

BREEDING HORTICULTURAL CROPS FOR ABIOTIC STRESS TOLERANCE: GENETIC RESOURCES, MECHANISMS AND FUTURE PROSPECTS: A REVIEW

¹Sagar, ²Ashutosh Kumar, ³Radhey Shyam Singh*, ⁴Yogita, ⁵N.K. Tiwari, ⁶Suraj Luthra, ⁷Shivam Maurya, ⁸Subhash Verma

¹Assistant Professor, Genetics and Plant Breeding, Faculty of Agricultural Sciences, GLA University, Mathura, Uttar Pradesh-281406

²Dr. Rajendra Prasad Central Agricultural University Pusa Samastipur, ACTO (SMS Horticulture) KVK Narkatiyaganj RPCAU Pusa

³Assistant Professor-cum-Junior Scientist, Department of Genetics and Plant Breeding, Veer Kunwar Singh College of Agriculture, Dumraon, Buxar-802136 (BAU, Sabour) Bihar

⁴Ph.D. (Vegetable Science), Maharana Pratap Horticultural University, Karnal, Haryana pincode- 132 001

⁵Associate Professor, Faculty of Agriculture, Maharishi Markandeshwar (Deemed to be University), Mullana, Ambala, Haryana, India - 133207

⁶Assistant professor School of Agriculture, Dev Bhoomi Uttarakhand University Dehradun Chakrata Road, Navgaon, Manduwala, Dehradun - 248007, Uttarakhand, India.

⁷Assistant Professor, Department of Plant Pathology, School of Agriculture, Lovely Professional University, Jalandhar Punjab

⁸Assistant Professor, School of Agriculture, Eklavya University, Damoh (Madhya Pradesh)-470661

*Corresponding author: Radhey Shyam Singh, E-mail- singhrrsco@gmail.com

ABSTRACT

Abiotic stresses are one of the major limitations affecting the productivity, quality, profitability and sustainability of horticultural crops. Rising temperatures, erratic precipitation, drought, salinity in soil and water, low temperatures and chilling/frost, waterlogging, imbalance in nutrients and heavy metal toxicity are the growing stresses experienced by fruit, vegetable, spice, plantation, ornamental and medicinal crops. The impact of such stresses is particularly pronounced in horticultural crops since apart from the total yield, the size, color, texture, flavor, nutritive value and marketable quality of fruits and vegetables are of considerable importance. Climate change has made such stresses even more unpredictable, severe and frequent, making it necessary to develop horticultural varieties with stable yields and quality under stress conditions. The genetic stock, which includes landraces, traditional varieties, wild relatives, introduced species, mutants and germplasm collections, is a major source of alleles for development of stress tolerant varieties. Abiotic stresses are tolerated by plants through a variety of physiological, biochemical and molecular mechanisms, which include osmoregulation, ionic regulation, antioxidative defenses, membrane stability, root system modifications, photosynthetic control and phytohormonal signaling. At the molecular level, transcription factors, stress response genes, transporters, protein kinases, reactive oxygen species and calcium-based signaling pathways play an important role. Traditional breeding techniques still hold significance, however, the efficiency of such techniques can be improved by adopting marker assisted selection, quantitative trait locus analysis, genome wide association studies, genomic selection and phenomics. The recent advances in genomics, pangenomics, transcriptomics, proteomics, metabolomics and epigenomics have made it easier to find out the candidate genes and favourable alleles that confer stress tolerance traits. Genome editing technology including the CRISPR/Cas system, base editing and prime editing has opened up new avenues for manipulating the genes of interest in stress adaptation. The combination of genetic resources, physiology, genomics, multi-omics, phenomics, artificial intelligence and genome editing will help develop more resilient cultivars in horticulture against the changing climatic conditions. This review article covers the important abiotic stresses impacting horticulture crops, genetic resources for crop breeding, physiological and molecular mechanisms of stress tolerance, traditional and advanced breeding techniques and future strategies for breeding resilient horticultural crops using genome editing technology.

KEYWORDS: Abiotic stress, horticulture crops, Abiotic stress, molecular breeding, and CRISPR/Cas,

1. INTRODUCTION

Horticultural crops form an important part of agriculture as they produce fruits, vegetables, spices, plantation crops, medicinal and aromatic plants and ornamental crops which make an important contribution to food security, nutritional security, farmer's income and rural employment. Fruits and vegetables play a major role as the source of vitamins, minerals, dietary fiber, antioxidants and bioactive compounds. The yield of horticultural crops also provides raw material for processing industries such as food processing, pharmaceutical industry, nutraceuticals and cosmetics. The yield of these crops is very much dependent on the environmental conditions, (Kumar et al., 2021).

Abiotic stresses are defined as environmental stresses which cause negative impact on the growth and development of the plant and include drought, salinity, heat, chilling, freezing, waterlogging, flooding, nutrient deficiency, nutrient toxicity and heavy metal stress (Paliwal, et al., 2021). The level of abiotic stresses is increasing at many locations due to climatic changes, unstained irrigation, soil degradation, higher temperature and

precipitation. The Food and Agriculture Organization has highlighted the significance of plant genetic resources in ensuring the adaptive capacity of the agricultural system. Genetic diversity provides the raw material required for selection and breeding of cultivars capable of performing under stressful environments, (Patil et al., 2026).

There is the possibility that abiotic stress could affect horticultural crops since many commercial varieties have been selectively developed to ensure higher yields and better fruit quality and preference when grown in favorable environments. The process of intensive selection may lead to the loss of the genetic diversity within the elite breeding lines and cause the genetic base to be narrow, (Padilla, et al., 2025). Also, many horticultural crops are complicated in their reproductive processes, highly heterogeneous, have long generation periods and genotypic × environmental interactions, thus making breeding relatively time-consuming.

Abiotic stress can influence horticultural crops at all the stages of their development. There may be low seed germination, leaf growth and photosynthetic rates, flower induction and fruit development due to drought. Heat stress can cause pollen sterility, flowers abortion, low fruit set and sun scalding. Salinity induces both osmotic and ionic stresses that cause low water absorption, nutrient imbalance and high level of toxic ions in cells. Freezing and chilling affect the cell membranes and metabolic processes of plants whereas waterlogging leads to oxygen deficiency in roots, (Kumar et al., 2021).

Plants' reactions to abiotic stress are multifaceted and include interaction of processes of physiological, biochemical, molecular and genetic nature. Stress reaction is associated with immediate adjustments in stomata regulation, root growth, osmolyte production, antioxidative capacity, changes in membrane composition and hormone metabolism. On the molecular level, stress perception is associated with signaling pathways involving calcium, reactive oxygen species and hormones which lead to changes in transcription factors and stress responsive genes expression, (Saharam et al., 2022).

Conventional plant breeding has made great contribution into creation of adapted cultivars. However, most of abiotic stress-related traits show quantitative inheritance what complicates phenotypic selection (Rai et al., 2021). New molecular tools give an opportunity to resolve this problem. Marker-assisted selection, QTL mapping, genome wide association studies and genomic selection can make breeding process more efficient. Genomics and high throughput phenotyping allow more efficient characterization of large populations, (Muhammad, et al., 2025).

Rise of next generation sequencing methods made possible the study of the genetics of stress tolerance in great detail. Transcriptomics provides the possibility to detect stress-inducible genes. Proteomics and metabolomics give information about protein and metabolite changes, respectively. Epigenomics proved the importance of DNA methylation and histone modification in stress adaptation, (Kumar et al., 2021).

Genome editing techniques have further revolutionized the prospects of improving crop plants. The use of CRISPR/Cas systems can enable the editing of genes responsible for stress responses, thus accelerating the improvement of crop varieties ((Patil et al., 2026). Other forms of genome editing that can be exploited include base editing and prime editing. Some recent reviews suggest the increasing interest in applying genome editing to drought, salinity, heat, cold, and other abiotic stresses of horticultural and agronomic crops, (Chennakesavulu, et al., 2022 and Yadav et al., 2023). Thus, breeding of abiotic stress-tolerant horticultural crops will require a coordinated effort using genetic materials, conventional plant breeding, physiological evaluation, molecular genetics, genomics, phenomics, multi-omics and genome editing (Mickelbart, et al., 2015). This review gives an overview of these approaches and their application in the future in climate-resilient horticultural production systems.

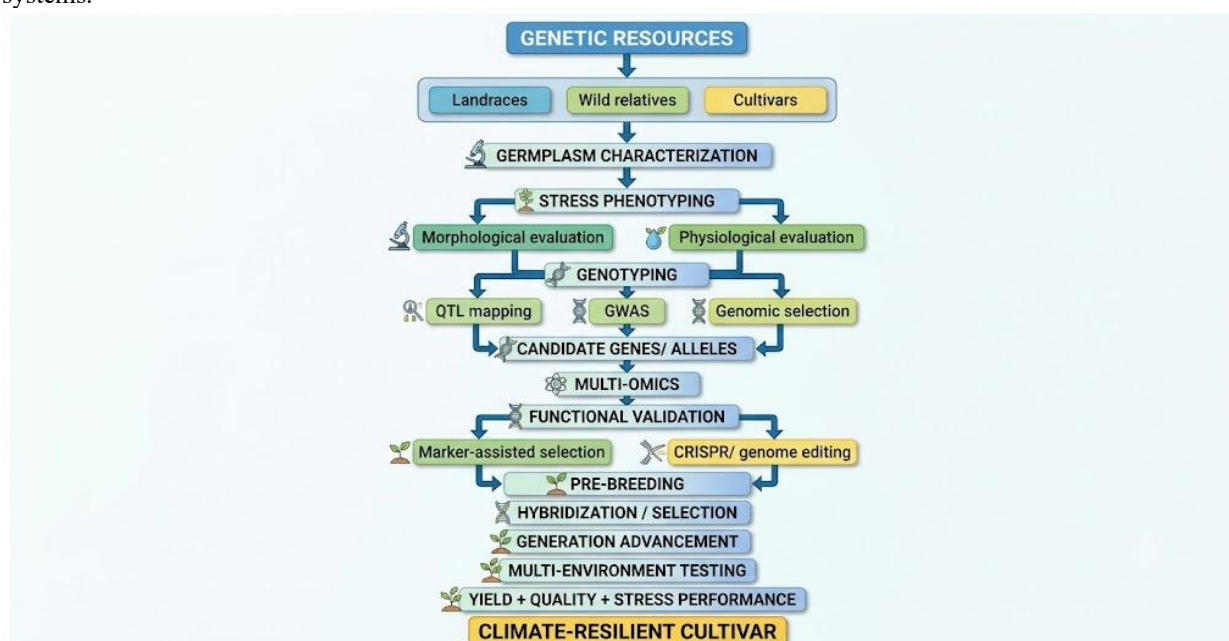


Figure 1. Breeding Pipeline for Development of Climate-Resilient Horticultural Cultivars

Table 1. Genetic Resources Used for Abiotic-Stress Breeding in Major Horticultural Crops

Crop	Genetic resources	Major stress targets	Breeding value
Tomato	Landraces, wild <i>Solanum</i> species and breeding lines	Drought, salinity, heat	Novel alleles for physiological and reproductive tolerance
Chilli/pepper	Landraces, cultivars and wild <i>Capsicum</i> species	Heat, drought, salinity	Variation for reproductive and physiological resilience
Brinjal	Landraces and wild <i>Solanum</i> species	Drought, salinity, heat	Root and stress-response variation
Potato	Wild <i>Solanum</i> species and landraces	Heat, drought, salinity	Tuberization and stress-adaptation traits
Cucumber	Landraces and <i>Cucumis</i> relatives	Heat, salinity, drought	Stress-responsive physiological traits
Melon	Landraces and wild <i>Cucumis</i> species	Drought, salinity	Root and water-use-efficiency traits
Brassica crops	Landraces and wild relatives	Heat, drought, salinity	Genetic variation for resilience
Onion	Local cultivars, landraces and wild <i>Allium</i> species	Drought, heat, salinity	Bulb yield and adaptation
Mango	Traditional cultivars and diverse germplasm	Drought, heat	Adaptation to tropical and dry environments
Citrus	Diverse rootstocks and wild relatives	Salinity, drought, cold	Particularly valuable for rootstock breeding
Grape	Cultivars and wild <i>Vitis</i> species	Drought, salinity, heat	Water-use efficiency and fruit-quality adaptation
Banana	Cultivars and wild <i>Musa</i> species	Drought, salinity, cold	Novel adaptive alleles
Pomegranate	Traditional cultivars and diverse germplasm	Drought, salinity, heat	Adaptation to arid/semi-arid environments
Strawberry	Cultivars and wild <i>Fragaria</i> species	Heat, drought, cold	Stress-adaptive flowering and fruiting traits

2. Abiotic Stresses that Influence the Growth of Horticultural Crops

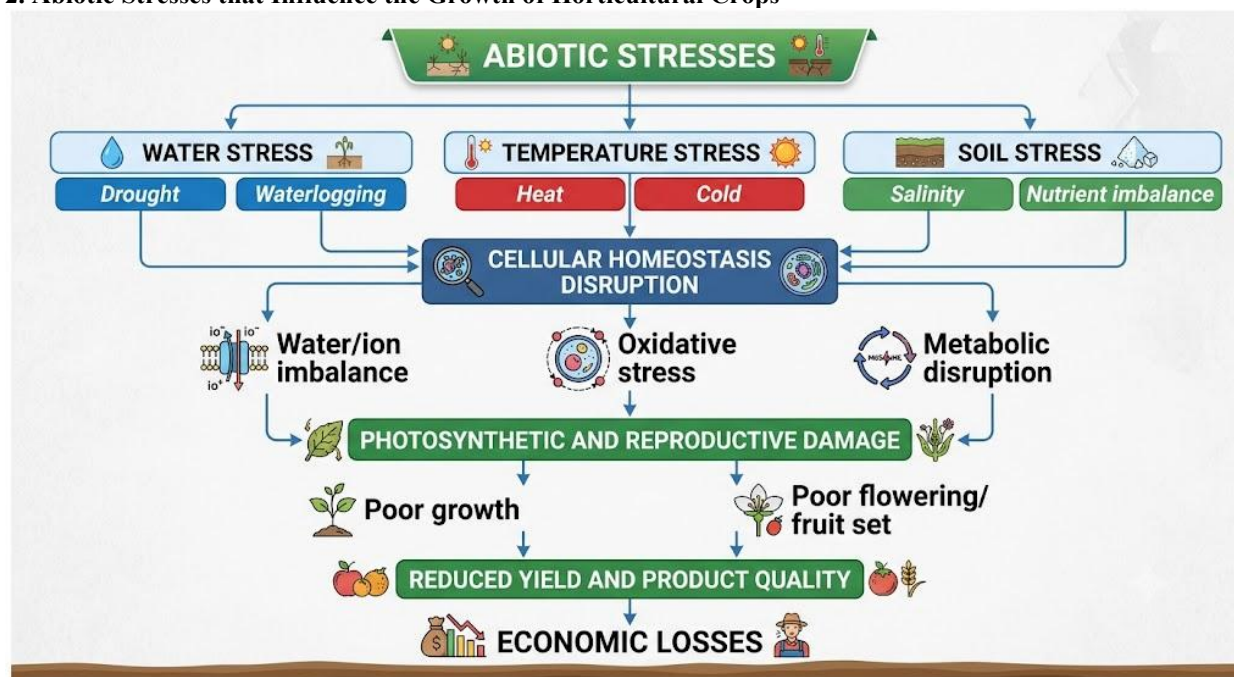


Figure 2. Major Abiotic Stresses and Their Effects on Horticultural Crops

2.1 Drought Stress

Drought is one of the major abiotic stresses influencing the production of horticultural crops. It arises due to the inadequacy of water to satisfy the needs of plants and can be caused by insufficient precipitation, excessive evaporation, inadequate irrigation or lack of moisture in the soil. Drought impacts water status of plants and hence

affects the process of cell expansion, photosynthesis, nutrient absorption, flowering and reproduction, (Francini, and Sebastiani, 2019).

In vegetable crops, drought causes decreased height of the plant, leaf area and total biomass. In fruits, prolonged water deficit can lead to decrease in the number of flowers, flower retention, fruit size and total yield. Nevertheless, limited water may positively influence quality of the product, indicating that plants' reactions to drought depend on a crop type, genotypic features and developmental stage of the plant and severity of stress, (Yadav et al., 2023).

Plants respond to drought through stomatal closure, changes in root growth, osmotic adjustment, accumulation of compatible solutes and increased activities of antioxidant systems. Abscissic acid regulates stomata functions and expression of drought-related genes. As a result, breeding programs nowadays focus on root morphology, canopy temperature, relative water content, water use efficiency, membrane stability and yield stability under water-limited conditions, (Kumar, et al., 2023).

2.2 Salt Stress

Salt stress is one of the major constraints to irrigated horticulture, especially where poor quality of irrigation water and drainage lead to accumulation of salts in the rhizosphere. Salt stress poses both osmotic and ionic stresses to the plants. Osmotic stress limits the capacity of the roots to take up water, while excessive levels of sodium and chlorine cause ionic stress to the plants, (Zheng et al., 2023). Salt sensitive horticultural crops show symptoms such as chlorosis, necrosis, stunted growth, flower and fruit yield reduction. Salt stress is also known to influence fruit quality, causing changes in sugar accumulation, acidity, and mineral content, (Begna et al., 2026).

There are various strategies used by the plants to achieve salt tolerance. These strategies include limiting salt absorption, keeping a high ratio of potassium to sodium, sequestration of toxic salts into vacuoles, accumulation of compatible solutes, and increased antioxidative activity. Important members of transporter families involved in ion homeostasis include SOS, HKT, and NHX transporters, (Patil et al., 2026).

2.3 Heat Stress

Heat stress is gaining more relevance since global temperature is rising, and heat waves are becoming common. Vegetables crops are very sensitive to high temperature, especially during their reproductive stages, (Ahmad et al., 2024). High temperature causes membrane injury, increased respiration rate, reduced photosynthesis, and pollen sterility. High temperature during reproductive stage in tomato, pepper, cucumber and other vegetable crops leads to pollen sterility, flower abortion and reduced fruit set. Fruit crops suffer from sunburn, rapid ripening and deterioration of fruit quality due to extreme temperature.

Plants cope with heat by synthesizing heat shock proteins, activation of heat shock transcription factors, changes in membrane composition and enhanced antioxidants. Therefore, heat resistant breeding needs screening both vegetative and reproductive stages. Current horticulture research emphasizes the role of transcription factors, heat shock proteins, reactive oxygen species signaling, calcium signaling and hormones in heat stress tolerance, (Wu et al., 2026).

2.4 Cold and Chilling Stress

Temperature influences agricultural crops through reduced enzymatic action, change in membrane fluidity, inhibition of photosynthesis, and disruption of reproductive growth. Crops belonging to tropical and subtropical regions are more sensitive to chilling stress, (Altaf et al., 2023).

Chilling stress may also occur at temperatures above freezing while freezing stress includes the formation of ice within plant cells. Both stresses may lead to membrane damage, cellular leakage, and tissue necrosis, (Pandey, et al., 2021). Plants that are cold-tolerant have higher antioxidant capacity, membrane lipid changes, osmoprotectant accumulation, and cold-response transcriptional regulation. ICE-CBF-COR pathway is one of the important molecular mechanisms of cold stress adaptation.

2.6 Nutrient Stress and Heavy-Metal Toxicity

Deficiency and toxicity of nutrients could also be sources of significant stress to horticultural crops. Deficiencies of nitrogen, phosphorus, potassium, iron, zinc and other nutrients could limit photosynthesis, enzyme activity and growth. On the other hand, higher concentrations of some nutrients might cause toxicity and oxidative stress, (Hassan, et al., 2026). Cadmium, lead, and chromium are heavy metals that could affect root development, photosynthesis, and cellular metabolism. However, plants could defend against heavy metals through chelation, sequestration, limited uptake, and antioxidants. Plant breeding programmes could utilize genetic variability of nutrient-use efficiency and low accumulation of harmful elements. (Lal et al., 2023).

Table 2. Major Abiotic Stresses, Symptoms, Physiological Effects and Tolerance Mechanisms

Abiotic stress	Major symptoms	Physiological effects	Important tolerance mechanisms
Drought	Wilting, leaf rolling, reduced leaf expansion and premature senescence	Reduced water potential, stomatal closure and impaired photosynthesis	Root-system adaptation, osmotic adjustment, ABA signalling and improved water-use efficiency
Heat	Leaf scorching, flower abortion, pollen sterility and poor fruit set	Membrane damage, reduced photosynthesis and reproductive impairment	Heat-shock proteins, antioxidant defence, membrane stabilization and thermotolerance

Salinity	Chlorosis, necrosis, stunting and reduced fruit development	Osmotic stress, Na ⁺ /Cl ⁻ toxicity and nutrient imbalance	Ion exclusion, Na ⁺ sequestration, K ⁺ /Na ⁺ homeostasis and osmotic adjustment
Chilling	Reduced growth, chlorosis and poor germination	Membrane rigidification, enzyme inhibition and oxidative stress	Membrane-lipid modification, antioxidants and cold-responsive genes
Freezing	Tissue necrosis and cellular leakage	Ice formation and membrane disruption	Cold acclimation, osmoprotectants and protective proteins
Waterlogging	Yellowing, root decay and reduced growth	Root hypoxia, reduced respiration and nutrient uptake	Aerenchyma formation, adventitious roots and anaerobic metabolism
Nutrient deficiency	Chlorosis, poor growth and abnormal development	Impaired enzyme activity and metabolic processes	Improved nutrient acquisition, remobilization and nutrient-use efficiency
Heavy-metal toxicity	Root inhibition, chlorosis and necrosis	ROS accumulation, enzyme inhibition and metabolic disruption	Chelation, sequestration and antioxidant defence
Combined stresses	Severe growth, reproductive and yield reduction	Simultaneous osmotic, ionic, oxidative and metabolic disturbances	Integrated signalling, hormonal regulation and broad-spectrum tolerance

3. Genetic Resources for Abiotic-Stress Breeding

Genetic variability is the basis of all plant breeding. Without genetic variability, plant breeding for better abiotic-stress tolerance is very limited. Horticultural genetic resources include traditional landraces, farmer varieties, cultivated varieties, breeding lines, wild species, exotic accessions, mutagenized populations and germplasm stored in national and international gene banks. Landraces are particularly valuable because they have evolved under local environmental conditions and may contain favourable alleles associated with adaptation to drought, salinity, heat and other stresses. Although landraces may not possess the yield and quality characteristics required by commercial agriculture, they can serve as important donors in pre-breeding programmes, (Yadav et al., 2023). Wild relatives serve as another key source of variation. While undergoing domestication and selective breeding, certain alleles linked to adaptation to the environment could be lost by crops. As a result, wild relatives could contribute novel alleles conferring drought tolerance, salt tolerance, disease resistance, thermal adaptation and nutrient use efficiency. Utilization of wild relatives may also be limited due to issues of reproductive isolation and linkage drag. Methods like advanced backcrossing, marker assisted selection, genomic selection and genome editing can aid in overcoming these constraints, (Ahmad et al., 2024). Thus, the conservation of genetic resources is not only about preserving biodiversity but also is important for future agricultural adaptation to climate change. According to FAO, genetic resources of plants represent an essential element of food and agriculture systems with particular emphasis on adaptation to new environmental conditions, (FAO, 2007).

Table 3. Important Genes/Gene Families Associated with Abiotic Stress Tolerance

Stress	Gene/gene family	Major function	Breeding relevance
Drought	DREB/CBF	Activates dehydration/cold-responsive genes	Drought and temperature adaptation
Drought	AREB/ABF	ABA-dependent transcriptional regulation	Drought-response regulation
Drought	Aquaporins	Membrane water transport	Cellular water regulation
Salinity	SOS1	Plasma-membrane Na ⁺ extrusion	Na ⁺ homeostasis
Salinity	HKT	Na ⁺ transport and exclusion	Maintenance of shoot ion balance
Heat	HSP70/HSP90	Protein protection and folding	Thermotolerance
Heat	HSF	Regulation of heat-shock genes	Heat-response activation
Heat	HSP100	Protein protection during heat stress	Thermotolerance
Multiple stresses	NAC	Stress-responsive transcription	Broad stress adaptation
Multiple stresses	WRKY	Stress signalling and transcriptional regulation	Abiotic-stress response
Multiple stresses	MYB	Regulation of stress-responsive genes	Drought/salt/temperature response
Cold	CBF/DREB	Cold-responsive transcription	Cold acclimation
Cold	COR genes	Cellular protection during cold	Chilling/freezing tolerance

These gene families are supported by recent reviews of abiotic-stress mechanisms in horticultural crops and genome-editing literature, (Wu et al., 2026).

4. Physiological Mechanisms of Abiotic Stress Tolerance

Abiotic stress tolerance is a multifaceted process that involves various physiological mechanisms.

4.1 Osmotic Adjustment

Osmotic adjustment helps in maintaining water uptake and turgor in plants subjected to water deficiency and salinity. Compatible solutes such as proline, soluble sugars, glycine betaine and some amino acids get accumulated. The accumulation of such solutes enables the cells to maintain the protein structure, membrane integrity and osmotic balance. Since the ability to accumulate osmolytes varies among different species and genotypes, osmotic adjustment can be used as one of the physiological criteria in plant breeding programs, (Zivcak et al., 2016).

4.2 Ion Homeostasis

Salt tolerance often requires ion homeostasis which allows maintaining potassium, calcium and other mineral ions by limiting the effect of excessive concentrations of sodium and chloride ions on such nutrients. Salt tolerant genotypes have better mechanisms of exclusion or storage of sodium ions in vacuoles, (Brini, and Masmoudi, 2012).

4.3 Plant Defense Against Antioxidants

The abiotic stress leads to overproduction of the reactive oxygen species. Even though ROS act as a signal molecule, high amounts of ROS can oxidize the proteins, fats, nucleic acid and cellular membrane. Plant cells defend themselves from abiotic stress through antioxidant enzymes including superoxide dismutase, catalase, ascorbate peroxidase and glutathione reductase. There are also some non-enzymatic antioxidants which include ascorbate, glutathione, carotenoids and phenolics, (Mishra et al., 2023).

4.4 Photosynthetic Defense

Photosynthesis process is quite sensitive to drought, heat, salt and low temperature conditions. Stomata closure due to the stress affects the intake of CO₂ while the damages to the photosynthetic membranes and proteins further reduce the carbon fixation. Stress-tolerant genotypes often maintain higher chlorophyll content, photosynthetic efficiency and photochemical activity under stress, (Sachdev et al., 2021).

4.5 Adaptation of Roots to Stress

Root system development has a key role in obtaining water and nutrients. Extensive and deep-rooted plants may adapt to drought stress better, while aerenchyma formation and adventitious roots might contribute to adaptation to flooding. The root traits need to be given more attention in horticultural breeding because the above-ground selection has been traditionally more important, (Koevoets, et al., 2016).

5. Molecular Mechanisms of Abiotic Stress Resistance

Perception of environmental stress triggers a molecular signalling process based on calcium, reactive oxygen species, protein kinases, phytohormones, and transcription factors, (Bechtold, and Field, 2018). Calcium acts as a second messenger. The changes in cytosolic calcium levels are perceived through calcium-binding proteins that lead to activation of signaling pathways further. Transcription regulation is performed by protein kinases among others, such as calcium-dependent protein kinase and mitogen-activated protein kinases, (Roychoudhury, and Banerjee, 2017). ROS have two main functions they take part in signaling when their concentration is moderate and cause oxidative damage when it is too high. Thus, plants need precise regulation of ROS production and elimination, (Sachdev et al., 2021).

Abscisic acid, ethylene, jasmonic acid, salicylic acid, auxins, cytokinins, and brassinosteroids take part in signalling in relation to environmental stresses. Abscisic acid is especially important in drought and salinity response due to its regulates stomatal closure and stress-responsive gene expression. Transcription factors such as DREB, NAC, WRKY, MYB, bZIP, AP2/ERF, HSF and bHLH regulate large networks of stress-responsive genes. These genes encode proteins involved in osmotic adjustment, ion transport, antioxidant defence, protein protection and cellular repair, (Chaffai et al., 2024).

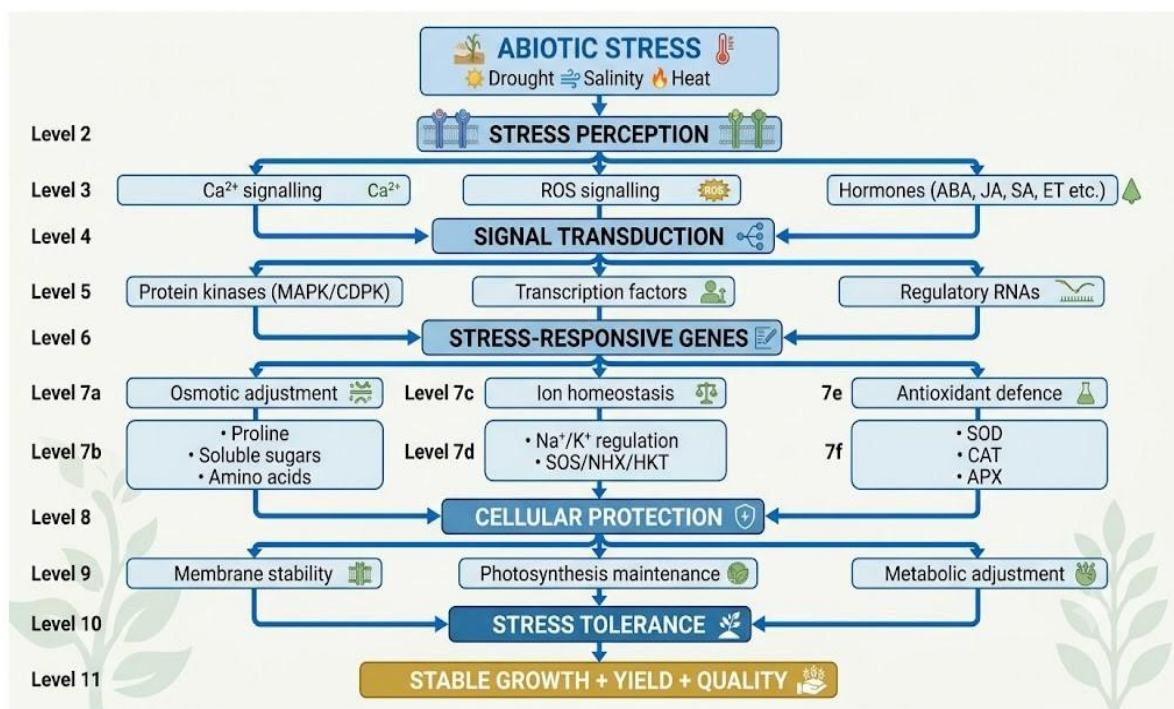


Figure 3. Physiological and Molecular Mechanisms of Abiotic Stress Tolerance

6. Conventional Breeding for Abiotic Stress Tolerance

Conventional breeding continues to serve as the basis for improving horticultural crops. It involves the use of tolerant genetic resources, crossing them with superior cultivars and selection of the offspring with stress tolerance and good agronomic and economic traits (Kumar et al., 2021). Selection could be performed in controlled conditions, field conditions or in a combination of both of them. But since abiotic stress is environment-dependent, selection at a single site or in one season will not guarantee selection of stable genotypes. Crossing is useful in combining the desired traits from two genetically different parents. While backcrossing is a useful method to introgress the desired stress tolerance gene or genomic region into a superior cultivar, (Kumar et al., 2021). While mutation breeding can create novel genetic variation when there is not enough natural genetic variation available. Interspecific hybridization is another method which can help in accessing stress tolerance genes from wild relatives. In case of perennial fruit crops, breeding becomes even more difficult because the plants take several years before reaching maturity stage. Hence, genomic prediction, marker-assisted selection and speed breeding methods become valuable in perennials.

Table 4. Conventional and Molecular Breeding Approaches for Abiotic-Stress Tolerance

Approach	Principle	Advantages	Limitations	Application
Introduction	Direct use of adapted germplasm	Rapid access to variation	Poor adaptation may occur	Germplasm enhancement
Selection	Selection of tolerant plants	Simple and inexpensive	Strong environmental effects	Drought/heat/salinity
Hybridization	Combination of contrasting parents	Creates new combinations	Requires several generations	Broad application
Backcrossing	Transfer of target allele into elite background	Maintains elite phenotype	Time-consuming	Major genes/QTL
Recurrent selection	Accumulation of favourable alleles	Suitable for quantitative traits	Large populations required	Polygenic tolerance
Mutation breeding	Generation of novel variation	Useful when natural variation is limited	Random mutations	Stress-tolerance improvement
Interspecific hybridization	Introgression from wild relatives	Accesses novel alleles	Linkage drag and incompatibility	Stress-adaptive traits

Marker-assisted selection	DNA-marker-based selection	Early selection	Requires validated markers	Major genes/QTL
QTL mapping	Identification of genomic regions	Genetic dissection of complex traits	Population-dependent	Quantitative tolerance
GWAS	Association between markers and traits	High-resolution allele discovery	Population structure effects	Natural variation
Genomic selection	Prediction using genome-wide markers	Useful for complex traits	Requires training population	Yield stability
High-throughput phenotyping	Automated stress phenotyping	Rapid and non-destructive	Equipment/data requirements	Large germplasm screening
Speed breeding	Accelerated generation turnover	Shortens breeding cycles	Crop-dependent	Rapid cultivar development
Genome editing	Precise modification of target genes	High precision	Transformation/regulatory challenges	Functional improvement
Multi-omics	Integration of molecular datasets	Identifies regulatory networks	Cost and data complexity	Candidate-gene discovery

Source: Synthesized from literature on conventional and genomic-assisted breeding for abiotic-stress management in horticultural crops, (Rai et al., 2021).

7. Marker-Assisted Selection and QTL Mapping

Marker-assisted selection employs molecular markers associated with genes or chromosomal regions regulating desired traits. This approach helps increase efficiency by enabling selection at an early stage of development prior to expression of the trait. QTL mapping is especially relevant for determining the chromosomal regions involved in quantitative traits, e.g., drought tolerance, salt tolerance, root systems, water-use efficiency, and stable yields, (Younis, et al., 2020). On the other hand, QTL effects may differ between different genetic backgrounds and environments. Thus, QTL validation is necessary in independent populations and environments prior to practical applications, (Rai et al., 2021).

8. Genome-Wide Association Studies

In GWAS, naturally occurring genetic variations in diverse germplasm resources are utilized. Molecular markers associated with phenotypic variations can help to determine chromosomal regions responsible for stress tolerance traits, (Hammad et al., 2026).

The relevance of GWAS for horticultural plants is high because horticultural crops have great diversity of landraces and cultivars. However, population structure, linkage disequilibrium, and environmental variation should be taken into account. Combination of GWAS with transcriptomics and functional validation can improve the efficiency of candidate gene discovery, (Rai et al., 2026).

9. Genomic Selection

In contrast to marker-assisted selection, genomic selection is based on the use of whole genome marker data in the prediction of breeding value of the individual without using a few markers associated with major genes. Genomic selection would be very beneficial for breeding of abiotic-stress tolerant varieties because many stress-responsive characteristics have polygenic nature and are controlled by multiple genes with low effect, (Budhlakoti, et al., 2022).

Genomic selection can be especially important in case of breeding of horticultural crops due to long generation intervals and high cost of phenotypic assessment of plants. This method will allow breeders to decrease the number of plants to be tested in the field, (Parmar et al., 2017).

10. Multi-Omics Approaches in Abiotic-Stress Breeding

Modern breeding techniques are shifting from analysis of individual genes to multi-omics studies. Genomics discovers DNA polymorphisms, while transcriptomics finds gene expression changes in response to stress. Proteomics allows finding stress-responsive proteins and metabolomics detects metabolite and metabolic pathway changes.

Additional data is provided by epigenomics that includes DNA methylation, histone modifications and chromatin regulation. Epigenetics might be responsible for the stress memory and transgenerational effects. The integration of all these data can help us find regulatory networks that are impossible to understand by a single molecular approach, (Shankar, et al., 2026).

11. High-Throughput Phenotyping

Phenotyping is one of the major challenges in abiotic stress breeding. Conventional phenotyping methods such as plant height, leaf area, biomass, and yield are often time-consuming and do not reflect physiological response at

an earlier stage. High-throughput phenotyping approaches offer the possibility to evaluate large populations through RGB imaging, thermal imaging, hyperspectral imaging, chlorophyll fluorescence, and root imaging. Thermal imaging detects the changes in canopy temperature related to stomatal conductance and plant water status. Hyperspectral imaging reveals the changes in pigments, plant water status, and biochemistry. Integration of phenomic data with genome information can greatly increase the efficiency of selection, (Hanjagi, 2025).

12. Genomic Editing and CRISPR/Cas Approach

Genomic editing is one of the greatest innovations in plant breeding. CRISPR/Cas systems permit to modify the genes and regulatory elements involved in stress responses. CRISPR/Cas9 system has been extensively applied for gene knockout and validation of function. However, there are other CRISPR/Cas systems, for example, Cas12a, which have their own characteristics of target-site recognition, (Yadav et al., 2023). Base editing allows to make nucleotide substitutions without creating double-stranded DNA breakage. Prime editing provides even greater possibilities for making precise substitutions, insertions, and deletions, (XiuJuan, et al., 2026).

Table-5: CRISPR/Cas-mediated targeting of genes in fruits and vegetables for imparting resistance against abiotic stress.

Stress	Plant species	Delivery method	Targeted gene	Phenotype	References
Drought stress	<i>Solanum lycopersicum</i>	CRISPR/Cas9; <i>Agrobacterium tumefaciens</i> -mediated transformation	<i>Mitogen Activated Protein Kinase 3</i>	Sensitive to drought stress	(Wang et al., 2017)
Drought stress	<i>Solanum lycopersicum</i>	CRISPR/Cas9; <i>Agrobacterium tumefaciens</i> -mediated transformation	<i>Non-expressor of Pathogenesis-Related 1</i>	Sensitive to drought stress	(Li et al., 2019)
Drought stress	<i>Solanum lycopersicum</i>	CRISPR/Cas9; <i>Agrobacterium tumefaciens</i> -mediated transformation	<i>Lateral Organ Boundaries Domain 40</i>	Tolerance to drought stress	(Liu et al., 2020)
Drought stress	<i>Solanum lycopersicum</i>	CRISPR/Cas9; <i>Agrobacterium tumefaciens</i> -mediated transformation	<i>Gibberellin-Insensitive Dwarf 1a</i>	Resistance to drought stress	(Illouz-Eliaz et al., 2020)
Drought stress	<i>Solanum lycopersicum</i>	CRISPR/Cas9; <i>Agrobacterium tumefaciens</i> -mediated transformation	<i>Aberrant Growth and Death 2-like Defense Response Protein 1</i>	Tolerance to drought stress	(Wang et al., 2021a)
Drought stress	<i>Solanum lycopersicum</i>	CRISPR/Cas9; <i>Agrobacterium tumefaciens</i> -mediated transformation	<i>Flavin-dependent Monooxygenase 1</i>	Sensitive to drought stress	(Wang et al., 2021a)
Drought stress	<i>Solanum lycopersicum</i>	CRISPR/Cas9; <i>Agrobacterium tumefaciens</i> -mediated transformation	<i>Auxin Response Factor 4</i>	Tolerance to drought stress	(Chen et al., 2021)
Drought stress	<i>Solanum lycopersicum</i>	CRISPR/Cas9; <i>Agrobacterium tumefaciens</i> -mediated transformation	<i>Histone H3 Lysine Methyltransferases Set Domain Group 33 and 34</i>	Resistance to drought stress (both single and double mutants)	(Bvindi et al., 2022)
Drought stress	<i>Solanum tuberosum</i>	CRISPR/Cas9; <i>Agrobacterium tumefaciens</i> -mediated transformation	<i>FLORE</i> (long non-coding RNA counterpart of <i>Cycling DOF Factor 1</i>)	Sensitive to drought stress	(Ramírez Gonzales et al., 2021)
Salinity stress	<i>Solanum lycopersicum</i>	CRISPR/Cas9; <i>Agrobacterium tumefaciens</i> -mediated transformation	<i>Auxin Response Factor 4</i>	Tolerance to salinity stress	(Bouzroud et al., 2020)
Salinity stress	<i>Solanum lycopersicum</i>	CRISPR/Cas9; <i>Agrobacterium tumefaciens</i> -mediated transformation	<i>High-affinity K⁺ 20</i>	Sensitive to salinity stress	(Wang et al., 2020)
Salinity stress	<i>Solanum lycopersicum</i>	CRISPR/ LbCas12a; <i>Agrobacterium tumefaciens</i> -mediated transformation	<i>High-affinity K⁺ Transporter 1;2</i>	Tolerance to salinity stress	(Vu et al., 2020)
Salinity stress	<i>Solanum lycopersicum</i>	CRISPR/Cas9; <i>Agrobacterium tumefaciens</i> -mediated transformation	<i>Hybrid Proline-rich Protein 1</i>	Tolerance to salinity stress	(Tran et al., 2021)
Salinity stress	<i>Solanum lycopersicum</i>	CRISPR/Cas9; <i>Agrobacterium tumefaciens</i> -mediated transformation	<i>Salt Overly Sensitive 1</i>	Sensitive to salinity stress	(Wang et al., 2021b)

Salinity stress	<i>Solanum lycopersicum</i>	CRISPR/Cas9; <i>Agrobacterium tumefaciens</i> -mediated transformation	<i>Mitogen Activated Protein Kinase 3</i>	Sensitive to salinity stress	(Shu et al., 2022)
Salinity stress	<i>Solanum tuberosum</i>	CRISPR/Cas9; RNP delivery using biolistics or vacuum infiltration methods	<i>Coilin</i>	Tolerance to salinity and osmotic stress	(Makhotenko et al., 2019)
Salinity stress	<i>Cucurbita moschata</i>	CRISPR/Cas9; <i>Agrobacterium rhizogenes</i> -mediated transformation	<i>Respiratory Burst Oxidase Homolog D</i>	Sensitive to salinity stress	(Huang et al., 2019)
Heat stress	<i>Solanum lycopersicum</i>	CRISPR/Cas9; <i>Agrobacterium tumefaciens</i> -mediated transformation	<i>Agamous-like 6</i>	Capable of seedless fruit production under heat stress	(Klap et al., 2017)
Heat stress	<i>Solanum lycopersicum</i>	CRISPR/Cas9; <i>Agrobacterium tumefaciens</i> -mediated transformation	<i>Brassinazole Resistant 1</i>	Sensitive to heat stress	(Yin et al., 2018)
Heat stress	<i>Solanum lycopersicum</i>	CRISPR/Cas9; <i>Agrobacterium tumefaciens</i> -mediated transformation	<i>Mitogen Activated Protein Kinase 3</i>	Tolerance to heat stress	(Yu et al., 2019)
Heat stress	<i>Solanum lycopersicum</i>	CRISPR/Cas9; <i>Agrobacterium tumefaciens</i> -mediated transformation	<i>Calcium-Dependent Protein Kinase 28</i>	Sensitive to heat stress	(Hu et al., 2021)
Heat stress	<i>Lactuca sativa</i>	CRISPR/Cas9; <i>Agrobacterium tumefaciens</i> -mediated transformation	<i>9-cis-Epoxycarotenoid Dioxygenase 4</i>	Seed germination at high temperature	(Bertier et al., 2018)
Cold stress	<i>Solanum lycopersicum</i>	CRISPR/Cas9; <i>Agrobacterium tumefaciens</i> -mediated transformation	<i>C-Repeat Binding Factors/ Dehydration-Responsive Element Binding Factor 1</i>	Sensitive to cold stress	(Li et al., 2018)
High light stress	<i>Solanum tuberosum</i>	CRISPR/Cas9; <i>Agrobacterium tumefaciens</i> -mediated transformation	<i>Alternative oxidase</i>	Resistance to high light stress	(Hua et al., 2020)

(Source, Sardar, 2023)

These technologies may be particularly useful for horticultural crops where conventional introgression of wild alleles may introduce undesirable characteristics. However, genome editing is not without limitations. Transformation and regeneration can be difficult in many horticultural species, and genotype-dependent tissue culture responses may restrict application. Regulatory frameworks, off-target effects, editing efficiency and public acceptance also require consideration, (Yadav et al., 2023).

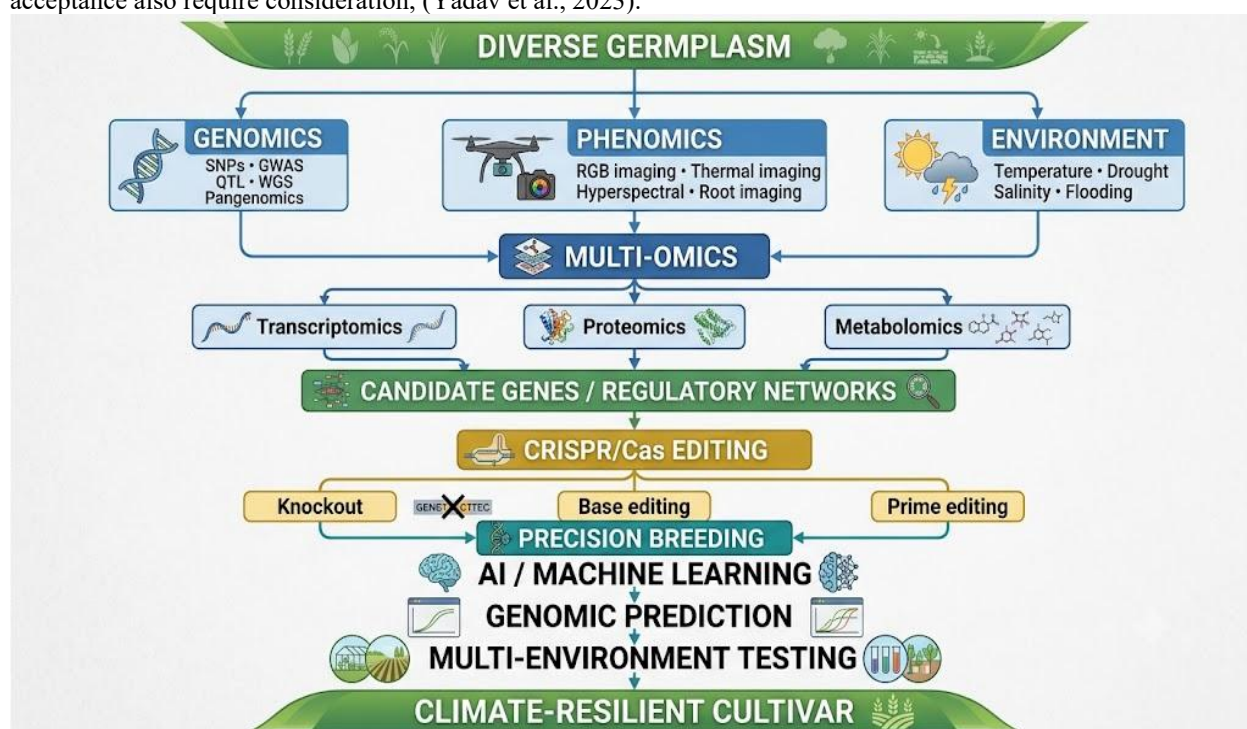


Figure 4. Integration of Genomics, Phenomics, Multi-Omics and CRISPR in Stress Breeding

13. Breeding for Combined Abiotic Stresses

One weakness of the traditional method of stress breeding is the practice of studying individual stressors in isolation. However, in reality, there could be simultaneous occurrences of different abiotic stressors, (Padilla, et al., 2025).

For example, drought could happen with heat, whereas salinity could increase because of high temperatures. At times, flooding could occur during high temperatures, thus making oxygen deficit and heat stress possible at the same time. The reaction to different stresses in combination might be very different from reactions to individual stressors. As a result, selection for individual stress tolerance could lead to cultivars poorly performing in field conditions, (Nehanjali Parmar et al., 2017). Thus, future breeding programmes should include the experiment with the combined stresses and test for yield stability in different environments.

14. Use of Rootstocks in Abiotic Stress Tolerance

Breeding of rootstocks is one of the most promising approaches for vegetables and fruits. A tolerant rootstock will enhance water absorption, nutrition and ions regulation, thus making it possible to use the scion of commercial value, (Schwaz et al., 2010).

Grafting technique was used successfully with a number of vegetable crops, such as tomatoes, eggplants, cucumbers, watermelons and melons. Salt-tolerant or drought-tolerant rootstocks can mitigate the negative effects of environmental stress on scion growth and yield, (Rouphael, ET AL., 2017). In fruit crops, rootstocks are especially important because they influence tree vigour, water relations, nutrient uptake and adaptation to soil conditions. Future rootstock breeding should combine physiological screening with genomic approaches to identify root traits associated with stress tolerance.

15. Function of plant-microbe interactions

Plant-associated microbes may assist in developing tolerance to abiotic stress through increased nutrient availability, hormonal balance, enhanced antioxidant defense, and improved root system development. PGPRs, AMF and other beneficial microorganisms may be helpful in increasing plant productivity under conditions of drought, salinity, and nutrient stress.

Combining microbiome science with conventional plant breeding provides a new frontier. Plant breeders could use genotypes capable of maintaining favorable and stable associations with plant microorganisms. In this context, the application of a new approach called microbiome-assisted breeding, in which the plant genotype and its associated microbiome are studied in parallel, could be suggested, (Muhammad et al., 2024).

16. Artificial intelligence and machine learning in stress breeding

With the expansion of genomic, phenomic, and environmental data, the use of artificial intelligence and machine-learning strategies becomes possible. Machine learning techniques may discover correlations between genomic markers, environmental variables, and phenotypes. They may also help in forecasting the behavior of genotypes under certain environmental conditions., (Gou, et al., 2024). Thus, artificial intelligence can contribute to genotype selection, stress classification, disease and stress phenotyping, yield forecasting, and environmental adaptation pattern detection, (Gerakari, et al., 2025).

17. Challenges to the Development of Horticultural Crops that are Tolerant to Abiotic Stresses

Despite significant technological advancements, some challenges remain.

Tolerance to abiotic stresses is a quantitative trait with many genes controlling it. These genes are affected by the environment leading to significant genotype x environment interaction.

Another challenge is phenotyping. It is because tolerance to stress cannot always be phenotyped by a single trait and survival under stress does not necessarily mean yield or marketable product.

While a certain genotype may be tolerant to drought, it may have smaller fruits. Likewise, a genotype that is tolerant to salinity may accumulate unwanted ions and also have reduced fruit quality. Hence, breeding objectives should combine tolerance with yield, nutritional quality and market acceptability.

The genetic diversity of some horticultural crops is limited and hence the source of variation is also limited. While wild species can contribute important genes, there is linkage drag and reproductive isolation.

Long juvenile phase of perennial crops poses yet another challenge. Genomic selection and early molecular screening may help in reducing the breeding cycles.

Genome editing offers new opportunities but is limited by low transformation efficiencies, regeneration methods, genotype dependency, regulatory issues and social acceptability.

18. Future Prospects

Future development of breeding for abiotic stresses will involve use of complementary methods of breeding in combination, rather than use of one single breeding approach.

Firstly, it is important to conduct systematic characterization of genetic resources. Landraces, wild relatives and underutilized horticultural plants should be examined under controlled and field conditions to detect novel alleles associated with stress adaptation.

Secondly, it is important to develop phenotyping systems that will allow accurate and fast evaluation of stress response.

Thirdly, it is important to conduct integration of genomics and phenomics in order to increase the precision of genomic prediction and detection of stable genomic regions.

Use of multi-omics approaches will be an increasingly useful strategy in the understanding of the molecular mechanism of tolerance. Candidate genes revealed through GWAS or QTL analysis can be confirmed using transcriptomics, proteomics and metabolomics studies, and then used for editing of the genome.

Pangenomics will become increasingly important. The whole diversity of a species cannot be captured by a single reference genome. Pangenomic approaches allow detection of genes and structural variants that may be not present in the reference genome and carry useful variation for stress adaptation.

CRISPR-based technologies are expected to become more precise through base editing, prime editing and multiplex editing. These approaches may allow breeders to modify favourable alleles without introducing large genomic segments from wild relatives.

Artificial intelligence will provide another important layer of integration. Genomic, phenotypic, environmental and climatic datasets can be analysed simultaneously to predict which genotypes are likely to perform well under future climatic scenarios.

Future breeding should also move from single-stress screening towards multi-stress resilience. Cultivars should be evaluated under realistic combinations of drought, heat, salinity and other stresses because these conditions frequently occur together in farmers' fields.

Table 6. Major Constraints and Future Opportunities in Climate-Resilient Horticultural Breeding

Constraint	Major consequence	Future opportunity
Complex genetic inheritance	Slow genetic gain	Genomic selection and multi-omics
Strong genotype × environment interaction	Unstable performance	Multi-environment testing
Difficult stress phenotyping	Low selection efficiency	High-throughput phenotyping
Narrow genetic base	Limited adaptive variation	Wild relatives and landraces
Genetic erosion	Loss of useful alleles	Conservation and characterization of germplasm
Linkage drag	Undesirable traits transferred	Fine mapping and genome editing
Long juvenile phase	Long breeding cycles	Genomic prediction and speed breeding
Combined stresses	Single-stress screening is inadequate	Multi-stress screening
Limited validated markers	Difficult molecular selection	GWAS and pangenomics
Transformation barriers	Restricted CRISPR application	Improved regeneration and delivery systems
Yield–stress tolerance trade-off	Tolerance may reduce productivity	Precision allele editing and gene pyramiding
Variable environments	Poor repeatability	Controlled + field phenotyping
High omics cost	Limited accessibility	Targeted and integrated omics
Regulatory uncertainty	Delayed deployment	Clear science-based regulatory pathways
Root–shoot complexity	Incomplete understanding of tolerance	Rootstock breeding
Rhizosphere interactions	Underused biological adaptation	Microbiome-assisted breeding
Public acceptance	Adoption barriers	Transparent risk assessment and communication
Climate unpredictability	Cultivar instability	Predictive and environment-specific breeding

19. Integrated Breeding Strategy for Climate-Resilient Horticultural Crops

An effective future breeding strategy can be represented as:

Genetic resources → Germplasm characterization → Stress phenotyping → Genotyping → QTL/GWAS → Candidate-gene identification → Multi-omics validation → Marker-assisted/genomic selection → Genome editing → Multi-environment testing → Farmer-oriented evaluation → Climate-resilient cultivar

This integrated approach combines the strengths of conventional and modern breeding. Conventional breeding provides the framework for combining complex traits, while molecular technologies improve the precision and speed of selection.

The final breeding objective should not simply be the development of plants that survive abiotic stress. Instead, breeders should develop cultivars that maintain commercial yield, nutritional quality, sensory quality and marketability under realistic environmental stress conditions.

20. CONCLUSION

Abiotic stresses pose major challenges for sustainable horticultural production in a changing climate. Drought, salinity, heat, chilling, flooding, waterlogging, nutrient imbalance and heavy-metal toxicity can adversely influence growth, reproductive development, productivity and quality of horticultural crops.

Genetic resources serve as a basis for developing cultivars tolerant of stress. Landraces, traditional cultivars, wild relatives, exotic genotypes and germplasm collection contain useful alleles that could be used in breeding. Hence, their systematic study and exploitation need to be an integral part of climate-adaptive horticultural breeding.

Phenomena underlying the mechanisms of stress tolerance include osmoregulation, ionic regulation, antioxidation, membrane stability, photosynthesis protection and root system adaptations. At the molecular level, calcium, reactive oxygen species, phytohormones, transcription factors and stress-related genes constitute interrelated regulatory systems.

While conventional breeding is inevitable, it can become more efficient due to marker-assisted selection, QTL analysis, GWAS and genomic selection. High-throughput phenotyping serves as a tool for assessing large breeding material, and transcriptomics, proteomics, metabolomics and epigenomics can help understand complex molecular mechanisms of stress responses. CRISPR/Cas and other genomic engineering methods have the potential to edit genes that affect plant stress resistance. But effective use of these tools is likely to be dependent on the improvement in transformation technologies, regeneration, target gene verification, off-target analysis and regulation.

The future of horticultural stress breeding involves an integrated precision breeding system where genetic diversity, physiological, genomics, phenomics, multi-omics, artificial intelligence, microbiome research and gene editing technologies are used together. In an integrated system of precision breeding, faster development of horticultural cultivars that can sustain their performance and quality under drought, salinity, heat, cold and multiple stresses is possible.

In essence, horticultural stress breeding should not only involve selection for stress tolerance but also high productivity, nutritional value, marketable yield, resource efficiency and adaptation ability. Development and utilization of such varieties would become critical for sustainable horticultural production, food and nutrition security and farmers' income in changing climatic conditions.

REFERENCE

1. Ahmad, Y., Haakim, Z., Iqbal, J., Abbasi, B. A., Mahmood, T., & Kazi, M. (2024). Technological innovations for abiotic stress resistance in horticultural crops. *OMICs-based techniques for global food security*, 233-244.
2. Altaf, M. A., Shahid, R., Kumar, R., Altaf, M. M., Kumar, A., Khan, L. U., ... & Naz, S. (2023). Phytohormones mediated modulation of abiotic stress tolerance and potential crosstalk in horticultural crops. *Journal of Plant Growth Regulation*, 42(8), 4724-4750.
3. Bechtold, U., & Field, B. (2018). Molecular mechanisms controlling plant growth during abiotic stress. *Journal of Experimental Botany*, 69(11), 2753-2758.
4. Begna, T., Gichile, H., Teressa, T., Yali, W., & Asrat, Z. (2026). Crop production under abiotic stresses: Management options and crop reactions. *Ecological Genetics and Genomics*, 100454.
5. Bertier, L. D., Ron, M., Huo, H., Bradford, K. J., Britt, A. B., & Michelmore, R. W. (2018). High-resolution analysis of the efficiency, heritability, and editing outcomes of CRISPR/Cas9-induced modifications of NCED4 in lettuce (*Lactuca sativa*). *G3: Genes, Genomes, Genetics*, 8(5), 1513-1521.
6. Bouzroud, S., Gasparini, K., Hu, G., Barbosa, M. A. M., Rosa, B. L., Fahr, M., ... & Zouine, M. (2020). Down regulation and loss of auxin response factor 4 function using CRISPR/Cas9 alters plant growth, stomatal function and improves tomato tolerance to salinity and osmotic stress. *Genes*, 11(3), 272.
7. Brini, F., & Masmoudi, K. (2012). Ion transporters and abiotic stress tolerance in plants. *International scholarly research notices*, 2012(1), 927436.
8. Budhlakoti, N., Kushwaha, A. K., Rai, A., Chaturvedi, K. K., Kumar, A., Pradhan, A. K., ... & Kumar, S. (2022). Genomic selection: A tool for accelerating the efficiency of molecular breeding for development of climate-resilient crops. *Frontiers in Genetics*, 13, 832153.
9. Bvindi, C., Lee, S., Tang, L., Mickelbart, M. V., Li, Y., and Mengiste, T. (2022). Improved pathogen and stress tolerance in tomato mutants of SET domain histone 3 lysine methyltransferases. *New Phytologist*. 235 (5), 1957–1976.
10. Chaffai, R., Ganesan, M., & Cherif, A. (2024). Transcriptional regulation of gene expression in plant abiotic stress response. In *Plant adaptation to abiotic stress: from signaling pathways and microbiomes to molecular mechanisms* (pp. 303-343). Singapore: Springer Nature Singapore.
11. Chen, M., Zhu, X., Liu, X., Wu, C., Yu, C., Hu, G., ... & Hao, Y. (2021). Knockout of auxin response factor SlARF4 improves tomato resistance to water deficit. *International Journal of Molecular Sciences*, 22(7), 3347.
12. Chennakesavulu, K., Singh, H., Trivedi, P. K., Jain, M., & Yadav, S. R. (2022). State-of-the-art in CRISPR technology and engineering drought, salinity, and thermo-tolerant crop plants. *Plant cell reports*, 41(3), 815-831.
13. FAO, F. (2007). Commission on genetic resources for food and agriculture. Rome: <http://www.fao.org/nr/cgrfa/cgrfa-about/cgrfa-history/en>.
14. Francini, A., & Sebastiani, L. (2019). Abiotic stress effects on performance of horticultural crops. *Horticulturae*, 5(4), 67.

15. Gerakari, M., Katsileros, A., Klefogianni, K., Tani, E., Bebeli, P. J., & Papasotiropoulos, V. (2025). Breeding of solanaceous crops using AI: Machine learning and deep learning approaches—A critical review. *Agronomy*, 15(3), 757.
16. Gou, C., Zafar, S., Fatima, N., Hasnain, Z., Aslam, N., Iqbal, N., ... & Abbas, M. (2024). Machine and deep learning: artificial intelligence application in biotic and abiotic stress management in plants. *Frontiers in Bioscience-Landmark*, 29(1).
17. Hammad, M., Talib, U., Sher, A., Shafiq, M., & SHERAZI, S. (2026). Climate-resilient horticulture through genomic tools: A decade of genome-wide association studies (GWAS) applications amidst a changing climate. *Bulletin of Biological and Allied Sciences Research*, 2026(1), 115-115.
18. Hanjagi, P. S. (2025). High Throughput Phenotyping for Abiotic Stress Management. *Spatial & Agricultural System Modeling for Abiotic Stress Management*, 4.
19. Hassan, K. M., Ali, M. A., & Nasser, M. A. (2026). Effects of abiotic stress on the performance of horticultural crops. In *Melatonin in Horticultural Plants* (pp. 1-29). Academic Press.
20. Hu, Z., Li, J., Ding, S., Cheng, F., Li, X., Jiang, Y., ... & Shi, K. (2021). The protein kinase CPK28 phosphorylates ascorbate peroxidase and enhances thermotolerance in tomato. *Plant Physiology*, 186(2), 1302-1317.
21. Hua, D., Ma, M., Ge, G., Suleman, M., & Li, H. (2020). The role of cyanide-resistant respiration in *Solanum tuberosum* L. against high light stress. *Plant Biology*, 22(3), 425-432.
22. Illouz-Eliaz, N., Nissan, I., Nir, I., Ramon, U., Shohat, H., & Weiss, D. (2020). Mutations in the tomato gibberellin receptors suppress xylem proliferation and reduce water loss under water-deficit conditions. *Journal of Experimental Botany*, 71(12), 3603-3612.
23. Klap, C., Yeshayahou, E., Bolger, A. M., Arazi, T., Gupta, S. K., Shabtai, S., ... & Barg, R. (2017). Tomato facultative parthenocarp results from *Sl AGAMOUS-LIKE 6* loss of function. *Plant biotechnology journal*, 15(5), 634-647.
24. Koevoets, I. T., Venema, J. H., Elzenga, J. T. M., & Testerink, C. (2016). Roots withstanding their environment: exploiting root system architecture responses to abiotic stress to improve crop tolerance. *Frontiers in plant science*, 7, 1335.
25. Kumar, A., Rai, A. C., Rai, A. K., Rai, K. K., & Rai, V. P. (Eds.). (2021). *Stress tolerance in horticultural crops: challenges and mitigation strategies*. Woodhead Publishing.
26. Kumar, M., Prusty, M. R., Pandey, M. K., Singh, P. K., Bohra, A., Guo, B., & Varshney, R. K. (2023). Application of CRISPR/Cas9-mediated gene editing for abiotic stress management in crop plants. *Frontiers in plant science*, 14, 1157678.
27. Lal, M. K., Tiwari, R. K., Altaf, M. A., Kumar, A., & Kumar, R. (2023). Abiotic and biotic stress in horticultural crops: insight into recent advances in the underlying tolerance mechanism. *Frontiers in Plant Science*, 14, 1212982.
28. Li, R., Liu, C., Zhao, R., Wang, L., Chen, L., Yu, W., ... & Shen, L. (2019). CRISPR/Cas9-Mediated *SINPR1* mutagenesis reduces tomato plant drought tolerance. *BMC plant biology*, 19(1), 38.
29. Li, R., Zhang, L., Wang, L., Chen, L., Zhao, R., Sheng, J., & Shen, L. (2018). Reduction of tomato-plant chilling tolerance by CRISPR–Cas9-mediated *SICBF1* mutagenesis. *Journal of agricultural and food chemistry*, 66(34), 9042-9051.
30. Liu, L., Zhang, J., Xu, J., Li, Y., Guo, L., Wang, Z., ... & Zhang, N. (2020). CRISPR/Cas9 targeted mutagenesis of *SILBD40*, a lateral organ boundaries domain transcription factor, enhances drought tolerance in tomato. *Plant Science*, 301, 110683.
31. Makhotenko, A. V., Khromov, A. V., Snigir, E. A., Makarova, S. S., Makarov, V. V., Suprunova, T. P., ... & Taliansky, M. E. (2019, January). Functional analysis of coilin in virus resistance and stress tolerance of potato *Solanum tuberosum* using CRISPR-Cas9 editing. In *Doklady biochemistry and biophysics* (Vol. 484, No. 1, pp. 88-91). Moscow: Pleiades Publishing.
32. Mickelbart, M. V., Hasegawa, P. M., & Bailey-Serres, J. (2015). Genetic mechanisms of abiotic stress tolerance that translate to crop yield stability. *Nature Reviews Genetics*, 16(4), 237-251.
33. Mishra, N., Jiang, C., Chen, L., Paul, A., Chatterjee, A., & Shen, G. (2023). Achieving abiotic stress tolerance in plants through antioxidative defense mechanisms. *Frontiers in plant science*, 14, 1110622.
34. Muhammad, A., Kong, X., Zheng, S., Bai, N., Li, L., Khan, M. H. U., ... & Zhang, Z. (2024). Exploring plant-microbe interactions in adapting to abiotic stress under climate change: a review. *Frontiers in plant science*, 15, 1482739.
35. Muhammad, M., Basit, A., Ameen, N., Khan, A., Wahab, A., Nazim, M., ... & Li, L. (2025). Insights into molecular and biochemical approaches of multi-stress responses to horticultural crops. *Plant Growth Regulation*, 105(6), 1889-1910.
36. Nehanjali Parmar, N. P., Singh, K. H., Deepika Sharma, D. S., Lal Singh, L. S., Pankaj Kumar, P. K., Nanjundan, J., ... & Thakur, A. K. (2017). Genetic engineering strategies for biotic and abiotic stress tolerance and quality enhancement in horticultural crops: a comprehensive review.
37. Padilla, Y., Fotopoulos, V., Ntatsi, G., Calatayud, Á., Penella, C., Sabatino, L., & Mozafarian, M. (2025). Strategies for enhancing resilience in horticultural crops against combined abiotic stresses. *Physiologia Plantarum*, 177(5), e70502.

38. Padilla, Y., Fotopoulos, V., Ntatsi, G., Calatayud, Á., Penella, C., Sabatino, L., & Mozafarian, M. (2025). Strategies for enhancing resilience in horticultural crops against combined abiotic stresses. *Physiologia Plantarum*, 177(5), e70502.
39. Paliwal, R., Singh, G., Mir, R. R., & Gueye, B. (2021). Genomic-assisted breeding for abiotic stress tolerance in horticultural crops. In *Stress Tolerance in Horticultural Crops* (pp. 91-118). Woodhead Publishing.
40. Pandey, H., Singh, D., Pandey, A. K., Suthar, K. P., Mehta, R., & Pandey, D. (2021). Current approaches in horticultural crops to mitigate the effect of cold stress. *Stress Tolerance in Horticultural Crops*, 241-257.
41. Parmar, N., Singh, K. H., Sharma, D., Singh, L., Kumar, P., Nanjundan, J., ... & Thakur, A. K. (2017). Genetic engineering strategies for biotic and abiotic stress tolerance and quality enhancement in horticultural crops: a comprehensive review. *3 Biotech*, 7(4), 239.
42. Patil, A. H., Pawar, R. M., Negi, R., Singh, R. A., Singh, B., Tiwari, S., ... & Beese, S. (2026). GENETIC AND MOLECULAR MECHANISMS OF ABIOTIC STRESS TOLERANCE IN HORTICULTURAL CROPS: ADVANCES IN GENOMICS AND GENOME EDITING-A REVIEW. *Genetics and Molecular Research*
43. Rai, A., Vatov, E., Georgieva, A. W., Bogdanova, S., Wittenberg, M. F., Anachkov, N., ... & Alseekh, S. (2026). Integrated genome-wide association and quantitative trait locus mapping elucidate the genetic basis of fruit yield and quality traits in pepper under water stress. *Journal of Experimental Botany*, erag385.
44. Rai, K. K., Kumar, A., Rai, A., Rai, V. P., & Rai, A. C. (2021). Conventional breeding approaches for abiotic stress management in horticultural crops. In *Stress Tolerance in Horticultural Crops* (pp. 21-32). Woodhead Publishing.
45. Rai, K. K., Kumar, A., Rai, A., Rai, V. P., & Rai, A. C. (2021). Conventional breeding approaches for abiotic stress management in horticultural crops. In *Stress Tolerance in Horticultural Crops* (pp. 21-32). Woodhead Publishing.
- Younis, A., Ramzan, F., Ramzan, Y., Zulfikar, F., Ahsan, M., & Lim, K. B. (2020). Molecular markers improve abiotic stress tolerance in crops: a review. *Plants*, 9(10), 1374.
46. Ramírez Gonzales, L., Shi, L., Bergonzi, S. B., Oortwijn, M., Franco-Zorrilla, J. M., Solano-Tavira, R., et al. (2021). Potato CYCLING DOF FACTOR 1 and its lncRNA counterpart StFLORE link tuber development and drought response. *Plant J.* 105 (4), 855–869.
47. Roupael, Y., Venema, J. H., Edelstein, M., Savvas, D., Colla, G., Ntatsi, G., ... & Schwarz, D. (2017). Grafting as a tool for tolerance of abiotic stress. In *Vegetable grafting: principles and practices* (pp. 171-215). Wallingford UK: CABI.
48. Roychoudhury, A., & Banerjee, A. (2017). Absciscic acid signaling and involvement of mitogen activated protein kinases and calcium-dependent protein kinases during plant abiotic stress. *Mechanism of plant hormone signaling under stress*, 1, 197-241.
49. Sachdev, S., Ansari, S. A., Ansari, M. I., Fujita, M., & Hasanuzzaman, M. (2021). Abiotic stress and reactive oxygen species: Generation, signaling, and defense mechanisms. *Antioxidants*, 10(2), 277.
50. Sachdev, S., Ansari, S. A., Ansari, M. I., Fujita, M., & Hasanuzzaman, M. (2021). Abiotic stress and reactive oxygen species: Generation, signaling, and defense mechanisms. *Antioxidants*, 10(2), 277.
51. Saharan, B. S., Brar, B., Duhan, J. S., Kumar, R., Marwaha, S., Rajput, V. D., & Minkina, T. (2022). Molecular and physiological mechanisms to mitigate abiotic stress conditions in plants. *Life*, 12(10), 1634.
52. Sardar, A. (2023). Genetic amelioration of fruit and vegetable crops to increase biotic and abiotic stress resistance through CRISPR genome editing. *Frontiers in Plant Science*, 14, 1260102.
53. Schwarz, D., Roupael, Y., Colla, G., & Venema, J. H. (2010). Grafting as a tool to improve tolerance of vegetables to abiotic stresses: Thermal stress, water stress and organic pollutants. *Scientia horticulturae*, 127(2), 162-171.
54. Shankar, K., Singh, D., Sharma, P., Singh, N., Shukla, R., Goel, P., ... & Meena, M. (2026). Multi-Omics Insights into Climate-Driven Abiotic Stress Responses and Tolerance Mechanisms in Fruit Crops. *Stresses*, 6(3), 66.
55. Shu, P., Li, Z., Min, D., Zhang, X., Ai, W., Li, J., ... & Li, X. (2020). CRISPR/Cas9-mediated SIMYC2 mutagenesis adverse to tomato plant growth and MeJA-induced fruit resistance to *Botrytis cinerea*. *Journal of Agricultural and Food Chemistry*, 68(20), 5529-5538.
56. Tran, M. T., Doan, D. T. H., Kim, J., Song, Y. J., Sung, Y. W., Das, S., ... & Kim, J. Y. (2021). CRISPR/Cas9-based precise excision of SlHyPRP1 domain (s) to obtain salt stress-tolerant tomato. *Plant Cell Reports*, 40(6), 999-1011.
57. Vu, T. V., Sivankalyani, V., Kim, E. J., Doan, D. T. H., Tran, M. T., Kim, J., ... & Kim, J. Y. (2020). Highly efficient homology-directed repair using CRISPR/Cpf1-geminiviral replicon in tomato. *Plant biotechnology journal*, 18(10), 2133-2143.
58. Wang, L., Chen, L., Li, R., Zhao, R., Yang, M., Sheng, J., & Shen, L. (2017). Reduced drought tolerance by CRISPR/Cas9-mediated SIMAPK3 mutagenesis in tomato plants. *Journal of agricultural and food chemistry*, 65(39), 8674-8682.
59. Wang, P., Luo, Q., Yang, W., Ahammed, G. J., Ding, S., Chen, X., ... & Shi, K. (2021). A novel role of pipercolic acid biosynthetic pathway in drought tolerance through the antioxidant system in tomato. *Antioxidants*, 10(12), 1923.
60. Wang, Z., Hong, Y., Li, Y., Shi, H., Yao, J., Liu, X., ... & Zhu, J. K. (2020). Natural variations in SlSOS1 contribute to the loss of salt tolerance during tomato domestication. *Plant Biotechnology Journal*, 19(1), 20.

61. Wang, Z., Hong, Y., Zhu, G., Li, Y., Niu, Q., Yao, J., ... & Zhu, J. K. (2020). Loss of salt tolerance during tomato domestication conferred by variation in a Na⁺/K⁺ transporter. *The EMBO journal*, 39(10), EMBJ2019103256.
62. Wu, W., Wang, R., Li, J., Zhang, Z., Yao, W., Zhang, N., & Xu, W. (2026). Engineering climate-resilient horticultural crops: advances in transcriptional regulation, genome editing, and synthetic networks. *Horticulture Research*, 13(8), uhag119.
63. XiuJuan, W., Faisal, M., Muhammad, S., Aslam, A., Razzaq, M. K., Masroor, A., ... & Osman, H. E. S. (2026). Clustered Regularly Interspaced Short Palindromic Repeats (CRISPR)-Cas genome editing transforming crop stress tolerance for global food security. *PeerJ*, 14, e21450.
64. Yadav, R. K., Tripathi, M. K., Tiwari, S., Tripathi, N., Asati, R., Chauhan, S., ... & Payasi, D. K. (2023). Genome editing and improvement of abiotic stress tolerance in crop plants. *Life*, 13(7), 1456.
65. Yadav, R. K., Tripathi, M. K., Tiwari, S., Tripathi, N., Asati, R., Chauhan, S., ... & Payasi, D. K. (2023). Genome editing and improvement of abiotic stress tolerance in crop plants. *Life*, 13(7), 1456.
66. Yin, Y., Qin, K., Song, X., Zhang, Q., Zhou, Y., Xia, X., & Yu, J. (2018). BZR1 transcription factor regulates heat stress tolerance through FERONIA receptor-like kinase-mediated reactive oxygen species signaling in tomato. *Plant and Cell Physiology*, 59(11), 2239-2254.
67. Yu, W., Wang, L., Zhao, R., Sheng, J., Zhang, S., Li, R., & Shen, L. (2019). Knockout of SIMAPK3 enhances tolerance to heat stress involving ROS homeostasis in tomato plants. *BMC plant biology*, 19(1), 354.
68. Zheng, Y., Wang, X., Cui, X., Wang, K., Wang, Y., & He, Y. (2023). Phytohormones regulate the abiotic stress: An overview of physiological, biochemical, and molecular responses in horticultural crops. *Frontiers in Plant Science*, 13, 1095363.
69. Zivcak, M., Brestic, M., & Sytar, O. (2016). Osmotic adjustment and plant adaptation to drought stress. In *Drought stress tolerance in plants, Vol 1: physiology and biochemistry* (pp. 105-143). Cham: Springer International Publishing