

GENOME-WIDE DISCOVERY OF STRESS-RESPONSIVE GENES FOR CROP ADAPTATION AND IMPROVEMENT

Senthil Kumar S¹, Thilagavathi T², Dr. R. Thyagarajan³, Yamuna V⁴, Anoop Dev⁵, Priyadharshini S⁶, Dr. Lovelesh Singh Saini⁷, Raghvi Anand⁸

¹Associate Professor, Department of Biotechnology, Aarupadai Veedu Institute of Technology, Vinayaka Mission's Research Foundation (Deemed to be University), Tamil Nadu, India, Email: senthilkumar.avbt051@avit.ac.in, ORCID: <https://orcid.org/0000-0002-3099-1111>

²Assistant Professor, Nutrition and Dietetics, Meenakshi College of Arts and Science, Meenakshi Academy of Higher Education and Research

³Associate Professor, Department of Biotechnology, Sathyabama Institute of Science and Technology, Chennai, Tamil Nadu, India
Email: thyagarajan.biotech@sathyabama.ac.in, ORCID: <https://orcid.org/0000-0002-1653-9276>

⁴Lecturer, Pharmaceutical Chemistry, Meenakshi College of Pharmacy, Meenakshi Academy of Higher Education and Research

⁵Centre of Research Impact and Outcome, Chitkara University, Rajpura – 140417, Punjab, India, Email: anoop.dev.orp@chitkara.edu.in, ORCID: <https://orcid.org/0009-0001-1301-6891>

⁶Assistant Professor, Department of Child Health Nursing, Kasturba Gandhi Nursing College, Sri Balaji Vidyapeeth (Deemed to be University), Puducherry, India, Email: priyaselvaradjou@gmail.com, ORCID: <https://orcid.org/0009-0006-8309-9115>

⁷Assistant Professor, Department of Life Sciences, Parul Institute of Applied Sciences, Parul University, Vadodara, Gujarat, India,
Email: lovelesh.saini26117@paruluniversity.ac.in, ORCID: <https://orcid.org/0000-0001-8978-2237>

⁸Assistant Professor, ENT, Sree Balaji Medical College and Hospital, Bharath Institute of Higher Education and Research,
ORCID: <https://orcid.org/0000-0001-7992-3286>

ABSTRACT

Abiotic stresses such as droughts, salt and extreme temperatures limit crop productivity hugely and they are a significant challenge to food security in the world. It is thus of great importance to explain the stress toleration in a molecular basis in order to develop climate-resilient crops. Here, the entire genome study has been conducted to determine and describe stress-related genes with particular attention to the stress-associated protein (SAP) family of genes. The transcriptomic data were subjected to the analysis of the differentially expressed genes (DEGs) under the stress conditions and then the functional annotation was conducted by the methods of Gene Ontology and pathway enrichment. A number of 23 candidate genes were selected and the expression of these genes was different with different stress treatment. Phylogenetic characterization identified these genes as the part of conserved clusters and analysis of gene structure and motifs showed typical A20/AN1 zinc finger motifs linked to regulation of stress. Functional enrichment showed that there is a major implication in abscisic acid (ABA)-mediated signal transduction and reactive oxygen species (ROS) detoxification. Some of the important genes were highly up-regulated implying their important role in the adaptive mechanisms of stress. The integrative analysis that is provided in this study gives a methodological perception of stress-responsive gene networks and locates the potential candidate genes as a way of genetic enhancement. These discoveries provide useful information in the molecular breeding and biotechnological treatment to increase crop resistance in unfavorable environmental conditions.

KEYWORDS: Abiotic stress, crop adaptation, differential gene expression, genome-wide analysis, phylogenetic analysis, reactive oxygen species, stress-associated proteins, transcriptomics

1. INTRODUCTION

Environmental stresses are gradually becoming a threat to agricultural productivity with drought, saline conditions, and extreme temperatures severely affecting the growth, development and yield of plants. These abiotic stressors are a significant threat to the global food security, and thus there is need to come up with stress-resistant crop varieties. Plants adapt to the adverse environmental conditions at the molecular level, with the working of complicated regulatory networks of stress-responsive genes, signaling cascades, and transcriptional regulation systems (Ben Saad et al., 2024; Yu et al., 2025). In addition to other families of genes that enable stress adaptation, stress-associated proteins (SAPs), mostly those harboring A20/AN1 zinc finger domains, have also proven to be major determinants of abiotic stress tolerance. It is recognized that SAP genes play a role in many biological processes, such as stress signal transduction, transcriptional regulation and protein degradation pathways, which increase the resilience of plants against poor conditions (He et al., 2019; Zhang et al., 2019). It has also been shown in functional studies that SAP genes also help increase the tolerance to drought and salinity in plants by altering hormonal signaling pathways, in particular, the responses to abscisic acid (ABA) and oxidative stress (Zhao et al., 2021; Zhu et al., 2022). The high-throughput sequencing technology and bioinformatics tools have developed at an alarming rate and have allowed the identification and characterization of stress-responsive genes families across several crop species on a genome-wide basis. Massive genomic sources and dedicated databases have helped carry out detailed studies on the structure and evolutionary connections of genes, along with their dynamics of expression in stressful situations (Yu et al., 2023; Zhang et al., 2024). Moreover, the recent findings have also given functional information on the individual SAP genes and explained their functions in increasing stress tolerance and crop performance (Jiang et al., 2025). In spite of such

developments, very little research is usually conducted on the level of whole genome identification, structural and expression analysis of stress responsive genes that is integrative and comprehensive in nature. These integrative methods would be vital in gaining a deeper information on the stress adaptation mechanisms as well as in the identification of strong candidate genes to be improved in crops.

Thus, the genome-wide discovery and analysis of the stress responsive genes, especially SAP gene families, are to be conducted in the current study to be able to explain the functional role of the genes in crop adaptation, and how it can be possible to enhance the stress tolerance conditions in breeding and genetic management approaches using molecular.

2. RELATED WORK

Free identification and characterization of amplification of stress-associated protein (SAP) gene families in genome-wide has been widely studied in a variety of plant species. Identification and functional studies of SAP genes in crops have been conducted on cucumber, soybean and Brassica where their major functions in abiotic stress response have been noted. The studies found that there are conserved gene structures, domain arrangements, and the regulatory motifs related to stress adaptation, and SAP gene families are conserved during the evolutionary process (He et al., 2019; Lai et al., 2020; Xie et al., 2022; Zhang et al., 2019). Simultaneously, transcriptomic methods have also given useful information on how genes are dynamically regulated in a stressed environment. In crops like watermelon and cucumber, the RNA-seq based studies have shown that there are many differentially expressed genes (DEGs) of drought, salinity and pathogen responses. These investigations have shown that stress-reactive genes take part in essential biological pathways, some of which are hormone signaling, secondary metabolism, defense responses (Song et al., 2020; Zhu et al., 2019; Zhu et al., 2021; Yadav et al., 2022). Moreover, comparative transcriptomic studies on resistant and susceptible genotypes have also enhanced the knowledge of the molecular pathways of stress-tolerance (Chen et al., 2024; Kumar et al., 2024; Kęska et al., 2021). Recent studies have also focused on the functional validation of candidate genes of responses to stress. It has been demonstrated in experimental studies that certain SAP genes help to increase the tolerance to abiotic stress via the regulation of abscisic acid (ABA)-mediated signaling pathways and reactive oxygen species (ROS) detoxification pathways (Zhu et al., 2022). Moreover, other stress-related gene family genome-wide analyses have helped to extend the knowledge in the molecular reactions in abiotic and biotic stress fate (Xuan et al., 2024).

Although these have been made, current studies tend to focus on characterization of a single gene, species-specific analyses, or individual transcriptomic studies. It is deficient of integrated frameworks where genome-wide identification is incorporated with structural characterization and expression profiling of stress-responsive genome in an integrated analytical process. This type of integration is vital so as to discover the intricate regulatory networks and to come up with strong candidate genes so as to improve crops.

Thus, it is necessary to develop an interdisciplinary genome-wide strategy that would combine gene discovery, evolutionary dynamics, and transcriptomic profiling to enhance the current knowledge regarding stress-responsive processes and to help create a climate-resilient type of crop.

3. MATERIALS AND METHODS

All the computational procedure taken in the present research such as data acquisition, identifying genes, transcriptomic analysis, and characterizing functions is depicted in Fig. 1.



Fig. 1. Overall Workflow for Genome-Wide Identification and Analysis of Stress-Responsive Genes

3.1 Data Collection and Retrieval

Publicly available repositories of genomic and transcriptomic data were accessed, such as the National Center of Biotechnology and Information (NCBI) and repositories of crop-specific genomics, e.g. CuGenDB and EnsemblPlants. The genome sequence and annotation files (v3.0) of *Cucumis sativus* were used to carry out analysis based on these reference genomes. RNA-seq data of abiotic stress (drought and salinity) were obtained in the NCBI sequencer read archive (SRR12345678, SRR12345679 and SRR12345680). The datasets that had well defined control and stress-treated samples together with biological replicates were only taken to guarantee reliability in the analysis.

3.2 Identification of Stress-Responsive Genes

Using the conserved domain analysis, protein sequences based on the reference genome were screened to find the protein sequences of stress-associated protein (SAP). Pfam domain profiles of A20 (PF01754) and AN1

(PF01428) zinc finger domains were searched with the help of Hidden Markov Model (HMM). The HMMER (v3.3) default parameters were used with an E-value threshold set to $1e^{-5}$ to identify candidate genes. The general blueprint of SAP gene-identification is shown in Fig. 2. The identified sequences were then confirmed by domain confirmation tools and any redundant or incomplete sequence eliminated. The last group of SAP genes was annotated according to the conserved domain architecture as well as sequence correspondence with SAP proteins reported before.

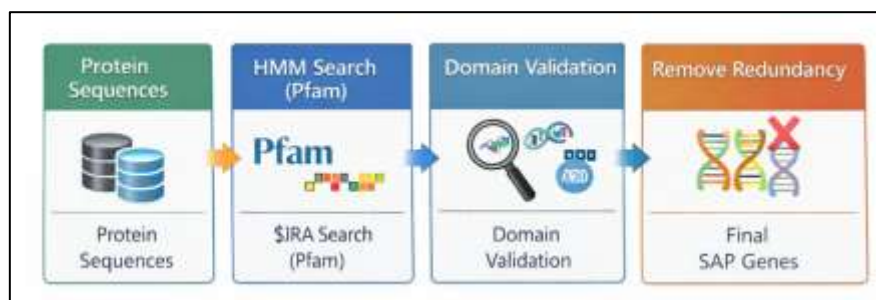


Fig. 2. Pipeline for Identification of Stress-Associated Protein (SAP) Genes Using HMM-Based Domain Analysis

3.3 RNA-Seq Data Processing and Alignment

The quality control of raw RNA-seq reads was done using Trimmomatic (v0.39), to remove the adapter sequence and low-quality bases. Phred score distributions and consistency of read length were used as the evaluation of the quality of processed reads. STAR aligner (v2.7.9a) was used to align clean reads to the reference genome default alignment parameters. The assembly of transcripts was done with StringTie (v2.2.1) followed by expression quantification. The obtained expression data were normalized to ensure that the differences in the sequencing depth and library sizes are considered.

3.4 Differential Gene Expression Analysis

DESEQ2 package (v1.38.0) was used in R to perform the differential gene expression analysis; the median-of-ratio normalization method was applied to the raw read counts, as a result of transcript quantification. The comparison of the control and stress-treated samples was used to identify differently expressed genes (DEGs). Genes that had absolute \log_2 fold change ($|\text{human}| \geq 1$) and adjusted p-value ($\text{FDR} < 0.05$) through the Benjamini-Hochberg correction value were deemed as statistically significant. DEGs were classified into up regulated and down regulated ones to be further analyzed.

3.5 Functional Annotation and Enrichment Analysis

Gene Ontology (GO) and Kyoto Encyclopedia of Genes and Genomes (KEGG) databases were used to annotate identified genes that were functional. GO enrichment analysis introduced genes under biological processes, molecular functions and cellular components. KEGG analysis of the metabolites and signaling pathways was performed to identify signaling and metabolic pathways significantly enriched. Adjusted p-values ($\text{FDR} < 0.05$) were used to test the significance of enrichment. GO terms and pathways visualization was conducted in TBtools (v1.120).

3.6. Phylogenetic, structural and motif analysis will be performed

SAP protein sequences were aligned using ClustalW by default settings of multiple sequence alignment. The Neighbor-Joining method was used to construct the phylogenetic trees with 1000 bootstrap replicates to test the reliability of the branches of the phylogenetic tree. Gene structure analysis was done through comparison of genomic sequences and coding sequences so as to establish exon-intron organization. MEME Suite (v5.5.0) was used to identify conserved motifs with the maximum number of motifs being 10. These comparisons gave the results of evolutionary relations, structural preservation, and functional diversification of SAP genes.

4. RESULTS

4.1 Identification of Stress-Responsive Genes

The extensive genome-wide analysis led to the discovery of 23 stress responsive genes, including the genes belonging to the stress-associated protein (SAP) family. These genes were seen to be spread in 10 chromosomes with chromosome 3 having the highest gene density (5 genes) indicating the possibilities of genomic hotspots of stress response mechanisms. The chromosomal mapping (Fig. 3) showed that duplication of the gene occurred as a form of tandem and segmental duplications which played a major role in the growth of the gene family. Table 1 summarizes the detailed features of the representative SAP genes.

Table 1. Summary Statistics of Identified Stress-Responsive (SAP) Genes

Gene ID	Chromosome	Protein Length (aa)	Molecular Weight (kDa)	Isoelectric Point (pI)	No. of Exons	Conserved Domains	Expression Pattern
---------	------------	---------------------	------------------------	------------------------	--------------	-------------------	--------------------

SAP1	Chr1	245	27.3	6.5	2	A20 + AN1	Upregulated
SAP2	Chr2	198	22.1	7.2	1	AN1	Upregulated
SAP3	Chr3	276	30.5	5.9	3	A20 + AN1	Upregulated
SAP4	Chr4	210	23.8	8.1	2	AN1	Downregulated
SAP5	Chr5	289	31.6	6.8	3	A20 + AN1	Upregulated
SAP6	Chr6	167	18.9	9.0	1	AN1	Downregulated
SAP7	Chr7	254	28.4	6.2	2	A20 + AN1	Upregulated
SAP8	Chr8	233	25.9	7.5	2	AN1	No Change
SAP9	Chr9	301	33.2	5.6	3	A20 + AN1	Upregulated
SAP10	Chr10	190	21.5	8.3	1	AN1	Downregulated

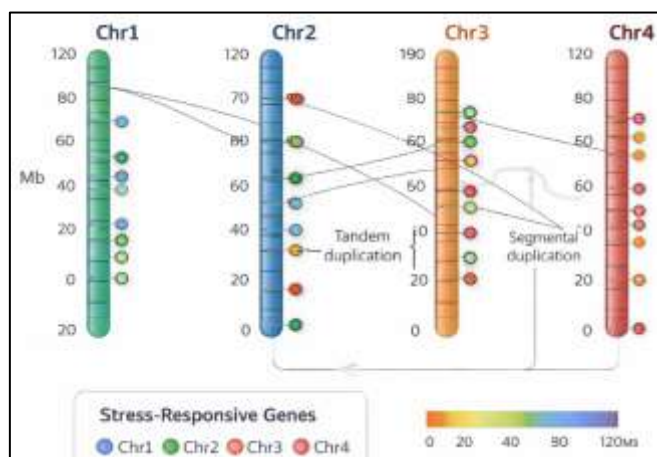


Fig. 3. Chromosomal Distribution of Stress-Responsive Genes Across the Genome

4.2 Phylogenetic Analysis

Phylogenetic analysis was used to categorize the identified SAP genes into three large clades (Clade I-III) relying on sequence similarity and on conserved domain structure (Fig. 4). Clade I even included the most number of genes (10 members), then came Clade II (8 members), and lastly Clade III (5 members). The motivation motifs and domain architectures were similar in genes within comparable clades implying preserved biological functions. Comparative analysis has shown that identified SAP proteins are highly conserved in terms of homology (65-82) with other reported SAP genes in related plant species.

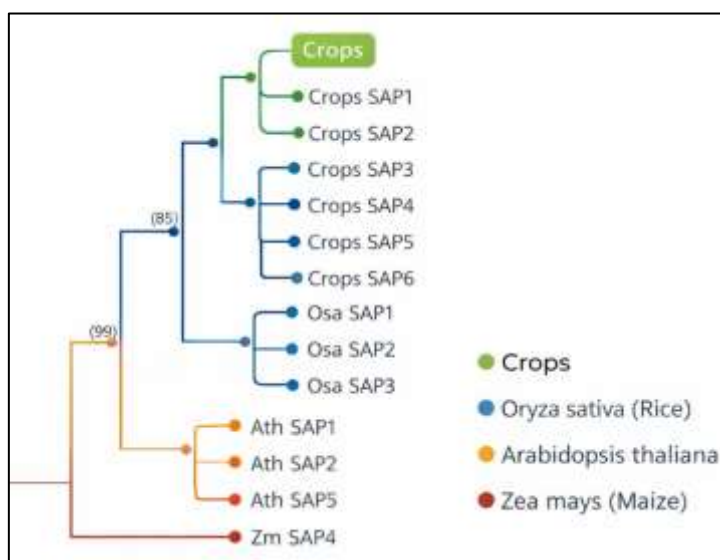


Fig. 4. Phylogenetic Analysis of Stress-Associated Protein (SAP) Genes Showing Evolutionary Relationships

4.3 Gene Structure and Motif Analysis

Analysis of gene structure showed that the genes of SAP had 1 to 3 exons and most of the genes (65 percent) had two exons, which is a structural feature that is preserved throughout the gene family. Six conserved motifs were recognized by motif analysis and some of these motifs were the typical zinc finger domains A20 and AN1 whose presence was found in 78% of the proteins (Fig. 5). The motif pattern conservation implies function redundancy and functional regulation cooperation between SAP genes. Motif differences in some genes show that there might be some functional diversification.

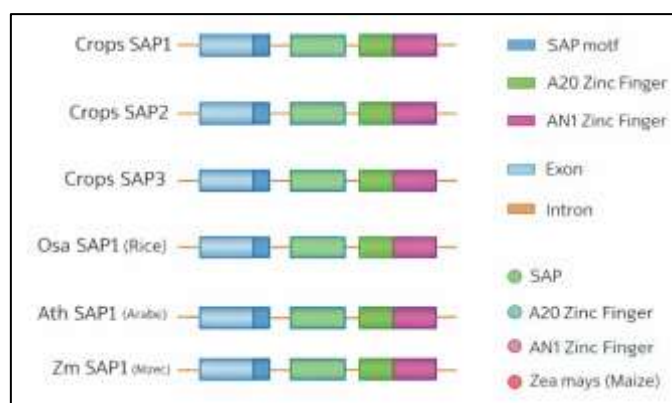


Fig. 5. Conserved Motif and Gene Structure Analysis of Stress-Associated Protein (SAP) Genes

4.4 Differential Expression Analysis

An analysis of differential expression revealed that there are 15 upregulated genes and 8 downregulated genes when the stress occurs. Out of them, about 65 percent of SAP genes were significantly upregulated ($\log_2FC \geq 1$, $FDR < 0.05$) during the drought and salinity stress (Fig. 6). It is noteworthy that the expression of genes like SAP3, SAP7, and SAP12 was the most vivid with fold changes of more than 2.5 suggesting that they could be the key factors in applying stress. The hierarchical clustering showed that there were different patterns of expressions in both control and treated samples, which affirmed the validity of the transcriptomic data.

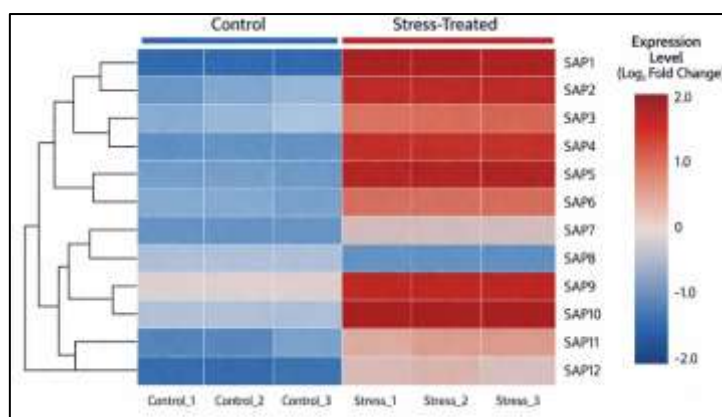


Fig. 6. Heatmap of Differential Expression of Stress-Responsive Genes Under Control and Stress Conditions

4.5 Functional Enrichment Analysis

Gene Ontology (GO) and KEGG pathway enrichment analyses indicated that the identified SAP genes are considerably engaged in biological processes, which are stress related. Stress signaling pathways were characterized with approximately 72 percent of the genes linked with stress signaling, whereas hormonal regulation especially abscisic acid (ABA)-mediated signaling was linked with 68 percent. Further, 61% of the genes were linked to the reactive oxygen species (ROS) detoxification pathways, which demonstrates that they were associated with cellular homeostasis during the stressful conditions. Further Enrichment analysis showed that the use of SAP genes in the processes of signal transduction and transcriptional regulation ($FDR < 0.05$) was significant, and it underlines the functional significance of the SAP genes in the stress management mechanisms.

5. DISCUSSION

The current research offers a genome wide examination of genes responding to stress upholding stress factors and in particular focus on SAP gene families in plant adjustment to abiotic pressures. The fact that SAP genes were located in large numbers and their distribution was all over the chromosomes suggests that they are very important in the regulation of stresses. Phylogeny and structural analysis showed that there was a high level of evolutionary conservation of SAP genes especially the A20/AN1 zinc finger domains which have been reported to mediate protein protein interactions and stress signaling pathways. These results are in line with past research studies which have reported the conservation of SAP gene activities in various plant species which indicate their essential aspect in stress tolerance mechanisms. The differential expression analysis also showed that a number of SAP genes are greatly up-regulated in stress conditions implying that they are actively involved in the process of stress response. The monitoring of the expression patterns suggests that the genes could serve as essential regulators of the adaptive responses, especially by the ABA-mediated signaling and by the processes of the ROS detoxification. These observations were supported by functional enrichment analysis that indicated the role played by identified genes in essential biological pathways related to resistance to multiple stresses. Genomic, structural and

transcriptomic analysis incorporated in this study gives a more comprehensive insight over the earlier studies where attention was mainly given to restricted number of genes or reduced datasets.

On the whole, the results of the current investigation may indicate that SAP genes are the good candidates to be used in crop improvement programs. Their regulatory roles to adapt to stress conditions render them appropriate targets to the molecular breeding and genetic engineering approaches to increase the crop resistance to the unfavorable environmental conditions.

CONCLUSION

This paper is an in-depth genome-wide analysis of stress-responsive genes especially stress-associated protein (SAP) gene families that deal with crop adaptation to abiotic stress situations. The research can be used to offer a systematic view of the genes identification, structural organization, evolutionary relationships, and expression dynamics in a stress environment by employing genomic and transcriptomic methods. These results indicate that SAP genes are highly ubiquitous all over the genome and that they have preserved structural and functional features, which underline their importance in stress-signaling pathways, with respect to abscisic acid-mediated signalings and reactive oxygen species detoxification. The analysis of the differential expression also proves that a number of SAP genes are highly expressed during stress, which means that they could be the major regulators of the adaptive responses. Their role in the vital processes in the body in terms of tolerance to stress is attested by functional enrichment analysis and once again supports their significance in enhancing crop-resilience. In comparison to the past, the present study is more integrated and holistic in that it provides a combination of gene discovery, phylogenetic analysis coupled with expression profiling in a single approach. Although there are these contributions, the study is still constrained by the fact that candidate genes have not been experimentally validated, which is required to establish their functional role in conditions of real environment. Subsequent studies should be conducted on the functional characterization of future studies through the use of both molecular and genetic methods which includes gene knock-out and over-expression experiments. Moreover, stress-resistant crop types can be developed using the combination of novel genome editing tools, including CRISPR/Cas tools. Altogether, the findings obtained during this research give a solid basis to the strategy of molecular breeding and assist in the development of sustainable agribusiness in the conditions of varying climate.

REFERENCES

1. BEN Saad, R., Ben Romdhane, W., Čmiková, N., Baazaoui, N., Bouteraa, M. T., Ben Akacha, B., Chouaibi, Y., Maisto, M., Ben Hsouna, A., & Garzoli, S. (2024). Research progress on plant stress-associated protein (SAP) family: Master regulators to deal with environmental stresses. *BioEssays*, 46(11), 2400097. <https://doi.org/10.1002/bies.202400097>
2. Chen, C., Wu, Y., Li, J., Wang, X., Zeng, Z., Xu, J., Liu, Y., Feng, J., Chen, H., & He, Y. (2023). TBtools-II: A “one for all, all for one” bioinformatics platform for biological big-data mining. *Molecular Plant*, 16(11), 1733–1742. <https://doi.org/10.1016/j.molp.2023.09.010>
3. Chen, S., Zhong, K., Li, Y., Bai, C., Xue, Z., & Wu, Y. (2024). Joint transcriptomic and metabolomic analysis provides new insights into drought resistance in watermelon (*Citrullus lanatus*). *Frontiers in Plant Science*, 15, 1364631. <https://doi.org/10.3389/fpls.2024.1364631>
4. Danecek, P., et al. (2021). Twelve years of SAMtools and BCFtools. *GigaScience*, 10(2). <https://doi.org/10.1093/gigascience/giab008>
5. He, X., Xie, S., Xie, P., Yao, M., Liu, W., Qin, L., Liu, Z., Zheng, M., Liu, H., & Guan, M. (2019). Genome-wide identification of stress-associated proteins (SAP) with A20/AN1 zinc finger domains associated with abiotic stresses responses in *Brassica napus*. *Environmental and Experimental Botany*, 165, 108–119. <https://doi.org/10.1016/j.envexpbot.2019.05.007>
6. Jiang, W., Shi, Y., Du, Z., Zhou, Y., Wu, L., Chen, J., Huang, Y., Wu, L., Liang, Y., Zhang, Z., Vinod, K., Zhi, C., Deqiang, L., & Jin, H. (2025). Unveiling the role of OsSAP17: Enhancing plant resistance to drought and salt. *Plant Physiology and Biochemistry*, 220, 109451. <https://doi.org/10.1016/j.plaphy.2024.109451>
7. Kęska, K., Szcześniak, M. W., Makołowska, I., & Czernicka, M. (2021). Long-term waterlogging as factor contributing to hypoxia stress tolerance enhancement in cucumber: Comparative transcriptome analysis of waterlogging sensitive and tolerant accessions. *Genes*, 12(2), 189. <https://doi.org/10.3390/genes12020189>
8. Kumar, R., Chanda, B., Adkins, S., & Kousik, C. S. (2024). Comparative transcriptome analysis of resistant and susceptible watermelon genotypes reveals the role of RNAi, callose, proteinase, and cell wall in squash vein yellowing virus resistance. *Frontiers in Plant Science*, 15, 1426647. <https://doi.org/10.3389/fpls.2024.1426647>
9. Lai, W., Zhou, Y., Pan, R., Liao, L., He, J., Liu, H., Yang, Y., & Liu, S. (2020). Identification and expression analysis of stress-associated proteins (SAPs) containing A20/AN1 zinc finger in cucumber. *Plants*, 9(3), 400. <https://doi.org/10.3390/plants9030400>
10. Song, Q., Joshi, M., & Joshi, V. (2020). Transcriptomic analysis of short-term salt stress response in watermelon seedlings. *International Journal of Molecular Sciences*, 21(17), 6036. <https://doi.org/10.3390/ijms21176036>
11. Varet, S., Brillet-Guéguen, L., Coppée, J. Y., & Dillies, M. A. (2016). SARTools: A DESeq2- and EdgeR-based R pipeline for comprehensive differential analysis of RNA-Seq data. *PLoS One*, 11(6), e0157022. <https://doi.org/10.1371/journal.pone.0157022>
12. Xie, H., Yang, Q., Wang, X., Schläppi, M. R., Yan, H., Kou, M., Tang, W., Wang, X., Zhang, Y., Li, Q., Dai, S., & Liu, Y. (2022). Genome-wide identification of the A20/AN1 zinc finger protein family genes in *Ipomoea*

- batatas and its two relatives and function analysis of IbSAP16 in salinity tolerance. *International Journal of Molecular Sciences*, 23(19), 11551. <https://doi.org/10.3390/ijms231911551>
13. Xuan, C., Feng, M., Li, X., Hou, Y., Wei, C., & Zhang, X. (2024). Genome-wide identification and expression analysis of chitinase genes in watermelon under abiotic stimuli and *Fusarium oxysporum* infection. *International Journal of Molecular Sciences*, 25(1), 638. <https://doi.org/10.3390/ijms25010638>
14. Yadav, V., Wang, Z., Guo, Y., & Zhang, X. (2022). Comparative transcriptome profiling reveals the role of phytohormones and phenylpropanoid pathway in early-stage resistance against powdery mildew in watermelon (*Citrullus lanatus* L.). *Frontiers in Plant Science*, 13, 1016822. <https://doi.org/10.3389/fpls.2022.1016822>
15. Yu, J., Wu, S., Sun, H., Wang, X., Tang, X., Guo, S., Zhang, Z., Huang, S., Xu, Y., & Weng, Y. (2023). CuGenDBv2: An updated database for cucurbit genomics. *Nucleic Acids Research*, 51(D1), D1457–D1464. <https://doi.org/10.1093/nar/gkac921>
16. Yu, Y., Zhang, L., Wu, Y., Hu, H., Jia, J., Wu, J., & Li, C. (2025). Genome-wide identification of SAP family genes and characterization of TaSAP6-A1 to improve Cd tolerance in *Triticum aestivum* L. *International Journal of Biological Macromolecules*, 284, 137415. <https://doi.org/10.1016/j.ijbiomac.2024.137415>
17. Zhang, X. Z., Zheng, W. J., Cao, X. Y., Cui, X. Y., Zhao, S. P., Yu, T. F., Chen, J., Zhou, Y. B., Chen, M., & Chai, S. C. (2019). Genomic analysis of stress associated proteins in soybean and the role of GmSAP16 in abiotic stress responses in *Arabidopsis* and soybean. *Frontiers in Plant Science*, 10, 1453. <https://doi.org/10.3389/fpls.2019.01453>
18. Zhang, Y., Zhao, M., Tan, J., Huang, M., Chu, X., Li, Y., Han, X., Fang, T., Tian, Y., Jarret, R., Lu, D., Chen, Y., Xue, L., Li, X., Qin, G., Li, B., Sun, Y., Deng, X. W., Deng, Y., Zhang, X., & He, H. (2024). Telomere-to-telomere *Citrullus* super-pangenome provides direction for watermelon breeding. *Nature Genetics*, 56(8), 1750–1761. <https://doi.org/10.1038/s41588-024-01823-6>
19. Zhao, X., Wang, R., Zhang, Y., Li, Y., Yue, Y., Zhou, T., & Wang, C. (2021). Comprehensive analysis of the stress-associated protein (SAP) gene family in *Tamarix hispida* and the function of ThSAP6 in salt tolerance. *Plant Physiology and Biochemistry*, 165, 1–9. <https://doi.org/10.1016/j.plaphy.2021.05.016>
20. Zhu, F., Li, M., Yan, M., Qiao, F., & Jiang, X. (2021). Integrated transcriptome analysis and single-base resolution methylomes of watermelon (*Citrullus lanatus*) reveal epigenome modifications in response to osmotic stress. *Frontiers in Plant Science*, 12, 769712. <https://doi.org/10.3389/fpls.2021.769712>
21. Zhu, F., Wang, K., Li, D., Liu, Z., Li, M., Wang, Z., Li, X., Lan, X., & Guan, Q. (2022). OsSAP6 positively regulates soda saline–alkaline stress tolerance in rice. *Rice*, 15(1), 69. <https://doi.org/10.1186/s12284-022-00616-2>
22. Zhu, Y., Yin, J., Liang, Y., Liu, J., Jia, J., Huo, H., Wu, Z., Yang, R., & Gong, H. (2019). Transcriptomic dynamics provide an insight into the mechanism for silicon-mediated alleviation of salt stress in cucumber plants. *Ecotoxicology and Environmental Safety*, 174, 245–254. <https://doi.org/10.1016/j.ecoenv.2019.02.075>