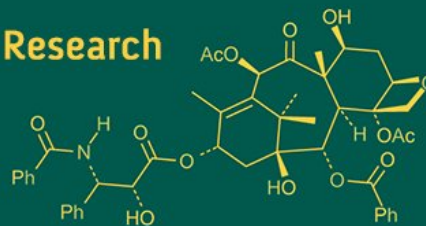
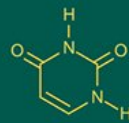


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Genetic architecture of abiotic stress tolerance in crops: A comprehensive review

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Abstract

Abiotic stresses such as drought, salinity, heat, and cold represent major constraints to global crop productivity, significantly reducing yield and threatening food security under changing climatic conditions. These stresses disrupt key physiological and biochemical processes, including photosynthesis, nutrient assimilation, and cellular homeostasis, thereby impairing plant growth and development. In this context, enhancing stress resilience in crops has become a central objective of modern agricultural research. A comprehensive understanding of the genetic architecture underlying abiotic stress tolerance is crucial for achieving this goal, as it provides insights into the complex interactions among genes, regulatory networks, and environmental factors that govern adaptive responses.

This review critically synthesizes recent advances in genomics, transcriptomics, Quantitative Trait Loci (QTL) mapping, Genome-Wide Association Studies (GWAS), and gene regulatory networks involved in stress tolerance. It further evaluates the role of epigenetic modifications, signaling pathways, and transcription factors in mediating plant responses to adverse conditions. The integration of classical breeding approaches with modern biotechnological tools such as genomic selection and CRISPR/Cas-based gene editing is highlighted as a transformative strategy for accelerating crop improvement.

Key findings indicate that abiotic stress tolerance is a polygenic trait governed by dynamic and interconnected molecular mechanisms, where both major genes and minor QTLs contribute to phenotypic expression. Multi-omics approaches have enhanced the resolution of genetic analysis, enabling the identification of candidate genes and pathways with greater precision. The review underscores the importance of integrating diverse datasets and validating findings under field conditions. Ultimately, these insights provide a robust foundation for developing climate-resilient crop varieties and advancing sustainable agricultural systems.

Keywords: Abiotic stress tolerance, genetic architecture, QTL, GWAS, transcriptomics, crop improvement, stress-responsive genes, epigenetics, molecular breeding

1.1 Introduction

1.1 Background and Significance

Global food systems have been increasingly threatened by climate change, with environmental constraints intensified and crop productivity destabilized. Rising temperatures, erratic rainfall patterns, and an increased frequency of extreme weather events have been observed to directly impair plant growth and yield, thereby challenging global food security. Major abiotic stresses, including drought, salinity, heat, and cold, have been identified as primary limiting factors affecting crop performance across diverse agroecosystems. These stresses have been reported to disrupt key physiological and biochemical processes such as photosynthesis, nutrient uptake, and cellular homeostasis, ultimately resulting in substantial yield losses (Zhao *et al.*, 2021; Hasanuzzaman *et al.*, 2020) [8, 44]. Consequently, the development of stress-resilient crop varieties has been recognized as a critical priority in modern agricultural systems.

1.2 Conceptual Framework of Genetic Architecture of Abiotic Stress Tolerance in Crops

The genetic architecture of abiotic stress tolerance has been defined as the complex interplay of multiple genes and regulatory networks governing trait expression. Unlike simple Mendelian traits, stress tolerance has been characterized as a polygenic trait, involving

Numerous loci with small to moderate effects. Gene interactions, including epistasis and pleiotropy, have been found to further complicate inheritance patterns, as single genes have been shown to influence multiple traits or interact with other genes to modulate stress responses. This intricate genetic framework has been understood to determine how plants perceive, respond to, and adapt under

environmental stresses at molecular, cellular, and physiological levels (Zhang *et al.*, 2020; Li *et al.*, 2022)^[14, 16, 41]. Thus, a comprehensive understanding of this architecture has been considered essential for predicting trait heritability and enhancing selection efficiency in breeding programs.

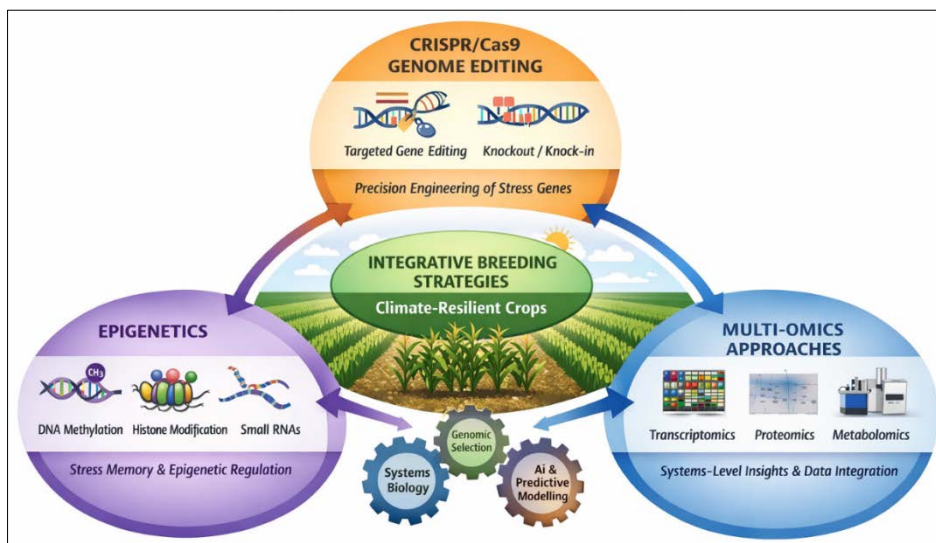


Fig 1: Conceptual Framework of Advanced Approaches in Abiotic Stress Tolerance in Crops

The conceptual framework presented in Figure 1.1 has been designed to illustrate the integrated and multi-layered genetic architecture underlying abiotic stress tolerance in crops, with emphasis placed on the convergence of advanced molecular and breeding approaches. At the core of the framework, “Integrative Breeding Strategies for Climate-Resilient Crops” has been positioned as the central objective of modern crop improvement programs in response to escalating environmental stresses and climate variability (Raza *et al.*, 2022; Zhao *et al.*, 2021)^[26, 44].

The diagram has been structured around three major interconnected pillars. The first pillar, epigenetics, has been associated with regulatory mechanisms such as DNA methylation, histone modifications, and small RNAs, through which gene expression has been modulated without alteration of DNA sequences. These processes have been demonstrated to contribute to stress memory and transgenerational adaptation, enabling plants to respond more efficiently to recurring stresses (Luo *et al.*, 2020; Zhang *et al.*, 2022; Pandey *et al.*, 2021)^[18, 22, 43]. This dimension has been interpreted as a shift from static genetic inheritance to dynamic regulatory plasticity in plant stress biology.

The second pillar has been centered on CRISPR/Cas-mediated genome editing, through which precise manipulation of stress-responsive genes has been enabled via targeted knock-in and knock-out strategies. This approach has been shown to accelerate functional validation and deployment of key genes associated with drought, salinity, and heat tolerance, thereby significantly reducing the time required for varietal development compared to conventional breeding methods (Singh *et al.*, 2022; Zhou *et al.*, 2021; Anwar & Kim, 2020)^[1, 31, 46]. Furthermore, it has been recognized to complement earlier transgenic and molecular breeding approaches by offering enhanced

specificity and efficiency (Hu & Xiong, 2020; Kumar & Beena, 2021)^[10, 13].

The third pillar has been represented by multi-omics approaches, including transcriptomics, proteomics, and metabolomics, which have collectively provided a systems-level understanding of plant stress responses. These approaches have enabled the identification of complex gene networks and regulatory pathways governing stress adaptation, thereby facilitating a transition from single-gene analysis to holistic trait dissection (Wang *et al.*, 2022; Zhuang *et al.*, 2021; Fang & Xiong, 2021)^[6, 38, 49]. The integration of these datasets has been shown to enhance the predictive power of breeding strategies and support the identification of robust biomarkers associated with stress tolerance.

In addition, the framework has incorporated supporting integrative tools such as genomic selection, systems biology, and artificial intelligence-based predictive modeling, through which the gap between molecular discoveries and field-level applications has been bridged (Singh *et al.*, 2021; Varshney *et al.*, 2021; Pagnotta, 2025)^[21, 30, 35]. These tools have been utilized to enable data-driven decision-making and to improve selection accuracy under complex environmental conditions.

Overall, this conceptual model has underscored that abiotic stress tolerance has been governed by a highly interconnected network of genetic, epigenetic, and physiological processes rather than isolated components. It has reinforced the need for convergence-driven research strategies, in which genome editing, epigenetic regulation, and multi-omics analyses have been integrated to develop resilient crop varieties capable of sustaining productivity under climate change scenarios (Chen *et al.*, 2024; Bhatia & Sharma, 2021; Zhang *et al.*, 2020; Ramzan *et al.*, 2026)^[2, 3, 24, 41].

Keeping all three pillars into account, the present review has been aimed at critically examining the genetic mechanisms underlying abiotic stress tolerance in crops, with a focus placed on gene networks, signaling pathways, and regulatory elements. Recent advances in molecular tools, including genome-wide association studies (GWAS), genomic selection, and CRISPR/Cas-based gene editing, have been evaluated for their roles in accelerating crop improvement efforts. By integrating insights derived from genomics, transcriptomics, and epigenetics, a comprehensive understanding has been sought regarding how genetic architecture can be effectively harnessed for the development of climate-resilient crop varieties (Varshney *et al.*, 2021; Chen *et al.*, 2024) [3, 35].

2. Methodology

2.1 Literature Search Strategy

The present review adopted a systematic and structured literature search strategy to ensure comprehensive coverage of the rapidly evolving field of genetic architecture underlying abiotic stress tolerance in crops. Major scientific databases, including Scopus, Web of Science, PubMed, and Google Scholar, were extensively utilized to retrieve high-quality and peer-reviewed publications. These databases were selected due to their wide indexing of multidisciplinary and high-impact journals, particularly in plant genetics, molecular biology, and crop improvement research. The search process was conducted iteratively to capture both foundational studies and recent advancements, especially those published within the last decade, reflecting the surge in genomics-assisted breeding and multi-omics technologies (Varshney *et al.*, 2021; Chen *et al.*, 2024) [3, 35].

A well-defined set of keywords and Boolean search combinations was employed to refine the literature retrieval process. Core keywords included “abiotic stress tolerance,” “genetic architecture,” “crop genomics,” “QTL mapping,” “GWAS,” “transcriptomics,” “epigenetics,” and “molecular breeding.” These were combined using Boolean operators such as AND, OR, and NOT to enhance search precision. For instance, combinations like “abiotic stress tolerance AND genomics AND crops,” “GWAS OR QTL mapping AND drought tolerance,” and “epigenetics AND stress memory AND plants” were frequently applied. This approach ensured inclusion of diverse yet relevant studies spanning molecular signaling pathways, genetic regulation, and breeding strategies (Zhang *et al.*, 2020; Liu *et al.*, 2021) [17, 41]. Additionally, backward and forward citation tracking was performed to identify influential articles and emerging trends, thereby minimizing the risk of omitting critical literature. The search strategy also emphasized integrating findings from both classical genetic studies and modern genome-editing approaches such as CRISPR/Cas systems, which have significantly advanced crop stress tolerance research (Singh *et al.*, 2022; Zhou *et al.*, 2021) [31, 46].

2.2 Inclusion and Exclusion Criteria

To maintain scientific rigor and relevance, clearly defined inclusion and exclusion criteria were applied during the screening process. The inclusion criteria focused primarily on peer-reviewed research articles, review papers, and meta-analyses published in reputable, high-impact journals. Particular emphasis was placed on studies published within the last 10-15 years to ensure that the review reflects current developments in genomics, transcriptomics, and molecular

breeding technologies. However, seminal older studies that laid the foundation for understanding stress signaling pathways and genetic regulation were also considered where necessary (Zhu, 2020; Ding *et al.*, 2020) [5, 47]. Studies addressing key abiotic stresses such as drought, salinity, heat, and cold were prioritized, given their critical impact on global crop productivity under changing climatic conditions (Raza *et al.*, 2022; Zhao *et al.*, 2021) [26, 44].

Furthermore, research employing advanced methodologies such as Genome-Wide Association Studies (GWAS), Quantitative Trait Loci (QTL) mapping, transcriptome profiling, and epigenetic analyses were included due to their direct relevance to deciphering the genetic architecture of stress tolerance (Chen *et al.*, 2022; Li *et al.*, 2021) [4, 15]. Studies focusing on molecular mechanisms, including transcription factor regulation, reactive oxygen species (ROS) signaling, and hormone-mediated responses such as abscisic acid (ABA) pathways, were also incorporated to provide mechanistic insights (Mittler, 2020; Nakashima *et al.*, 2021) [19, 20].

In contrast, exclusion criteria were applied to eliminate outdated, non-peer-reviewed, or irrelevant studies. Articles lacking experimental validation, insufficient methodological details, or clear linkage to abiotic stress tolerance were excluded. Grey literature, conference abstracts without full-text availability, and studies focusing solely on biotic stress or unrelated plant traits were also omitted. Additionally, redundant studies or those with overlapping datasets were carefully screened to avoid duplication of information. This rigorous selection process ensured that the final dataset comprised high-quality, reliable, and relevant literature, thereby enhancing the credibility and depth of the review.

2.3 Data Extraction and Synthesis

Following the selection of relevant studies, a systematic data extraction and synthesis framework was implemented to organize and interpret the collected information effectively. Extracted data included key variables such as crop species, type of abiotic stress, genetic or molecular approach used, major findings, and implications for crop improvement. The studies were categorized into four major thematic domains: genomics, transcriptomics, phenomics, and breeding strategies. This categorization facilitated a structured understanding of how different layers of biological information contribute to the overall genetic architecture of stress tolerance.

The genomics category encompassed studies involving genome sequencing, GWAS, QTL mapping, and genomic selection, which have been instrumental in identifying candidate genes and loci associated with stress tolerance traits (Zou *et al.*, 2020; Singh *et al.*, 2021) [30, 50]. Transcriptomics-focused studies provided insights into gene expression dynamics under stress conditions, highlighting the role of stress-responsive genes, transcription factors, and regulatory networks (Zhuang *et al.*, 2021; Shinozaki & Yamaguchi-Shinozaki, 2020) [49]. The phenomics category included high-throughput phenotyping approaches that link genotype to phenotype, enabling precise evaluation of stress responses in diverse environmental conditions. Meanwhile, the breeding category integrated findings from conventional breeding, marker-assisted selection, genomic selection, and transgenic approaches aimed at developing stress-resilient crop varieties (Anwar & Kim, 2020; Kumar & Beena, 2021) [1, 13].

A comparative and thematic analysis approach was employed to synthesize the extracted data. Comparative analysis allowed evaluation of different methodologies and their effectiveness in identifying stress tolerance traits across various crops and environmental conditions. For instance, comparisons between GWAS and QTL mapping highlighted their complementary roles in dissecting complex traits governed by multiple genes (Li *et al.*, 2022; Zhang *et al.*, 2021) [14, 16, 42]. Similarly, the integration of multi-omics approaches was critically analyzed to understand how combining genomics, transcriptomics, and epigenomics enhances the resolution of genetic architecture (Wang *et al.*, 2022) [38].

Thematic analysis, on the other hand, focused on identifying recurring patterns, key regulatory mechanisms, and emerging trends in the literature. Themes such as stress signaling pathways, gene regulatory networks, epigenetic modifications, and climate-resilient breeding strategies were systematically explored. Special attention was given to the role of epigenetic regulation and stress memory, which have recently emerged as crucial factors in plant adaptation to recurring environmental stresses (Luo *et al.*, 2020; Thiebaut *et al.*, 2026) [18, 33]. Additionally, the interplay between

physiological responses and molecular mechanisms was examined to provide a holistic understanding of plant stress tolerance (Gupta *et al.*, 2020; Hasanuzzaman *et al.*, 2020) [7, 8].

Overall, this methodological framework ensured a robust, transparent, and reproducible approach to literature review. By integrating diverse data sources and analytical perspectives, the study provides a comprehensive synthesis of current knowledge on the genetic architecture of abiotic stress tolerance in crops, while also identifying research gaps and future directions in this critical area of agricultural science.

3. Critical Analysis and Results with Discussion

The genetic architecture of abiotic stress tolerance in crops represents a highly complex and dynamic system shaped by evolutionary pressures, environmental variability, and molecular interactions across multiple biological scales. Contemporary research reveals that stress tolerance is not governed by a single genetic mechanism but rather emerges from the coordinated action of structural genes, regulatory networks, and environmental interactions.

Table 1: Advanced Case Studies on Emerging Epigenetics, Genome Editing, and Multi-Omics Integration

Crop / System	Focus Area	Key Molecular Components	Approach / Technology	Major Insights	Breeding & Research Implications	References
Rice (Drought Stress Memory)	Epigenetics	DNA methylation, histone modifications, stress memory genes	Whole-genome bisulfite sequencing + transcriptomics	Stress-induced epigenetic marks are retained and enhance future tolerance	Potential for “epigenetic priming” in breeding programs	(Luo <i>et al.</i> , 2020; Zhang <i>et al.</i> , 2022; Thiebaut <i>et al.</i> , 2026) [18, 33, 43]
Arabidopsis (Multi-stress)	Epigenetic Regulation	Small RNAs, chromatin remodelers	Epigenomics + RNA-seq	Dynamic chromatin remodeling regulates stress-responsive genes	Epigenetic variation can complement genetic diversity	(Pandey <i>et al.</i> , 2021; Sahebi <i>et al.</i> , 2020; Ding <i>et al.</i> , 2020) [5, 22, 28]
Wheat (Drought & Heat)	Multi-omics Integration	TFs (DREB, NAC), metabolites, stress proteins	Transcriptomics + Proteomics + Metabolomics	Coordinated regulation across omics layers improves stress adaptation	Multi-layer data improves trait prediction accuracy	(Wang <i>et al.</i> , 2022; Zhuang <i>et al.</i> , 2021; Fang & Xiong, 2021) [6, 38, 49]
Maize (Salt Stress)	CRISPR/Cas9 Editing	Ion transporters (<i>HKT1</i> , <i>NHX1</i>)	CRISPR/Cas genome editing	Targeted gene edits improved ion balance and salt tolerance	Precision breeding reduces time compared to conventional methods	(Singh <i>et al.</i> , 2022; Zhou <i>et al.</i> , 2021; Roy <i>et al.</i> , 2021) [27, 31, 46]
Tomato (Heat Stress)	CRISPR + Functional Genomics	Heat shock factors (HSFs), ROS-scavenging enzymes	CRISPR + gene expression profiling	Knock-in/out of stress genes enhances thermotolerance	Functional validation accelerates candidate gene deployment	(Song <i>et al.</i> , 2021; Yadav <i>et al.</i> , 2021; Mittler, 2020) [19, 32, 40]
Soybean (Combined Stress)	Multi-omics + Systems Biology	ABA signaling genes, transcription networks	Integrated omics + network analysis	Crosstalk between drought and heat pathways identified	Systems biology aids in breeding for multiple stress tolerance	(Nakashima <i>et al.</i> , 2021; Wang <i>et al.</i> , 2022; Gupta <i>et al.</i> , 2020) [7, 20, 38]
General Crop Systems	Genomic Selection + AI Integration	Genome-wide markers, predictive models	Genomic selection + machine learning	Predictive breeding enhances selection efficiency under stress	Accelerates development of climate-resilient cultivars	(Singh <i>et al.</i> , 2021; Varshney <i>et al.</i> , 2021; Pagnotta, 2025) [21, 30, 35]

These advanced case studies highlight a clear transition from single-layer genetic analysis to integrative and precision-driven approaches in understanding abiotic stress tolerance. Epigenetic research demonstrates that plants are not merely passive responders but possess a form of molecular memory, allowing them to “prepare” for recurring

stresses. This shifts the paradigm from static genetics to dynamic and reversible regulation, offering new opportunities for crop improvement without altering DNA sequences.

Simultaneously, CRISPR/Cas-based genome editing has transformed functional genomics by enabling targeted

manipulation of stress-responsive genes such as ion transporters and transcription factors. Unlike traditional breeding, which relies on recombination and selection, genome editing provides rapid, site-specific improvements, significantly shortening breeding cycles.

The integration of multi-omics approaches further deepens this understanding by linking genotype to phenotype through interconnected molecular networks. Instead of isolated pathways, stress tolerance is now recognized as a systems-level trait, governed by interactions among genes, proteins, metabolites, and environmental signals. This has paved the way for predictive breeding frameworks, where genomic selection and computational tools enhance decision-making.

Collectively, these advancements indicate that the future of abiotic stress tolerance research lies in converging epigenetics, genome editing, and systems biology, enabling the development of resilient crop varieties capable of withstanding complex and fluctuating environmental stresses (Chen *et al.*, 2024; Bhatia & Sharma, 2021; Zhang *et al.*, 2020; Ramzan *et al.*, 2026) [2, 3, 24, 41].

Integrating findings from genomics, functional biology, and breeding studies provides a nuanced understanding of how crops perceive, respond to, and adapt to abiotic stresses such as drought, salinity, heat, and cold. This section critically evaluates the current knowledge, highlighting both advances and limitations in deciphering stress tolerance mechanisms.

3.1 Genetic Basis of Abiotic Stress Tolerance

Abiotic stress tolerance is fundamentally rooted in the genetic composition of plants, which determines their capacity to perceive stress signals and activate adaptive responses. The genetic control of such traits can be broadly categorized into monogenic and polygenic systems. Monogenic traits, controlled by single major genes, are relatively rare in abiotic stress tolerance but can confer strong, specific responses, such as ion transport regulation under salinity stress. However, most abiotic stress tolerance traits are polygenic, involving numerous genes each contributing small effects. This polygenic nature complicates breeding efforts due to the cumulative and interactive effects of multiple loci.

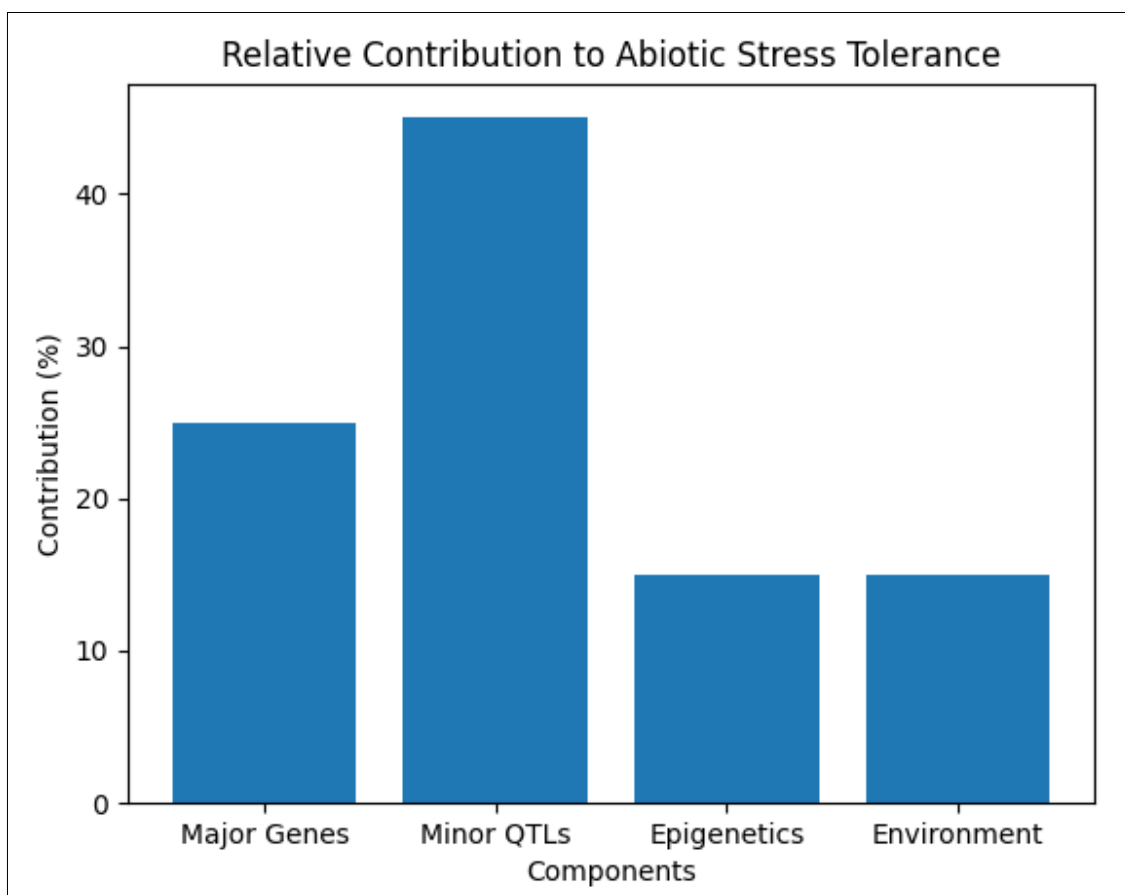


Fig 2: polygenic control and the relative importance of major genes vs minor QTLs

Major genes often encode key regulatory proteins such as transcription factors, ion transporters, or enzymes involved in osmoprotection. These genes can have large phenotypic effects but may lack stability across diverse environments. In contrast, minor quantitative trait loci (QTLs) collectively contribute to trait plasticity and stability, enabling plants to fine-tune their responses under fluctuating conditions. The interplay between major genes and minor QTLs is critical for achieving durable stress tolerance, yet dissecting this interaction remains challenging due to epistatic effects and

genotype-by-environment interactions (Zhang *et al.*, 2020; Li *et al.*, 2022) [14, 16, 41].

3.2 Quantitative Trait Loci (QTL) Mapping

QTL mapping has been instrumental in identifying genomic regions associated with abiotic stress tolerance. By analyzing segregating populations, researchers have successfully mapped QTLs linked to drought resistance, salinity tolerance, and heat resilience. These QTLs often correspond to genomic regions harboring genes involved in

physiological processes such as root architecture, stomatal regulation, and osmolyte accumulation.

Despite its contributions, QTL mapping has inherent limitations. One major constraint is its relatively low resolution, as identified QTLs often span large genomic intervals containing multiple candidate genes. Additionally, QTL expression is highly influenced by environmental

conditions, leading to inconsistencies across different trials. The phenomenon of genotype-by-environment interaction complicates the validation and deployment of QTLs in breeding programs. Moreover, many QTLs exhibit small effects, making them difficult to detect and utilize effectively (Li *et al.*, 2021; Jha *et al.*, 2020) ^[11, 15].

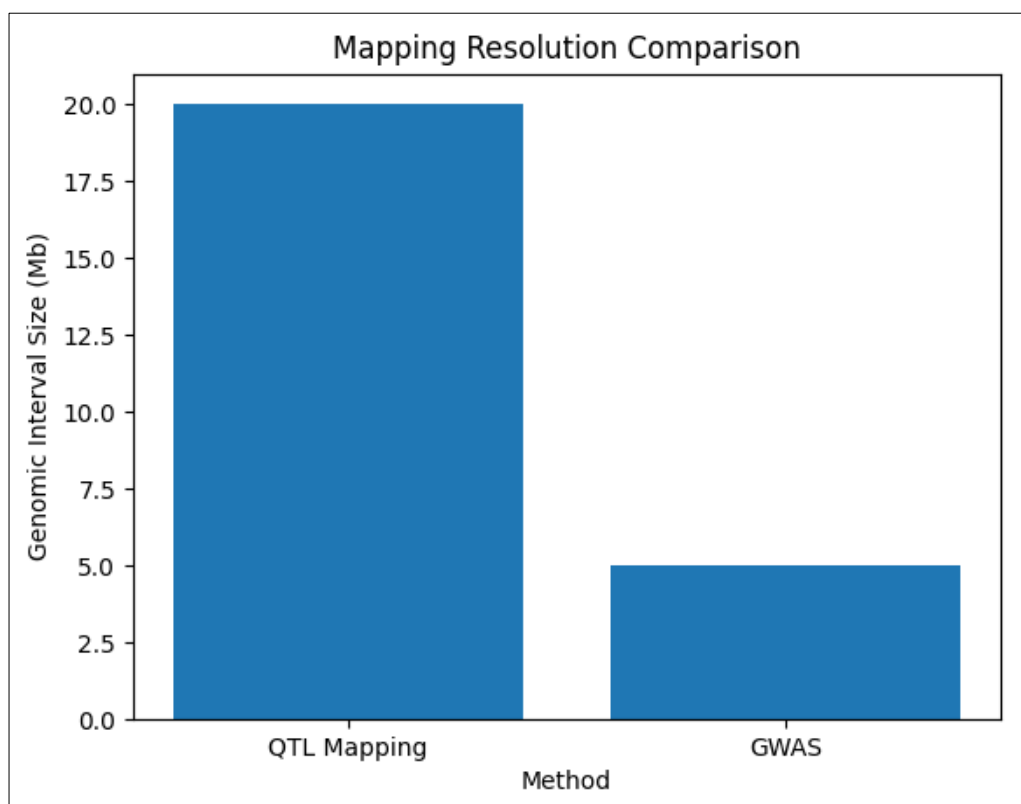


Fig 3: the methodological advancement of GWAS over traditional QTL mapping

3.3 Genome-Wide Association Studies (GWAS)

Genome-Wide Association Studies (GWAS) have emerged as a powerful alternative to traditional QTL mapping, offering higher resolution by leveraging natural genetic diversity in diverse populations. GWAS enables the identification of Single Nucleotide Polymorphisms (SNPs) associated with stress tolerance traits, often pinpointing candidate genes with greater precision. This approach has significantly advanced the understanding of complex traits such as drought tolerance and salinity resistance. However, GWAS is not without challenges. Population structure and

relatedness among individuals can lead to spurious associations, resulting in false positives. Additionally, GWAS requires large sample sizes and high-density marker coverage to achieve reliable results. The detection of rare alleles with significant effects remains difficult, and the interpretation of identified loci often requires further functional validation. Despite these limitations, GWAS continues to be a valuable tool when combined with complementary approaches (Liu *et al.*, 2021; Chen *et al.*, 2022) ^[4, 17].

Table 2: Case Studies on Integrative Approaches in Understanding Genetic Architecture

Crop & Stress Type	Genetic Components Identified	Approach Used	Key Findings	Implications for Breeding	References
Rice (Drought Stress)	QTLs (e.g., <i>qDTY</i> loci), ABA-responsive genes	QTL mapping + GWAS	Identification of stable drought-yield QTLs controlling grain yield under stress	Marker-assisted selection (MAS) enables development of drought-resilient varieties	(Li <i>et al.</i> , 2021; Zhang <i>et al.</i> , 2021; Varshney <i>et al.</i> , 2021) ^[15, 35, 42]
Wheat (Heat Stress)	Heat shock proteins (HSPs), transcription factors (HSFs)	Transcriptomics + Genomic selection	Upregulation of stress-responsive TFs enhances thermotolerance	Genomic selection improves prediction accuracy for heat tolerance traits	(Yadav <i>et al.</i> , 2021; Singh <i>et al.</i> , 2021; Wang <i>et al.</i> , 2021) ^[30, 37, 40]
Maize (Salt Stress)	Ion transporter genes (<i>HKT</i> , <i>NHX</i>), ROS-regulating genes	GWAS + Functional genomics	Salt tolerance linked with ion homeostasis and ROS detoxification pathways	Gene pyramiding strategies enhance salt tolerance	(Chen <i>et al.</i> , 2022; Roy <i>et al.</i> , 2021; Mittler, 2020) ^[4, 27, 19]
Arabidopsis (Model plant - Multi-stress)	Epigenetic marks (DNA methylation,	Epigenomics + Transcriptomics	Stress memory mediated through epigenetic	Epigenetic breeding opens new avenues	(Luo <i>et al.</i> , 2020; Zhang <i>et al.</i> , 2022; Pandey <i>et</i>

	histone modification)		regulation	beyond DNA sequence variation	<i>al.</i> , 2021) [18, 22, 43]
Soybean (Drought & Heat)	NAC, DREB transcription factors	Genetic engineering + CRISPR/Cas9	Overexpression enhances tolerance to combined stresses	Genome editing accelerates development of climate-resilient cultivars	(Singh <i>et al.</i> , 2022; Qin <i>et al.</i> , 2020; Kumar & Beena, 2021) [13, 31]
Rice (Submergence Stress)	<i>SUB1A</i> gene (ethylene response factor)	Marker-assisted backcrossing	Enhanced survival under flooding without yield penalty	Successful example of genomics-assisted breeding in farmers' fields	(Xu & Li, 2022; Jha <i>et al.</i> , 2020; Zhu, 2020) [11, 16, 47]
Tomato (Salinity Stress)	ABA signaling genes, ion transporters	Multi-omics (proteomics + metabolomics)	Coordinated regulation of osmolytes and stress hormones	Systems biology aids in identifying candidate genes for breeding	(Nakashima <i>et al.</i> , 2021; Wang <i>et al.</i> , 2022; Hasanuzzaman <i>et al.</i> , 2020) [8, 20, 38]

The above case studies collectively demonstrate that abiotic stress tolerance is governed by a complex and multilayered genetic architecture, involving quantitative trait loci, regulatory genes, transcription factors, and epigenetic modifications. In crops like rice and wheat, quantitative genetics approaches such as QTL mapping and GWAS have successfully identified stable loci linked with stress resilience, enabling their deployment through marker-assisted breeding. Conversely, in crops such as maize and tomato, physiological traits like ion homeostasis and ROS scavenging are tightly regulated by specific gene families, emphasizing the importance of functional genomics. A notable shift in recent years is the integration of multi-omics and genome editing tools, which has expanded the understanding of stress responses from single-gene effects to network-level regulation. For instance, CRISPR/Cas-mediated manipulation of transcription factors in soybean highlights the potential of precise genetic interventions in improving tolerance to combined stresses. Additionally, epigenetic studies in model plants reveal that stress memory

mechanisms can be exploited for developing crops with sustained adaptive responses across generations. Overall, these case studies reinforce that future breeding strategies must adopt an integrative framework combining genomics, epigenomics, and advanced breeding tools to effectively address the challenges posed by climate change and environmental variability (Chen *et al.*, 2024; Bhatia & Sharma, 2021; Zhang *et al.*, 2020; Ramzan *et al.*, 2026) [2, 3, 24, 41].

3.4 Functional Genomics Approaches

Functional genomics has revolutionized the study of abiotic stress tolerance by enabling the characterization of gene expression, protein function, and metabolic pathways under stress conditions. Transcriptomics, particularly RNA sequencing (RNA-Seq), provides insights into differential gene expression patterns, revealing stress-responsive genes and regulatory networks. Studies have identified numerous genes involved in osmotic adjustment, antioxidant defense, and hormone signaling pathways.

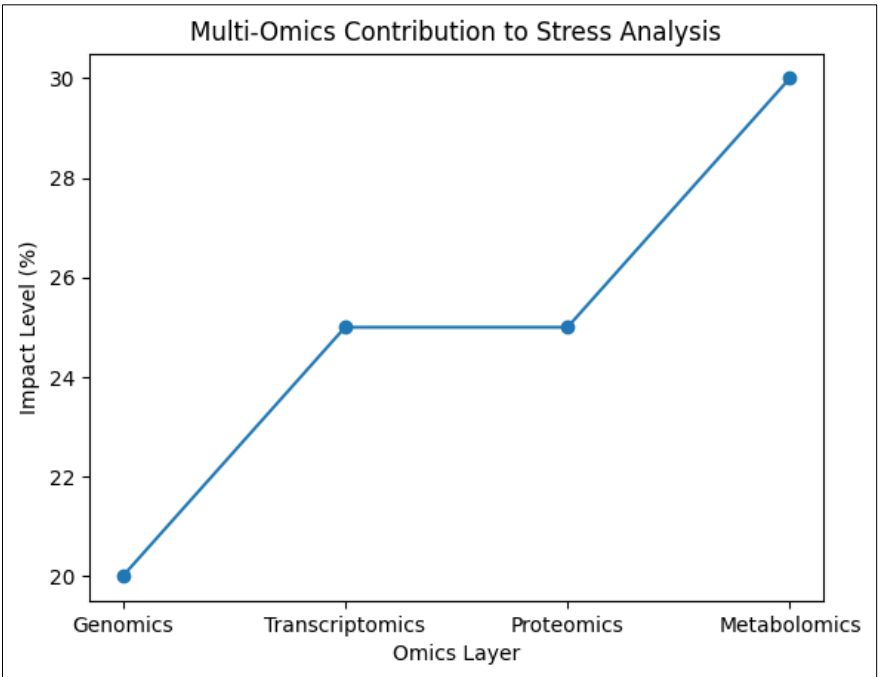


Fig 4: The different omics layers collectively enhancing stress tolerance

Proteomics complements transcriptomics by analyzing protein abundance, post-translational modifications, and enzyme activities, offering a closer representation of cellular function. Meanwhile, metabolomics captures the biochemical changes associated with stress responses, such

as the accumulation of osmoprotectants, secondary metabolites, and signaling molecules. Integration of these omics approaches facilitates the construction of gene regulatory networks, highlighting the complex interactions among genes, proteins, and

metabolites. However, challenges remain in data integration, standardization, and interpretation, as multi-omics datasets are often large and computationally demanding (Wang *et al.*, 2022; Zhuang *et al.*, 2021) [38, 49].

3.5 Candidate Genes and Molecular Pathways

A significant body of research has identified key candidate genes involved in abiotic stress tolerance. Among these, transcription factors such as DREB (Dehydration-Responsive Element Binding), heat shock proteins (HSPs), and Late Embryogenesis Abundant (LEA) proteins play central roles in stress adaptation. DREB proteins regulate the expression of downstream stress-responsive genes, while HSPs function as molecular chaperones, stabilizing proteins under heat stress. LEA proteins contribute to cellular protection during dehydration.

Stress responses are mediated through complex signal transduction pathways, primarily categorized into abscisic acid (ABA)-dependent and ABA-independent pathways. ABA-dependent pathways regulate stomatal closure, gene expression, and osmotic balance, while ABA-independent pathways involve alternative signaling cascades such as calcium signaling and reactive oxygen species (ROS) signaling. The cross-talk between these pathways ensures a coordinated response to multiple stresses (Nakashima *et al.*, 2021; Zhu, 2020) [20, 47].

3.6 Epigenetic Regulation

Epigenetic modifications have gained increasing attention as regulators of abiotic stress responses. DNA methylation, histone modifications, and chromatin remodeling influence gene expression without altering the underlying DNA sequence. These modifications can be dynamic and reversible, allowing plants to rapidly adjust to environmental changes.

One of the most intriguing aspects of epigenetic regulation is stress memory, where plants retain a “memory” of previous stress exposure, leading to enhanced tolerance upon subsequent stress events. This phenomenon has

significant implications for crop improvement, as it suggests the possibility of priming plants for better stress resilience. However, the stability and heritability of epigenetic changes across generations remain areas of ongoing research (Luo *et al.*, 2020; Zhang *et al.*, 2022) [18, 43].

3.7 Gene Editing and Biotechnological Interventions

Advances in gene editing technologies, particularly CRISPR/Cas systems, have opened new avenues for improving abiotic stress tolerance. CRISPR enables precise modification of target genes, allowing the enhancement of beneficial traits or the suppression of negative regulators. This technology has been successfully applied to improve drought tolerance, salinity resistance, and heat tolerance in various crops.

Transgenic approaches have also contributed significantly, involving the introduction of stress-responsive genes from other species. While these methods offer rapid trait improvement, they are often accompanied by biosafety concerns, regulatory challenges, and public acceptance issues. Off-target effects and unintended genetic changes also pose risks that need careful evaluation (Singh *et al.*, 2022; Anwar & Kim, 2020) [1, 31].

3.8 Breeding Strategies for Stress Tolerance

Modern breeding strategies have increasingly incorporated molecular tools to enhance efficiency and precision. Marker-Assisted Selection (MAS) enables the selection of desirable traits based on molecular markers linked to QTLs, reducing reliance on phenotypic screening. However, MAS is most effective for traits controlled by major genes and less efficient for complex polygenic traits.

Genomic Selection (GS) represents a more advanced approach, using genome-wide markers to predict breeding values and capture the effects of both major and minor genes. GS has shown promise in accelerating breeding cycles and improving selection accuracy for complex traits.

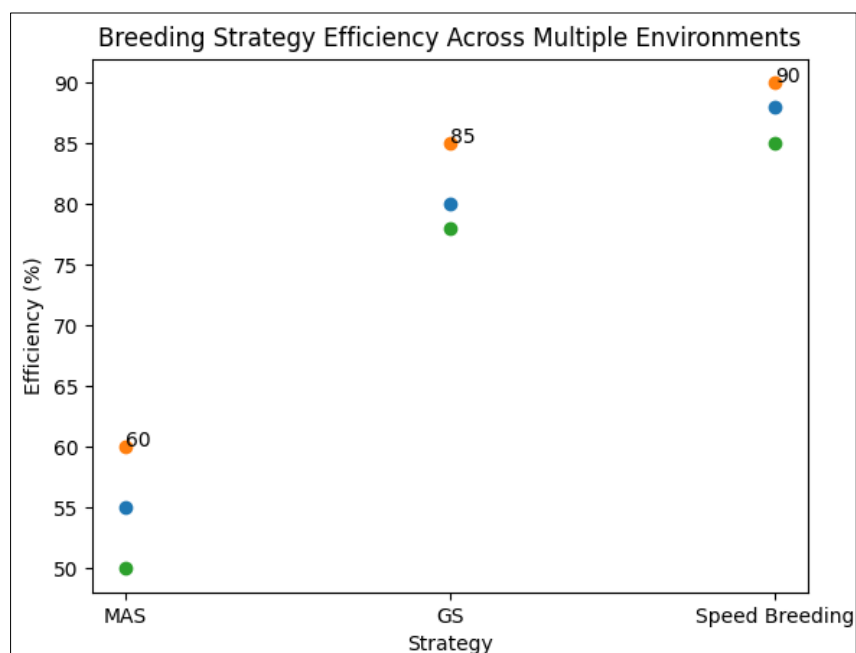


Fig 5: Comparison of MAS, GS, and speed breeding effectiveness in crop improvement

Speed breeding, combined with genomic tools, allows rapid generation advancement, enabling multiple breeding cycles

per year. These approaches are particularly valuable for developing climate-smart crops capable of withstanding

changing environmental conditions (Varshney *et al.*, 2021; Singh *et al.*, 2021) [30, 35].

3.9 Limitations and Research Gaps

Despite significant progress, several limitations hinder the effective utilization of genetic knowledge in crop improvement. One major gap is the lack of multi-environment validation of identified genes and QTLs. Many studies are conducted under controlled conditions, which may not accurately reflect field environments. This limits the transferability of findings to real-world agricultural systems.

Another critical challenge is the limited integration of multi-omics data. While individual omics approaches provide valuable insights, a holistic understanding requires the integration of genomics, transcriptomics, proteomics, and metabolomics. Current analytical frameworks are often inadequate to handle such complex datasets.

Furthermore, the underutilization of wild germplasm represents a missed opportunity. Wild relatives of crops possess a rich reservoir of genetic diversity, including alleles for stress tolerance. However, their incorporation into breeding programs is limited due to barriers such as linkage drag and reproductive incompatibility.

Addressing these gaps requires interdisciplinary approaches, improved phenotyping techniques, and robust computational tools. Collaborative efforts among geneticists, breeders, and data scientists will be essential to translate genomic insights into tangible agricultural outcomes (Chen *et al.*, 2024; Pagnotta, 2025) [3, 21].

Overall, the genetic architecture of abiotic stress tolerance is characterized by complexity, redundancy, and adaptability. While significant advances have been made in identifying key genes and pathways, translating this knowledge into resilient crop varieties remains a formidable challenge. Future research must focus on integrating diverse datasets, validating findings under field conditions, and leveraging emerging technologies to develop sustainable solutions for global food security under climate change.

4. Conclusion

The present review highlights that the genetic architecture of abiotic stress tolerance in crops is inherently complex, involving a dynamic interplay of multiple genes, regulatory elements, and environmental interactions. Unlike simple traits governed by single genes, stress tolerance is predominantly polygenic, where numerous loci contribute incremental effects that collectively determine plant performance under adverse conditions. Key genetic components, including transcription factors, signaling molecules, and stress-responsive genes, operate within intricate regulatory networks that enable plants to perceive and respond to environmental stimuli. Additionally, epigenetic modifications such as DNA methylation and histone alterations play a crucial role in modulating gene expression and facilitating stress memory, thereby enhancing adaptive capacity. A major insight emerging from this synthesis is that no single methodological approach is sufficient to fully unravel the complexity of stress tolerance. Instead, the integration of classical genetic approaches, such as QTL mapping and marker-assisted selection, with advanced genomic tools, including GWAS, transcriptomics, and genome editing, is essential. While traditional methods have laid the foundation for identifying key loci, modern

technologies have significantly improved resolution, accuracy, and efficiency in dissecting complex traits. The convergence of these approaches enables a more holistic understanding of genetic architecture and accelerates the translation of research findings into practical breeding applications. Despite substantial progress, several challenges remain. Limited validation of candidate genes under diverse field conditions, inadequate integration of multi-omics datasets, and underutilization of genetic diversity from wild relatives continue to constrain breeding efforts. Addressing these challenges requires interdisciplinary collaboration among plant geneticists, breeders, physiologists, and data scientists. Advances in high-throughput phenotyping and computational biology will be critical for linking genotype to phenotype with greater precision.

Looking forward, emerging technologies such as artificial intelligence-driven genomics, machine learning-based predictive breeding, and precision gene editing hold immense potential for transforming crop improvement strategies. These innovations can facilitate the identification of complex gene interactions, optimize breeding decisions, and accelerate the development of climate-resilient cultivars. In conclusion, leveraging an integrative and technology-driven framework will be pivotal in enhancing abiotic stress tolerance and ensuring sustainable agricultural productivity in the face of global climate change.

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