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Abiotic Stress Tolerance and Breeding Strategies in Rice: A Comprehensive Review

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Abstract**—** *Abiotic stresses such as drought, salinity, and temperature extremes, as well as their combinations, often occur during rice production, negatively affecting rice growth, yield, and quality. The impacts include reduced leaf area and photosynthesis, inhibition of spikelet formation and development, and oxidative stress. At the same time, tolerance is determined by the combination of germination capacity, root volume, root number, plant height, and tiller number. The latest research identifies genetic and epigenetic mechanisms of tolerance, including cold tolerance linked to DNA hypomethylation, which underlies acquired and heritable tolerance. The gene pool of wild, weedy, and pre-breed rice varieties can be used to improve cultivated rice's yield potential and tolerance to multiple stresses. Studies on rice's response to salt stress reveal the role of QTL Saltol and mechanisms of ion homeostasis and antioxidant defense that can be harnessed to improve tolerance. The authors conclude that combined physiological, genetic, molecular, epigenetic, and multi-omics approaches, along with the utilization of the wild rice gene pool, speed breeding technologies, genome editing, transgenics, marker-assisted selection, QTL mapping, and GWAS, could be used to develop novel varieties with increased tolerance to multiple stresses, stable yield, and improved grain quality.*

Keywords**— Rice, abiotic stress, marker-assisted selection, genome-wide association studies, multi-stress tolerance and breeding strategies.**

I. INTRODUCTION

Rice (*Oryza sativa* L.) is a staple crop in which the biotic and abiotic environmental conditions, including high temperatures, drought, and salinity, affect plant growth, yield, and quality. Abiotic stresses are increasingly recognized as critical threats to global food security, given rice productionis high vulnerability to adverse environmental conditions. The growth, yield, and quality of rice are often compromised by unfavorable edaphic and climatic factors. Therefore, rice's response to abiotic stress is critical to investigate to improve stress-resistance breeding and ensure food security and ecosystem services (Sokra *et al*., 2025). Advancements in breeding techniques, such as genetics and genetic engineering, offer novel opportunities to develop crops with improved tolerance and resistance to biotic and abiotic stresses. Genetic breeding can be done in various rice varieties; however, those widely used as wild types for genetic modification include Nipponbare, Zhonghua 11, 9311, and IR64 due to their genome sequence, genetic background, and tissue culture response – attributes ideal for gene function identification and breeding application (Wang *et al*., 2025). Diverse abiotic stresses usually interact in different ways to impair rice productivity. Besides, multiple stresses are often present in the same environment and at the same time or sequentially, and/or one abiotic stressor causes another, for instance, osmotic stress causes salt stress. The interactions of multiple abiotic stresses usually disrupt normal rice growth and development, therefore reducing yield and quality (Yao *et al*., 2025). Generally, abiotic stress tolerance in rice is

determined using germination percentage, root volume, root number, plant height, and tiller number (Yao *et al*., 2025).

II. MECHANISMS OF ABIOTIC STRESS IN RICE

1. Drought Stress

Insufficient rainfall is a major non-biological factor hindering rice cultivation across different geographical regions. The growth and maturation of these plants require a large volume of water, making this cereal crop highly sensitive to changes in environmental moisture (Wang *et al*., 2025). In response to water scarcity, rice biological systems undergo multiple changes to remain alive. As the soil begins to dry, root systems extend deeper and expand their physical reach to collect remaining moisture, but as the dry period continues, these physical changes fail to provide sufficient hydration, and the roots stop growing in length and density (Wang *et al*., 2025). The pores on the surface of the leaves manage the intake of carbon dioxide and the release of water vapor. Under dry conditions, those pores close to prevent water loss, but this also prevents the plant from converting sunlight into energy (Pedrozo *et al*., 2025). To survive the conditions, internal cells increase their concentration of dissolved substances to draw in more water, thereby preserving the physical integrity of the cellular walls. On farms, growers use methods such as periodic flooding, measured water delivery, and precise tubing systems to provide crops with the necessary moisture. By using those strategies, agricultural workers provide sufficient water for rice and use less of the available freshwater supply (Wang *et al*., 2025).

2. Salinity Stress

Worldwide, about 100 million hectares of land are estimated to be salt-affected, representing 7% of the world's land area. Salt (salinity) buildup in the soil results from salts (mainly sodium chloride/NaCl) in the irrigation water and, as a consequence, causes osmotic and ionic stress. At a soil soluble salt concentration of approximately 0.3%, rice production is estimated to fall by more than half on average (Wang *et al*., 2025). Due to climate change and suboptimal irrigation practices, the global habitable area is expected to further expand (Saleem *et al*., 2025).

Salinity stress limits rice growth and yield through osmotic and ionic effects, disrupting water and nutrient uptake and homeostasis. A study in 2026 indicated that shoot biomass and photosynthesis, along with nitrogen, phosphorus, and potassium concentrations, were generally decreased with increasing salinity levels, whilst Na+ concentration in leaves and the Na+/K+ ratio increased. At high salinity, rice yield was also significantly reduced, with a yield penalty of 34.2-54.9%, demonstrating the impact of salt stress. Salinity also had a significant effect on rice during reproductive development, with relative water content, chlorophyll, grain yield, and 1000-seed weight decreasing, while electrolyte leakage and proline increased, illustrating the physiological effects. Molecular studies now indicate oxidative damage caused by increased reactive oxygen species, and the use of antioxidants, osmo-protectants, and transporters, including sodium-hydrogen potassium transporters (HKT) and Na+/H+ antiporters (NHX), helps adapt to salt stress by maintaining cellular water balance and ionic homeostasis. The integration of physiologically based screening strategies and molecular studies is important for improving rice tolerance to salt stress by maintaining ion balance, photosynthesis, and yield (Wei et al., 2026).

3. Temperature Stress

Extreme temperatures, both high and low, limit rice production. High temperatures during flowering reduce pollen viability and, consequently, spikelet fertility. Moreover, prolonged exposure to high temperatures increases respiration and reduces the dry matter available for yield. On the other hand, low temperatures during the establishment phase or at the booting stage slow down plant development and may cause sterility in the panicle. These factors indicate that temperature-tolerant varieties and appropriate growing techniques are critical for rice production (In et al., 2025).

4. Oxidative Stress

In rice, reactive oxygen species (ROS) are primarily produced in response to environmental stresses such as drought, salinity, heat, and pathogen infections. Cell organelles such as chloroplasts, mitochondria, peroxisomes, and the plasma membrane, as well as NADPH oxidases, are the main sites of ROS generation under these stress conditions. Drought stress, for instance, increases photorespiration in chloroplasts and, as a consequence, produces more ROS, which can cause oxidative damage to various biomolecules, including proteins, lipids, and DNA. During drought, peroxisomes also act as ROS generators, worsening oxidative stress. Genes like OsRbohA encode plasma membrane NADPH oxidases, which are induced in response to salt and heat stress, thereby further increasing reactive oxygen species (ROS) activity. Overproduction of ROS may cause cell death, DNA fragmentation, and membrane damage; however, ROS can also act as second messengers to mediate and enhance stress-tolerance mechanisms (Tavu and Redillas, 2025).

Antioxidant Defense Systems in Rice

To eliminate damaging free radicals in plant cells, rice employs an antioxidant defense system that includes both enzymatic and non-enzymatic components. As one of the principal antioxidant enzymes, SOD works by converting O2- into H2O2, which is then broken down into water and oxygen by CAT and/or APX. In addition, the enzymatic action of GPX and GR helps maintain redox homeostasis by reducing H2O2 and hydroxyorganic compounds. These stress-responsive gene-controlled proteins have a preventive role against cellular oxidative injuries (Tavu and Redillas.,2025).

Physiological and Molecular Responses to Abiotic Stress

Osmotic stress occurs very soon after saline stress, whereas ion toxicity from excess Na+ and Cl occurs much later. Excessive accumulation of sodium and chloride ions in intracellular compartments in rice can cause ionic imbalance, also known as toxic ion stress, leading to abnormalities in cellular metabolism and, ultimately, early leaf fall and plant death. Several pathways contribute to Na+ toxicity. Initially, it reduces the rate of enzyme activity and influences metabolism by replacing K+. Excess sodium ions in the cytoplasm also limit the transport and absorption of K+ and macro- and micronutrients such as zinc (Zn2+), calcium (Ca2+), nitrogen (N), and phosphorus (P) (Saleem *et al*., 2025).

Na+ causes plasma membrane depolarization, resulting in K+ efflux into the cytoplasm. This activates endonucleases and caspase-like proteases, leading to cell death and further injury. Toxicity is another major cause of ionic injury, as it can damage N and S accumulated in rice. To cope with ionic disruption, many processes have evolved, including exclusion and tissue tolerance. It has been reported that low-level NaCl (5 mM) improves plant growth by increasing shoot and root dry weights. A NaCl (5 mM) treatment resulted in an increase in K, S, Zn, and Cu levels. These increases could not be observed and were not immune to the NaCl treatments. These resulting increased elements could promote higher processes like photosynthesis and faster cell growth. Noted: S plasma levels were prominent across all studies, with high plasma cysteine levels in high-NaCl treatments. This can be explained by the fact that increased S plasma levels confer considerable growth-promoting effects (Saleem *et al*., 2025).

Plants cope with osmotic stress mainly by accumulating small molecules such as trehalose and proline that help maintain osmotic balance. Key genes involved in osmotic stress response include the trehalose biosynthesis gene OsTrehalose-6-Phosphate Phosphatase 1 (OsTPP1) and the proline synthesis gene OsPyrroline-5-Carboxylate Synthetase (OsP5CS). (Ma *et al*., 2025).

There are many genes responsible for water stress adaptation and rice yield, such as DROT1 RoLe1 ZIP23 MYB ERF/DREB, and NAC, among others. DROT1 is responsible for increased drought tolerance via higher cellulose deposition and retention of cellulose crystallinity. As a result, cellulose wall strengthening and water transport are affected; its expression is drought-response ERF3 and ERF71 dependent. NAC TFs are part of broader stress-response networks, while OsNAC15 boosts OsNCED1, OsNCED2, and OsNCED5 (ABA pathways), thereby regulating the plant's ability to survive drought and salt stress. And it was recently shown that DREB, NAC, and MYB transcription factors, together with ABA signaling and ROS homeostasis, form complex regulatory networks that contribute to osmotic adjustment, antioxidant defense, and drought adaptation in rice. From all of that, it appears that combining drought-tolerant genes with physiological screening and molecular breeding will yield promising results for developing drought-tolerant rice cultivars (Wang *et al*., 2025).

1. Molecular adaptations and breeding implications

At the molecular level, rice regulates kinases, phosphatases, and transcription factors to stabilize ROS levels and enhance stress resilience. Antioxidant defense is modulated by polyamine and proline metabolic pathways, while QTLs such as sub1A are known to contribute to oxidative stress tolerance, particularly in genetically bred varieties for submersion resistance. Many studies have found that more than 50 transcription factors are differentially expressed between resistant and susceptible rice varieties under oxidative stress. These findings support breeding of multi-stress-resistant rice varieties by utilizing the underlying genetic variability (Tavu and Redillas, 2025).

Molecular investigations are pointing more clearly towards Really rice has to be improved on molecular level targeting not single stresses but multiple abiotic stress response pathways. A recent meta-transcriptomic analysis pinpointed the regulatory factors, which are common to drought and iron toxicity, including ROS-related genes and transcription factors like DREB2A, ERF95 and ERF102. These discoveries give an opportunity for molecular breeding of rice plants having tolerance to various stresses.

With the help of recent progress in understanding rice genomics and genome editing, we can say it will become increasingly possible not only to identify the regulatory genes and metabolic pathways but also to pinpoint those genes that will be useful to produce ROS-scavenging proteins, maintain ion balance, and communicate stress signals that will allow for the development of crops with

specific desirable traits. Besides that, the most recent research shows that breeding can be A lot improved when molecular techniques are combined with conventional ones; an example is the manipulation of a rice TPP riboswitch that brought together the benefits of increased yield, higher nitrogen use, better quality of grain nutrition, greater cold adaptability, and better resistance to pests (i.e., blast). Because of this, future rice breeding programs should focus on both stress resistance and nutrient-utilization efficiency, combining them with yield stability and adaptability to changing climates (environmental changes) to develop rice cultivars suited to the changing conditions. Bottom line: a cross-cutting (multidisciplinary) collaboration among genomics, plant physiology, metabolomics, and breeding has great potential to enable climate-smart and environmentally sustainable rice production (Ahmdikhah *et al*., 2025).

III. GENETIC BASIS OF ABIOTIC STRESS TOLERANCE

1. Genetic diversity in wild and weedy rice and its relevance to abiotic stress

Weedy rice (*Oriza sativa* f. spontanea) represents a crop wild relative (CWR) to domesticated rice (*Oriza sativa*) with the same genome type AA (2n = 24). Weedy rice is considered a weed in rice cultivation fields across the globe, primarily in temperate zones and the tropics.1 Due to its reddish color of pericarp, it is popularly named 'red rice'. Although research of this type is progressing, the exact origin of weedy rice remains a major mystery, and as a result, it is often regarded as the clearest case of convergent evolution among rice plants (Roy *et al*., 2023).

Genetic differences between wild and weedy rice varieties are an important source of adaptive traits that increase abiotic stress tolerance in cultivated rice. A broad genomic comparison of 180 wild rice accessions revealed significant genomic differences, including millions of SNPs and InDels, and wild rice being overall more genetically diverse than domesticated rice; meanwhile, some good adaptive alleles might have been lost during the selection of desirable varieties. *Oryza rufipogon* retains genes that enable the plant to survive drought, cold, and salinity stress and to resist diseases, and WRKY67 has proven to be a useful gene for developing salt-resistant rice. In addition, weedy rice exhibits substantial genetic and morphological variation, as well as traits that could aid the study of genotype-environment interactions and the discovery of desirable alleles.

So, the conservation and use of wild and weedy rice materials may expand the genetic base of rice and help create rice varieties that are more resistant to climate change (Tao et al., 2026).

2. Pre-breeding with *Oryza rufipogon* and RIL population

Before one actually begins cross-breeding, parental breeding is required, as it helps develop improvement programs in rice, where several challenges, such as climate change, food security, malnutrition, and sustainability, are being addressed. Through the activation of the latent genetic resources of wild relatives (O. rufipogon), we managed to set up two major large-scale pre-breeding (F8:9) populations, each containing 100 RILs (BWF and CWF), against the background genes of two local indica cultivars, i.e., Badshabhog and Chenga. When the results of an ANOVA test together with an estimate of broad-sense heritability (H percent), the level to which the change of a trait can be passed on through generations, genetic variation, PCA, and Mahalanobis D2 test statistics have been examined, there is a convergence among them that indicates a significant widening of the genetic variation of BWF and CWF RILs which is the combined effect of alien introgression of underutilized wild rice (O. *rufipogon*) with the previously hidden genes (Roy and Shil, 2025).

3. Variation among traditional, modern, and genetically engineered varieties

Different studies have compared how rice cultivars respond to different stress conditions. Traditional, modern, and genetically modified rice cultivars have all demonstrated a difference for how well they tolerate stress. As a traditional variety, Co13 exhibited strong tolerance to oxidative stress - by having efficient photosystem II function and low ion leakage - both suggesting a good maintenance of membrane integrity when under stress. Korgut is a rice variety that contains more unsaturated fatty acids than Jaya, which promotes membrane fluidity and allows it to better tolerate salinity-induced oxidative stress. These features show that local traditional varieties have undergone natural selection and adaptation to their environments and, as a result, are useful in saline or drought-prone areas (Tavu and Redillas, 2025).

Modern Japanese-style rice cultivars like Koshihikari and Indian-type varieties like IR58 have demonstrated a similar level of resistance to oxidative damage, comparable to traditional varieties. This happened mainly because they were bred to select stress-tolerant traits. Such advancements are in line with changes in rice breeding, where the focus has shifted from biotic to abiotic stress resistance to support productivity under varied environmental conditions (Tavu and Redillas, 2025).

Through genetic engineering, we can better harness rice plants' potential against oxidative stress. The technique involves adding genes into rice genome which results in an increase in rice plants' ability to resist the effects of stress through the enhancement of the plants' antioxidant system. The SUB1 gene, which has been introduced into varieties such as Binadhan-11 and BRRI dhan52, increases the abundance of antioxidant enzymes, namely ascorbate peroxidase and peroxidase, so these SUB1 rice varieties are more stress-tolerant than the non-SUB1 varieties. Such modifications allow rice varieties to achieve higher yields even under stress and to show greater resilience to environmental changes (Tavu and Redillas, 2025).

IV. BREEDING STRATEGIES FOR ABIOTIC STRESS TOLERANCE

1. Traditional breeding and selection

Traditional methods of rice plant breeding simply involve identifying rice varieties with desirable traits and then hybridizing them. By using a screen between generations, plants that are better able to resist stress and exhibit other traits have been developed. The main point is to identify genes involved in stress resistance that can be introduced into offspring by crossing parent plants with the trait of interest. For instance, one may cross drought-resistant wild rice varieties with drought-sensitive yet high-yielding cultivated varieties of the plant so that offspring would show both high-yielding and drought-resistant characteristics. Some of the techniques used in traditional plant breeding include family selection, recurrent selection, backcrossing, and induced mutations, to name but a few (Sokra *et al*., 2025).

2. Molecular marker-assisted selection and GWAS

Molecular MAS makes contemporary plant breeding much easier and faster. By identifying molecular markers closely linked to resistance traits to abiotic and biotic stresses, breeders are better equipped to select plants with the desired genes, resulting in higher breeding efficiency and success rates (Wang *et al*., 2025). A thorough study of the abiotic stress response genes will pave the way for the emergence of molecular markers that are closely linked to these genes and, in some cases, virtually interchangeable with them. In rice, such markers enable early screening of breeding materials for resistance to various stresses, allowing breeders to work faster and deliver stress-tolerant varieties on time (Wang *et al*., 2025).

3. Gene Editing Technologies

Current gene-editing technologies enable us to develop varieties of high-yield rice that meet consumer expectations and are highly robust (Wang *et al*., 2025). Using CRISPR/Cas9 technology, which can edit multiple genes simultaneously, researchers induced mutations in the GS3 and GL3.1 genes, which are responsible for determining rice grain shape. The double-mutant gs3 gl3.1 rice they developed had larger, rounder grains, with major benefits in grain appearance, fullness, yield, and stress resistance compared with the single-mutant gs3 rice (Wang *et al*., 2025). Also, deleting the OsPAO5 gene leads to much longer, fatter rice grains and higher grain yields, along with increased stress tolerance and enhanced embryo elongation (In *et al*., 2025).

Adding CRISPR/Cas9 to rice breeding methods opens an avenue for creating new rice varieties with strong, long-lasting resistance (Pedrozo et al., 2025). Since genome-editing techniques target weak points, such as host-susceptibility genes, and build resistance mechanisms, they accelerate the development of high-quality rice varieties and reduce our reliance on pesticides (Pedrozo *et al*., 2025).

Table 1. Quantitative evidence directly relevant to abiotic-stress tolerance and breeding in rice. Values are reported by the cited studies and are not pooled estimates.

Dataset	Stress or breeding context	Rice sample	Important Traits	Breeding implication
Wei *et al.* (2026)	High salinity (HS) vs low salinity (LS)	4 cultivars; 2-year field study	Grain yield reduced 34.2–54.9% at HS	Strong yield penalty supports screening for yield stability and ion-homeostasis traits
Wei *et al.* (2026)	Salinity tolerance comparison	2 tolerant vs 2 susceptible cultivars	Tolerant rice yielded 10.1% more at LS and 27.1% more at HS	Tolerance traits can preserve yield under stronger salinity
2Ma *et al.* (2025)	Modern cultivar genomic/phenomic diversity	6,044 cultivars; 212 datasets	3,131 QTLs linked to 53 phenotypes	Large diversity panels can support breeding-by-design and GWAS
Roy & Shil	Pre-breeding with O. *rufipogon*	100 BWF + 100 CWF RILs	Heritability 74.42–99.87%; first four PCs explained	Wild-rice introgression can broaden selectable variation

(2025)			73.74% in BWF	
Tao *et al.* (2026)	AA-genome wild-rice pan-genomics	180 wild accessions; 5 species	67–224 Mb novel sequence per species	Wild rice contains substantial sequence diversity lost or selected during domestication
Ahmdikhah *et al.* (2025)	Multiple abiotic stresses	Transcriptomic meta-analysis	DREB2A, ERF95 and ERF102 were among shared response factors	Shared regulatory nodes are candidates for multi-stress breeding
Song *et al.* (2025)	Cold stress / epigenetics	Multigenerational cold exposure	Heritable ACT1 promoter hypomethylation associated with acquired cold tolerance	Stable epialleles may complement conventional genetic resources

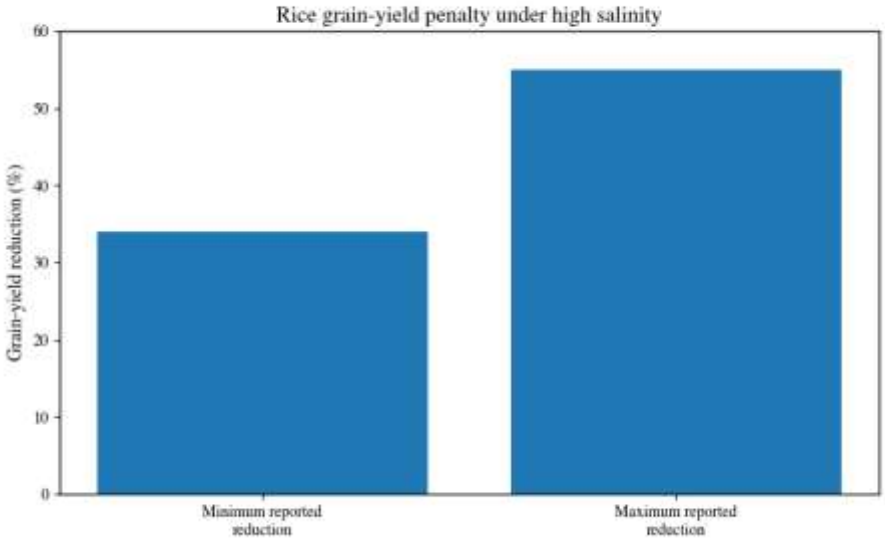

Fig 1. Reported grain-yield reduction of rice under high salinity relative to low salinity in a two-year field study. Source: (Wei et al.,2026).

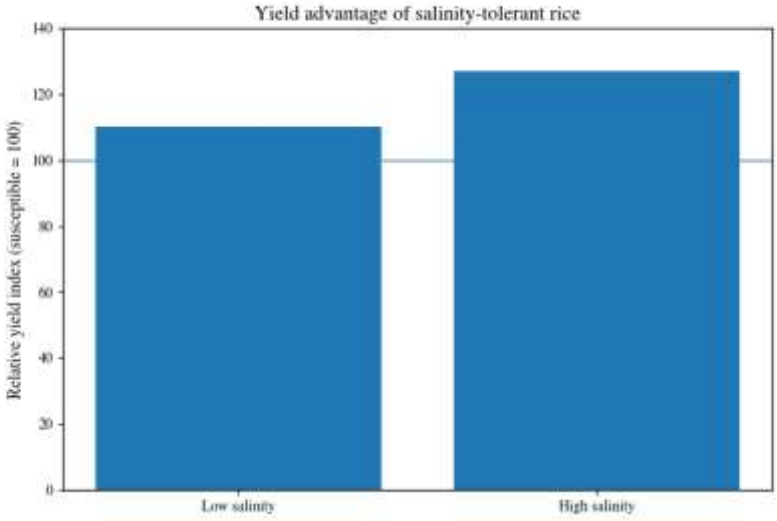

Fig. Relative yield index derived from the reported yield advantage of salinity-tolerant rice over susceptible rice (susceptible = 100). Source: (Wei et al.2026).

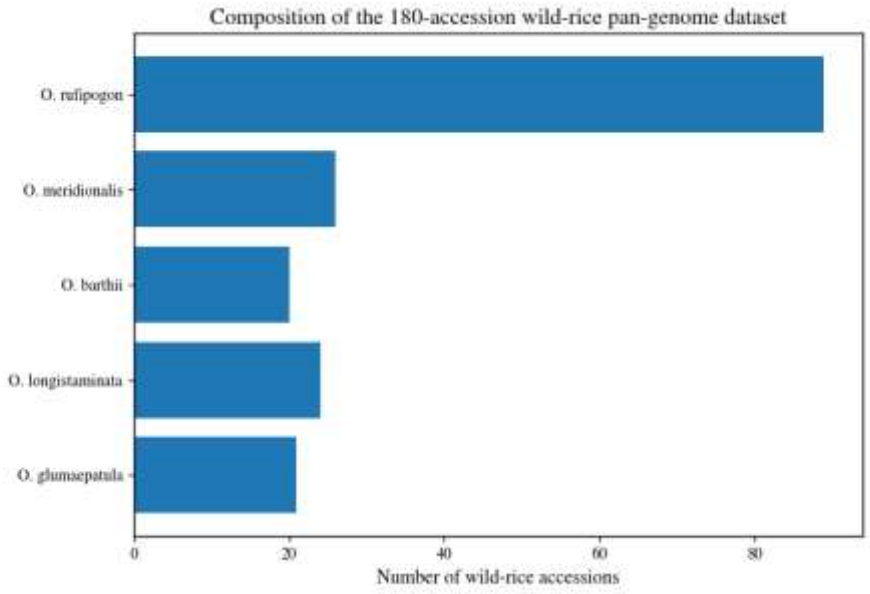

Fig 3. Composition of the 180-accession AA-genome wild-rice dataset used for pan-genome analysis. (Tao et al,.2026).

V. DISCUSSION

The evidence compiled in this review indicates that rice tolerance to abiotic stress should be considered a problem of yield stability rather than merely a physiological trait. Field data under salinity clearly show the scale of the problem: high salinity resulted in a 34.2-54.9% grain yield decrease compared to low salinity, whereas salinity-tolerant cultivars still had a 10.1% yield advantage under low salinity and a 27.1% advantage under high salinity. Notably, tolerant cultivars exhibit lower leaf Na+ and Na+/K+ ratios, along with higher photosynthetic capacity, biomass potassium concentration, and accumulation of N, P, and K, indicating that ionic homeostasis and source-sink maintenance are tightly linked to yield protection (Wei et al., 2026).

The review further illustrates why breeding for a single stressor is not enough. Transcriptome meta-analysis has identified regulatory factors that are common under stress conditions, including DREB2A, ERF95, and ERF102 in drought- and iron-toxicity-related responses. Studies in these fields have shown that salinity combined with drought can be even more detrimental to the crop than either stress alone. These data support a breeding approach that focuses on conserved signaling, ROS regulation, osmotic adjustment, and ion homeostasis while still allowing sufficient growth and reproductive performance (Ahmdikhah et al., 2025).

Another major implication is the use of genetic resources. The 2026 wild-rice pan-genome research work sequenced 180 wild accessions from five AA-genome species and discovered many novel sequences, including, on average, 224 Mb of non-redundant novel sequence per species. Also, the authors pinpointed sequences lost or deliberately selected during domestication and stress-response genes that are located in these regions. For the RIL work using O. *rufipogon*, the results confirm that wild and weedy rice are valuable reservoirs of genetic diversity from which new breeding lines can be developed, mapped, and marker-assisted selection performed (Tao et al., 2026; Roy and Shil, 2025).

Genomic tools of today's data further strengthen this method. An extensive study of 6,044 currently grown rice cultivars identified 3,131 QTLs associated with 53 phenotypes across 212 datasets, illustrating the extent to which genotype, phenotype, and environmental data can be integrated. Such tools can enhance traditional selection by enabling breeders to identify groups of alleles linked to adaptation, productivity traits, and stress responses rather than selecting for stress tolerance alone (Ma et al., 2025).

Epigenetic variability introduces yet another level in the breeding scheme. Song et al. (2025) showed that repeated cold stress caused heritable hypomethylation of the ACT1 promoter, thereby enhancing cold tolerance. This result does not mean that epigenetic variation can substitute for traditional genetic breeding; on the contrary, it suggests that stable epialleles may be another source of adaptive variation to be explored alongside DNA sequence polymorphisms.

Generally, the most logical, scientifically justifiable breeding structure which is backed by evidence points towards a hybrid program: first alter the genetic makeup by introducing genes from wild and weedy rice; testing

under both single and combined realistic environmental stresses; detecting loci, genes, and epigenetic alleles that are consistent; further study the underlying physiological and molecular candidate mechanisms; then integrating mating based on markers, genome-wide association studies genomics targeted gene modification, and traditional breeding. The primary basis for choosing the best one in the end should be high, stable yields across multiple environments, coupled with grain quality and efficient use of resources. This aligns with recent findings that climate, soil, cultivar, and management factors collectively explain rice yield stability, calling for genetic improvement aimed at environmental variability rather than at a single stress treatment (Wang et al., 2025).

VI. CONCLUSION

Rice plant growth and development are controlled by genetic, hormonal, and environmental factors, whereas abiotic stresses like drought, salinity, temperature extremes, and heavy metals severely disrupt growth, yield, and grain quality. These single or combined stress conditions lead to reduced leaf area, altered photosynthesis, impaired spikelet development, oxidative damage, ROS accumulation, and changes in grain composition. Besides cultivated varieties, wild and weedy rice sources such as O. rufipogon have provided not only useful traits for drought, cold, salinity, and other stresses but also the genetic and epigenetic basis of tolerance. Rice's genetic base has been diversified, and new breeding materials with stress tolerance and yield-related traits have been developed through pre-breeding and interspecific hybridization. Besides, epigenetic changes, such as ACT1 promoter hypomethylation, can improve heritable cold tolerance. Mainly for salinity tolerance, integrated approaches including soil and microbial management, genetic resources, marker-assisted introgression of major loci such as Saltol, transgenic approaches, and agronomic practices are required. Today, traditional selection, MAS, GWAS, QTL mapping, genome editing, gene stacking, speed breeding, multi-omics, and systems biology are increasingly combined in modern breeding to produce high-yielding, environmentally adapted rice varieties.

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