



REVIEW ARTICLE

Multi-omics approaches for abiotic stress tolerance in rice (*Oryza sativa* L.)

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Abstract

Rice, one of the world's staple crops, faces significant challenges due to abiotic stresses such as drought, salinity and extreme temperatures, which threaten global food security. Traditional breeding methods have limitations in developing stress-tolerant rice varieties within a short time frame. Thus, there is a growing interest in employing multi-omics approaches, integrating genomics, transcriptomics, proteomics, metabolomics and epigenomics, to unravel the complex molecular mechanisms underlying abiotic stress tolerance in rice. In contrast to a single-omics method, this combination of multi-dimensional approaches provides an extensive understanding of cellular dynamics under abiotic stress conditions. This review discusses recent advances in multi-omics technologies and their applications in dissecting the molecular responses of rice to abiotic stresses. It highlights the integration of multi-omics data to identify critical genes, pathways and regulatory networks involved in stress responses and tolerance mechanisms.

Furthermore, it explores the potential of multi-omics-assisted breeding strategies for developing stress-tolerant rice varieties with improved agronomic traits. The challenges and future perspectives in utilizing multi-omics approaches to enhance rice's abiotic stress tolerance are also discussed. Overall, multi-omics approaches offer a comprehensive platform to understand the molecular basis of stress tolerance in rice and accelerate the development of resilient varieties to ensure global food security.

Keywords

abiotic stress; genomics; proteomics; transcriptomics

Introduction

"Rice, often called the "queen of cereals," is a cornerstone of global food security, sustaining billions of people worldwide. Beyond being a dietary staple, rice is rich in essential nutrients such as vitamins, minerals, dietary fibre, and phytochemicals that help prevent various diseases" (1). With a genome size of 430 Mb, rice is also a pivotal model crop in plant genomics and breeding research (2). As the global population is projected to surge to 10 billion by 2050, the demand for rice is expected to escalate, with estimates suggesting that production must rise to 852 million tonnes by 2035 to meet this growing need (3).

"However, climate change poses a serious threat to rice production, as abiotic stresses such as drought, salinity, submergence and extreme

temperatures become more prevalent." These stresses have already contributed to yield losses across approximately 50% of the global rice-growing regions(4).

Drought stress during the reproductive stage of rice severely disrupts pollination and grain filling. This leads to yield loss and potential sterility, while the damage during earlier stages, like seedling and vegetative growth, is less severe and more recoverable. The reproductive phase is the most vulnerable, with drought effects often being irreversible (5), (6). Salinity stress during early seedling and vegetative stages impairs water uptake and ion balance, leading to poor plant growth. In contrast, at the reproductive stage, it reduces grain filling and seed viability (7). Temperature extremes, such as heat stress during flowering, can result in pollen sterility, while cold stress during germination hinders seedling establishment. Flooding, especially during early growth stages, can cause oxygen deprivation, but some rice varieties exhibit resilience at later stages due to genetic adaptations (6). The advent of molecular biology and high-throughput technologies has facilitated the identification of numerous quantitative trait loci (QTLs) and genes associated with abiotic stress tolerance in rice. For instance, the *Sub1A-1* allele on chromosome 9 has enhanced submergence tolerance by inhibiting excessive leaf elongation, enabling rice plants to endure waterlogged conditions for up to two weeks(8). Additionally, the *COLD1* QTL interacts with G-protein to activate calcium channels, a crucial mechanism for conferring chilling tolerance in japonica rice varieties (9). *OsDREB1F* has been shown to enhance drought tolerance when over-expressed, leading to improved water-use efficiency and high survival rates under water-deficit conditions (10).

Drought tolerance QTLs such as *qDTY_{1.1}*, *qDTY_{3.1}* and *qDTY_{12.1}* which are identified in rice and are associated with improved grain yield under drought conditions. For instance, *qDTY_{3.1}* from the drought-tolerant donor variety, Nagin22 has been widely used in breeding programs to enhance drought tolerance in high-yielding rice cultivars (11). *Saltol* identified initially in the Pokkali variety is located on chromosome 1 and plays a significant role in Na^+ uptake regulation and K^+ ion balance critical for rice survival in saline environments (12). *OsHKT1;5* associated with salt tolerance in rice encodes a Na^+ transporter that limits K^+ accumulation in shoots by facilitating its retrieval into the roots. Varieties with functional genes *OsHKT1;5* demonstrate higher tolerance to salinity due to reduced sodium accumulation in leaf tissues (13). The rice roots' ability to absorb K^+ ions depend on the potassium channel proteins encoded by *OsAKT1* and *OsAKT2*. The combination of *OsCBL1-OsCIPK23* significantly improved the K^+ uptake mediated by *OsAKT1* or *OsAKT2* (14).

In recent years, innovative approaches such as marker-assisted selection (MAS) and genome editing have emerged as transformative tools in developing stress-resilient rice varieties. These techniques offer precision and efficiency in incorporating traits for abiotic stress tolerance, enabling faster and more accurate breeding outcomes than traditional methods. MAS has been

instrumental in introgressing the *qDTY* QTLs associated with drought tolerance into high-yielding rice varieties. , *qDTY_{3.1}*, a QTL conferring enhanced grain yield under drought conditions, has been successfully integrated into popular varieties such as Sahbhagi Dhan and IR64 using MAS (11). Similarly, MAS incorporated the *Saltol* QTL for salinity tolerance from the donor variety Pokkali into elite lines, improving rice performance under saline conditions (12), (15).

The future of rice production faces further challenges as climate change intensifies. Projections indicate that by 2050, approximately 27% of the global rice harvesting area will experience temperatures exceeding critical thresholds during the reproductive stage, posing severe risks to crop yield and quality (15). Consequently, there is an urgent need to develop new rice cultivars endowed with enhanced yield potential and robust resistance to multiple abiotic stresses. Advances in omics technologies, particularly transcriptomics and proteomics, have provided valuable insights into the molecular mechanisms underlying stress responses. For example, E3-ubiquitin has been identified as a crucial modulator of rice's response to diverse abiotic stresses, offering potential targets for genetic improvement (16). This review explores the role of multi-omics approaches in enhancing our understanding of abiotic stress tolerance in rice, focusing on crucial gene families, regulatory pathways, and the potential applications of omics-assisted breeding for developing resilient rice varieties."

2. Gene Families involved in Abiotic Stress Response

Figure 1 illustrates the different gene families involved in abiotic stress response, showing their roles and interactions. Many genes, which encode transcription factors or proteins involved in signal transduction pathways, influence rice plant growth. Transcription factors may be classified into several types based on the domains that bind to specific DNA sequences in the regulatory regions of downstream target genes. In rice, multi-omics studies integrating RNA-seq and metabolomics revealed *WRKY* TFs like *OsWRKY11* and *OsWRKY45*. These are seemingly essential regulators of drought, salt and heat stress responses (17). Crosstalk mechanisms involve the degradation of JAZ (Jasmonate zim-domain) proteins, allowing transcription factors like *MYC2* to activate defence genes. JA (Jasmonic acid) also modulates developmental processes like root formation, senescence and response to abiotic stresses (18). Multi-omics analyses have shown that *MYB* proteins, such as *OsMYB2* and *OSMYB3R*, regulate drought and cold tolerance genes. Multi-omics have demonstrated that *NAC* TFs such as *OsNAC6*, *OsSNAC1* and *OsNAC10* regulate a broad spectrum of stress-responsive genes involved in drought, salinity and heat tolerance. *OsSNAC1* enhanced drought tolerance by promoting stomatal closure and water loss and improving root architecture (19). In the plant kingdom, various (Transcription factor) TF families-including ethylene response factors (*AP2/ERF* (Ethylene Response Factor)), *WRKY*, *NAC* and *MYB*-are essential for regulating the metabolism of reactive oxygen species (ROS). The study

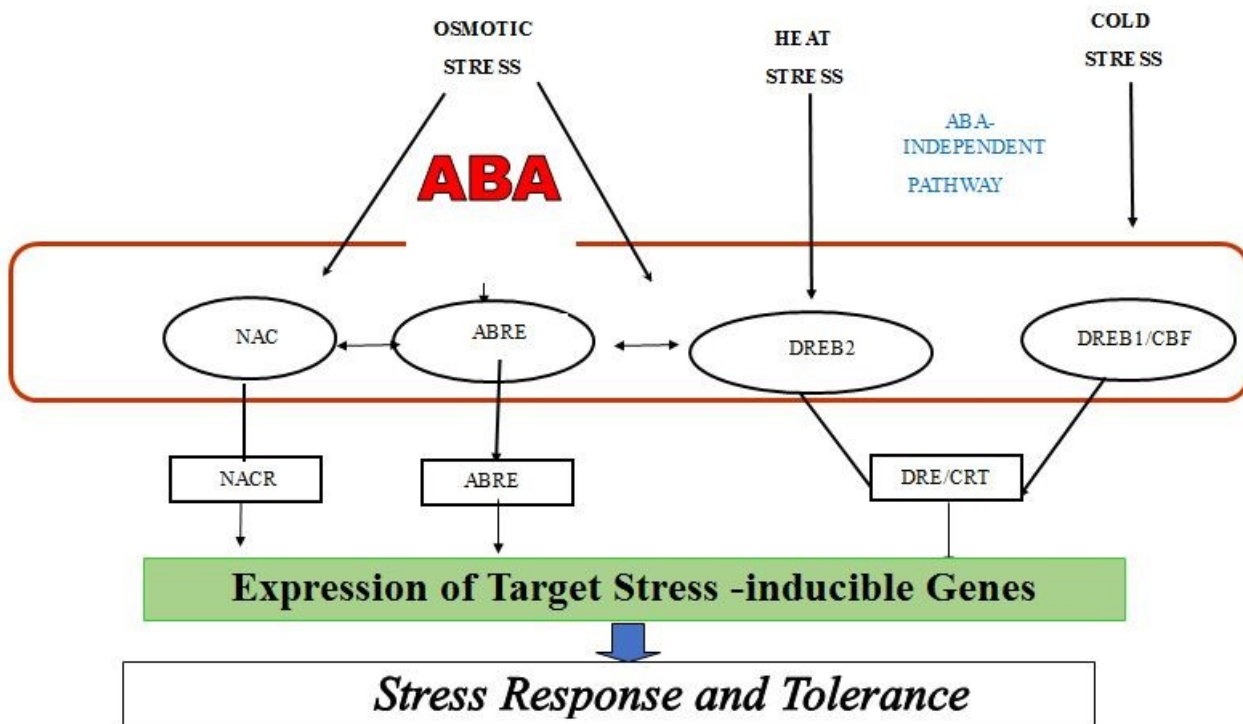


Fig. 1: A diagram illustrating the different gene families involved in abiotic stress response, showing their roles and interactions.

shows that *AP2/ERF*, *WRKY* and *NAC* primarily govern the enzymatic antioxidant system, which helps combat oxidative stress in challenging environments.

Additionally, *bHLH* (Basic helix-loop-helix), *MYB*, *bZIP* (Basic leucine zipper) and *Dof* (DNA-binding with one zinc finger) transcription factors are involved in regulating nonenzymatic antioxidant systems, including the biosynthesis of tocopherols, flavonoids, proline and carotenoids. These transcription factors are crucial in orchestrating enzymatic and nonenzymatic antioxidant responses, highlighting their importance in plant resilience against stress (20). Multi-omics approaches have revealed that the expression of *OsDREB1A* and *OsDREB1B* is specifically induced by cold stress, while *OsDREB2A* responds to dehydration and high-salt conditions. Both *OsDREB1A* and *OsDREB2A* proteins bind to the DRE sequence, activating the transcription of a GUS reporter gene in rice protoplasts. Transgenic *Arabidopsis* overexpressing *OsDREB1A* exhibited elevated levels of *DREB1A* target genes, conferring enhanced tolerance to drought, salinity, and freezing stresses (21). Multi-omics approaches have revealed that *AP2/ERF* transcription factors like *OsERF1* and *OsERF3* regulate key stress-responsive pathways in rice. These TFs control genes involved in ethylene signalling, antioxidant defence (e.g., SOD and CAT) and ion homeostasis (e.g., HKT and NHX transporters). This regulatory network enhances rice tolerance to drought and salinity stress (22). Detailed investigations of fully sequenced genomes show that transcription factors (TF) account for many encoded proteins. These can be grouped into gene families based on the presence of specific DNA binding motifs.

2.1 PPR (Pentatricopeptide-repeat proteins)

PPR proteins, grouped into P and PLS subfamilies based on motif properties, show varied distribution across rice chromosomes. Comparative genomic analysis indicates *O. rufipogon* has more PPR genes than *O. sativa*. These genes are vital in rice's response to abiotic stresses (23). A genome-wide study identified 491 PPR genes in rice, with most lacking introns, of which 246 belong to the P subfamily and 245 belong to the PLS subfamily. They're spread across all 12 chromosomes, showing distinct phylogenetic differences. Many target chloroplasts or mitochondria, with *LOC_Os10g34310* confirmed in mitochondria.

Additionally, three genes (*LOC_Os03g17634*, *LOC_Os07g40820*, *LOC_Os04g51350*) are miRNA targets (24). PPR proteins, characterized by tandem 35-amino acid repeats, bind specific RNA sequences to regulate RNA stabilization, cleavage, and editing processes. In mitochondria and chloroplasts, they prevent RNA degradation by binding to 5' to 3' untranslated regions (UTRs), ensuring proper processing and translation. This RNA stabilization is critical under stress conditions like drought and salinity, where maintaining metabolic function in organelles is essential for plant survival (25). PPR proteins are required for splicing introns in chloroplast and mitochondrial transcripts (26). Chloroplast PPR proteins regulate the splicing of plastid transcripts that encode essential photosynthetic proteins, allowing plants to maintain photosynthetic efficiency during stress (27). One of the ways PPR proteins contribute to top organellar genome maintenance is by preventing the degradation of essential transcripts. In mitochondria, PPR proteins protect mRNAs from endo-nucleolytic cleavage, ensuring the stable accumulation of transcripts required for electron transport

and ATP synthesis (25). PPR proteins practice in RNA editing, a process by which specific cytidines are converted to uridines, resulting in the reproduction of functional proteins (28). PPR protein *CBL19* is required for RNA editing in chloroplasts, and its loss leads to defects in the editing of transcripts involved in photosynthetic electron transport (29). Under heat stress, the PPR protein HCF152 stabilises RNA-encoding components of the chloroplast ATP synthase, ensuring continued energy production and maintaining photosynthesis (30). Under drought or salinity stress, PPR proteins regulate the expression of chloroplast-encoded genes involved in repairing photosystem II, a critical complex in the photosynthetic electron transport chain (27).

2.2 DIR (Dirigent) gene family

The study conducted for Insilico identification and validation of miRNAs and their DIR-specific targets in *Oryza sativa indica* under abiotic stress aimed to identify miRNAs targeting 61 DIR genes in *Oryza sativa indica* through computational methods. Three miRNAs and their respective DIR-specific target genes were identified. Expression analysis via PCR under five abiotic stress conditions (Heavy metal, low temperature, high temperature, drought and salinity) confirmed miRNA regulation of DIR gene expression in rice (31). The study conducted a genome-wide analysis of 49 DIR or DIR-like genes in rice, arranged into ten clusters. Phylogenetic analysis revealed clustering into five subfamilies: DIR-a and four DIR-like subfamilies (DIR-b/d, DIR-g, DIR-c, DIR-e) 23 OsDIRs or OsDIR-likes were responded to abiotic stress (32). The DIR gene protein is crucial in compound stereochemistry and lignification against various stresses. Lignin is synthesized by polymerising phenolic compounds, specifically monolignols (coniferyl alcohol, sinapyl alcohol and p-coumaryl alcohol). The DIR proteins are involved in the stereospecific coupling of these monolignols into lignin polymers, guiding the formation of specific linkages that impact lignin structure and composition. By controlling this process, DIR proteins form a robust and more cross-linked lignin matrix, which enhances the mechanical properties of the plant cell wall (33). The enhanced lignification of cell walls increases their resistance to mechanical damage while reducing the permeability to harmful ions, particularly sodium, under saline conditions (34). During drought stress, the DIR-mediated lignin reinforcement of the cell wall reduces water loss by limiting transpiration and preventing the collapse of cells under reduced water availability (35).

2.3 DHN (Dehydrins) gene family

Dehydrins, characterized by their intrinsic disorder and high hydrophilicity, are critical in mitigating osmotic stress-induced protein denaturation. Interacting with partially unfolded proteins stabilises these structures, preventing irreversible aggregation and preserving functional conformations, thus ensuring cellular resilience under dehydration (36). In rice, dehydrins localize to both cytoplasmic and nuclear compartments, where they bind to exposed hydrophobic regions of misfolded proteins, effectively preventing further denaturation. Functioning analogously to well-known molecular chaperons heat shock proteins, dehydrins are uniquely adapted to safeguard

cellular integrity under extreme dehydration and low water potential conditions (37). **OsDhn1** is a rice gene responsive to cold and drought stress, encoding a hydrophilic protein with motifs typical of acidic dehydrins. Its expression is induced in roots and seed coat tissues under stress conditions, regulated by the CBF/DREB pathway (38). Comparative analysis of 11 rice species revealed 65 DHNs, with three well-preserved. Domesticated species like *Oryza sativa ssp. indica*, *Oryza nivara* show conserved evolution, whereas wild species such as *Oryza sativa ssp. Japonica* *Oryza rufipogon* exhibit adaptive evolution, suggesting selection for advantageous genes over detrimental alleles (39).

2.4 MATE (Multidrug And toxic compound extrusion) gene family

Du and others identified 46 MATE proteins in rice, grouped into four subfamilies. Using qRT-PCR analysis, the expression changes in eight OsMATE genes varied under salt and drought stresses. MATE42 and MATE46 were downregulated post-treatment, while others showed different degrees of upregulation. MATE2 and MATE4 (Group 1) increased sharply 6 hours after salt stress, MATE16 and MATE45 (Group 3) peaked after 24 hours, and MATE42 and MATE46 (Group 4) decreased after salt stress (40). During salt or drought stress, MATE proteins help maintain cellular ion balance by regulating the transport of metal ions such as aluminium and excess sodium, which otherwise accumulate to toxic levels under high salinity conditions. By extruding these ions, MATE proteins maintain osmotic balance and protect cellular components from ion toxicity, thus enhancing the plant's resilience to stress (41). In addition to their role in ion regulation, MATE transporters detoxify harmful metabolites and stress-induced compounds, such as secondary metabolites or xenobiotics, which can accumulate to detrimental levels under stress conditions. By exporting these compounds out of the cytosol, MATE proteins reduce cellular damage and maintain metabolic stability, thereby supporting plant survival under adverse environmental conditions.

2.5 BURP (BNM2, Universal stress protein, RD22, Polygalacturonase 1 β) gene family

Ding et al. identified 17 BURP family genes (*OsBURP01–17*) in rice, classifying them into seven subfamilies. Two gene clusters, BURP V and BURP VI, were located on chromosomes 5 and 6. Under stress conditions, all genes except OsBURP01 and OsBURP13 were induced, with OsBURP05 and OsBURP16 responsive to all stresses (42).

The significance of DUF221 domain-containing genes (DDP genes) in various aspects of plant biology, including development, hormone signalling and stress responses, is widely acknowledged. Comparative genomics has discovered that both cultivated and wild rice (*Oryza sativa* L.) harbour a minimum of nine DDP gene members. Microarray data coupled with subsequent qRT-PCR analysis have unveiled that *OsDDP6* exhibits heightened expression across all developmental stages in FL478, a rice genotype known for its salt tolerance, despite previous studies suggesting its upregulation under salt stress. Furthermore,

investigations have revealed the involvement of *OsDDP6* in proline metabolism (43).

2.6 RP (Ribosomal protein) gene family

In rice, 56 ribosomal protein small subunits (RPS) are dispersed across the 12 chromosomes. The rice RP gene family comprises at least 70 genes, including small and large subunits (RPL). Over 50% of RP genes were upregulated in shoot and root tissues under limited water and drought conditions. RPL6, 7, 23A, 24, and 31, along with RPS4, 10, and 18a, showed significant upregulation under water limitation and drought (44). *RPL6*, a Ribosomal Protein Large subunit, validated for salt stress tolerance in rice. Overexpression of *RPL6* enhanced tolerance to moderate (150 mM) and high (200 mM) salt levels. Network analysis revealed *RPL6* interactions with translation-related proteins and helicases. *RPL6* contributes to a comprehensive signalling network, enhancing tolerance and promoting growth and yield under salt stress (45). Ribosomal proteins (RPs) participate in ribosome biogenesis and translation. During stress, specific ribosomal proteins may be preferentially incorporated into ribosomes, modulating their function to translate mRNAs encoding stress-related proteins selectively. The reprogramming of translational machinery enables rice cells to prioritize the synthesis of proteins involved in stress tolerance while downregulating global protein synthesis to conserve energy and resources (46). Ribosomal proteins also play a vital role in ribosome biogenesis, ensuring the restoration of translational capacity during stress recovery. Upregulation of the ribosomal protein gene facilitates the synthesis of new ribosomes, which is crucial for resuming normal cellular functions. This post-stress ribosome biogenesis is tightly linked to stress recovery, ensuring cells can efficiently transition from a stress-induced program to a growth-promoting one.

3. Genomics

Genomics has profoundly advanced the study of abiotic stress tolerance in rice, driven by innovations in next-generation sequencing (NGS) technologies. NGS platforms such as Illumina and PacBio have enabled the high-throughput sequencing of rice genes and quantitative trait loci (QTLs). Techniques like RNA-seq have provided detailed insights into gene expression changes under stress, identifying crucial genes involved in tolerance mechanisms (47). Furthermore, NGS has facilitated high-resolution QTL mapping and genome-wide association studies (GWAS), pinpointing genetic loci associated with stress resistance (48). Integrating NGS data with genomic and phenotypic information has deepened our understanding of the genetic architecture underlying stress responses (49). Genomics is an effective bioinformatics tool for determining the genetic underpinnings of agricultural plants' resistance to abiotic stress, which has produced extensive information on candidate genes and changes in their expression patterns during abiotic stress. Conventional and modern breeding methods for creating abiotic tolerant agricultural plants are ineffective until the molecular processes behind grain yield stability are fully understood (50). Genomic-assisted

breeding (GAB) represents a paradigm shift from conventional breeding methods by leveraging advanced genomic tools to expedite the development of stress-tolerant rice varieties. Unlike traditional approaches, which rely on phenotypic selection and empirical trial-and-error, GAB utilizes genomic data to identify and target specific genes and quantitative trait loci (QTLs) associated with stress tolerance (51). By focusing on well-characterized genetic loci, GAB accelerates the breeding cycle, enhances the accuracy of trait selection and facilitates the development of varieties with improved resilience to abiotic stresses, thus overcoming the limitations of traditional methods (52). Abiotic stress-responsive genes identified using genomic approaches were mentioned in Table 1.

3.1 Drought tolerance in rice

Recent genomic studies have identified critical regions and candidate genes linked to drought and salt tolerance in rice. Jiang et al. discovered 47 genomic regions associated with drought tolerance and 4,006 elite variants linked to salt tolerance, highlighting *AIM1*, *OsSIRP4*, and *ws1* as essential genes (53). The study conducted by (54) identified 42 QTLs for drought-related traits, with four candidate genes pinpointed through haplotype analysis. In rice, several QTLs linked to root traits have been found. For example, *qDTY_{12.1}* which is found on chromosome 12 improves root depth and branching, which in turn improves water uptake in deeper soil layers (55). Similarly, *qDTY_{3.1}* found on chromosome 3 increases root biomass and length contributing to greater water absorption capacity (56). QTLs influencing water-use efficiency primarily affect transpiration and stomatal conductance. For instance, *qDTY_{1.1}*, located on chromosome 1 enhances WUE by reducing stomatal conductance, thereby minimizing water loss through transpiration (57).

3.2 Salinity tolerance in rice

A comprehensive genome-wide analysis of DNA polymorphisms across five rice genotypes with varying salt tolerance revealed significant differences, particularly on chromosome 1, with notable variations in the frequency of SNPs and InDels across several chromosomes (58). They integrate these polymorphism data with salt-tolerant QTLs, allowing for the identification of differentially expressed genes (DEGs) associated with salt tolerance. Essential genes such as *OsSAP16*, linked to *qRSL7*, have been shown to regulate relative shoot growth under salt stress (59). The study combined linkage mapping and genome-wide association studies (GWAS) to investigate salt tolerance in japonica rice at the seedling stage. They identified a 195-kb region on chromosome 12, containing the candidate gene *LOC_Os12g34450*, associated with seedling survival rate, potassium concentration in roots, and sodium concentration in shoots, thereby highlighting its potential role in salt tolerance (60). *Saltol* is located on chromosome 1 and is vital in salinity tolerance. This gene encodes a protein in ion homeostasis, maintaining sodium and potassium balance within cells. It enhances the uptake of potassium while limiting sodium uptake. This selective ion transport prevents ionic toxicity and

Table 1: Abiotic stress-responsive genes identified using genomic approaches

S.No.	Gene	Method of Validation	Associated stress response	References
1	<i>OsPIN5</i>	CRISPR-Cas9 mutagenesis	Cold Stress	(97)
2	<i>OsHSP40</i>	T-DNA insertional mutation	Salt stress	(98)
3	<i>Os02g0528900</i>	TILLING	Heat stress	(99)
4	<i>OsRRR22</i>	CRISPR-Cas9 mutagenesis	Salinity stress	(92)
5	<i>OsCYP19-4</i>	T-DNA insertional mutation	Cold stress	(100)
6	<i>OsAKT1, OsHKT6, OsNSCC2, OsHAK11, OsSOS1</i>	TILLING	Salt stress	(101)
7	<i>OsMDH1, OsSRFP1, OsCDPK7</i>	GWAS (Genome-wide association study)	Salt stress at the bud burst stage	(102)
8	<i>STG5</i>	Combined eQTL and GWAS	Salt stress	(73)
9	<i>OsDST</i>	CRISPR-Cas9 mutagenesis	Drought and salt stress	(103)
10	<i>OsAHL1</i>	Genome-wide profiling and analysis	Drought tolerance and avoidance	(104)
11	<i>OsLEA3-2</i>	T-DNA insertional mutation	Salt and drought stress	(105),(106)
12	<i>OsMIR528</i>	CRISPR-Cas9 mutagenesis	Salt stress	(107)
13	<i>OsGSK1</i>	T-DNA insertional mutation	Cold and Salt stress	(108)
14	<i>OsTP1</i>	T-DNA insertional mutation	Drought stress	(106)
15	<i>VP14</i>	ECOTILLING	Drought stress	(109)
16	<i>SNAC1</i>	TILLING	Drought stress	(110)
17	<i>OsTEF1</i>	T-DNA insertional mutation	Drought stress	(111)
18	<i>OsSAP1</i>	T-DNA insertional mutation	Drought stress	(112)

maintains cellular functions under saline conditions. **Saltol** also impacts osmotic balance by influencing the synthesis and accumulation of osmoprotectants such as proline and soluble sugars. Rice varieties with the Saltol gene exhibit improved osmotic adjustment capabilities, enhancing salt tolerance and maintaining growth and yield under saline conditions (61).

3.3 Heat

Heat Shock Factors (HSFs) are vital in the heat stress response. HSFs are activated and translocate to the nucleus, binding to heat shock elements (HSEs) in the promoter regions of heat shock protein (HSP) genes. The binding of HSFs to HSEs initiates the transcription of these genes, leading to the synthesis of HSPs (62). Under heat stress, HSF1 undergoes a conformational change that enhances its DNA-binding affinity and promotes HSP gene expression (63). The interaction between HSFs and HSPs is a well-orchestrated process. Upon heat stress, HSFs activate the transcription of HSP genes, increasing HSP levels. In turn, elevated levels of HSPs assist in refolding denatured proteins and prevent aggregation. This reciprocal regulation helps to restore protein homeostasis and protect cells from thermal damage. HSPs also play a role in regulating HSF activity. Some HSPs can bind to HSFs, preventing them from entering the nucleus and activating the stress response. However, during heat stress, this interaction is disrupted, allowing HSFs to accumulate in the nucleus and drive the expression of HSPs (64). Rice HSFs are grouped into conserved classes A, B and C. Six HSFs are segmentally duplicated, with four pairs undergoing pseudo-functionalization. Expression analysis reveals eight *OsHsfs* unregulated during seed development and six in all abiotic stresses. *OsHsfA2a* highly responsive to heat stress across various tissues and developmental stages. *OsHsfA3* more responsive to cold and drought stress, *OsHsfA7* and *OsHsfA9* exhibit seed-specific expression. Hormones like ABA, brassinosteroids, and salicylic acid influence *OsHsf* gene expression. *OsHsfA1*

shows stable constitutive expression across tissues and stresses (65).

3.4 Submergence Tolerance in Rice

SUB1C homolog *SUB1A-1* regulator gene-carrying cultivars seem to express *SUB1C* at low levels. To put it briefly, rice cultivars (*Oryza sativa* L.) expressing the *SUB1A-1* gene exhibit decreased GA responsiveness, which forces them to use up carbon pools for leaf elongation and impedes plant growth in general. Their adaptability allows them to withstand large-scale floods (66). Additionally, the research demonstrated that while membrane peroxidation and malondialdehyde (MDA) generation were significantly lower in transgenic rice (*Oryza sativa* L.) plants than in non-transgenic rice (*Oryza sativa* L.) plants, transgenic rice plants had substantially higher superoxide dismutase activity (67). *SUB1A* gene confers a remarkable ability to survive complete submergence for up to 2 weeks, a trait that has dramatically benefited farmers in regions prone to flash floods. The discovery and incorporation of the *SUB1A* gene began with identifying submergence-tolerant rice landraces like FR13A, which are traditionally grown in India and Bangladesh. *SUB1A* gene encodes for a specific ethylene-responsive transcription factor that helps plants remain dormant during flooding, thereby conserving energy and preventing rapid elongation, which is typically detrimental in submerged conditions (66). Using marker-assisted selection, scientists could transfer *SUB1A* widely grown high-yielding rice varieties. This led to the development of popular varieties such as Swarna-Sub1, which combines submergence tolerance with the desirable traits of Swarna, a high-yielding rice variety cultivated across millions of hectares in South Asia (68). Adopting these varieties has succeeded, with millions of farmers in Bangladesh, India and Southeast Asian countries now cultivating *SUB1A*-carrying rice. The yield advantages in flood-prone regions have been substantial, providing resilience to farmers facing increasingly erratic weather patterns (69).

4. Transcriptomics

Transcriptomics, the comprehensive study of RNA transcripts in a given cell or tissue, has become a fundamental tool in molecular biology for understanding gene regulation. It plays a crucial role in identifying differentially expressed genes (DEGs) under stress conditions by comparing gene expression profiles between stressed and non-stressed states. Identifying DEGs helps elucidate the molecular mechanisms governing stress responses contributing to fields such as plant stress biology (70),(71). Transcriptomics is vital for analysing gene expression in rice under abiotic stresses like drought, salinity, and flooding. This approach helps uncover vital regulatory pathways and stress-responsive genes contributing to improved stress tolerance and crop resilience (72). Table 2 represents the QTLs for rice trait improvement and stress management.

4.1 eQTL Mapping and Salt Tolerance

Transcriptome analysis of 202 rice accessions under normal and salt stress conditions revealed 22,345 eQTLs for 7,787 eGenes in normal conditions and 27,610 eQTLs for 9,361 eGenes under salt stress. Integration with GWAS identified *STG5* as a critical gene at the major salt tolerance locus *qSTS5*, crucial for maintaining Na^+ / K^+ Homeostasis by regulating the *OsHKT* gene family (73). High-generation recombinant inbred lines (RILs) developed from a cross between Luohui 9 and RPY geng revealed four novel salt tolerance QTLs: *qST-3.1*, *qST-5.1*, *qST-6.1* and *qST-6.2* on chromosomes 3, 4, 5, 6 and 8. Candidate genes such as *LOC_Os05g14880*, *LOC_Os06g01250* and *LOC_Os06g37300* were identified in association with these QTLs (74).

4.2 Cold Tolerance in Weedy and Cultivated Rice

Cold stress poses significant challenges to rice at the seedling stage as low temperatures can delay or inhibit germination, reduce seedling vigour and impair early plant development. Seedlings exposed to cold stress often exhibit stunted growth, chlorosis and poor root development, ultimately compromising plant survival and yield potential (75). Cold stress induces floret sterility, resulting in grain abortion and low grain yield. Cold stress causes pollen sterility due to tapetal hypertrophy and nutrient imbalances (76).

The research analysed cold tolerance in weedy rice lines (WR 03-35, WR 03-26) and cultivated rice lines (Kongyu 131, 9311) during the seedling stage. "RNA-seq identified more differentially expressed genes (DEGs) in cold-tolerant genotypes, with semi-quantitative RT-PCR and qRT-PCR validation. These findings underscore the potential weedy rice gene resources for enhancing cold tolerance in breeding programs" (77).

4.3 Heat Stress Response

Heat stress during the reproductive phase significantly impairs rice growth by affecting pollen viability, fertilization and grain filling, leading to reduced spikelet fertility and lower grain yield (78). Prolonged exposure to high temperatures during the reproductive phase increases sterility and poor grain quality, thus compromising yield potential (76). Heat stress disturbs another dehiscence, resulting in low pollen dispersal and fewer pollen on the stigma. Heat stress reduces starch biosynthesis in developing grain, which reduces starch accumulation (76). Moreover, heat stress accelerates plant senescence, shortening the grain-filling period and reducing overall biomass (79).

The research conducted by (80) identified vital genes associated with heat stress survival, including *LOC Os02g12890* and *OsCML4*. The study employed GWAS and transcriptome analysis to identify 11 genes linked to heat stress response, with specific mutations in *LOC Os03g16460* and *LOC Os05g07050* contributing to heat tolerance, especially in indica rice accessions (81).

4.4 Drought Tolerance

The research focused on drought stress in rice seedling roots, finding 1,098 upregulated genes, with 68% previously unreported. The study highlighted the role of RING-box E3-ligases in the ubiquitin-proteasome pathway and identified 29 genes linked explicitly to drought tolerance, predominantly involved in protein degradation and metabolism. *OsPhyB* helps modulate ROS processing, underscoring the potential for manipulating drought tolerance in rice through these newly characterized genes (82). NAC, MYB and HD-ZIP transcription factors were also implicated in the salt stress response (83).

Table 2: QTLs for rice trait improvement and stress management

S.No.	QTL	Trait/Stress	References
1	qSSISFH8.1	Reproductive stage salinity tolerance	(113)
2	qHTT8	Heat tolerance at the flowering stage	(114)
3	qDTY3.2	Grain yield under drought stress	(115)
4	qTT4 and qTT5	Heat stress	(116)
5	qSTS5	Salt stress	(73)
6	qST-3.1, qST-5.1, qST-6.1, and qST-6.2	Salt stress	(74)
7	qSTIPSS9.1, qSSIPSS12.1 and qSSIY3.1	Heat stress	(117)
8	qHTSF4.1	Heat stress	(118)
9	Sub1	Submergence	(119)
10	<i>Saltol</i>	Salinity stress	(119)
11	qDTY12.1	Grain yield under drought	(87)

4.5 Meta-Transcriptomics and Abiotic Stress Tolerance

"Meta-transcriptomics, which analyzes gene expression across multiple species or conditions, has been employed to identify 6,596 abiotic stress-tolerant (ASTR) genes, including significant hub regulatory genes and transcription factors. Among these, 73 ASTR genes were located within known QTLs for abiotic stress traits. The functional annotation of uncharacterized ASTR genes revealed their potential roles in stress response, with over 65% showing differential expression in tolerant genotypes under stress conditions (84).

5. Proteomics Approaches in Rice Abiotic Stress Research

Proteomic approaches involve the systematic identification and quantification of proteins, often utilizing techniques such as two-dimensional electrophoresis (2-DE), mass spectrometry (MS), and isobaric tags for relative and absolute quantitation (iTRAQ). These methods allow for detecting differentially expressed proteins (DEPs) under stress conditions, providing a deeper understanding of the molecular mechanisms involved in stress responses.

5.1 Drought Stress Responses

Drought stress significantly impacts rice growth and yield, and proteomic analyses have identified numerous drought-responsive proteins across different rice genotypes and developmental stages.

5.1.1 Drought-Responsive Proteins

The study conducted by (85) identified 42 proteins exhibiting significant abundance changes in rice plants under gradual water stress. Among these, proteins involved in photosynthesis, antioxidant defence and protein biosynthesis were notably altered. The study conducted by (86) highlighted the significance of the ABA-GA antagonistic relationship in drought resistance, as evidenced by the varied expression patterns of 31 proteins during the panicle emerging stage under drought stress.

5.1.1 Metabolic Pathways and Drought Adaptation

Proteomic studies have revealed that metabolic pathways related to sugar, starch, and amino acid metabolism are crucial for drought tolerance. According to the study, a tandem mass tag (TMT)-based proteomic approach is used to identify proteins associated with drought-specific morpho-physiological responses in a near-isogenic line (NIL) carrying the *qDTY12.1* QTL (87).

5.2 Salinity Stress Responses

Salinity stress, another major abiotic factor limiting rice productivity, induces significant proteomic changes, particularly in salt-tolerant and sensitive genotypes.

5.2.1 Salt-Responsive Proteins and Mechanisms

"According to the study, iTRAQ was used to analyze proteomic differences between salt-sensitive IR64 and salt-tolerant pokkalice rice seedlings, revealing that Pokkali roots accumulated more Na^+ ions and stress tolerance-related proteins compared to IR64" (88). Similarly, another study identified stress-responsive proteins in *Saltol* QTL-carrying FL478 rice, highlighting the importance of maintaining mitochondrial activity and amino acid

metabolism under salt stress (89).

5.2.2 Key Proteins in Salt Tolerance

OsCYP2, identified by (90), significantly enhances salt stress tolerance in transgenic rice seedlings by preserving photochemical efficiency and minimizing lipid peroxidation, highlighting its crucial role in stress mitigation." This highlights the importance of specific proteins in mitigating the effects of salinity stress.

5.3 Heat Stress Responses

Heat stress severely affects rice growth and development, with proteomic studies identifying several vital proteins and pathways involved in heat tolerance.

5.3.1 Heat-Responsive Proteins

"A proteomic analysis of the heat-sensitive rice genotype IET21405 identified proteins involved in energy production, photosynthesis, and protein synthesis (91). Two-dimensional difference gel electrophoresis (2D-DIGE) was used to identify early heat stress-regulated proteins, including ubiquitin-specific protease *OsUBP21*, which plays a critical role in heat stress tolerance (92)."

5.3.2 Proteomic Insights into Heat Stress

"Heat stress was shown to alter the abundance of proteins related to glycolysis, the TCA cycle, and redox homeostasis in rice grains, highlighting the importance of metabolic adjustments in response to elevated temperatures (93)."

5.4 Cold Stress Responses

Cold stress is particularly detrimental to rice, especially during the early stages of development. Proteomic analyses have identified several cold-responsive proteins that contribute to cold tolerance.

5.4.1 Cold-Responsive Proteins

Ji and Zhou compared cold-sensitive and cold-resistant rice varieties, identifying 59 proteins linked to cold stress resistance (94). Similarly, Wang JinZi and Wang Jun found that cold-tolerant hybrid wild rice showed quicker expression of cold-responsive proteins, which improved cell integrity under cold (95).

5.4.2 Mechanisms of Cold Tolerance

Research has shown that nystose treatment enhances root growth and cold tolerance by modulating signaling pathways such as abscisic acid, jasmonate and MAPK cascades (96)."

Conclusion

Functional characterisation and analysis of genes essential to agronomic parameters are the keys to increasing rice output. "For several years, high-throughput technologies have provided valuable insights into the molecular mechanisms underlying rice development and stress responses." While transcriptomics helps to clarify the intricate RNA expression networks in rice that might be critical to yield or stress responses, genomics gives information on the dominant or recessive genes in different rice types. Proteomics similarly helps identify critical proteins that increase rice quality. Bioinformatics

databases integrate data from the omics sciences to provide a comprehensive understanding of the variables influencing rice's ability to respond to stress or improve its quality, quantity, or both. To improve rice crops, omics-generated datasets can speed up gene discoveries and functional characterizations. Furthermore, studying plant system biology has improved research on integrative omics, metabolism, and stress responses. "The advent of CRISPR/Cas9 genome editing technology, applied in conjunction with omics research, has further expanded the potential of rice science. This technology has significantly broadened the scope of rice research, enabling more precise gene editing to optimize traits. Integrating state-of-the-art technologies with omics-based research presents a promising avenue for addressing stress management and boosting rice yields."

Authors' contributions

PA- collected literature and wrote the manuscript; RP - helped in securing research funds and approved the manuscript; helped in editing, summarizing and revising the final manuscript; SM- helped in summarizing and revising the manuscript; MR- helped in summarizing and revising the manuscript, AS - helped in summarizing and revising the manuscript, KPK - helped in summarizing and revising the manuscript.

Compliance with ethical standards

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Declaration of generative AI and AI-assisted technologies in the writing process

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