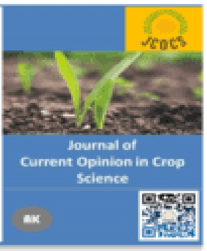
JCOCS

Journal of
Current Opinion in Crop Science

Journal homepage: www.jcocs.com; ISSN(O):2583-0392



REVIEW ARTICLE

Integrative omics approaches for enhancing abiotic stress resilience in maize

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Article history:

Received: August 30, 2025
Accepted: September 25, 2025
Published: September 30, 2025

Citation:
Ashokkumar, K., & Shobhana, V. G., Mani, P., Thangaraj, T., & Muniyandi, S. J. (2025). Integrative omics approaches for enhancing abiotic stress resilience in maize. *Journal of Current Opinion in Crop Science, 6*(3), 213-233. https://doi.org/10.62773/jcocs.v6i3.347

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ABSTRACT

Abiotic stresses such as drought, heat, salinity, and nutrient imbalances severely threaten maize productivity, necessitating innovative strategies for developing resilient cultivars. Omics technologies have emerged as transformative tools to unravel the complex molecular and physiological mechanisms. Each omics layer, genomics, transcriptomics, proteomics, metabolomics, ionomics, and phenomics, provides unique insights into how maize perceives and adapts to adverse environments. When integrated, these approaches generate a systems-level perspective that connects molecular signals with biochemical pathways, physiological responses, and morphological traits, thereby advancing our understanding of resilience at multiple biological scales. Integrating multi-omics with high-throughput phenotyping has accelerated the identification of biomarkers, regulatory networks, and candidate genes associated with stress tolerance. Significantly, omics-driven approaches facilitate the development of climate-smart cultivars capable of sustaining yield stability under fluctuating and extreme conditions. Future studies will depend on coupling omics with advanced analytics, machine learning, and environmental datasets to strengthen predictive capacity. Emerging innovations, including field-deployable omics platforms and AI-integrated decision-support tools, hold promise for real-time trait selection and adaptive management strategies. Ultimately, the successful translation of omics-derived knowledge into breeding programs will require global collaboration, open-access databases, and integration into precision agriculture frameworks. Such efforts will help ensure food security, resource-use efficiency, and sustainable maize production in a changing climate.

Keywords: abiotic stress tolerance; genomics; ionomics, maize, metabolomics, proteomics; phenomics; transcriptomics

1. INTRODUCTION

Maize (*Zea mays* L.) is one of the most widely cultivated cereal crops worldwide, serving simultaneously as a staple food, livestock feed, and industrial raw material. It is grown in over 160 countries and consistently ranks first among cereals in production, with global production outstanding 1.2 billion metric tons annually (Meng et al., 2024; Shiferaw et al., 2011). In India, maize contributes more than 2% to overall agricultural output and supports the livelihoods of over 15 million farmers, highlighting its socio-economic significance (Rani & Kumar, 2022; Dass et al., 2016).

Nutritionally, maize provides a rich source of carbohydrates, dietary fiber, and key micronutrients such as magnesium, phosphorus, and B-complex vitamins (Bouis & Welch, 2010). It also contains a diverse array of bioactive phytochemicals, including carotenoids, phenolic compounds, and phytosterols, which are associated with antioxidant properties and the prevention of chronic diseases (Shah et al., 2016; Adiaha, 2017; Ali et al., 2021). Additionally, quality protein maize (QPM) varieties have been developed to overcome deficiencies in essential amino acids, particularly lysine and tryptophan, thereby enhancing their nutritional profile (Prasanna et al., 2001). Beyond its role in food and nutrition security, maize is a vital raw material for the fodder, bioethanol, bioplastics, and pharmaceutical industries, underscoring its versatility and strategic importance to sustainable agriculture and economic development in both developing and industrialized economies (Tester & Langridge, 2010; Shiferaw et al., 2011).

Maize productivity is highly sensitive to abiotic stresses such as drought, salinity, heat, cold, and waterlogging. These stresses disrupt physiological and metabolic processes, often resulting in substantial yield losses up to 90% under severe drought conditions (Sheoran et al., 2022). Molecular breeding has emerged as a key strategy to mitigate these effects. A meta-analysis of 33 QTL mapping studies identified 542 QTLs associated with abiotic stress tolerance, of which 244 major QTLs accounted for more than 10% phenotypic variance. These were refined into 32 meta-QTLs linked to transcription factors, including ERF, MYB, bZIP, NAC, and WRKY, which govern stress responses (Sheoran et al., 2022). Marker-assisted selection (MAS), using SSR and SNP markers, has facilitated introgression of stress-resilient alleles into elite maize germplasm, thereby enhancing tolerance and expediting cultivar development (Arabzai & Gul, 2021; Beyene et al., 2016)

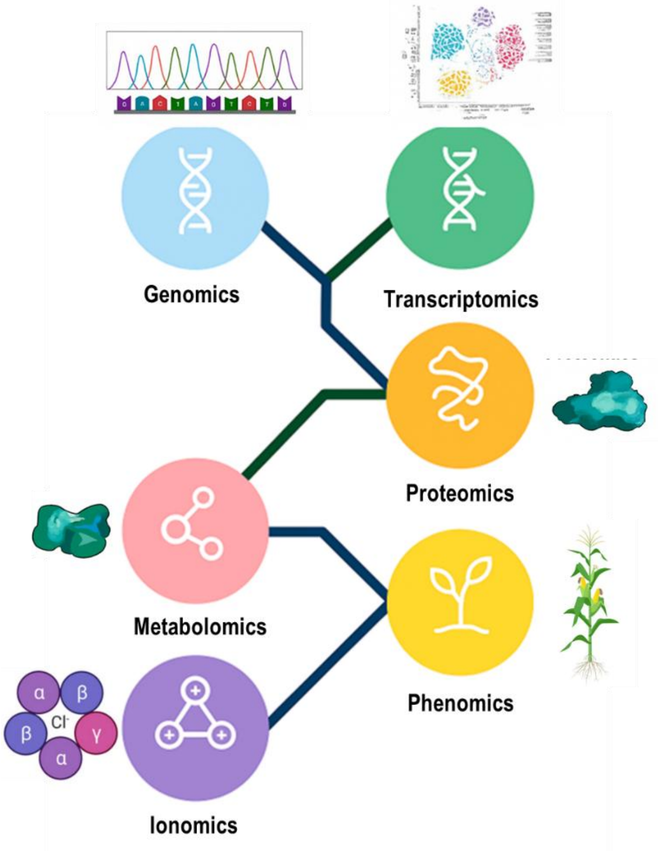

Figure 1. Schema of omics approaches used in abiotic stress tolerance in maize.

Omics technologies have revolutionized maize stress biology by delivering multilayered insights into plant adaptation. Genomics has uncovered key loci for drought and salinity tolerance through genome-wide association studies (GWAS) and CRISPR-Cas9 editing (Meng et al., 2024). Transcriptomics, particularly RNA-Seq, has revealed dynamic gene expression profiles during stress, delineating regulatory networks and critical transcription factors (Singh, 2024). Proteomics has mapped stress-induced protein modifications, identified enzymes and signaling proteins crucial for tolerance (Yang et al., 2021). Metabolomics characterizes stress-responsive metabolites such as osmoprotectants, flavonoids, and antioxidants that link biochemical shifts to resilience (Sahoo et al., 2025). The omics approaches used in abiotic stress tolerance in maize were illustrated in Figure 1. Integrated multi-omics approaches offer systems biology frameworks for dissecting complex stress responses, guiding precision breeding (Yang et al., 2021; Deshmukh et al., 2025). Based on the above interests, this study comprehensively reviews genomic, transcriptomic, proteomic, and metabolomic tools used to enhance abiotic stress tolerance in maize, providing a roadmap for future research and breeding initiatives aimed at climate-resilient cultivars.

2. GENOMICS FOR ABIOTIC STRESS TOLERANCE IN MAIZE

2.1. Molecular markers /MAS for abiotic stress tolerance

Molecular markers and marker-assisted selection (MAS) have become foundational tools in maize breeding programs targeting abiotic stress tolerance. DNA-based markers such as simple sequence repeats (SSRs), single-nucleotide polymorphisms (SNPs), and amplified fragment length polymorphisms (AFLPs) enable the precise identification of stress-responsive genes and quantitative trait loci (QTLs). For example, SSR markers have been used to map QTLs linked to drought tolerance traits like root depth, leaf rolling, and stay-green phenotypes (Wani et al., 2018; Younis et al., 2020). SNP markers, due to their abundance and high-throughput genotyping capacity, have facilitated genome-wide association studies (GWAS) that uncover key loci such as ZmDREB2A and ZmPP2C-A10 involved in drought and heat stress signaling (Meng et al., 2024; Xu & Crouch, 2008). Additionally, RAPD and RFLP markers have supported early-stage salinity and cold tolerance screening in maize genotypes (Ashraf et al., 2012). These molecular tools allow breeders to bypass environmental variability and select genotypes with favorable alleles even in early generations, enhancing breeding efficiency and precision.

Marker-assisted backcrossing (MAB) further accelerates the introgression of stress-tolerant alleles into elite maize cultivars. Genes such as *saltol* (salinity tolerance), *dehydrin* (drought resilience), and *ZmNAC111* (heat tolerance) have been successfully incorporated into high-yielding lines using MAB strategies (Choudhary et al., 2018; Collard et al., 2005) (Table 1). Integrating molecular markers with multi-omics platforms, including genomics, transcriptomics, proteomics, and metabolomics, has enabled pyramiding of multiple stress-tolerance traits, ensuring adaptability across diverse agro-climatic zones (Xu, 2010; Younis et al., 2020). Furthermore, molecular breeding is increasingly complemented by CRISPR/Cas-based gene editing, offering precise manipulation of stress-responsive loci and accelerating trait fixation (Meng et al., 2024). As climate variability intensifies, MAS and MAB provide a robust framework for developing climate-resilient maize varieties, contributing to sustainable agriculture and food security.

Table 1. Molecular Markers and Breeding Strategies for Abiotic Stress Tolerance in Maize

Abiotic stress	Marker type	Key Genes / QTLs	Breeding Strategy	References
Drought	SSR & SNP	*ZmDREB2A*, *ZmPP2C-A10*, *qDTY1.1*, *ZmNAC111*, *ZmVPP1*	MAS, MAB, GWAS, QTL mapping	Wani et al., 2018; Meng et al., 2024; Xu & Crouch, 2008; Li et al., 2024.
Salinity	SSR & SNP	*Saltol*, *HKT1*, *NHX1*, *ZmSOS1*, *ZmWRKY33*	MAB, MAS, introgression from tolerant lines	Choudhary et al., 2018; Younis et al., 2020; Sharma et al., 2019.

Heat	SNP & AFLP	*HSPs*, *ZmNAC111*, *ZmPP2C-A10*, *ZmHsfA2*, *ZmPIP2;5*	GWAS, MAS, transcriptomics, RNA-seq	Meng et al., 2024; Xu, 2010; Farooqi et al., 2022.
Cold	RAPD, SSR & SNP	*CBF/DREB1*, *ICE1*, *COR15a*, *ZmMPK3*, *ZmMYB31*	MAS, early-generation selection, QTL mapping	Ashraf et al., 2012; Younis et al., 2020; Fracheboud et al., 2002.
Multiple stress	SNP, SSR, & RFLP	*Dehydrin*, *LEA*, *ABA-responsive genes*, *ZmSnRK2*, *ZmAP2*	Pyramiding, multi-omics MAS, gene stacking	Collard et al., 2005; Xu, 2010; Meng et al., 2024
Heavy metal	SSR & SNP	*ZmPCS1*, *ZmMT2*, *ZmZIP4*	MAS, transgenic introgression	Farooqi et al., 2022; Bagri et al., 2020.
Oxidative stress	SNP & SSR	*ZmCAT*, *ZmSOD*, *ZmAPX*, *ZmGST*	MAS, functional genomics, CRISPR/Cas	Meng et al., 2024; Sharma et al., 2019.
Waterlogging	SSR & SNP	*ZmEREB180*, *ADH1*, *ZmRBOH*, *ZmPDC1*	MAS, GWAS, transcriptomics	Farooqi et al., 2022; Xu, 2010.
UV stress	SNP & AFLP	*ZmUVR8*, *ZmHY5*, *ZmCHS*	MAS, gene expression profiling	Meng et al., 2024; Bagri et al., 2020.

2.2. Identification of loci governing abiotic stress tolerance in maize

Identifying loci governing abiotic stress tolerance in maize has advanced significantly through quantitative trait loci (QTL) mapping, multi-parent populations, and genome-wide association studies (GWAS). QTL mapping has long served as a foundational approach for dissecting complex traits such as drought resilience, salinity tolerance, and cold adaptation. Using biparental populations like recombinant inbred lines (RILs) and doubled haploids (DHs), researchers have mapped key QTLs, including *qDTY1.1* for grain yield under drought, *qASI7.1* for anthesis-silking interval, and *qLR5.2* for leaf rolling (Sharma et al., 2019). A meta-analysis by Sheoran et al. (2022) synthesized data from 33 studies, consolidating 542 QTLs into 32 stable meta-QTLs (MQTLs) with high phenotypic variance. These MQTLs span chromosomes 1 to 10 and are enriched for transcription factor families such as *DREB*, *NAC*, *WRKY*, and *bZIP*, which are central to abiotic stress signaling (Table 2). Such loci are now prioritized for marker-assisted selection (MAS), gene pyramiding, and functional validation in climate-resilient maize breeding programs.

To overcome the limitations of biparental mapping, MAGIC (Multi-parent Advanced Generation Inter-Cross) populations have emerged as powerful tools for high-resolution mapping. These populations capture broader allelic diversity and recombination events, enabling the detection of minor-effect loci and epistatic interactions. In maize, Caicedo et al. (2021) evaluated 672 RILs derived from a MAGIC population and identified 36 candidate genes associated with drought-induced senescence and nutrient remobilization. Notably, *Zm00001d043586* was linked to chlorophyll degradation during late developmental stages, a key determinant of stress-induced leaf senescence. MAGIC designs thus offer a robust framework for dissecting polygenic traits and accelerating trait discovery under variable environmental conditions.

Genome-Wide Association Studies (GWAS) complement QTL mapping by leveraging natural variation across diverse germplasm panels. GWAS has identified loci associated with drought (*ZmDREB2A*, *ZmPP2C-A10*), heat (*ZmHsfA2*, *ZmPIP2;5*), salinity (*ZmSOS1*, *ZmWRKY33*), and cold tolerance (*ICE1*, *CBF/DREB1*) (Meng et al., 2024; Hu et al., 2016). These studies integrate high-density SNP genotyping with multi-environment phenotyping, enabling the discovery of environment-specific and pleiotropic loci. For instance, Zhao et al. (2018) used GWAS to identify SNPs linked to drought-induced leaf senescence and grain filling, while Hu et al. (2016) combined GWAS with transcriptomic data to uncover cold-responsive genes. Increasingly, GWAS is supported by multi-omics platforms like genomics, transcriptomics, and metabolomics, which enhance candidate gene discovery and accelerate breeding cycles for abiotic stress resilience.

Table 2. Identification of QTL governing abiotic stress tolerance in maize

Stress	Traits	QTL name	Chromosome number	Position (Cm)	LOD (score)	Reference
Drought	Seedling root length	qRL1.1	1	45.2	3.8	Li et al. (2024)
Drought	Grain yield under stress	MQTL5.1	5	78.0	5.2	Sheoran et al. (2022)
Salinity	Germination rate	qGR3.2	3	62.5	4.1	Sharma et al. (2019)
Heat	Pollen viability	qPV9.1	9	101.3	3.5	Meng et al. (2024)
Cold	Seedling vigor	qSV2.1	2	33.7	4.6	Fracheboud et al. (2002)
Drought	Anthesis-silking interval (ASI)	MQTL7.1	7	59.4	6.0	Sheoran et al. (2022)
Combined stress	Inflorescence development	MQTL9.2	9	110.5	5.8	Sheoran et al. (2022)
Salinity	Seedling shoot biomass	qSB4.1	4	41.9	3.9	Sharma et al. (2019)
Cold	Germination rate	qGR2.3	2	28.6	4.2	Rodríguez et al., 2008
Drought	Leaf rolling	qLR5.2	5	84.0	3.7	Li et al. (2024)
Drought	Plant height under stress	MQTL2.1	2	36.0	4.9	Sheoran et al. (2022)
Heat	Tassel blast resistance	qTB6.1	6	72.4	3.6	Meng et al. (2024)
Cold	Chlorophyll content	qCC1.2	1	50.3	4.4	Jompuk et al. (2005)
Drought	Ear height	MQTL5.6	5	90.1	5.5	Sheoran et al. (2022)
Salinity	Root-to-shoot ratio	qRSR3.1	3	66.7	4.0	Sharma et al. (2019)

2.3. Genomic selection (GC) for abiotic stress tolerance

Genomic selection (GS) has emerged as a powerful and predictive breeding strategy for improving abiotic stress tolerance in maize, particularly under the pressures of climate change and resource-limited environments. Unlike marker-assisted selection, which targets specific QTLs and GS leverages genome-wide marker data to estimate the breeding value of individuals, enabling early and accurate selection for complex traits such as drought, heat, and salinity tolerance (Mittal et al., 2017; Sheoran et al., 2023). These traits are typically polygenic and exhibit strong genotype-by-environment interactions, making traditional phenotypic selection inefficient. GS models such as Bayes B, ridge regression, and reproducing kernel Hilbert space (RKHS) have demonstrated high prediction accuracies for drought-related traits in subtropical maize lines, with Bayes B outperforming others in multi-environment trials by identifying SNPs linked to transcription factors regulating stomatal closure, root development, and hormonal signaling (Mittal et al., 2017).

Furthermore, GS is being integrated into hybrid breeding programs to enhance the efficiency of parental selection and predict hybrid performance under stress conditions (Lohithaswa et al., 2022). This integration allows breeders to bypass extensive field evaluations and accelerate the development of climate-resilient cultivars. Also, GS has shown promising results in maize and other cereals like wheat and rice, where it has improved yield and stress tolerance traits (Kumar et al., 2022). GS complements high-throughput phenotyping and multi-environment testing, refining prediction models and enhancing their robustness across diverse agroecological zones (Sheoran et al., 2023). As abiotic stresses threaten global food security, GS offers a scalable, data-driven framework for sustainable maize improvement, aligning with ecological resilience and breeding efficiency. The comparison of genomic selection models for abiotic stress traits was presented in Table 3.

Table 3. Comparison of genomic selection models for abiotic stress traits

Model	Statistical Basis	Strengths	Limitations	Use
Bayes B	Bayesian variable selection	High accuracy for sparse traits; handles major QTLs.	Computationally intensive	Drought tolerance & root traits.
RR-BLUP	Ridge regression	Fast & robust for polygenic traits.	Assumes equal marker effects	Grain yield & flowering time.
RKHS	Kernel-based non-parametric	Captures non-linear effects.	Requires tuning and large datasets	Multi-environment prediction.
Bayes A	Bayesian shrinkage	Flexible for trait-specific variance.	Sensitive to prior assumptions	Stress-adaptive physiological traits

3. TRANSCRIPTOMICS FOR ABIOTIC STRESS TOLERANCE IN MAIZE

Transcriptomics has become a pivotal tool for unraveling the molecular mechanisms underlying abiotic stress tolerance in maize, enabling researchers to capture genome-wide gene expression changes in response to environmental challenges. High-throughput RNA sequencing (RNA-seq) has revealed thousands of differentially expressed genes (DEGs) in maize leaves and roots under drought, salinity, heat, and cold stress, many of which are involved in hormone signaling, transcriptional regulation, lipid metabolism, and antioxidant defense (Li et al., 2017). For example, transcriptomic profiling of the B73 inbred line identified 5,330 DEGs across four stress types, with 167 genes, primarily transcription factors such as ERF, NAC, MYB, and HD-ZIP, being commonly regulated, suggesting the existence of core stress-responsive networks (Li et al., 2017). Such insights provide candidate genes for functional validation and targeted breeding, accelerating the development of stress-resilient cultivars.

Beyond single-stress studies, integrative transcriptomic analyses have shed light on maize responses to combined stresses, such as drought and heat, which often co-occur in the field. Yang et al. (2022) demonstrated that primary root responses to combined stress are mediated by salicylic acid metabolism and phenylpropanoid pathways, with key regulatory genes like *ZmWRKY106* showing significant induction. These findings underscore the complexity of stress adaptation, where transcriptomic plasticity enables maize to fine-tune physiological and metabolic processes under fluctuating environments. Coupled with genomics, metabolomics, and functional assays, transcriptomics offers a systems-level framework for identifying biomarkers and engineering multi-stress tolerance in maize. The major functional genes involved in various abiotic stress tolerance in maize were summarized in Table 4.

Table 4. Transcriptomics for abiotic stress tolerance in maize

Stress type(s)	Tissue/stage	Major functional pathways/genes	Results/remarks	Reference
Drought, salinity, heat, & cold	Seedling leaves	Hormone signaling, lipid metabolism, & antioxidant defense	Identified 5,330 DEGs; 167 common to all stresses; core TF families (ERF, NAC, MYB, & HD-ZIP)	Li et al. (2017)
Salinity, drought, & cold	Seedlings	Gibberellin metabolism, MAPK cascades, DREB, bZIP TFs	Digital gene expression profiling revealed GA metabolic pathway modulation; generated a	Shan et al. (2013)

			candidate gene list for functional studies	
Combined drought + heat	Primary roots	SA biosynthesis, phenylpropanoid metabolism & WRKY TFs	Salicylic acid metabolism and the phenylpropanoid pathway are central to the combined stress response; *ZmWRKY106* upregulated	Yang et al. (2022)
Multiple abiotic stresses	Various tissues	Chitinase activity, phosphorelay signal transduction & stress-related metabolic modules	560 DEGs identified; co-expression network revealed hub genes (e.g., *Zm.7361.1.A1_at*); logistic LASSO regression validated candidates	Nazari & Zinati (2023)
Cold & drought (seed germination)	Germinating seeds	Stress-responsive TFs, osmoprotectant biosynthesis & ROS scavenging	12,299 DEGs; distinct and overlapping responses; cold stress induced more DEGs than drought	Zhang et al. (2021)
Salinity, drought, & cold	Seedlings	Gibberellin metabolism, MAPK cascades, DREB & bZIP TFs	Digital gene expression profiling revealed GA metabolic pathway modulation; it generated a candidate gene list for functional studies	Shan et al. (2013)

4. PROTEOMICS FOR ABIOTIC STRESS TOLERANCE IN MAIZE

Proteomics has become an indispensable approach for elucidating the molecular mechanisms of abiotic stress tolerance in maize, offering a direct link between gene expression and functional protein networks (Table 5). By profiling the complete set of proteins expressed under stress conditions, proteomics reveals post-translational modifications, protein–protein interactions, and metabolic adjustments that cannot be inferred from transcriptomics alone (Farooqi et al., 2022). Comparative proteomic analyses between stress-tolerant and stress-sensitive maize genotypes have identified differentially expressed proteins (DEPs) involved in antioxidant defense, osmotic adjustment, energy metabolism, and signal transduction. For example, under salt stress, tolerant lines exhibit upregulation of proteins linked to phenylpropanoid biosynthesis, starch and sucrose metabolism, and MAPK signaling, which collectively enhance osmotic regulation, ROS scavenging, and cellular homeostasis (Chen et al., 2019).

Recent studies have also highlighted the dynamic nature of the maize proteome in response to drought and osmotic stress. Short-term osmotic stress triggers rapid accumulation of antioxidant enzymes such as catalase (CAT) and superoxide dismutase (SOD), alongside proteins involved in ATP synthesis and energy metabolism, enabling roots to maintain metabolic activity under water deficit (Wang et al., 2025). Integrating proteomics with other omics platforms, such as transcriptomics and metabolomics, provides a systems-level understanding of stress adaptation, facilitating the identification of robust biomarkers and candidate proteins for breeding climate-resilient maize cultivars. This multi-omics collaboration is increasingly being adopted in breeding programs to accelerate the development of varieties capable of withstanding multiple abiotic stresses (Farooqi et al., 2022).

Table 5. Functional proteomics of maize under environmental stress conditions

Stress Type(s)	Tissue / Stage	Major functional pathways/proteins	Results/ remarks	Reference

Salt stress (180 mM NaCl, 10 days)	Seedling roots (salt-tolerant 8723 vs. salt-sensitive P138)	Phenylpropanoid biosynthesis, starch/sucrose metabolism, MAPK signaling, nitrogen metabolism	1,056 DEPs; the tolerant line showed stronger osmotic regulation, antioxidant synergy, and energy metabolism	Chen et al. (2019)
Short-term osmotic stress (PEG-induced)	Roots	ROS scavenging, energy metabolism, and osmotic adjustment	Rapid accumulation of antioxidant enzymes (CAT, SOD) and ATP-synthesis proteins; maintained metabolic activity under water deficit	Wang et al. (2025)
Drought stress during kernel filling	Developing kernels (tolerant YE8112 vs. sensitive MO17)	Protein processing in the ER, tryptophan metabolism, and oxidative phosphorylation	5,175 DAPs; tolerant line enriched in HSPs, redox regulation and secondary metabolite biosynthesis	Wang et al. (2019)
Water deficit	Leaves (maize vs. sorghum comparison)	Antioxidant defense, osmoprotectant biosynthesis, and ROS detoxification	Maize showed higher oxidative damage; sorghum had better water retention and proline accumulation	Ali, (2019)
Drought stress	Leaves (tolerant vs. sensitive hybrids)	Calvin cycle enzymes, glycolysis, and stress-related chaperones	Stress-responsive proteins linked to photosynthesis stability and carbohydrate metabolism	Zenda et al. (2020)
Drought + herbicide stress in GM vs. non-GM maize	Leaves	Energetic/carbohydrate metabolism and phytohormone regulation	20 DEPs between GM and non-GM under stress; environment was the main driver of variation; differences in JA, MeJA, and CA levels	Benevenuto et al. (2017)
Cold stress	Seedling leaves	Photosynthesis, ROS detoxification, and stress-protective proteins	Identified cold-responsive proteins, including LEA, dehydrins, and antioxidant enzymes; tolerant genotypes maintained higher photosynthetic protein abundance	Gong et al. (2014)
High temperature + drought	Leaves and roots	Heat shock response, water transport and oxidative stress mitigation	Proteomic shifts in HSPs, aquaporins, and metabolic enzymes; coordinated regulation of ABA and ROS pathways	Meng et al. (2024)

5. METABOLOMICS FOR ABIOTIC STRESS TOLERANCE IN MAIZE

Earlier metabolomics work in maize positioned the approach as a systems-level window into the biochemical adjustments that underpin stress resilience. Arbona et al. (2013) first emphasized that profiling primary and secondary metabolites directly reflects a plant's physiological state, capturing osmotic adjustment, antioxidant defense, and energy homeostasis shifts not always visible through transcriptomic or proteomic analysis. Building on this conceptual foundation, Obata et al. (2015) used large-scale field trials under drought, heat, and combined stresses to link leaf metabolite profiles, such as increases in glycine, serine, myo-inositol, and raffinose family oligosaccharides, with grain yield stability, proposing these as biochemical markers for breeding.

The integration of metabolomics with genetic mapping accelerated in the following years. Farooqi et al. (2022) highlighted the application of metabolite-QTL (mQTL) mapping and metabolome-wide association studies (mGWAS) to identify loci controlling metabolite accumulation, with consistent markers including myo-inositol, trehalose, and flavonoids linked to yield stability under drought and heat stress (Table 6). Meng et al. (2024) synthesized multi-omics evidence to show that shifts in sugars, amino acids, and polyols are central to stress signal transduction, membrane stabilization, and redox balance across diverse abiotic stresses.

Most recently, targeted pathway studies have connected specific biosynthetic genes to metabolic resilience mechanisms. Wang et al. (2025) demonstrated that knockout of ZmCHS25, a chalcone synthase gene, disrupted flavonoid biosynthesis and phenylpropanoid metabolism, impairing osmotic regulation and salt tolerance in maize seedlings. This study pinpointed the dual roles of flavonoids in reactive oxygen species (ROS) scavenging and ion homeostasis under salinity. The chronological progression from broad profiling to gene-level functional metabolomics shows a clear trajectory toward predictive metabolic markers and integrated selection tools for breeding climate-resilient maize.

Table 6. Abiotic stress-induced metabolomic shifts in maize

Stress type(s)	Identified Metabolites	Primary pathways /processes	Results/ remarks	References
General framework for abiotic stresses	Proline, glycine betaine, & raffinose family oligosaccharides	Osmotic adjustment, antioxidant defense & energy homeostasis	Established a conceptual foundation for integrating metabolomics into stress physiology and breeding pipelines	Arbona, et al. (2013).
Drought & heat, combined stress	Glycine, serine, myo-inositol, & raffinose	Photorespiration, Osmo protection, & ROS scavenging	Identified metabolite markers correlating with grain yield under stress; proposed use in selection	Obata et al., (2015)
Drought, heat (multi-omics)	Myo-inositol, trehalose, & flavonoids	mQTL/mGWAS-linked metabolic traits, & carbohydrate metabolism	Integrated metabolomics with QTL mapping; positioned metabolites as selection criteria in genomic breeding	Farooqi (2022)
Multi-stress synthesis (drought,	Sugars (glucose, sucrose), & amino acids, polyols	Signal transduction, membrane stabilization, & redox homeostasis	Synthesized mechanistic roles of metabolites across stresses; informed multi-	Meng et al., (2024)

salinity, cold, & heavy metals)			trait breeding targets	
Salinity	Flavonoids & phenylpropanoids	Antioxidant defense, osmotic regulation, & ion homeostasis	Linked *ZmCHS25* function to metabolic regulation under salt stress; potential for targeted gene-based metabolic breeding	Wang et al., (2025)

6. IONOMICS FOR ABIOTIC STRESS TOLERANCE IN MAIZE

The high-throughput profiling of elemental composition in plant tissues has become an indispensable approach for elucidating nutrient homeostasis and mineral stress responses in maize under abiotic stress conditions. By simultaneously quantifying macro- and micronutrients, ionomics enables the identification of elemental signatures associated with tolerance to drought, salinity, heat, and nutrient deficiencies. For example, shifts in potassium (K), calcium (Ca), and magnesium (Mg) concentrations often reflect osmotic adjustment and membrane stabilization under water deficit (Table 7). At the same time, altered sodium (Na) and chloride (Cl) accumulation patterns are key indicators of salinity tolerance mechanisms (Baxter, 2015). In maize, ionomic analyses have revealed that genotypes maintaining higher K/Na ratios under saline conditions exhibit improved growth and photosynthetic efficiency, underscoring the role of selective ion uptake and compartmentalisation in stress resilience (Gupta et al., 2021).

Integrating ionomics with genomics and transcriptomics has further advanced the discovery of ion-related quantitative trait loci (QTLs) and candidate genes controlling elemental homeostasis under stress. High-resolution ionomic mapping has identified loci linked to zinc (Zn) and iron (Fe) efficiency under drought, as well as boron (B) and manganese (Mn) regulation under heat stress (Asaro et al., 2016). Such insights deepen our understanding of the physiological basis of abiotic stress tolerance and provide breeders with elemental biomarkers for selection. When combined with field phenotyping, ionomics offers a scalable, non-destructive tool to accelerate the development of maize cultivars optimized for nutrient use efficiency and resilience in climate-challenged agroecosystems.

Table 7. Abiotic stress induced Ionomics shifts in maize

Stress type(s)	Elemental shifts	Primary physiological/ molecular roles	Results/remarks	References
General abiotic stress ionomics framework	Multiple macro- and micronutrients (K, Ca, Mg, Na, Fe, & Zn)	Defined ionomics as a high-throughput elemental profiling approach; emphasized combined trait analysis	Provided a theoretical and methodological basis for integrating elemental profiling into crop stress physiology	Baxter (2015)
Multi-environment drought and nutrient variation	Zn, Fe, B, & Mn homeostasis shifts	G × E interactions for elemental traits; QTLs for nutrient efficiency	Identified stable elemental traits and loci; enabled breeding for nutrient-efficient, stress-resilient maize	Asaro et al. (2016)

Drought and low-N stress	Altered P, K, and micronutrient (Zn, Mn) levels	Coordinated nutrient remobilization and uptake efficiency under combined stresses	Suggested elemental efficiency traits as dual-stress breeding targets	Gu et al. (2018)
Salinity and drought	↑K/Na ratio, reduced Na accumulation, stable Ca and Mg	Ion homeostasis, osmotic adjustment, and membrane stabilization	Validated K/Na ratio and Ca stability as robust ionomic markers for multi-stress tolerance	Zhang et al. (2020)
Salinity	↑K/Na ratio, adjusted Cl levels	Osmotic adjustment, Na exclusion, selective K uptake	Demonstrated K/Na ratio as a reliable ionomic marker of salinity tolerance; applicable in selection programs	Gupta et al. (2021)
Heat stress	Increased B and Mn, stable Fe and Zn	Enzyme cofactor stability, ROS detoxification	Linked micronutrient regulation to thermotolerance; proposed B and Mn as heat-stress biomarkers	Liu et al. (2023)
Multi-stress (drought, salinity, cold, & heavy metals)	Stress-specific shifts in macro- and micronutrients	Integrated ionomics with transcriptomics to reveal nutrient-responsive regulatory networks	Provided a multi-omics framework for nutrient-based stress resilience breeding	Meng et al. (2024)

7. PHENOMICS FOR ABIOTIC STRESS TOLERANCE IN MAIZE

Phenomics, the large-scale, high-throughput measurement of plant traits, has become a cornerstone in dissecting the complex physiological responses of maize to abiotic stresses. By integrating advanced imaging, sensor technologies, and automated data analytics, phenomics enables precise, non-destructive monitoring of morphological, physiological, and biochemical traits over time and across environments (Furbank & Tester, 2011). In maize, phenomics platforms have been used to quantify traits such as canopy temperature, chlorophyll fluorescence, leaf wilting, anthesis–silking interval (ASI), and stay-green under drought, heat, and salinity stress (Araus & Cairns, 2014) (Table 8). These traits serve as proxies for underlying stress-adaptive mechanisms, allowing breeders to identify tolerant genotypes more efficiently than through conventional field scoring alone.

Recent advances in field-based high-throughput phenotyping (HTP), including uncrewed aerial vehicles (UAVs), multispectral and hyperspectral imaging, and LiDAR scanning, have expanded the scale and resolution of phenomics in maize breeding programs (Yang et al., 2020). For example, UAV-based thermal imaging has been used to detect genotypic variation in canopy temperature depression, a key indicator of transpiration efficiency under drought. Similarly, hyperspectral reflectance indices have been correlated with leaf nitrogen status, photosynthetic capacity, and water content, enabling early detection of stress responses before visible symptoms appear. When integrated with genomic selection models, phenomics data significantly improve the prediction accuracy for complex stress-related traits, accelerating the development of climate-resilient maize cultivars (Cabrera-Bosquet et al., 2012).

The future of phenomics for abiotic stress tolerance in maize lies in multi-environment, multi-trait data integration, where phenotypic datasets are combined with genomics, transcriptomics, metabolomics, and ionomics to build predictive models of plant performance. Such integrative approaches not only enhance the precision of selection but also deepen our understanding of the physiological and genetic architecture of stress adaptation, paving the way for breeding strategies that are both rapid and resource-efficient.

Table 8. Abiotic stress induced phenomics shifts in maize

Stress type	Phenomics platform / Scale	Traits measured	Results/ remarks	Reference
Drought	Field-based HTP (UAV + thermal imaging)	Canopy temperature depression (CTD), anthesis–silking interval (ASI), stay-green, & chlorophyll fluorescence (Fv/Fm)	CTD as proxy for transpiration efficiency; early ASI reduction linked to reproductive resilience; integrates with genomic selection.	Araus & Cairns (2014)
Heat	Fixed-platform RGB & hyperspectral imaging in growth chambers	Leaf senescence rate, NDVI, PRI, & pollen viability	Identifies heat-resilient genotypes via delayed senescence and stable photosynthesis under high temperature stress.	Cairns et al. (2013)
Salinity	Automated greenhouse conveyor phenomics (visible + NIR imaging)	Leaf area expansion rate, spectral water index (SWI), and ion leakage (via hyperspectral signatures)	Early detection of salinity tolerance through non-destructive water status indicators; accelerates screening before biomass loss.	Al-Tamimi et al. (2016)
Nutrient deficiency	UAV-based multispectral imaging (field trials)	Leaf nitrogen index, chlorophyll content (SPAD proxy via reflectance), & canopy uniformity	Precision phenotyping enables targeted nutrient management and supports QTL mapping for nutrient-use efficiency.	Li et al. (2018)
Combined drought + heat	LiDAR + hyperspectral fusion (field)	Canopy height dynamics, spectral stress indices, & reproductive success (kernel set %)	Multi-trait integration improves the prediction of yield stability under multi-stress field conditions.	Deery et al. (2019)
Cold stress	Growth chamber RGB +	Seedling vigor index,	Enables early-stage screening for cold	Revilla et al. (2016)

	chlorophyll fluorescence imaging	photochemical efficiency (Fv/Fm), & leaf color dynamics	tolerance; supports breeding for temperate and high-altitude adaptation.	
Flooding	Field phenomics with UAV multispectral + ground-based spectral sensors	Leaf chlorosis index, canopy cover %, & recovery growth rate	Identifies genotypes with rapid post-flood recovery; informs breeding for flood-prone lowland ecologies.	Zaidi et al. (2020)
Heavy metal stress (Cd)	Controlled-environment hyperspectral + fluorescence imaging	Leaf pigment degradation rate, PSII efficiency, & spectral stress indices	Non-destructive detection of Cd stress; potential for screening in phytoremediation and food safety breeding programs.	Zhang et al. (2021)
UV-B stress	Greenhouse phenomics with UV-B supplementation + multispectral reflectance	Leaf wax content (via spectral signature) & photoprotective pigment indices	Supports breeding for UV-B resilience in high-altitude or ozone-depleted regions.	Kataria & Guruprasa (2012)
Multi-environment trials	Integrated UAV + proximal sensing across locations and seasons	Stability indices for yield, canopy temperature, NDVI, & biomass accumulation	Links phenomics data to G×E interaction models; accelerates selection of broadly adapted stress-tolerant hybrids.	Prasanna et al. (2021)

8. INTEGRATION OF OMICS TECHNOLOGIES

The convergence of omics technologies, genomics, transcriptomics, proteomics, metabolomics, ionomics, phenomics, and epigenomics has revolutionized the study of abiotic stress tolerance in maize (*Zea mays* L.). Each omics layer captures a unique biological dimension: genomics identifies stress-responsive loci and alleles; transcriptomics reveals dynamic gene expression changes; proteomics uncovers protein abundance, modifications, and interaction networks; metabolomics profiles biochemical shifts in primary and secondary metabolism; ionomics quantifies nutrient and ion fluxes; phenomics measures whole-plant traits under stress; and epigenomics detects heritable changes in gene regulation without altering DNA sequence (Farooqi et al., 2022; Deshmukh et al., 2025). When integrated, these datasets provide a systems-level blueprint of maize's adaptive strategies, enabling the identification of master regulators and robust biomarkers for breeding (Table 9). The schematic representation of the integration of omics technologies for abiotic stress tolerance in maize was displayed in Figure 2.

Multi-omics integration has particularly impacted polygenic traits such as drought, heat, and combined stress tolerance, where genotype × environment interactions obscure single-layer signals. For example, coupling transcriptomic data on drought-induced transcription factors (e.g., *DREB*, *NAC*, *bZIP*) with proteomic profiles of antioxidant enzymes and metabolomic signatures of osmolytes has revealed coordinated defense pathways that maintain osmotic balance and protect photosynthetic machinery (Varadharajan et al., 2025). Similarly, integrating ionomic data on Na^+/K^+ homeostasis with transcriptomic profiles of transporter genes (*HKT*, *NHX*., & *SOS*) has clarified the molecular basis of salinity tolerance (Roychowdhury et al., 2023).

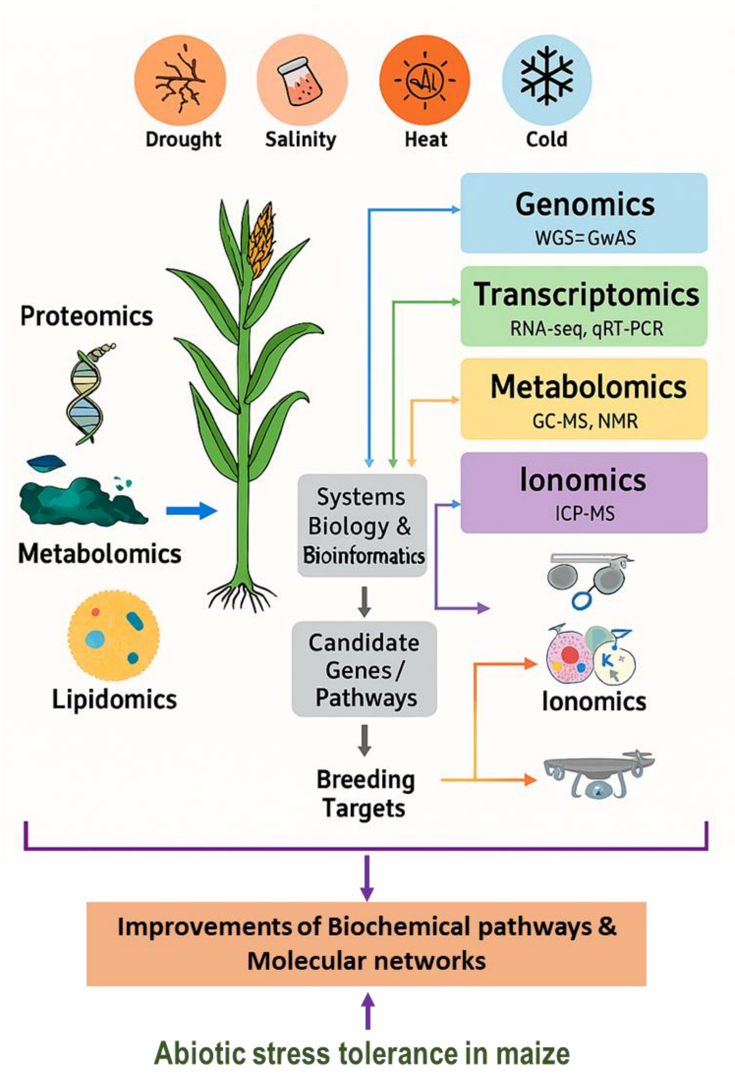

Figure 2. Integration of omics approaches for abiotic stress tolerance in maize

Recent advances in machine learning and network biology have amplified the value of integrated omics. Predictive models can now merge multi-layer datasets to construct gene–protein–metabolite–phenotype interaction maps, revealing regulatory hubs that would be invisible in single-omics studies. In maize, combining UAV-based phenomics data (e.g., canopy temperature depression, NDVI) with metabolomic profiles of stress-related compounds (e.g., proline & raffinose) has linked physiological performance to specific metabolic pathways, improving genomic prediction accuracy for yield under stress (Prasanna et al., 2021).

From a breeding perspective, integrated omics accelerates marker-assisted selection, genomic prediction, and genome editing by validating candidate genes across multiple biological layers and environments. This multi-evidence approach reduces false positives and ensures that selected targets confer stable tolerance. Moreover, integrating omics with environmental and agronomic datasets supports predictive modeling of genotype performance under future climate scenarios, aligning breeding pipelines with climate resilience and sustainability goals (Farooqi et al., 2022).

The future of integrated omics in maize lies in real-time, field-deployable multi-omics pipelines that combine portable sequencing, rapid metabolite profiling, and UAV-based phenotyping. Such systems will enable breeders to make data-driven selections in situ, drastically shortening breeding cycles and enhancing the precision of stress-tolerance improvement programs.

Table 9. Integration of omics technologies for improvement of abiotic stress tolerance in maize

Stress type	Omics layers integrated	Results/ remarks	Reference
Drought	Transcriptomics + Proteomics + Metabolomics	Coordinated upregulation of antioxidant enzymes, osmolyte biosynthesis, and ABA signaling pathways	Varadharajan et al., 2025
Heat	Genomics + Transcriptomics + Phenomics	Heat-responsive QTLs linked to stay-green and stable photosynthesis; identification of *HSP* gene clusters	Farooqi et al., 2022
Salinity	Ionomics + Transcriptomics + Proteomics	Regulation of Na^+/K^+ transporters (*HKT*, *NHX*), compatible solute accumulation, ROS detoxification	Roychowdhury et al., 2023
Cold Stress	Transcriptomics + Metabolomics + Proteomics	Induction of flavonoid biosynthesis and membrane lipid remodeling for cold acclimation	Revilla et al., 2016
Nutrient Deficiency	Metabolomics + Phenomics + Genomics	QTLs for nitrogen-use efficiency linked to amino acid metabolism and canopy reflectance indices	Farooqi et al., 2022
Flooding / Waterlogging	Transcriptomics + Proteomics + Phenomics	Upregulation of anaerobic respiration enzymes and aerenchyma formation genes	Zaidi et al., 2020
Heavy Metal Stress (Cd)	Ionomics + Proteomics + Metabolomics	Chelation via phytochelatins, sequestration in vacuoles, and antioxidant defense activation	Zhang et al., 2021
UV-B Stress	Transcriptomics + Metabolomics + Phenomics	Enhanced synthesis of UV-absorbing flavonoids and cuticular waxes	Kataria & Guruprasad, 2012

Combined Drought + Heat	Phenomics + Transcriptomics + Metabolomics + Proteomics	Shared and unique pathways for combined stress resilience; cross-talk between ABA and heat-shock pathways	Varadharajan et al., 2025
Multi-environment Trials	Genomics + Phenomics + Environmental Data	Stability indices for yield and physiological traits across diverse environments	Prasanna et al., 2021

9. FUTURE PROSPECTS

The future of omics approaches for abiotic stress tolerance in maize is poised to be shaped by deeper integration, real-time analytics, and precision breeding pipelines. Emerging technologies are moving beyond single-layer analyses toward multi-omics fusion, where genomics, transcriptomics, proteomics, metabolomics, ionomics, phenomics, and even epigenomics data are captured, processed, and interpreted in a unified framework. This integration will allow researchers to map genotype–phenotype–environment (G×P×E) interactions with unprecedented resolution, identifying the individual genes and pathways involved and the regulatory networks and cross-talk between biochemical, physiological, and developmental responses to stress.

One of the most promising prospects lies in real-time, field-deployable omics. Advances in portable sequencing platforms, rapid metabolite profiling devices, ionomic scanners, and drone-based phenotyping systems will enable high-throughput, non-destructive monitoring of stress biomarkers directly in farmers' fields. When paired with machine learning models, these real-time datasets could provide breeders and agronomists with predictive tools for selecting elite lines or adjusting management practices in response to environmental cues during the growing season.

Systems biology and AI-driven analytics will play a critical role in interpreting omics platforms' vast, complex datasets. Integrative network modeling can uncover multi-layer regulatory hubs, such as transcription factors that coordinate metabolic and ionomic shifts under drought or salinity, and feed these discoveries into genomic selection algorithms. These approaches will improve prediction accuracy for polygenic traits, reduce breeding cycles, and support the design of climate-smart maize varieties that perform consistently across diverse agroecological zones.

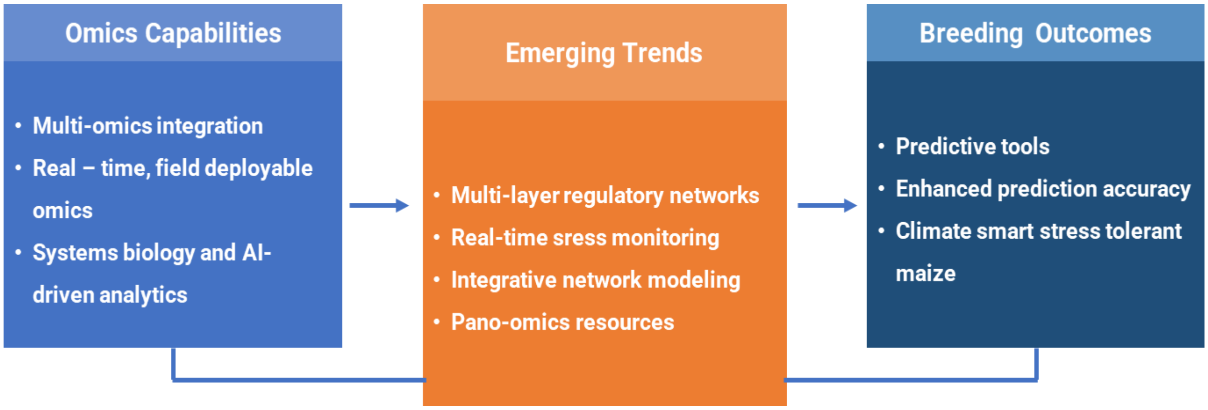

Figure 3. Prospects of the omics approach for abiotic stress tolerance in maize

The expansion of panomics resources, including reference pangenomes, multi-environment transcriptome atlases, proteome maps, metabolome databases, and ionome repositories, will further empower stress biology research in maize. These shared datasets will allow cross-study comparisons, meta-analyses, and the discovery of conserved and genotype-specific adaptive mechanisms. Coupled with genome editing tools such as CRISPR/Cas, this knowledge can be rapidly translated into targeted trait improvement, from modifying transporter genes for ion homeostasis to fine-tuning metabolic pathways for osmoprotection.

Combining omics technologies with climate forecasting, precision agriculture, and sustainable intensification strategies will shift breeding from a largely reactive process to a proactive, predictive science. In this envisioned future, maize improvement programs will not only respond to current stresses. However, they will anticipate and pre-adapt germplasm to the coming decades' environmental challenges, creating resilient, high-yielding, and resource-efficient cultivars under an increasingly variable climate. The overview of prospects of omics approaches for abiotic stress tolerance in maize was illustrated in Figure 3.

10. CONCLUSION

The rapid evolution and integration of omics technologies have revolutionized our understanding and improvement of abiotic stress tolerance in maize (*Zea mays* L.). The omics approaches like genomics, transcriptomics, proteomics, metabolomics, ionomics, and phenomics provide distinct yet interconnected insights into how maize responds to environmental stresses. These layers offer a comprehensive, systems-level perspective, uncovering the molecular, biochemical, physiological, and morphological networks driving stress resilience. By linking molecular data with large-scale phenotyping, integrated omics approaches speed up identifying reliable biomarkers and candidate genes, while enhancing predictive breeding tools for complex traits like drought, heat, and salinity tolerance.

This ability to connect genotype to phenotype and validate findings across biological scales reduces uncertainty in breeding programs. It improves the development of climate-resilient maize varieties capable of maintaining productivity under fluctuating and extreme conditions. Progress will hinge on interdisciplinary collaboration that merges omics data with advanced analytics, machine learning, and environmental monitoring. Innovations, such as portable omics devices and AI-based decision-support systems, promise real-time, genotype-specific crop management and selection.

This transition from reactive to predictive crop breeding represents a significant agricultural research and practice shift. Ultimately, the success of maize improvement amidst climate challenges will rely on translating omics discoveries into accessible and scalable solutions for farmers. Strengthening international cooperation and utilising multi-omics resources, while integrating these insights into precision breeding strategies, is essential for securing sustainable maize production and ensuring global food security.

ACKNOWLEDGEMENTS

Not applicable

AUTHORS CONTRIBUTIONS

K. A., & V.G.S. conceived the idea and wrote the manuscript. P.M., & T.V. collected the data and prepared figures. S.M.J. conceived the idea and edited the manuscript. All authors read and approved the final manuscript.

CONFLICT OF INTERESTS

The authors declare that they have no conflict of interest.

ETHICAL APPROVAL

Not applicable

FUNDING

No funds were obtained for this study.

AVAILABILITY OF DATA AND MATERIALS

All datasets analyzed and described during the present study are available from the corresponding author upon reasonable request.

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