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GENETIC AND MOLECULAR MECHANISMS OF ABIOTIC STRESS TOLERANCE IN HORTICULTURAL CROPS: ADVANCES IN GENOMICS AND GENOME EDITING- A REVIEW

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ABSTRACT

Abiotic stresses such as drought, salinity, heat, chilling, freezing, flooding, nutrient deficiency, heavy-metal toxicity and excessive radiation have a great impact on the yield and quality of horticulture crops. These products are especially susceptible as commercial success relies on yield, visual appearance, flavour, texture, nutritional makeup and postharvest behaviour. Stress tolerance is established through integrated processes, including environmental sensing, calcium and reactive oxygen species signaling, hormonal interplay, transcriptional control, ion homeostasis, osmotic adjustment, antioxidant defense, proteome protection, metabolic reprogramming and developmental pliancy. These phenotypic responses are governed by complex genetic bases, characterized by QTL, structural variations, regulatory polymorphisms, gene-family expansion, epistasis and genotype-by-environment interactions. Developments in long read sequencing including haplotype-resolved assemblies, pangenomics, genome-wide association studies, transcriptomics, epigenomics, proteomics, metabolomics, phenomics and envirotyping are allowing access to adaptive genes and alleles not available previously. CRISPR-Cas systems also allow their specific validation and modification, while base editing, prime editing, multiplex editing, CRISPR-mediated gene regulation provide superior precision to conventional methods of gene disruption. Nevertheless, transformation recalcitrance, polyploidy, heterozygosity, long juvenile periods, pleiotropic growth penalties and lack of sufficient field validation are still substantial obstacles in this regard. In this review, the genetic and molecular bases of abiotic-stress tolerance are discussed and how genomics and genome editing technologies can contribute to the development of robust, high-yielding and high-quality horticultural cultivars.

KEYWORDS: abiotic stress; horticultural crops; stress signalling; pangenome; multi-omics; CRISPR-Cas; base editing; prime editing

1. INTRODUCTION

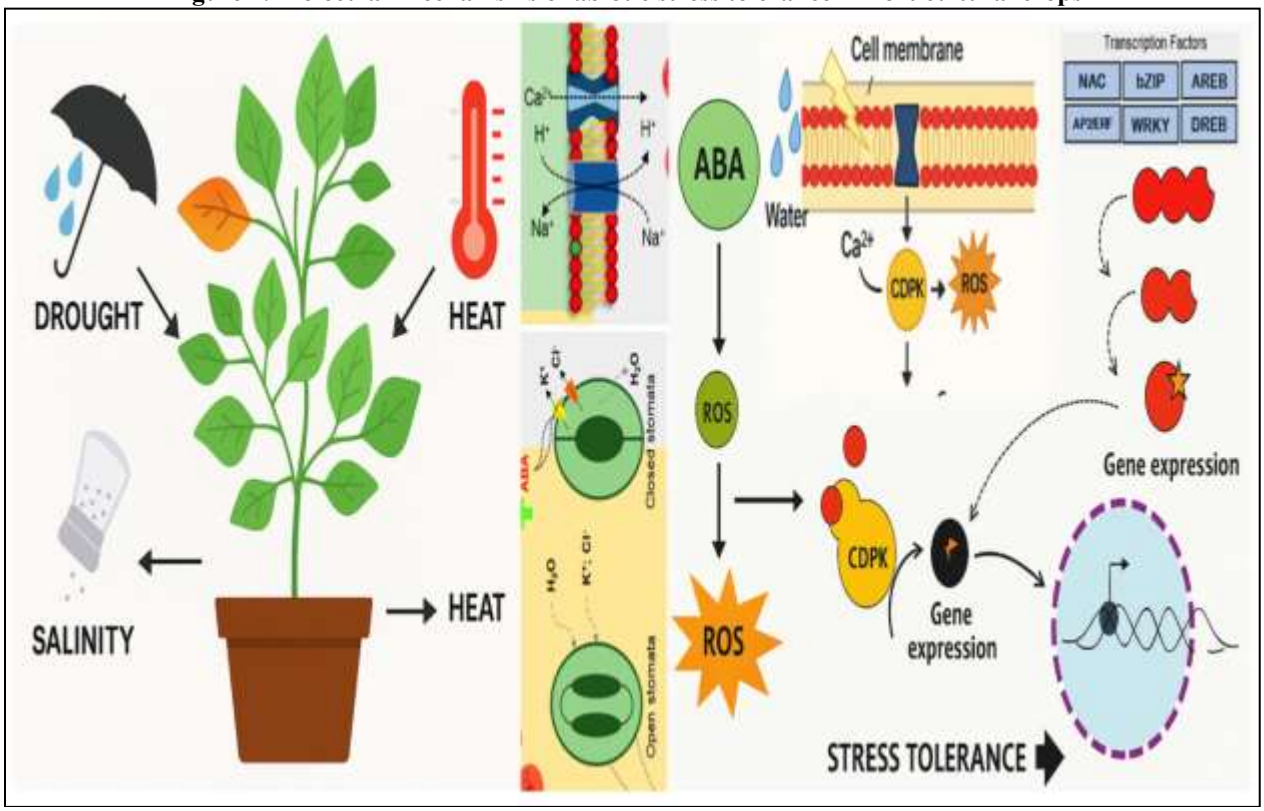
Horticultural crops are essential for food and nutrition security, agricultural diversification, rural income and employment, and foreign exchange. But their productivity, quality and market value are increasingly at risk due to climate fluctuations, global warming, droughts, salinization, floods, and deteriorating soil quality. Small variations in size, color, taste, firmness or appearance of fruits can result in huge financial loss (Savitha and Sundaram, 2026). Abiotic stresses influence plant growth, development, productivity, and postharvest quality during the entire crop life cycle. Thus, efficacious stress tolerance has to guarantee not only the survival of the plant but also a stable marketable yield, reproductive fitness, quality of the produce and recovery fitness after the stress (Dillon *et al*., 2020; Musacchi *et al*., 2023). Traditional breeding has produced stress-tolerant cultivars, but progress is frequently slow as tolerance

is a complex, polygenic trait, especially in perennial crops. With advances in genomics and genome editing, the prospect to elucidate and manipulate stress responsive genes, retaining favorable yield and quality traits to fast track development of climate resilient horticultural crops is becoming a reality (Daniel *et al*., 2023).

2. Genetic Architecture of Abiotic-Stress Tolerance

Tolerance to abiotic stress is a complex trait influenced by multiple genes with various effects and physiological aspects, such as root growth, stomatal regulation, ion exclusion, osmotic adjustment, antioxidant activity, pollen viability, and fruit detachment. It has also been shown that the response of stress responsive genes depends on the severity, duration, timing, developmental stage, and environment of the production and therefore, genotype-by-environment interactions become important in order to obtain stable yield and quality (Cosmulescu, 2026; Lee *et al*., 2026; He *et al*., 2018).

Figure 1. Molecular mechanisms of abiotic stress tolerance in horticultural crops



Source- Pagnotta, 2025

The reduced diversity caused by domestication and intensive breeding in many horticultural crops highlights the importance of landraces, traditional cultivars, wild relatives, and locally adapted rootstocks as sources of stress-resilience traits. Traditional introgression breeding may however bring along with it if also undesirable traits and involve a long breeding cycle (Salgotra and Chauhan, 2023). Recent progress in structural genomics, haplotype-resolved assemblies, and pangenomes are now allowing the discovery of novel genetic variation previously not associated with stress adaptation and environmental resilience (Su *et al*., 2020).

3. Perception and Early Stress Signalling

3.1 Environmental Perception

Plants sense stress by variations of water potential, membrane tension, temperature, ionic strength, oxygen availability, and macromolecular stability. Plasma-membrane receptors, receptor-like kinases, mechanosensitive proteins and osmosensitive calcium channels participate in environmental sensing. Salinity induces osmotic stress first prior to salt (sodium and chloride) toxicity. Heat changes membrane fluidity and favors protein unfolding, while chilling rigidifies membranes and leads to a metabolic desynchronization. These early physical and biochemical events trigger signalling cascades, which may allow the plant to successfully acclimate, or lead to irreversible cellular damage (Puniran-Hartley, 2022).

Stress perception is not confined to directly exposed cells. Root under dry or saline soil conditions send hydraulic and chemical signals to leaves whereas heat or light-stressed leaves send signals to meristems, flowers and fruits. Among long distance signalling molecules are hormones, electrical signals, calcium waves, reactive oxygen species, small

RNAs, peptides and mobile metabolites. This signalling enables the non-compromised tissues to induce protection prior to catastrophic damage. The rate, magnitude and duration of systemic signalling have profound effects on acclimation, resource allocation and recovery in the whole plant (Devireddy *et al*., 2021).

3.2 Calcium and Reactive Oxygen Species Signalling

Calcium is one of the earliest intracellular messengers generated after stress recognition. Different environmental stimuli induce characteristic Ca^{2+} signatures that differ in magnitude, frequency, length and subcellular delivery. Calmodulins, calcium-dependent protein kinases and calcineurin B like protein-interacting kinases interpret these patterns. They in turn modulate ion channels, transcription factors, metabolic enzymes, and membrane transporters. Specificity is not due just to a rise in Ca^{2+} concentration, but it depends on the spatial and temporal structure of the signal and the presence of certain Ca^{2+} decoding proteins (Li *et al*., 2024).

Reactive oxygen species are generated in the chloroplasts, mitochondria, peroxisomes and plasma membrane. Overproduction of this species oxidizes to lipids, proteins, pigments and nucleic acids, but a tightly regulated generation is an important signal. Calcium and reactive oxygen species (ROS) are mutually reinforcing and capable of generating waves that propagate through cells and organs. Nitric oxide, hydrogen sulphide, phospholipids and cyclic nucleotides provide additional layers of regulation. Brief and controlled signals activate acclimation, whereas prolonged accumulation can promote senescence, cellular dysfunction or programmed cell death (Castro *et al*., 2021).

3.3 Protein Kinase Cascades

Mitogen-activated protein kinase cascades mediate transduction of environmental signals into alterations of transcription, metabolism and development. Stomatal movement, ion transport and nutrient homeostasis are linked to calcium signatures by calcium-dependent kinases and CBL-CIPK complexes. Protein phosphatases limit hyperactivation and reset signalling networks to their basal states post-stress. Such contrasting regulatory activities enable the plant to have a rapid response, without the cost of turning on and off energy metabolism repeatedly. Genetic variation in phosphorylation sites, kinase-binding domains and phosphatase activity can therefore produce substantial differences in stress sensitivity among horticultural genotypes (Zhang *et al*., 2025).

Signalling proteins themselves are regulated by ubiquitination, proteasomal degradation and autophagy. Rapid protein turnover makes it possible for plants to discard damaged proteins and dynamically regulate the levels of receptors, kinases, transcription factors and repressor of regulation. Editing protein-interaction motifs or degradation signals might alter the length of protection responses without the need to switch on an entire pathway permanently. However, they often affect a multitude of developmental processes, thus the resulting lines should be scrutinized for unexpected alterations in plant architecture, flowering, ripening and reproductive fertility (Marshall and Vierstra, 2018).

3.4 Hormonal Integration

Abscisic acid (ABA) is a crucial determinant in drought and salinity tolerance, which triggers SnRK2 kinases and stress-induced cascades that facilitate stomatal closure, osmoprotectant synthesis, production of protective proteins, and adaptive root growth. Variation in ABA synthesis, transport, perception and signal transduction makes the contribution to cultivar specific stress responses. ABA is also cross-talk with auxin, cytokinin, ethylene, jasmonates, gibberellins, brassinosteroids, and strigolactones in the overall coordination of growth, senescence, antioxidant defense, and stress response (Gutmann *et al*., 2020; Salvi *et al*., 2021).

In Horticultural crops, the importance of hormonal regulation is emphasized as flowering, fruit set, fruit development, ripening and abscission are extremely stress sensitive. Heat and drought stress affect auxin and gibberellin levels and induce ethylene-mediated flower and fruit abscission, and ABA regulates sugar accumulation, color, and ripening. Therefore, genetic improvement should enhance stress protection without compromising reproductive development and produce quality, with tissue-specific and stress-inducible regulation offering promising strategies (Fatma *et al*., 2022).

4. Cellular and Molecular Mechanisms of Tolerance

4.1 Transcriptional Regulation

Stress responsive transcription factors (TFs) control intricate gene networks involved in drought, salinity, cold, heat and oxidative stress. The main TF families like DREB, CBF, AREB/ABF, NAC, WRKY, MYB, bZIP, ERF, HD-ZIP and Heat-shock factors (HSFs) regulate amongst others antioxidant defence, osmotic regulation, ion transport, cell-wall modification, senescence and reproductive fitness. They are subject to regulation at the transcription, alternative splicing, phosphorylation, protein-protein interactions, and degradation levels to facilitate rapid response to environmental changes (Debbarma *et al*., 2019; Abdelrahman *et al*., 2021).

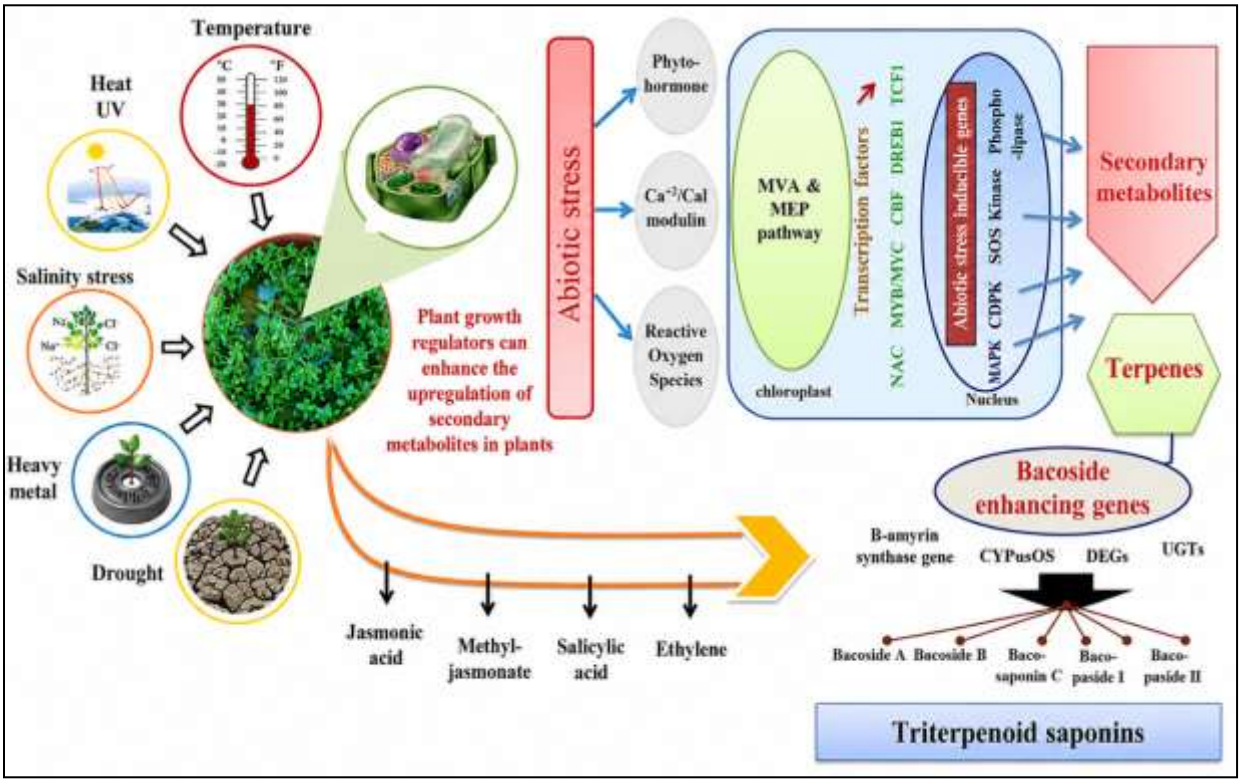
However, the upregulation of a stress-responsive gene does not always represent effective tolerance, as some responses could be a consequence of tissue injury. Thus, potential regulators need to be confirmed with physiological traits, recovery from capacity loss, reproductive performance, yield, and testing across multiple environments. Since a number of transcription factors have overlapping roles in critical developmental pathways, promoter editing, tissue-specific expression, or downstream targets modification might represent safer and more balanced strategies rather than whole gene knockout (Abdelrahman *et al*., 2021; Ahtisham and Obaid, 2024).

4.2 Osmotic Adjustment

Drought, salinity and freezing limit the availability of cellular water and alter turgor, and lead to proline, soluble sugars, raffinose-family oligosaccharides, glycine betaine, sugar alcohols and organic acids accumulation in plants. These osmolytes contribute to associated osmotic adjustment, membrane and protein stability, enzyme protection, and redox balance. However, their synthesis must be rapid and tissue-specific and should not heavily drain resources away from growth and reproduction, and remobilization of accumulated nutrients is very efficient and aids in recovery after stress (Roychowdhury *et al*., 2025).

Aquaporins, root system architecture, cuticular wax and stomatal traits together modulate plant water relations. Aquaporins affect water uptake and transport, and root growth, xylem differentiation, suberization, and root hairs influence hydraulic conductivity. Higher wax accumulation may decrease water loss and fruit protection while mild changes in stomatal density and responsiveness may lead to a better water-use efficiency without detriment on photosynthesis or canopy cooling. Therefore genetic engineering should focus on integrative, tissue-specific modulation of water uptake, retention, transport and utilization in concert with photosynthesis, canopy temperature and yield (Alam *et al*., 2026; Deng *et al*., 2025).

Figure 2. Abiotic Stress-Induced Regulation of Secondary Metabolite and Triterpenoid Saponin Biosynthesis in Plants



Source- Peleg *et al*., 2012

4.3 Ion Homeostasis

Salinity is a cause of osmotic stress, ion toxicity (Na^+ and Cl^-), nutrient imbalance, and oxidative stress. Tolerant plants restrict toxic-ion uptake, export Na^+ from the cytosol, recover it from the transpiration stream, and compartmentalize it within vacuoles concurrently with K^+ uptake and cellular pH homeostasis. The proton pumps generate the energy gradients necessary for these events, and transporter localization and tissue-specific activity can be more relevant than total transporter abundance (Alam *et al*., 2026).

The SOS pathway, HKT transporters, and NHX exchangers are involved in Na^+ sensing, long distance transport in the vasculature, and vacuolar sequestration, respectively, and K^+, Cl^- and Ca^{2+} homeostasis is ensured by other transporters. Specific regulatory editing may alter these processes with less impact under non-saline conditions (Zhang *et al*., 2025). In fruit and nut crops, rootstock-mediated ion exclusion and rootstock-scion signaling are the most notable. Ion partitioning needs to be assessed by breeding along with growth, yield and mineral content of the edible portion to achieve salinity tolerance as well as produce quality.

4.4 Antioxidant and Redox Defence

Drought, temperature extremes, salinity, flooding, and metals toxicity enhance ROS generation by interfering with cellular electron transport. Enzymatic antioxidants like SOD, catalase, ascorbate peroxidase, glutathione peroxidase,

and peroxiredoxins and non-enzymatic molecules such as ascorbate, glutathione, carotenoids, tocopherols, flavonoids, anthocyanins, and phenols prevent oxidative injury in plants (Alkmin *et al*., 2022). These systems maintain redox balance while preserving ROS as signalling molecules for stress acclimation (Sachdev *et al*., 2021).

Antioxidant metabolism also affects nutritional, sensory and commercial quality. While the increase of carotenoids, anthocyanins or ascorbate might result in a dual benefit of enhanced stress tolerance and produce value, coupled metabolic flux redirection could alter flavor, color, and maturation. Therefore, breeding should prioritize coordinated and tissue-specific redox regulation rather than continuous overproduction of single antioxidants. Redox proteomics in conjunction with metabolomics and physiological phenotyping can lead to the identification of regulators that potentiate stress responsiveness while causing minimal metabolic costs under non-stress conditions (Zhao *et al*., 2024; Huang *et al*., 2024).

4.5 Protein and Membrane Protection

Heat, dehydration, and freezing affect protein conformation and membrane integrity. Heat-shock proteins (HSPs) act as molecular chaperones, that have the anti-aggregation effect on proteins, promote refolding and cellular recovery process while the LEA proteins and dehydrins protect cellular structures during dehydration and cold stress. These protective genes are under the regulation of heat-shock factors that allow a rapid response to temperature stress (Bakery *et al*., 2024).

Membrane lipid remodeling ensures proper fluidity during temperature fluctuations and protein quality-control systems such as the unfolded-protein response, ubiquitin-mediated degradation and autophagy eliminate the damaged cellular components. Mild autophagy can promote survival and nutrient recycling, but over-activation may speed up senescence and yield loss. Therefore, breeding for genetic improvement in this regard should be aimed at achieving a coordinated, stress-responsive regulation of membrane stability, protein protection and cell recycling, using recovery and marketable yield as the main indicators of assessment (Chen *et al*., 2026; Wei *et al*., 2026).

4.6 Photosynthesis and Energy Balance

Photosynthesis is very vulnerable to drought, salinity, heat, chilling, and high light. Stomatal closure also limits CO_2 uptake, while stress may cause damage to photosystem II, the electron transport chain and the carbon-fixing enzymes, all of which lead to increased production of ROS. Plants guard photosynthesis by energy dissipation, antioxidant defense, pigment modification and by replacing damaged proteins, which in turn reduces photoinhibition (Didaran *et al*., 2024).

Chloroplasts, mitochondria, and peroxisomes are energetically positive organelles that couple energy metabolism, redox balancing, and stress recovery by inter-organelle communication. The problem is that survival by means of reduced growth and photosynthesis is not necessarily horticulturally useful tolerance. Good tolerance should preserve or return quickly to normal levels of carbon assimilation, reproductive development, source-sink transport, yield and fruit quality. Thus, chlorophyll fluorescence and gas-exchange analyses should be combined with yield and quality attributes during breeding and screening (Selinski *et al*., 2024; Vadez *et al*., 2024).

5. Major Abiotic Stresses and Their Specific Mechanisms

Table 1. Abiotic Stress Tolerance Mechanisms and Improvement Priorities in Horticultural Crops

Stress type	Key tolerance mechanisms	Horticultural improvement priorities	References
Drought	Water absorption and retention, ABA signalling, osmoprotection, antioxidants and quick recuperation..	Protect reproduction, fruit set and yield; improve post-rewatering recovery.	Franco-Navarro *et al*. (2025); Cardoso *et al*. (2025)
Salinity	Osmotic adjustment, ion exclusion/sequestration, K^+ retention and antioxidant defence.	Maintain yield and quality; develop salt-tolerant rootstocks.	Garcia-Daga *et al*. (2025); Badavath and Saski (2026)
Heat	Heat-shock proteins, Ca^{2+}/ROS signalling, thermotolerance and canopy cooling.	Prioritize reproductive-stage tolerance and tissue-specific genome editing.	Bakery *et al*. (2024); Ouonkap *et al*. (2024)
Cold & Freezing	CBF networks, membrane remodeling, sugars, dehydrins and antioxidants.	Maintain cold tolerance without disrupting dormancy, flowering and fruiting.	Muhammad *et al*. (2025); Sabir *et al*. (2025)
Flooding & Waterlogging	Aerenchyma, adventitious roots, fermentation, antioxidant defence and recovery.	Improve hypoxia survival and post-drainage recovery through rootstocks and genomics.	Pan *et al*. (2021); Manghwar *et al*. (2024); Mote *et al*. (2025)

Nutrient & Heavy-Metal	Nutrient sensing, transporter regulation, chelation, sequestration and antioxidants.	Improve nutrient-use efficiency while preventing toxic accumulation in edible parts.	Singh *et al*. (2024); Huang *et al*. (2024)

6. Advances in Genomics and Multi-Omics

6.1 High-Quality Genomes and Pangenomes

Sophisticated genomic methodologies, such as long-read sequencing, optical mapping and chromosome conformation capture, have enhanced the completeness and accuracy of horticultural crop genomes by addressing repetitive sequences, gene duplications, structural variants and chromosome-scale architecture. Haplotype-resolved assemblies are of particular utility for highly heterozygous fruit trees as well as for clonally propagated crops, allowing allele-specific expression studies, detection of structural variations and accurate guide-RNA design in case of duplicated or homologous genes (Schreiber *et al*., 2024). Because no single reference genome can represent all the genetic variation of the cultivated crop and its wild relatives, pangenome differentiate between core, variable and accession-specific sequences, whereas graph-based genomes model alternative alleles and structural variants. Super-pangenomes additionally integrate wild relatives with adaptive alleles for drought, salinity, heat, cold, and nutrient stress. The combination of these resources with genome editing may make it possible to breed advantageous alleles directly into elite cultivars, circumventing linkage drag and saving the time used for traditional backcrossing (Jayakodi *et al*., 2025).

6.2 QTL Mapping and Association Analysis

QTL mapping, genome wide association studies (GWAS), bulked segregant analysis sequencing (BSA-seq) and QTL-seq are useful methodologies to map genomic regions associated with abiotic-stress tolerance. Whereas linkage mapping identifies loci in structured populations, association analyses utilize historical recombination within diverse germplasm to attain higher resolution. Confidence for candidate loci is increased when linkage, association and environmental adaptation analyses identify the same genomic regions. Their identification, however, relies on accurate phenotyping using traits like canopy temperature, stomatal conductance, chlorophyll fluorescence, ion concentration, pollen viability, fruit set, yield, quality and post-stress recovery (Khunsanit *et al*., 2024). Integrating genomic variation and intermediate biological processes further promotes locus identification. Expression QTL and metabolite QTL analyses link genetic variation to transcript and metabolite abundance, and transcriptome-wide association studies identify genetically regulated genes that are associated with stress performance. Environmental association analyses identify alleles correlated with temperature, rainfall, salinity and altitude. Sequential measurements enable differentiation between stress avoidance, cellular tolerance, reproductive endurance and recuperative pathways. Population structure and demographic history also need to be accounted for, and candidate loci should be functionally validated prior to their utilization in breeding or genome editing (Torres-Rodríguez and Schnable, 2025).

6.3 Transcriptomics and Epigenomics

Transcriptomics offers a dynamic perspective on gene regulation in response to abiotic stress and enables early signalling events to be separated from later protective, injury and senescence responses. Comparisons between tissue-specific and tolerant–susceptible genotypes enable candidate genes for superior stress performance to be identified, while alternative isoforms and stress-dependent splicing are resolved by long-read sequencing. Promoter analysis, co-expression networks and chromatin-accessibility data specifically pinpoint core regulators of the multifaceted stress response (Alhabsi *et al*., 2025). The epigenome shows stress-induced alterations in DNA methylation, histone modifications, and chromatin structure, not all of which are necessarily involved in stress memory. MicroRNAs, long-non coding RNAs and allele specific expression analysis offer further regulatory information especially in heterozygous horticultural crops. Specific editing of the epigenome may one day alter stress-responsive gene expression without changing DNA sequence, but the stability, heritability, and phenotypic effects of such modifications must be confirmed prior to use in crop breeding (Zaid *et al*., 2026).

6.4 Proteomics, Metabolomics and Ionomics

Proteomics, metabolomics and ionomics offer functional interpretations that are not possible through genomic and transcriptomic data alone. Protein abundance can differ from transcript levels due to the effects of translation, degradation, localization and posttranslational modification on biological activity. Stress-responsive enzymes, transporters, chaperones and structural proteins are identified by proteomics, whereas phosphoproteomics captures rapid kinase-mediated signalling. Metabolomics analyses of sugars, amino acids, organic acids, lipids, hormones, phenolics and volatile compounds correlate stress response to horticultural traits such as flavour, aroma, colour, nutritional composition and postharvest quality (Siviya *et al*., 2025). Ionomics also complements these methods by analyzing mineral element patterns such as sodium exclusion, potassium retention, nutrient imbalances and heavy-metal accumulation. Omic technologies (e.g. genomics, transcriptomics, proteomics, metabolomics and ionomics) can bridge the gap between genetic diversity and molecular regulation, physiological reactions, and tolerance of environmental stress. Nevertheless, a successful multi-omics integration relies on a standardized sampling and on

comparable tissue and developmental stage, balanced genotype-treatment designs, suitable replication, and control of technical batch effects to effectively separate biological associations from experimental variance (Dakal *et al*., 2025).

6.5 Phenomics and Envirotyping

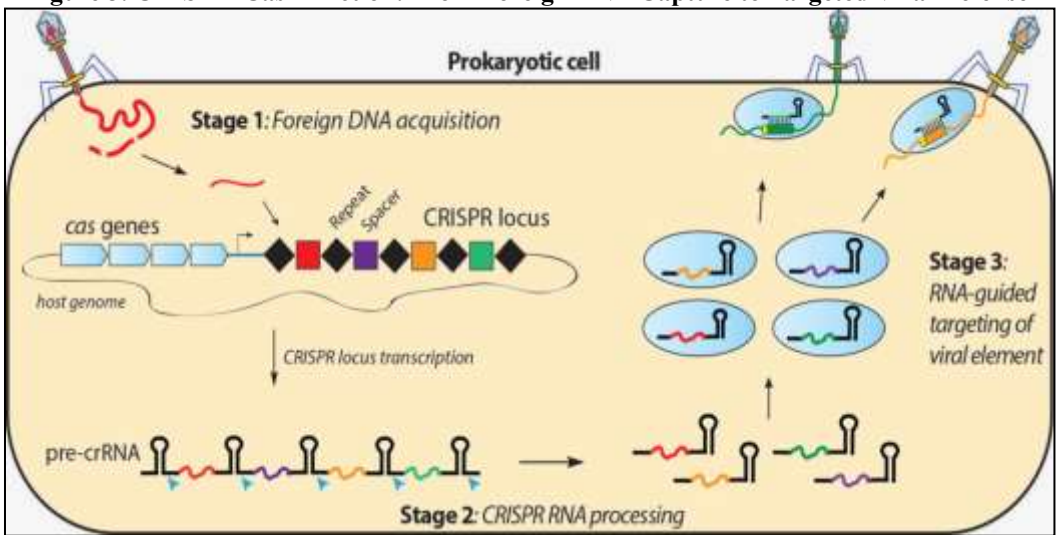
High-throughput phenomics facilitates repetitive, non-invasive monitoring of abiotic-stress responses using visible, thermal, fluorescence, hyperspectral and 3D imaging. Thermal and spectral data can be used to detect changes in canopy temperature, stomatal control, pigments, water status and metabolism prior to the development of visible symptoms, and root morphology (depth, branching and growth dynamics) can be quantified through automated root imaging. These technologies enhance the ability to screen and capture temporal responses to stress, but it is necessary to verify whether sensor-based traits are associated with plant physiological traits, reproduction performance, yield and produce quality to confer meaningful biological and breeding implications (Angidi *et al*., 2025). Envirotyping is a good companion to phenomics to describe temperature, radiation, humidity, soil moisture, salinity and management practices during developmental stages. The combination of envirotyping with genomic, phenotypic and multi-omics data has led to better predictions of genotype-by-environment interactions and environment-specific genomic selection. Most recently, deep learning has been used widely and probably artificial intelligence will further integrate markers, imaging, weather and molecular data in the future, but models need to be compared with interpretable statistical models and validated independently across years, sites and genetic background prior to routine implementation in breeding (Liang *et al*., 2026).

7. Genome Editing for Abiotic-Stress Improvement

7.1 CRISPR-Cas Systems

CRISPR-Cas systems employ customizable guide RNAs to target nucleases to specific sequences within the genome. Repair of the double-strand break often produces small insertions or deletions that disrupt gene function. This approach is useful when knocking out negative regulators, for example to reduce stress sensitivity or to remove competing metabolic routes. Cas12a cleaves different target motifs than Cas9, and can be used to process guide arrays, which allows multiplex editing. Engineered nuclease variants further increase the target space and mitigate off-target cleavage (Tuncel *et al*., 2025).

Figure 3. CRISPR-Cas in Action: From Foreign DNA Capture to Targeted Viral Defense



Source- https://doudnalab.org/research_areas/crispr-systems/

Complete knockouts are not always preferable since genes related to stress often have a role in normal development of the flower or fruit. Editing of promoters, enhancers, transcription-factor binding sites, or upstream open reading frames can result in quantitative changes in expression. These alleles may be more similar to beneficial natural variation rather than complete loss of the gene. It can therefore enhance stress responses in specific tissues or under specific environmental conditions and maintain essential gene function and normal performance under favorable production conditions (Ke *et al*., 2025).

7.2 Base and Prime Editing

Cytosine and adenine base editors allow for targeted base substitutions without making traditional double-stranded breaks, enabling the recreation of your favourable alleles, as well as amino acids, splice sites, and regulatory elements. Nevertheless, consideration of editing window-related limitations and bystander changes to adjacent bases is required in silico for guide design and in vitro for sequence validation, especially in heterozygous and polyploid horticultural species harboring homologous gene copies (Hillary and Ceasar, 2024). Prime editing uses a Cas nickase, reverse

transcriptase, and a specialized guide RNA to make a variety of changes, including substitutions and one or more small insertions or deletions. While it holds promise for precise allele or regulatory changes, its efficiency is still variable in a number of horticultural crops, thus improvements in the editor design, delivery, and tissue-culture systems would be needed to fully meet the demand of routine breeding applications (Vu *et al*., 2024).

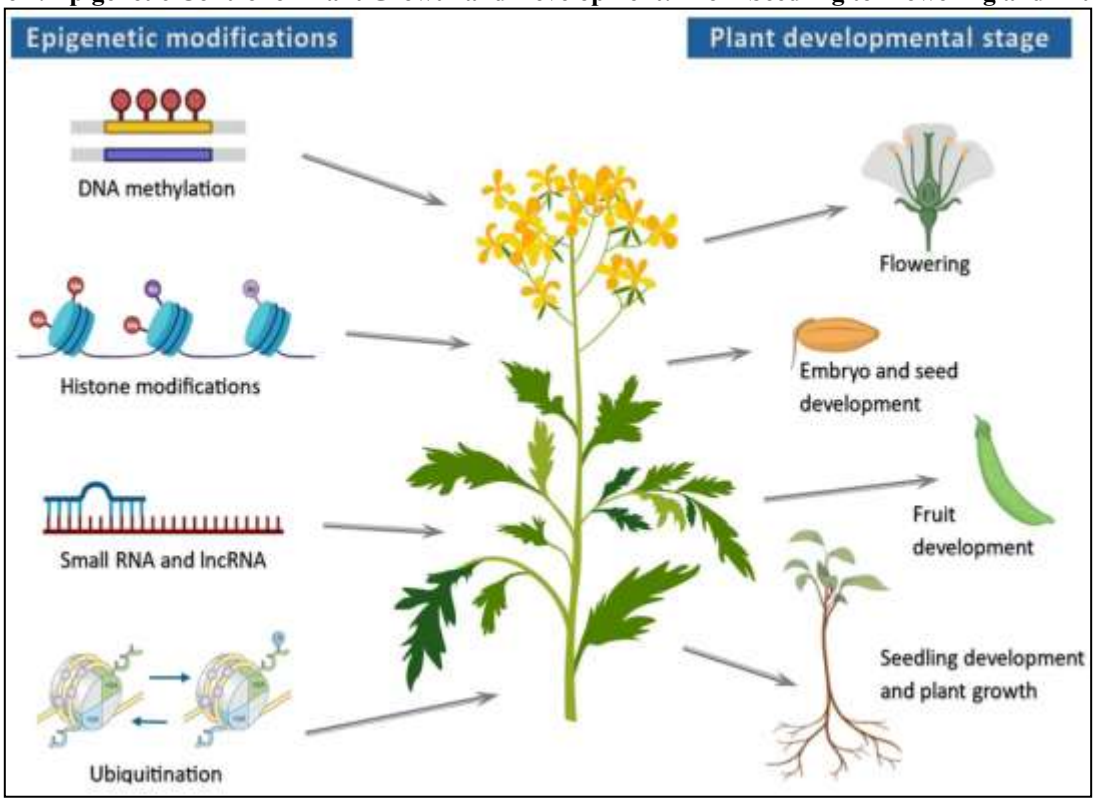
7.3 Multiplex and Allele-Specific Editing

Tolerance to abiotic stresses is likely to need the alteration of several pathways or members of redundant gene families. Multiplex editing can be used to target genes involved in ion transport, osmotic protection, root architecture and reproductive stability all at once, and is especially useful in polyploid crops where multiple homeologs need to be edited to see a phenotype. However, the intricate interactions among the genes may lead to unexpected results in growth, fertility or processing quality (Hwarari *et al*., 2024). Sequential editing and combinatory guide libraries can be used to discover ideal combinations of genes prior to final allele stack construction. Allele-specific editing is particularly advantageous in heterozygous and clonally propagated species as it allows for the targeted disruption of a deleterious allele whilst maintaining the intact version of a gene. Robust phased genomes are necessary to separate homologous copies and design unique guides to achieve precise editing and maintain normal growth in elite horticultural genotypes (Carlsen *et al*., 2025).

7.4 Gene Regulation and Epigenome Editing

Inactive dCas proteins fused to transcriptional repressors or activators allow CRISPRi and CRISPRa, respectively, enabling targeted control of gene expression without modifying the coding region. Such techniques can also reveal if slightly enhancing or reducing the activity of a gene yields a more advantageous compromise between stress resilience and growth than null mutation of the gene. Tissue-specific and inducible systems might even allow transient protection in sensitive developmental stages (Pan and Qi, 2023). Similarly, Cas proteins fused to DNA methyltransferase, demethylase or histone modifier enzymes allows targeted epigenome editing, which may regulate stress responsive genes or stress memory without altering DNA sequence. However, it is unknown whether edited epigenetic states can persist and be transmitted, and they may exert unknown off-target chromatin and developmental effects. Thus, epigenome editing is currently more valuable for functional studies than for direct breeding applications (Oberkofler and Baurle, 2024).

Figure 4. Epigenetic Control of Plant Growth and Development: From Seedling to Flowering and Fruiting



Source- Tresas *et al*., 2025

7.5 Transformation and Regeneration

Transformation and regeneration still pose significant technical challenges for genome editing in horticultural crops. The Agrobacterium-mediated transformation has a broad application but it is very much dependent on genotype and

tissue, while biolistic-mediated can be used for recalcitrant tissues, but DNA integration is often complex. Protoplast transfection allows delivery of CRISPR RNPs without DNA, but regeneration of fertile plants is challenging for many vegetable, fruit tree, plantation crop, and ornamental species (Pandey *et al*., 2025). Developmental regulators promote de novo meristem generation but need transient expression to prevent aberrant phenotypes. Viral vectors provide alternative means of delivery for guide RNAs and editing machinery, but they also have limitations in terms of cargo capacity, host range, and heritable transmission. Nanomaterial-mediated delivery is promising but it needs quality predictable, species-unrelated output. Therefore, the enhancement of regeneration biology is still necessary to convert the editing efficiency into viable and fertile plants (Niu *et al*., 2025).

In seed propagated annual crops, integrated editing constructs can often be eliminated by segregation. This approach is not applicable for sterile or highly heterozygous cultivars, as well as for clonally propagated cultivars since their specific elite genetic makeup could be lost due to sexual reproduction. Thus, DNA-free ribonucleoprotein delivery, transient expression, and precise construct-excision systems are of special relevance for applications in potato, banana, grapevine, fruit trees or ornamentals. Efficient transgene-free editing might also facilitate product characterization and help in getting regulatory acceptance in some regions (Van den Broeck *et al*., 2025).

8. Applications in Major Horticultural Crops

Genome editing holds crop-tailored potential to enhance abiotic-stress resilience in horticultural crops, but ploidy, transformation efficiency, reproductive sensitivity and market-quality maintenance are still the bottlenecks. Among horticultural crops, solanaceous and cucurbit crops are promising candidates for altering stress signalling, ion transport and root architecture, whereas polyploid Brassica, potato, sweet potato and strawberry are considered challengers in terms of allele dosage and gene redundancy. In the case of perennial and grafted species, rootstock editing may offer a feasible approach to enhance water relations and stress signalling without compromising elite scion traits.Stress tolerance should be assessed in conjunction with yield, reproductive behaviour, quality and postharvest traits in horticultural crops (Gao *et al*., 2019; Nguyen *et al*., 2024; Mohamed *et al*., 2024; Van Leeuwen *et al*., 2024; Mao *et al*., 2023).

Table 2. Crop-Specific Genomic and Genetic Strategies for Improving Abiotic Stress Tolerance in Major Horticultural Crops

Crop group	Major stress concerns	Key genomic/genetic improvement priorities	References
Solanaceous vegetables	Drought, salinity and heat	Modulate ABA signalling, ion transport and antioxidants, stomatal and root traits without compromising pollen viability, fruit set and fruit quality.	Gao *et al*. (2019); Ghabileh *et al*. (2024)
Cucurbitaceous crops	Chilling, heat, drought, salinity and waterlogging	Target aquaporins, ion transport, wax and root development genes; utilize edited rootstocks without compromising fruit set, quality or graft compatibility.	Nguyen *et al*. (2024); Kaleem *et al*. (2025)
Brassica vegetables	Heat, cold, drought, flooding and salinity	Apply haplotype-resolved genomes and multiplex editing to control redundant genes without compromising head/curd development, nutritional quality and harvest uniformity.	Mohamed *et al*. (2024); Yao *et al*. (2022)
Potato and sweet potato	Heat, drought, salinity and nutrient stress	Tackle polyploidy and allele dosage; assess storage-organ yield and quality and establish DNA-free editing and high-throughput regeneration platforms.	Aalborg and Nielsen (2024); Wu *et al*. (2025)
Grapevine and fruit trees	Drought, heat, salinity, cold and frost	Utilize pangenomes and natural adaptive alleles; employ rootstock editing to enhance stress tolerance without compromising fruit quality and clonal identity.	Van Leeuwen *et al*. (2024); Gabay and Flaishman (2024)
Citrus, banana and tropical crops	Drought, salinity, flooding, heat and occasional freezing	Enhance rootstock traits, regeneration and precise editing; address polyploidy maintaining flavour, quality and commercial biochemical traits.	Modica *et al*. (2024); Van den Broeck *et al*. (2025)
Strawberry and ornamental crops	Drought, salinity, heat and chilling	Use subgenome-aware editing in polyploid crops while maintaining fruit sensory traits or flower color, shape, fragrance and shelf life.	Mao *et al*. (2023); Pal *et al*. (2025)

9. Integration with Horticultural Breeding

A realistic crop breeding program should start with a target product profile specifying the crop, production situation, stress scenario, stage of development and expected marketable product. Representative germplasm should then be subjected to physiological, imaging and quality-based phenotyping . Candidate genes, favourable haplotypes and regulatory networks can be identified through genomic mapping, environmental association and multi-omics, and naturally occurring alleles endorsed by multiple lines of evidence are given priority for minimizing developmental penalties (Bhosale *et al*., 2025; Amin *et al*., 2025). Genome editing can be used to validate candidates and to introduce favorable variants into elite backgrounds via knockout, base/prime editing, promoter modification or multiplex editing. Edited lines need to be molecularly characterized and evaluated under controlled environment, and subsequently in multi-location field trials. Crucially, genome editing should be an adjunct to, not a substitute for, traditional breeding, genomic selection, rootstock improvement and grafting. Such synergistic approaches for wider allelic variation across variable genetic backgrounds may contribute to improved durability and environmental stability of abiotic-stress tolerance (Fritsche-Neto *et al*., 2025).

10. Challenges and Future Directions

A major challenge in developing climate-resilient horticultural crops is translating controlled-environment tolerance into field performance, where stresses often occur simultaneously and fluctuate over time. Future phenotyping should therefore incorporate realistic stress combinations, developmental stages, intensities and recovery periods. Breeding must also account for trade-offs between stress survival and photosynthesis, growth, yield and quality, with marketable productivity and performance under favourable conditions evaluated alongside tolerance (Jiang *et al*., 2025; Vadez *et al*., 2024).

Genome editing is still limited by genotype-dependent transformation, polyploidy, heterozygosity, tissue-culture variation, long juvenile periods, and potential off-target effects. The development of pangenomes, single-cell and spatial omics, cis-regulatory editing, tissue-specific regulation, DNA-free editing, enhanced base/prime editors and AI-guided design may potentially increase precision, particularly in perennial and clonal crops (Sakthivel *et al*., 2025; Schreiber *et al*., 2024; Alam, 2026). In the end, long-lasting climate resilience will be achieved by integrating genetic gain and rootstocks with precision irrigation, protected cultivation, soil health management, and climate-smart production practices (Arif *et al*., 2025).

CONCLUSION

Tolerance to abiotic stress in horticultural crops relies on coordination of signaling, hormonal responses, transcription, osmotic adjustment, ion homeostasis, antioxidant defence, protein protection, and developmental plasticity. Tolerance needs to go beyond survival to encompass maintenance of flowering, yield, nutritional and sensory quality, and postharvest performance over a range of environmental conditions. Progress in long-read sequencing, pangenomes, multi-omics, phenomics, and envirotyping are driving the discovery of adaptive genes and beneficial alleles. Genome editing strategies such as knockout, promoter editing, base and prime editing as well as multiplexing can further translate these findings into tailored solutions. Future developments will require molecularly accurate validation, genotype-flexible methods, and multi-environment validation. To this end, it will ultimately be necessary to combine natural diversity, traditional breeding, genomic prediction, genome editing, rootstock science as well as climate-smart management to breed productive, marketable and mineral-dense horticultural crops in a world of changing climates.

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