	2.922	275	Nucleus

2.2. Phylogenetic Relationships and Structural Features of *SIWOX*s

According to the current tomato genome annotation (SL4.0), the ten identified *SIWOX* genes were unevenly distributed on the twelve tomato chromosomes (Figure 2A). Indeed, only five of the twelve tomato chromosomes harbor *SIWOX* genes. For instance, three *SIWOX* genes (*SIWUS*, *SIWOX9* and *SIWOX13*) were physically located in chromosome 2 (chrom02). Meanwhile, chromosomes 3, 6 and 11 counted two genes each, with *SIWOX1* and *SIWOX5* distributed in chromosome 3, *SIWOX2* and *SIWOX11* in chromosome 6, and *SIWOX3a* and *SIWOX3b* on chromosome 11. The remaining *SIWOX* gene; *SIWOX4* was located in chromosome 4.

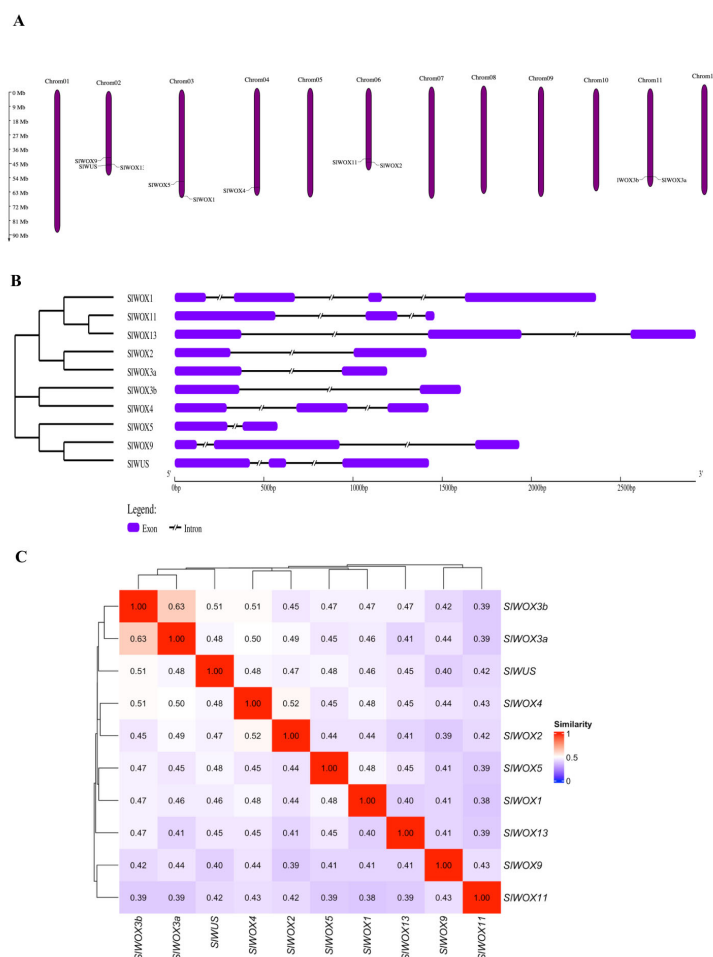


Figure 2. Integrated analysis of the physical position, gene structure and coding sequence (CDS) similarity of *SIWOX* gene family. (A) Physical position of the ten identified *SIWOX* genes, (B) gene structure with exons and introns represented by purple rectangles and single lines, respectively, (C) CDS similarity among the *SIWOX* genes represented by a heatmap. The colored bar indicated the correlation between the CDSs of two genes, with purple and red representing a low and high correlation, respectively. The detailed values are listed in Supplementary File S2.

SIWOXs gene's structure was examined to determine the exon–intron structure. This analysis revealed that the number of introns in the *SIWOX* genes varied from one (*SIWOX2*, *SIWOX3a*, *SIWOX3b* and *SIWOX5*) to three (*SIWOX1*). It is worth mentioning that the remaining seven *SIWOX* members exhibited two introns each (Figure 2B).

The identity matrix of the ten *WOX* CDSs of tomato showed that the similarity percentage ranged between 39% and 63%, with the highest percentage of 63% being registered for the pair *SIWOX3A* and *SIWOX3b* (Figure 2C). Interestingly, gene structures reasonably support this moderate similarity (Figure 2B). This finding strongly suggests that these two *SIWOXs* members are paralogous of the *WOX3* subclade, which probably originated from an ancient duplication event trailed by sequence divergence. In addition to this pair genes, the remaining *SIWOX* genes showed a low level of identity.

Consistent with these findings, collinearity analysis indicated that the 10 *SIWOX* genes are spread across several chromosomes without forming any collinear blocks. More importantly, no significant tandem or segmental duplications were able to be detected among these genes based on the applied criteria for block detection and sequence similarity. These results strongly suggest that, besides the *SIWOX3* paralogs (*SIWOX3a* and *SIWOX3b*), the other *SIWOX* genes have evolved independently, according to the absence of any duplication events thereby reflecting a dispersed and yet conserved genomic organization.

To elucidate the diversity and the phylogenetic relationships of *WOX* proteins, an evolutionary tree was built through the alignment of 10 tomato *SIWOXs*, 15 *Arabidopsis* *AtWOXs*, 11 *Cucumis sativus* *CsWOXs*, 11 *Cucumis melo* *CmWOXs* and 26 wheat *TaWOXs*. A total of 73 protein sequences were classified into three distinct clades (Figure 3): the ancient clade represented by 15 different *WOX* sequences, the intermediate clade counting 19 of the 73 clustered *WOX* protein sequences and the *WUS* clade gathering nearly 55% of the clustered *WOX* sequences (40 of the 73 aligned protein sequences). Regarding *SIWOXs* clustering, our results showed that the *WUS* clade comprised the largest number of *SIWOX*, with seven members in total. Meanwhile, the ancient and intermediate clades consisted of only one (*SIWOX13*) and two (*SIWOX9* and *SIWOX11*) members, respectively.

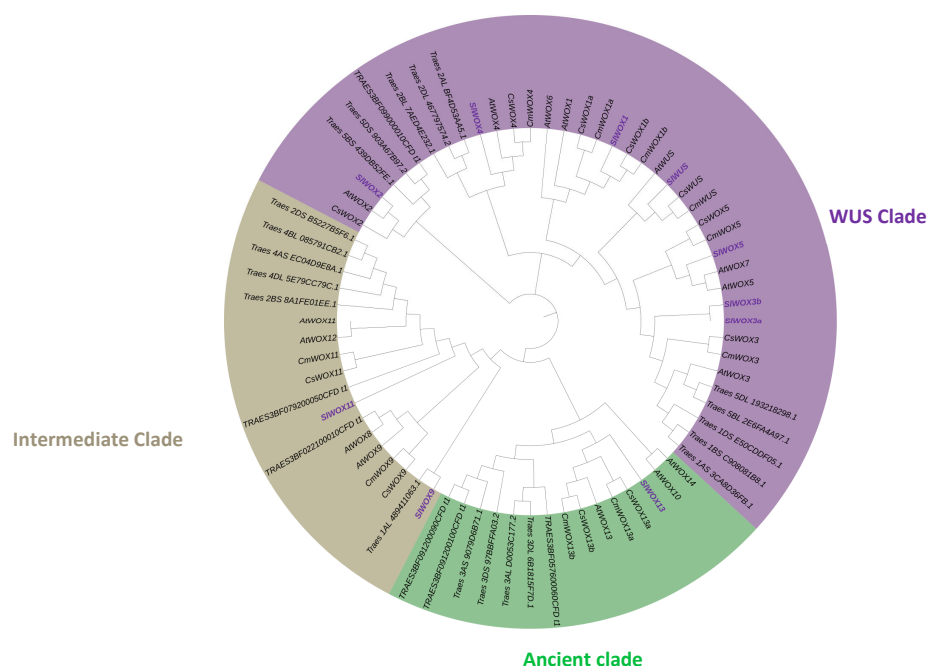


Figure 3. Evolutionary relationships between *SIWOX* gene family. The phylogenetic tree was constructed based on the alignment results generated by Mega12. The unrooted neighbor-joining tree was constructed using 73 protein sequences, including 10 from *Solanum lycopersicum*, 15 from *Arabidopsis thaliana*, 11 from *Cucumis melo* and *Cucumis sativus* and 26 from *Triticum aestivum*. The protein sequences

used are summarized in Supplementary File S3. The visualization and annotation were performed using iTol (v7). Different colors indicate the different WOX clades (WUS, modern and ancient).

According to phylogenetic and exon–intron analysis, it appears that the exon–intron organization showed a potential correlation with clade membership. For instance, members belonging to ancient and intermediate clades, namely *SIWOX13* (ancient) and *SIWOX9* and *SIWOX11*, harbor two introns (Figure 2B). This finding suggests that an ancestral *SIWOX* gene displayed this basic structure. In the meantime, a broad structural diversity was, however, noticed in the WUS clade, with the number of introns comprising between one (*SIWOX2*, *SIWOX3a*, *SIWOX3b*, *SIWOX4* and *SIWUS*) and three (*SIWOX1*), thereby reflecting not only a huge structural divergence within this clade but also potent intron gain or loss events during evolutionary processes.

2.3. Conserved Motifs and Three-Dimensional Structure Analysis

The conserved motifs of WOX TFs play a crucial role in controlling diverse plant development processes such as organ size (flower meristem size) and plant cell specificity. *SIWOX* proteins were examined for these motifs using MEME suite. The analysis revealed the presence of twenty conserved motifs (Figure 4A), spanning from six to 50 amino acids in length, within the ten *SIWOX* proteins. All the ten *SIWOX* proteins harbor motif 1 (50 amino-acids) and motif 2 (9 amino-acids), both encoding for the homeobox domain, defining their basic structural and functional roles (Figure 4B,C). Motif 3 is practically conserved across the proteins of the WUS clade. Additionally, its consensus sequence matches well with the one WUS box, indicating that motif 3 represent the WUS box. Also, motif 4 is present only in the intermediate clade. Notably, motif 4 and motif 6 were only present in the representants of the intermediate clade (*SIWOX9* and *SIWOX11*). It is worth noting that some motifs such as motif 5, motif 6, motif 9 and motif 10 were detected in a few members of the intermediate and WUS clades. Indeed, motif 5 was unique to *SIWOX3a* and *SIWOX3b*. Motif 9 was exclusively found in *SIWOX1* and motif 10 had been recorded in both *SIWUS* and *SIWOX11*. Overall, the divergence in the conserved motifs' composition supports the differences that have been observed in the structural composition (exon/intron mapping) and highlights the diversity of *SIWOX* members.

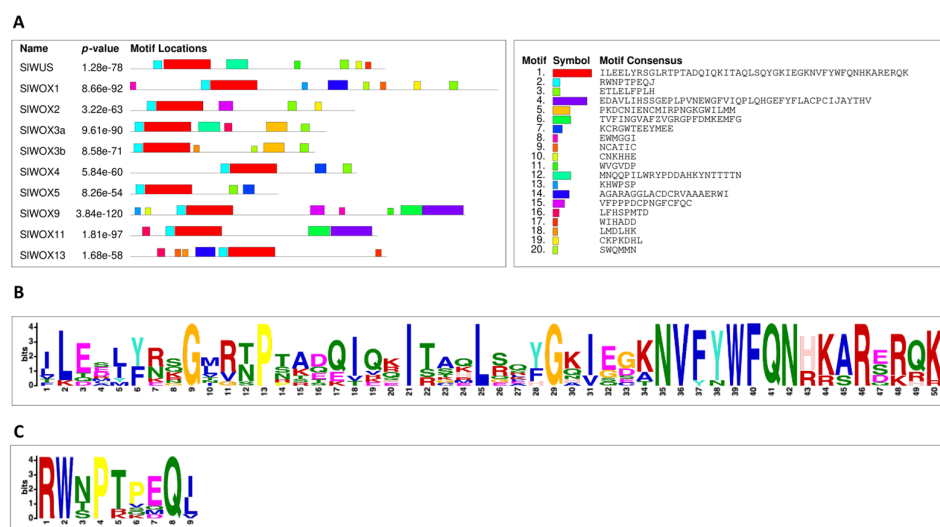


Figure 4. Conserved motifs analysis conducted by MEME suite software (v 5.5.8.). (A) Schematic representation of the position and statistical significance (*p*-values) of identified motifs within the gene sequences of *SIWOX*s, with each color representing a different motif, (B) composition in amino acids of motif 1 and (C) composition in amino acids of motif 2.

Consistent with previous findings [28], our analysis confirmed the exon–intron organization of the SIWOXs. To extend this characterization, we further explored the 3D structure of SIWOX proteins using the AlphaFold Protein Structure Database. This computational analysis revealed that all SIWOX proteins exhibited a highly conserved and well-folded homeodomain, in alignment with their conserved DNA-binding activities (Figure 5). However, the C-terminal and N-terminal regions were highly divergent, thereby underlying functional diversification.

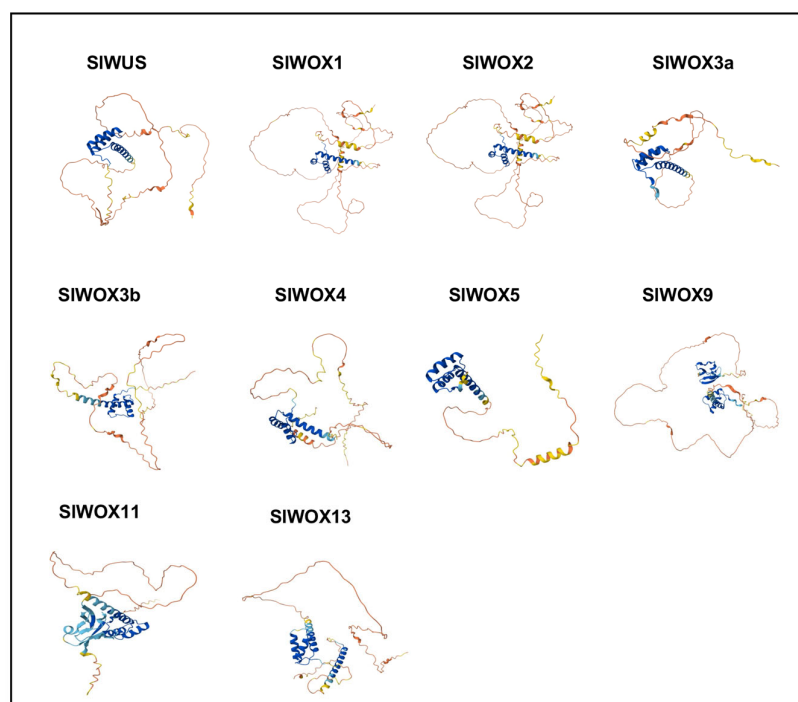


Figure 5. The three-dimensional structure of the ten identified SIWOX proteins using the AlphaFold Protein Structure Database.

2.4. Cis-Acting Regulatory Elements Analysis in SIWOX Promoters

To go further in depth into the biological features of *SIWOX*s, the 2kb-upstream promoter regions of the ten *SIWOX*s were retrieved and analyzed using the NEWPLACE database. The list of all the analyzed elements along with their respective sequences are listed in Supplementary File S4. A large panel of regulatory motifs was located in the promoter region of *SIWOX* genes in tomato (Figure 6A). These motifs were sorted into three distinct categories: plant growth development, hormone responsive and stress responsive. More importantly, plant growth and development-associated elements were the most abundant, followed by stress responsive-associated motifs. Meanwhile, hormone-responsive elements were the least represented, thereby suggesting a central role of *SIWOX* genes in the regulation of plant growth and development (Figure 6B,C). Indeed, motifs associated with plant development, namely ROOTMOTIFTAPOX1, GATABOX, GT1CONSENSUS, DOFCOREZM, and POLLEN1LELAT52, were present in several copies in the *SIWOX*s promoter region. These motifs were earlier described as involved in key developmental processes, including photosynthesis (GT1CONSENSUS), root (ROOTMOTIFTAPOX1) and pollen (POLLEN1LELAT52) development and carbon metabolism (DOFCOREZM). Among the sixteen examined plant growth-related motifs, GT1CONSENSUS, OSE2ROOTNODULE and ROOTMOTIFTAPOX1 represented the largest proportions, with 10.8%, 10.5% and 9.9% respectively. This finding strongly suggests a potential involvement of *SIWOX* genes in reproductive development and key development processes (photosynthesis) (Figure 6B).

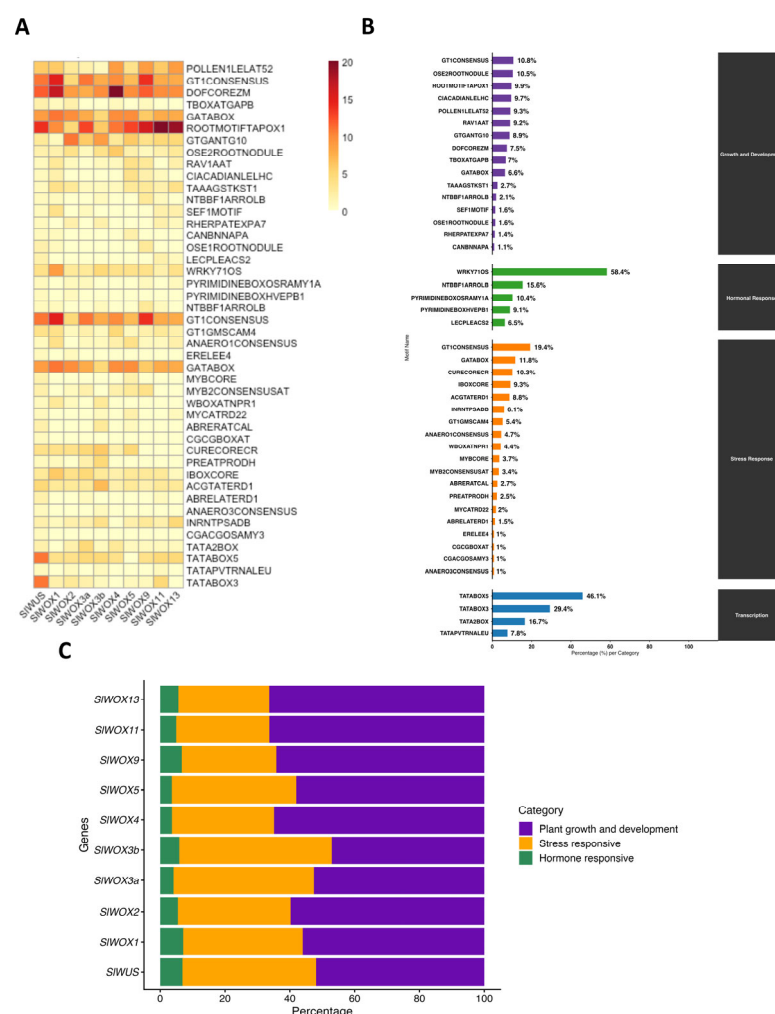


Figure 6. Cis-acting regulatory analysis of the promoter region of SIWOX genes. (A) Heatmap showing the occurrence of the different cis-elements, (B) the ratios of each motif from each category represented in the barplot, and (C) the proportion of motifs in each gene according to the three fixed categories (plant growth and development, hormone responsive and stress responsive).

In addition, multiple cis-acting regulatory elements related to biotic and abiotic stress responses were identified in the 2kb-upstream sequence. Indeed, GT1CONSENSUS (involved in biotic stress response), GATABOX and IBOXCORE (response to light), ACGTATERD1 (response to dehydration/drought stress) and CURECORCR (response to abiotic stresses, namely oxygen deprivation and copper stress) were found at different occurrence in the ten *SIWOX* genes. More importantly, it appears that GT1CONSENSUS motifs represented the largest proportion of 26.6%, followed by GATABOX (23.2%), thereby suggesting that *SIWOX* genes may participate in both biotic and abiotic stress responses (Figure 6B).

In agreement with the previous promoter analysis reported by Li et al. [28], several cis-acting elements associated with phytohormone response have been identified in the 2kb promoter region of the ten *SIWOX* genes. However, the in-depth analysis performed in the study enables the identification of additional cis-regulatory elements such as WRKY71OS (involved in GA-signaling pathway regulation), NTBBF1ARROLB (auxin induction), PYRIMIDINEBOXSRAMY1A (GA-response) and PYRIMIDINEBOXHVEPB1 (GA-induction). Notably, WRKY71OS accounted for the highest proportion of 58.4%, followed by NTBBF1ARROLB (15.6%), PYRIMIDINEBOXSRAMY1A (10.4%) and PYRIMIDINEBOXHVEPB1 (9.1%). It is worth mentioning that TATA box-associated motifs were

present in high numbers in the *SIWOX*s, reflecting a strong basic transcriptional regulatory framework (Figure 6B).

2.5. miRNA Regulation of *SIWOX* Genes

MicroRNAs play a central role in the post-transcriptional regulation of gene expression. This process can either occur through transcript cleavage or the prevention of protein translation. Using *SIWOX* genes as queries, the miRNA targeting *SIWOX*s were predicted. The results showed that several *SIWOX* genes were not predicted to be targeted by any tomato miRNA, suggesting differential post-transcriptional regulation across the tomato *SIWOX* gene family (Figure 7). Moreover, most *SIWOX*–miRNA interactions were through transcript cleavage except for the two interactions, involving sly-miR171c–*SIWOX*4 and sly-miR159–*SIWOX*9, for which the regulation was predicted to be through translational repression. Most miRNAs were associated with single or few *SIWOX* targets. For example, *SIWUS* and *SIWOX*13 interacted with multiple miRNAs each. sly-miR469-3p and sly-miR6026 were predicted to regulate *SIWUS*, while *SIWOX*13 was targeted by sly-miR478-3p, sly-miR476-3p, sly-miR156a, sly-miR156b and sly-miR156c through the cleavage mechanism. Overall, these data strongly suggest that miRNA-mediated regulation of *SIWOX* genes is gene-specific and more likely through transcript cleavage rather than translational repression.



Figure 7. Predicted microRNA–*SIWOX* regulatory interaction network with rows corresponding to individual miRNA and columns targeted *SIWOX*s. Interaction types are indicated by different colors.

2.6. *SIWOX*s Interactome and GO Enrichment Profiling

A protein–protein interaction (PPI) network was built using STRING analysis in *Solanum lycopersicum* with the purpose to decipher the biological functions and the regulatory network of the *SIWOX* family. The network showed *SIWUS* as a central node, displaying multiple interactions not only with other *WOX* members such as *SIWOX*2, *SIWOX*4, *SIWOX*5, *SIWOX*9 and *SIWOX*11 but also with other key proteins (Figure 8A).

For instance, FALSIFLORA appeared to interact with SIWUS and SIWOX9, along with different developmental regulators such as the MADS-box transcription factor EJ2. This clearly underscores the involvement of several WOX proteins in the floral architecture and transition. Moreover, four distinct WOX proteins, namely SIWUS and SIWOX4, showed direct and indirect interactions with SERK1 and SlmCLV2, known to be involved in meristem size regulation processes. This strongly suggests a potential functional diversification of some members of this family of TFs. It is worth mentioning that some SIWOXs (SIWOX3b and SIWOX13) appeared isolated and weakly connected to the other genes, ultimately indicating that they could operate independently or that their interaction network has not been yet characterized in tomato.

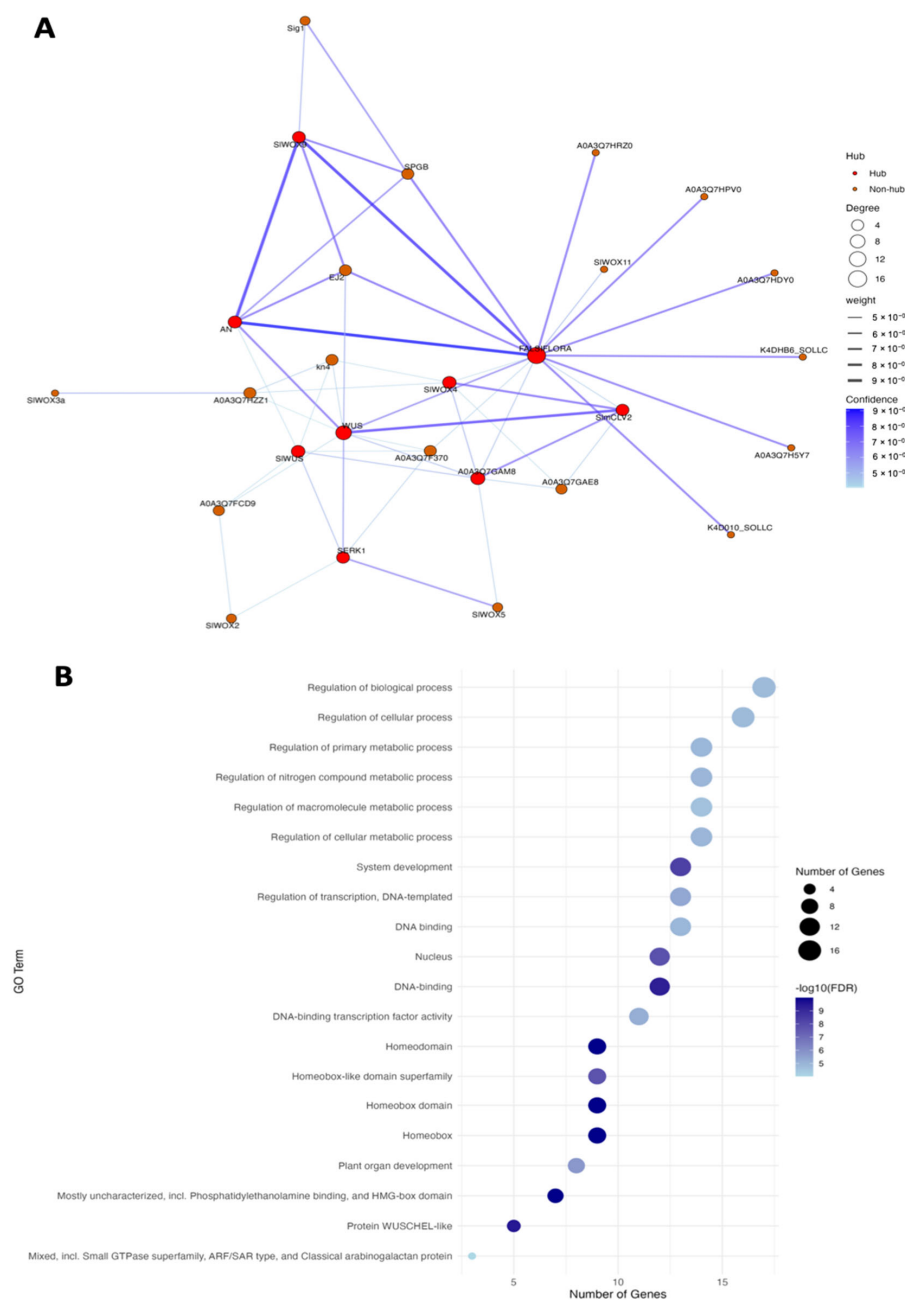


Figure 8. Protein–protein interaction (PPI) network and functional enrichment analysis of the *SIWOX* gene family. **(A)** PPT network, proteins are represented in nodes, with hub and non-hub genes shown in red and orange, respectively. **(B)** GO enrichment analysis represented in bubble plot displaying the top enriched GO terms across the different categories.

GO enrichment profiling provided additional information related to *SIWOX*s potential biological function. It appears that *SIWOX* genes are mainly enriched in the regulation of biological and cellular processes, including primary and nitrogen metabolic processes (Figure 8B). A notable enrichment in transcription-related categories, namely the regulation of transcription, DNA binding and DNA-binding transcription factor activity, was also recorded, along with nucleus activity/localization. Moreover, homeobox- and homeodomain-related terms were also represented, thereby highlighting the key features of *WOX* proteins. Overall, these data strongly emphasized the function of *WOX* genes as transcription factors involved in plant developmental and regulatory pathways, as they are operating from the nucleus.

2.7. Expression Profiling of *SIWOX*s Under Diverse Conditions

Expression profiling of the *SIWOX* gene family was firstly retrieved from the TomExpress database to explore the expression dynamics of the ten *SIWOX* genes across tissues, developmental stages and growth conditions (abiotic stress, biotic stress, hormonal treatment).

2.7.1. Expression Profiling of *SIWOX*s Across Vegetative and Reproductive Tissues

Exploring the expression of *SIWOX*s across the different vegetative and reproductive tissues revealed a high level of specificity across *SIWOX* genes (Figure 9A). Indeed, the majority of *SIWOX* genes displayed low to moderate expression levels, with *SIWUS*, *SIWOX1* and *SIWOX4* showing higher expression values in leaf, stem and flower. This finding was consistent with the RT-qPCR data published by Li et al. [28] and the interactome network (Figure 9A), thereby supporting an earlier hypothesis suggesting their implication in stem cell maintenance and organogenesis. Meanwhile, *SIWOX13* showed a broader expression pattern, with notable expression detectable across all the analyzed tissues, but more importantly in seeds, flowers, roots and stems. This expression profiling has not been fully detailed in previous reports. Overall, this result suggested that this gene could constitute a central hub controlling plant developmental processes.

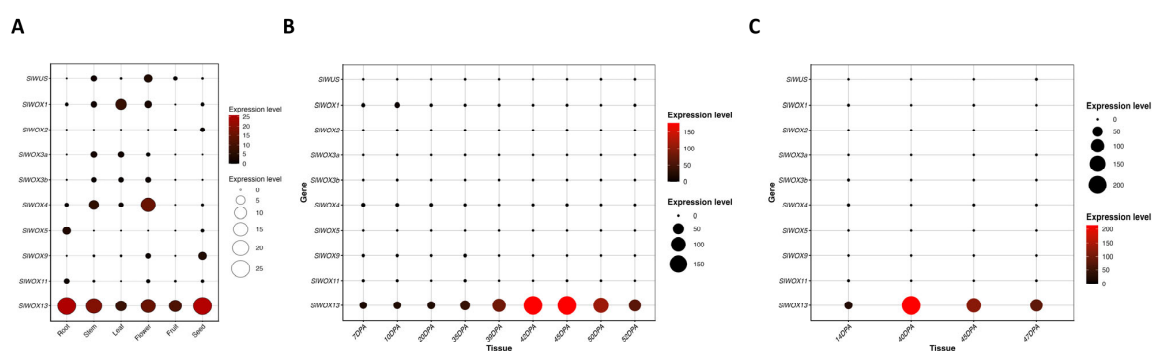


Figure 9. Expression profiling of *SIWOX* genes in vegetative and reproductive organs at different developmental stages. (A) Expression pattern of *SIWOX*s in vegetative and reproductive organs, (B) expression pattern of *SIWOX*s in the whole fruit at different fruit development and ripening stages, and (C) expression pattern of *SIWOX*s in the pericarp at different fruit development and ripening stages. Bubble size and color represent expression levels as indicated in the legend. The expression values are represented in Supplementary File S5.

Deciphering the expression of *SIWOX*s in the fruit during the ripening process revealed that most *SIWOX* genes displayed basic low expression values throughout fruit development, except for *SIWOX13* (Figure 9B). Indeed, its expression remained higher than the other *SIWOX*s, and showed a remarkable increase during the early developmental stages (7–20DPA), reaching a peak around 42–45DPA and remaining relatively high even

at late ripening stages (50–52DPA). This finding strongly suggests that *SIWOX13* is more involved in the mid and late stages of fruit development as indicated by the dynamic expression of this *SIWOX* across fruit developmental process. The examination of *SIWOX*s expression in the pericarp further corroborates previous observations. As clearly shown in Figure 9C, *SIWOX13* expression was highly dynamic, with a maximal expression detected at 40DPA, followed by stable and slightly reduced levels of transcripts at 45 and 47DPA.

2.7.2. Expression Profiling of *SIWOX*s in Response to Biotic and Abiotic Stimuli

Expression profiling of *SIWOX* genes in response to biotic and abiotic stresses was examined. The results showed that several *SIWOX*s displayed a notable increase in transcript levels in response to specific biotic and abiotic conditions. For example, *SIWOX4* and *SIWOX13* expression was highly induced, more particularly in response to cold and heat stresses. More striking, *SIWOX13* expression was remarkably higher in response to all the evaluate abiotic stimuli (drought, heat, cold and shade stresses) (Figure 10A) while negligible changes were recorded in the remaining *SIWOX*s.

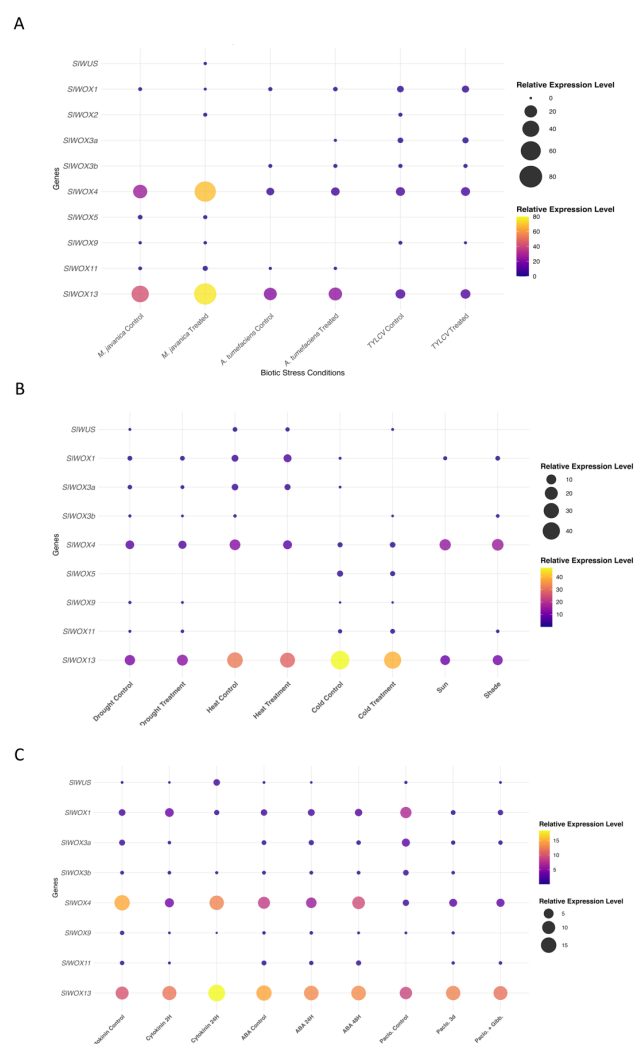


Figure 10. Expression profiling of *SIWOX* genes in response to various environmental and hormonal treatments. (A) Expression pattern of *SIWOX*s in response to biotic agents, namely *Meloidygne javanica*, *Agrobacterium tumefaciens* and *Tomato Yellow Leaf Curl Virus* (TYLCV), (B) expression pattern of *SIWOX*s in response to various abiotic stress conditions (drought, salinity, heat, light), and (C) expression pattern of *SIWOX*s in response to hormonal treatment (ABA, cytokinin, Paclobutrazol, and Paclobutrazol in combination with Gibberellin). Bubble size and color represent expression levels as indicated in the legend. The expression values are represented in Supplementary File S6.

In response to biotic agents, *SIWOX4* and *SIWOX13* showed the highest transcript accumulation levels, namely in response to *Meloidogyne javanica* infection (Figure 10B). A slight increase in transcript accumulation of both genes was also noticed in response to the two other biotic aggressors, *Agrobacterium tumefaciens* and Tomato Yellow Leaf Curl Virus (TYLCV). However, the remaining eight *SIWOXs*' expression was basically low, thereby suggesting a potential involvement of *SIWOX4*–*SIWOX13* in defense-related mechanisms.

2.7.3. Expression Profiling of *SIWOXs* in Response to Hormonal Treatment

Evaluating the expression of *SIWOX* genes in response to various hormonal treatments revealed that only *SIWOX13* demonstrated a distinct expression in response to all the tested treatments (Figure 10C). However, *SIWOX4* showed a substantial increase in transcript levels, more particularly in response to cytokinin and ABA exposure. The remaining *SIWOX* genes displayed, however, a low response to hormonal treatment, thereby suggesting the sole involvement of *SIWOX4* and *SIWOX13* in hormone signaling pathways.

2.7.4. Regulatory Network of *SIWOXs* Gene Family

Based on the RNA-seq data, an interaction network has been drawn summarizing the transcriptional regulation trends of *SIWOXs* in relationships with the different evaluated conditions. The integrative regulatory network showed once again the predominance of *SIWOX13* among stress and hormone responsive nodes, further proposing this transcriptional regulator as a central hub and orchestrating tomato response to biotic, abiotic and hormonal stimuli (Figure 11). In contrast, the other family members showed more restricted interactions compared to *SIWOX13*, which might reflect more specialized or limited developmental roles of these genes.

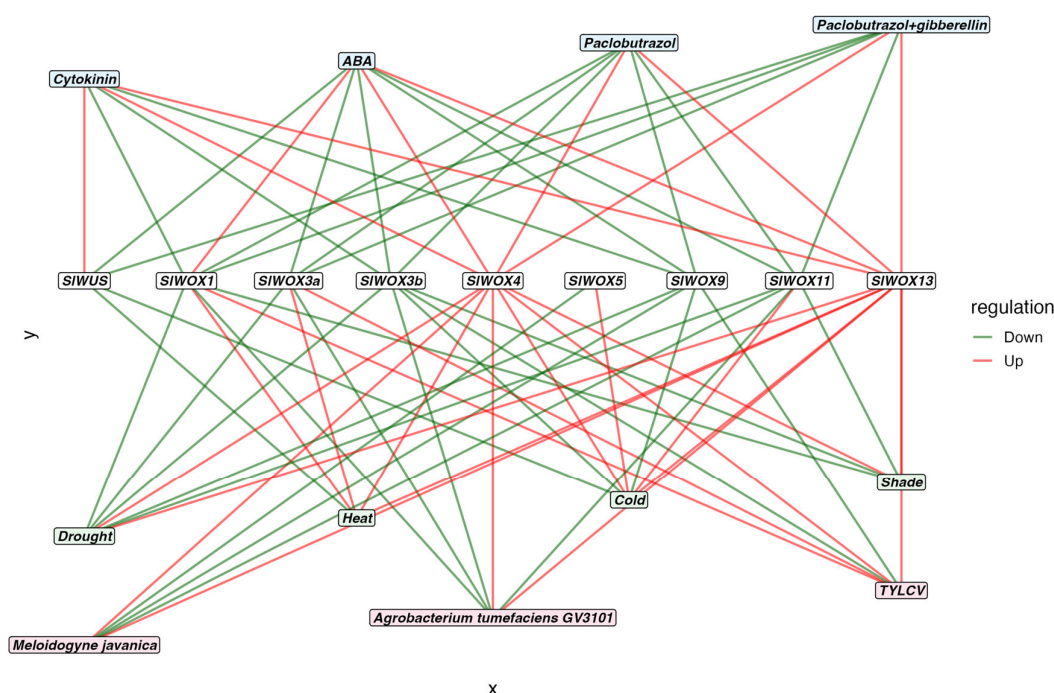


Figure 11. Regulatory network of *SIWOXs* gene family derived from RNA-seq dataset. The figure was drawn by R using all the expression data presented in Figures 9 and 10.

3. Discussion

The *WOX* gene family encodes unique transcription factors belonging to the homeodomain superfamily [31,32]. The first member of the *WOX* family was identified in *Arabidopsis thaliana* in 1996, establishing *WOX* genes as key regulators of embryo devel-

opment, stem maintenance and meristem organization [33]. Since then, there has been extensive work focusing on the identification and the characterization of this family of TFs in several plant species [34–38].

In the present study, 10 *SIWOX* gene family members were identified using a genome-wide mining approach. This finding was consistent with previously published data, underlying the presence of 10 *WOX* representative members in tomato [28]. The number of *WOX* genes is highly variable among species. For instance, 15 *WOX* genes were identified in *Arabidopsis thaliana* and 17 in *Camellia sinensis*, while 23 *WOX* encoding genes were reported in tobacco (*Nicotiana tabacum*) [20,27,39]. The gymnosperm species *Pinus massoniana* and *Picea abies* have only six *WOX* and 19 *WOX* genes, respectively [40,41]. This variation observed between species likely reflects species-specific evolutionary and duplication history rather than differences in the developmental complexity. This hypothesis is consolidated by the absence of tandem or segmental duplication events among *SIWOX* genes and the CDS similarity percentage < 80%, which strongly suggests that the low number of *SIWOX*s might result from evolutionary constraint rather than recent gene family expansion.

While previous studies mainly focus on genome mining and characterization of *WOX* members, the present work provides an in-depth physico-chemical characterization of the ten identified genes, providing additional information on the functional diversification and regulatory network among this family of transcriptional regulators. The instability index, for instance, revealed intriguing information regarding protein stability and functional regulation. Indeed, most proteins showed an instability index greater than 40, indicating a rapid degradation or post-translational changes for functional stability. Additionally, this innate instability can highlight the need for rapid protein turnover, to allow plants to modulate transcription factor levels during developmental stages or in response to environmental changes/stressors [42]. However, *SIWOX3b* showed remarkably a relatively stable profile with an instability index of instability of 42.16, thereby suggesting a prolonged lifespan in plant membranes.

Subcellular localization prediction showed that most *SIWOX* proteins are located in the nucleus, which is in alignment with their basic role as transcription factors. This conserved localization supports the basic function of this gene family [32]. Moreover, the low GRAVY appears to be crucial in maintaining *WOX* proteins stability in hydrophilic environs such as the nucleus, further confirming their DNA-binding properties. This stability is further confirmed with the aliphatic index of the identified *WOX* proteins. Indeed, the aliphatic index ranged between 40.30 and 80.80, in alignment with their basic function as transcription factors with DNA-binding properties. This function has been confirmed by the GO enrichment analysis, affirming the DNA-binding function and more importantly their nucleus localization. Interestingly, *SIWOX3a* showed a different localization (in the cytoplasm), which advocates a functional divergence. However, experimental validation is required to confirm this prediction.

Phylogenetic analysis enabled *SIWOX* genes to cluster into three clades, the ancient, the intermediate and the WUS clades, which fits perfectly with the lineage distribution in *Arabidopsis thaliana* and other dicot species [43]. Moreover, conserved motifs analysis revealed the conserved status of specific homeodomains (HDs) across orthologs, thus highlighting their DNA-binding functional specificity [44]. However, sequence divergence was mainly recorded in the remaining non-HD regions (C-terminal region). For instance, the WUS box was exclusively found in the WUS clade representatives, motifs 4 and 6, which are specific to the intermediate clade. This strongly highlights the existence of evolutionary mechanisms for transcriptional repression and activation. Furthermore, the WUS clade counted the higher number of members, with seven *SIWOX* genes, while the ancient and intermediate clades are represented by only one and two *SIWOX* genes, respectively. The

high proportion of WUS clade representatives has been reported in other plant species, including *Arabidopsis thaliana*, *Populus trichocarpa*, *Oryza sativa*, *Gossypium hirsutum*, *Triticum aestivum* and *Chimonanthus praecox* [27,32,45].

Expression profiling of the *SIWOX* gene family across different stages and growth conditions revealed broad functional variation among *SIWOX* members. Most *SIWOX* genes displayed low to moderate expression values throughout vegetative and reproductive tissues/organs, whereas *SIWUS*, *SIWOX1* and *SIWOX4* exhibited higher transcript levels in leaves, stems, and flowers. These findings were consistent with their conserved functions in meristem maintenance, organogenesis and floral development as previously reported by [11,20,32,46–49]. Remarkably, *SIWOX13* showed a dynamic expression pattern across all the analyzed tissues, underscoring its function as a central regulatory hub controlling diverse developmental processes. The expression *SIWOX13* remained interestingly induced during the different phases of fruit development, with a peak of expression detectable during fruit ripening. This expression pattern advocates its implication in cell expansion, tissue differentiation and fruit ripening. These findings remained consistent with earlier reports linking *WOX* function to fruit development and maturation processes [50–52]. It is worth mentioning that the expression profiles of several *SIWOX* genes are somehow similar to those reported in their orthologs, while others show notable divergence. For instance, *SILAM1* (*AtWOX1* ortholog) is known to promote the expansion of leaf margins [53]. In pea and Medicago, this gene is strictly required for blade development. In tomato, transcriptomic analysis further confirms its key role in leaflets' initiation and growth in tomato [53]. This suggests a functional diversification of *WOX1* resulting from evolutionary events in distant species. Inversely, the high expression of *SIWOX4* in stems reflects its conserved role in root and stem vascular procambium differentiation, as previously documented in both *Arabidopsis* and tomato by Ji et al. [54].

Under biotic and abiotic stresses, *SIWOX4* and *SIWOX13* were strongly induced, with *SIWOX13* displaying a broad response to all the tested stresses. However, discrepancies were observed between our findings and those reported by Li et al. [28]. For instance, Li et al. [28] reported a moderate expression of *SIWOW13* in response to cold application. Meanwhile, our results showed a strong expression of this gene in response to these abiotic stress conditions. These differences are mainly due to the differences in the experimental parameters such as the used cultivar, the intensity of the stress and time of application. It is worth mentioning that a major advancement of this study is the integration of the expression patterns of *SIWOX*s in response to biotic stressors. While prior research mainly focused on abiotic stresses such as salinity and cold stress, our work revealed another feature of *SIWOX4* and *SIWOX13*, associated with plant response to biotic stresses. With that, both genes can be proposed as multi-stress integration points, since they are actively involved in the set of adaptive response to both abiotic and biotic stresses. Additionally, some *SIWOX* members, mainly *SIWOX13* and *SIWUS*, appeared to be regulated at the post-transcriptional level by miRNA via transcript cleavage, allowing fine regulation of their expression in specific tissues and developmental stages.

Cis-acting regulatory element prospection provides additional clues regarding gene function [55]. Numerous previous studies have tinted the central role of *WOX* transcription factors in orchestrating developmental processes and plant response to external stimuli [56–62]. Computational mining of the promoter region (2kb-upstream initiation codon) of *SIWOX* genes revealed the presence of a broad number of *cis*-acting elements associated with plant growth and development and hormonal and stress response-related motifs. More interestingly, a huge proportion of these elements are specific to plant growth and development, further confirming their significant role in the regulation of several plant developmental processes. Additionally, the promoter regions of *SIWOX* genes, namely

SIWOX13 and *SIWOX4*, harbored *cis*-acting regulatory elements that are associated with plant response to abiotic and biotic stresses, which strongly suggest *SIWOX* involvement in the set of adaptive responses in addition to their core function. This hypothesis is consolidated by earlier studies underscoring WOX TFs' implication in biotic and abiotic stress responses [22,32,56,63]. The identification of these *cis*-regulatory elements in the promoters of *SIWOX4* and *SIWOX13* provides a regulatory basis for the biotic stress regulation observed in our study, further extending the *cis*-regulatory elements mining that had been previously established by Li et al. [28].

Protein–protein interaction analysis provides additional clues regarding the biological function of the *SIWOX* gene family, further confirming earlier conclusions. From this analysis, *SIWUS* emerges as a central interaction core, interacting with other WOX members and main floral regulators such as *FALSIFLORA* and the MADS-box factor *EJ2*. This finding was consistent with *WUS* implication in meristem maintenance and floral transition [33,47]. Moreover, the PPI analysis also highlighted the direct interaction of *SIWUS* and *SIWOX4* with *SERK1* and *SlmCLV2*, both described as meristem size regulators by [64,65], supporting their involvement in stem cell homeostasis and more importantly the functional diversification observed within the *SIWOX* TF family. By interacting with *SERK1*, these *SIWOX* proteins likely integrate brassinosteroid and other receptor-like kinase (RLK) signals, to modulate meristem size in response to internal physiological signals [66,67]. While the majority of *SIWOX*s appear to regulate developmental processes, *SIWOX13* along with *SIWUS* and *SIWOX4* arise as central regulatory hubs, ensuring the integration of developmental, hormonal and stress responsive pathways. Belonging to the ancient clade, *SIWOX13* likely functions as an evolutionary bridge connecting ancestral stress response pathways with modern developmental processes. By integrating ABA and ethylene signaling during water deficit or fruit maturation, these regulatory hubs act as molecular tuners. This mechanism allows the plant to set the balance between growth and survival under adverse environmental conditions [44,68].

In addition to the expression pattern and protein interactome, our study revealed a key feature regarding the regulatory network of *SIWOX* gene family members. For instance, *SIWOX13* and *SIWUS* appeared as highly regulated genes. Indeed, *SIWOX13* was found to be targeted by the *sly*-miR156 family. These post-transcriptional regulators are known for their involvement in the regulation of the initial stages of fleshy fruit development in tomato [69]. This hypothesis is further consolidated by the Jiang et al. work, describing *SIWOX13* as a positive regulator of tomato fruit ripening, which occurs through the modulation of key ripening-related transcription factors [29]. Similarly, while *SIWOX4* promotes procambial development, the identification of translational repression of this gene by *sly*-miR171c strongly suggests the existence of a fine-tuning mechanism associated with plant vascular system development [70]. Along with their involvement in the regulation of key developmental processes, *sly*-miR156 and *sly*-miR171c are significantly regulated by abiotic stresses, namely drought [71]. Here, we found that the expression of *sly*-miR156 and *sly*-miR171c targeted genes (*SIWOX13* and *SIWOX4*) was notably induced by drought, providing a direct link between miRNA control and stress response.

4. Materials and Methods

4.1. Genome-Wide Identification of *SIWOX* Genes

The identification of tomato WOX genes was conducted using genome sequence data (Tomato Genome CDS ITAG version 2.4) deposited at the Solanaceae Genomics Network (<https://solgenomics.net/>) (viewed on 20 April 2024), with the cultivar Heinz 1706 serving as the reference genome. Homologous protein sequences of *SIWOX* from *Arabidopsis thaliana*, *Nicotiana tabacum*, *Cucumis melo*, *Cucumis sativus*, and *Triticum aestivum* were

retrieved from PlantTFDB and employed as query sequences for search using TBLASTN (v 4.0). An expectation value (E-value) threshold of 1×10^{-10} was applied to guarantee high confidence of prediction. The identification was succeeded by the removal of redundant sequences according to their NCBI ID and Solyc number, ultimately yielding unique representative IDs of a singular WOX gene sequence. The identified *SIWOX* genes were named according to their homologous.

4.2. Physico-Chemical Characterization and Three-Dimensional Structure Prediction of *SIWOX* Proteins

The physico-chemical characteristics of the identified *SIWOX* proteins, namely the molecular weight (MW), theoretical isoelectric point (pI), the number of amino acids, instability index, aliphatic index, and GRAVY (grand average of hydropathicity), were predicted based on their predicted amino acid sequences using the ExPASy ProtParam tool (v 3.0) [72] (accessed on 20 January 2025). The physico-chemical characterization data were processed and visualized using R environment (version 4.5.0), with tidyr, dplyr and ggplot2 packages. The 3D structures of *SIWOX* proteins were predicted using the AlphaFold Protein Structure Database [73] (AlphaFold Monomer v2.0 pipeline, accessed 30 January 2025).

4.3. Gene Structure, Physical Position, Conserved Motifs and Cis-Acting Regulatory Elements Analysis

The ‘Gene Structure Display Server v2.0’ was used to analyze the gene structure of the identified *SIWOX*s [74]. The physical position of each identified *SIWOX* gene was shown using the Mapgene2chromosomeV2 program (http://mg2c.iask.in/mg2c_v2.0/) (accessed on 18 January 2025). The conserved domain search of the identified *SIWOX* genes was performed using Multiple Expectation Maximizations for Motif Elicitation (MEME) software (version 5.5.8) (accessible through: https://meme-suite.org/meme/meme_5.5.8/, (accessed on 12 February 2025) to search for a maximum of 20 motifs, with an amino acid width ranging from 6 to 50 and statistical cutoff of E-value < 0.05 [75]. The 2 kb-upstream DNA sequence of each *SIWOX* was extracted from the SGN database (Solanaceae Genomics Network) and then the PLACE database (<https://www.dna.affrc.go.jp/PLACE/?action=newplace>, accessed on 10 March 2025) was used for cis-regulatory elements mining [76]. A total of 44 elements were analyzed and the frequency of each element was recorded and summarized in a numerical matrix. Data visualization was performed using the R environment (version 4.5.0) using pheatmap, dplyr and ggplot2 packages.

4.4. Phylogenetic Analysis

The phylogenetic tree of *SIWOX* protein sequences was constructed using a pooled FASTA file gathering all WOX protein sequences from tomato and selected sequences from *Arabidopsis thaliana*, *Cucumis melo*, *Cucumis sativus* and *Triticum aestivum*. Multiple sequence alignment was performed using the MUSCLE algorithm implemented in Mega12 [77]. The alignment quality was maintained through the retrieve of poorly aligned regions. The tree was inferred using the Maximum Likelihood method with 1000 bootstrap replicates based on the JTT (Jones–Taylor–Thornton) substitution model. Tree visualization and annotation was realized using iTol (v 7) (<https://itol.embl.de/>), accessed on 12 March 2025 [78].

4.5. CDS Similarity Analysis

The coding DNA sequences (CDS) of the *SIWOX* genes were used for nucleotide sequence similarity analysis. For that, multiple sequence alignment was conducted in R environment (version 4.5.0) using the Biostrings package. Pairwise percentage identity values were computed using a custom R script enabling the generation of a nucleotide identity matrix. The results were visualized through a heatmap using the pheatmap

package in R. A pair of genes were considered as duplicated when they shared more than 80% of nucleotide sequence identity.

4.6. Collinearity and Duplication Events

Collinearity analysis was assessed using MCScanX (v1.0.0) to set the collinear relationships among *SIWOX* genes [79]. For that purpose, gene positions were retrieved from the GFF file (downloaded from the SGN platform), and BLASTN (v 2.0.0 x) results were used to identify homologous pairs. Duplicated genes were classified as tandem if they are positioned at the same chromosome with a distance ≤ 100 kb apart, or segmental/WGD if it concerned two genes located in different chromosomes, or singletons for pairs exhibiting no collinear relationship. Self-hits were also considered as singletons.

4.7. In Silico Prediction of miRNA Targets

The *in silico* prediction of miRNA targets in *SIWOX*s was performed using the psRNA Target Server (v2, 2017 update) (<https://www.zhaolab.org/psRNATarget/analysis>) [80] (accessed on 2 January 2025), using the available tomato miRNA database deposited in the same server. The analysis was conducted using default server parameters, with a maximum expectation value of 0.5 and a target accessibility penalty (UPE) maximum energy of 25.0 kcal/mol to ensure high confidence of prediction. Predicted miRNA–*SIWOX* interactions were compiled and subsequently visualized using the R (version 4.5.0) ggplot2 package and the geom_tile function for interaction type display.

4.8. Protein–Protein Interaction Analysis and GO Enrichment Profiling

Protein–protein interaction analysis of *SIWOX* proteins was carried out using the STRING database (<https://string-db.org/>) (accessed on 11 February 2026) against *Solanum lycopersicum* proteome. The network was constructed in the R environment, using igraph and tidygraph packages with the nodes representing the proteins. Proteins in the top 25% of degree were defined as hubs.

The GO enrichment profiling was conducted from *SIWOX*s data extracted from the STRING database, with the focus on biological processes, molecular function and cellular components. Significant terms (FDR < 0.05) were filtered, and the top 20 GO terms were visualized as a dot plot graphic using R environment, namely ggplot2 and forcats packages, with point size being proportional to gene count and color representing $-\text{Log}_{10}(\text{FDR})$.

4.9. Gene Expression and Regulatory Interactions Under Different Conditions

Gene expression analysis under different growth conditions and hormonal and stress treatments was extracted from the TOMEXPRESS RNA-seq database (accessed on 8 February 2026) [81]. The list of the different conditions and RNAseq dataset IDs is given in Supplementary File S7. The expression data were analyzed using the R environment (version 4.5.0) using tidyr and dplyr packages. Data visualization was performed using the ggplot2 package, as the expression patterns were represented as a bubble plot, with bubble size and color intensity being correlated with the expression levels across tissues, developmental stages or stress/hormonal conditions.

A bipartite gene-treatment network was constructed to feature the regulatory relationships between *SIWOX* genes and the different biotic, abiotic and hormonal treatments. Expression level values were used to set up-/down-regulated genes. Genes exhibiting ≥ 2 -fold change and ≤ 0.5 -fold change were considered up-regulated and down-regulated, respectively. Meanwhile, genes displaying changes ranging between 0.5- and 2-fold were discarded from the network analysis. Up-/down-regulated interactions were indicated in green and red, respectively.

5. Conclusions

The present study delivers a full genome-wide analysis of the WOX gene family in tomato. On this basis, ten *SIWOX* genes were identified and sorted into the three major clades. The identified genes displayed distinct gene structures, conserved motifs and a large panel of cis-acting regulatory motifs that are specific to plant development, hormonal signaling and both biotic and abiotic stress responses. Expression profiling and miRNA targets mining further revealed a specific regulation observed among *SIWOX* gene family members. More interestingly, functional analysis in combination with PPI analysis enabled the identification of key *SIWOX* genes that act as core regulatory components. Overall, this integrative analysis provides a deep functional basis for the *SIWOX* gene family. These findings deliver a robust groundwork for future functional studies and for the use of *SIWOX* genes, namely *SIWUS*, *SIWOX4* and *SIWOX13*, as targets for the improvement of tomato development and resilience to a wide range of environmental stresses.

Supplementary Materials: The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/stresses6020036/s1>, Supplementary File S1: CDS sequence of the ten identified *SIWOX* genes; Supplementary File S2: The correlated values of *SIWOX* genes; Supplementary File S3: the sequences of WOX proteins selected for phylogenetic analysis; Supplementary File S4: Summary of the cis-acting regulatory elements identified in the promoter regions of *SIWOX* genes. N = any nucleotide, W = A/T, K = G/T, R = A/G, Y, C/T, B = C/G/T, M = A/C according to the nucleotide ambiguity codes of IUPAC nomenclature.; Supplementary File S5: Estimated transcript number of *SIWOX* genes in different organs; Supplementary File S6: Estimated transcript number of *SIWOX* genes in response to different abiotic, biotic and hormonal treatments; Supplementary File S7: The list of the different conditions and RNAseq dataset IDs.

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