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Molecular Mechanisms of Rice Drought Resistance Genes and Their Prospects in Breeding

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Abstract Drought resistance in rice is a critical trait for ensuring stable yields in the face of increasing water scarcity. This review explores the molecular mechanisms underlying drought resistance genes in rice and their potential applications in breeding programs. Drought tolerance in rice is a complex trait influenced by various genetic and physiological factors. Recent advancements in genetic engineering, marker-assisted selection (MAS), and genome-wide association studies (GWAS) have identified key genes and quantitative trait loci (QTLs) associated with drought resistance. Several key genes closely associated with drought resistance have been appraised for their appreciable potential in drought resistance breeding. For instance, the overexpression of *OsERF71* in transgenic rice has been shown to enhance drought tolerance by modulating global gene expression and energy allocation. Additionally, the identification of drought-responsive genes through transcriptome analysis and gene co-expression networks has provided insights into the biological processes and metabolic pathways involved in drought tolerance. The integration of these molecular insights into breeding programs, such as the use of MAS and genetic transformation, has led to the development of rice varieties with improved drought resistance. This review highlights the importance of a multidisciplinary approach, combining molecular genetics, plant physiology, and advanced breeding techniques, to develop rice cultivars that can withstand drought conditions and ensure food security.

Keywords Drought resistance; Rice breeding; Molecular genetics; Gene expression; Marker-assisted selection (MAS)

1 Introduction

Rice (*Oryza sativa* L.) is a staple food for more than half of the world's population, particularly in developing countries (Hadiarto and Tran, 2011; Chen et al., 2013). However, rice cultivation is highly susceptible to drought stress, which significantly affects its growth, development, and yield (Sandhu and Kumar, 2017; Oladosu et al., 2019). Drought is one of the most severe environmental stresses, leading to substantial crop yield losses and posing a major threat to food security (Hu and Xiong, 2014; Pant et al., 2022). The increasing global population and changing climatic conditions exacerbate the challenge of ensuring stable rice production under water-deficit conditions. Therefore, developing drought-resistant rice varieties is crucial for sustaining rice production and ensuring food security (Hadiarto and Tran, 2011; Chen et al., 2013; Swamy and Kumar, 2013).

Drought resistance in rice is a complex trait governed by multiple genes and involves various physiological and molecular mechanisms (Chen et al., 2013; Selamat and Nadarajah, 2021). Key mechanisms include osmotic adjustment, scavenging of oxidative radicals, and regulation of endogenous hormones such as abscisic acid (ABA) and jasmonic acid (JA) (Chen et al., 2013; Pant et al., 2022). Advances in biotechnology have enabled the identification and manipulation of drought-responsive genes, including transcription factors (TFs), protein kinases, and other regulatory proteins (Hadiarto and Tran, 2011; Selamat and Nadarajah, 2021; Pant et al., 2022). QTL mapping and MAS have been instrumental in identifying genetic regions associated with drought tolerance and incorporating them into breeding programs (Swamy and Kumar, 2013; Sandhu and Kumar, 2017). Additionally, transgenic approaches have shown promise in enhancing drought tolerance by overexpressing specific genes or silencing negative regulators (Hu and Xiong, 2014; Pant et al., 2022). This review summarizes the molecular mechanisms underlying drought resistance in rice and explores their potential applications in breeding programs. Specifically, it seeks to identify and characterize key drought-responsive genes and their regulatory networks, investigate the physiological and biochemical pathways involved in drought tolerance and assess the effectiveness of genetic engineering and MAS in developing drought-resistant rice varieties. Additionally, the review will provide insights into integrating molecular and conventional breeding approaches to enhance drought resistance in rice. Ultimately, this review aims to support the development of rice varieties that can withstand drought stress, thereby ensuring stable rice production and food security in the face of increasing environmental challenges.

2 Drought Stress in Rice: Physiological and Molecular Responses

2.1 Impact of drought stress on rice growth and yield

Drought stress is a major abiotic factor that severely affects rice production, leading to significant reductions in growth and yield. Under drought conditions, rice plants experience reduced water availability, which directly impacts various physiological processes, such as photosynthesis, transpiration, and nutrient uptake. The severity of drought stress can cause stunted growth, delayed flowering, and reduced grain filling, ultimately leading to lower grain yield and quality (Lafitte et al., 2006). During the vegetative stage, drought reduces plant height, biomass, and tiller numbers, and causes leaf rolling in rice. The stress results from reduced soil moisture, which limits nutrient absorption and inhibits cell division in meristem tissues. At the tillering stage, water stress significantly impacts growth by hindering food production. Drought during flowering is especially damaging, disrupting pollination, inducing flower abortion, and leading to higher rates of unfilled grains. Prolonged moisture stress during the panicle initiation stage can reduce rice yields by 53.7%~63.5%, a major loss for farmers. Drought also hampers grain development during the reproductive stage, leading to spikelet infertility, decreased tillering capacity, and reduced photosynthesis due to leaf shrinkage. Water stress during the grain-filling stage accelerates plant senescence, shortens the grain-filling period, and reduces yield (Patnaik et al., 2021). Studies indicate that drought conditions during the critical flowering and grain-filling periods can reduce rice yields by up to 50%. Drought stress also affects the root system, reducing root length and density, which further impairs the plant's ability to absorb water and nutrients from the soil (Serraj et al., 2011).

2.2 Physiological responses to drought stress

Rice plants have developed a range of physiological responses to cope with drought stress. Chlorophyll is a key element in the photosynthesis of green plants and is positively correlated with the photosynthetic rate. Under drought stress, chlorophyll pigments can degrade and oxidize, which are common indicators of oxidative stress, resulting in a reduction in chlorophyll content. Both chlorophyll a and chlorophyll b are impacted by drought conditions (Islam et al., 2021). One of the primary responses is the closure of stomata to reduce water loss through transpiration. This stomatal closure, however, also limits CO_2 uptake, thereby reducing photosynthetic efficiency. Drought stress decreases the efficiency of photosystem II, impairing energy conversion in the chloroplasts (Flexas et al., 2006). Osmotic adjustment is another critical response, where plants accumulate compatible solutes such as proline, glycine betaine, and sugars to maintain cell turgor and protect cellular structures (Serraj and Sinclair, 2002). Relative water content (RWC) is an important indicator of a plant's water status, reflecting the metabolic activity within tissues and playing a crucial role in evaluating dehydration tolerance. RWC is associated with both water absorption by roots and water loss through transpiration. Many studies have reported a decrease in RWC in response to drought stress in various plant species (Nayyar et al., 2006). Additionally, rice plants enhance the expression of antioxidant enzymes like superoxide dismutase (SOD), catalase (CAT), and peroxidase (POD) to mitigate oxidative damage caused by reactive oxygen species (ROS) generated during drought stress (Mittler, 2002). Drought stress often leads to an increase in root-to-shoot ratio as plants invest more in root growth to enhance water uptake. Deeper and more extensive root systems help rice plants access water from deeper soil layers, improving drought tolerance (Henry et al., 2011).

2.3 Molecular responses and signaling pathways

At the molecular level, rice plants activate a complex network of signaling pathways and gene expression changes in response to drought stress. Key signaling molecules such as ABA play a central role in drought response by regulating stomatal closure and inducing the expression of drought-responsive genes (Shinozaki and Yamaguchi-Shinozaki, 2006). Former research has identified two primary regulatory pathways that influence gene expression patterns related to drought resistance mechanisms: (1) ABA-dependent pathways and (2) ABA-independent pathways. The ABA-dependent pathway is driven by MYB, NAC, and AREB/ABF TFs, whereas the ABA-independent pathways are regulated by DREB TFs (Du et al., 2011; Fu et al., 2017). TFs like DREB (dehydration-responsive element-binding), AREB/ABF (ABA-responsive element-binding protein/ABRE-binding factor), and NAC (NAM, ATAF, and CUC) are crucial for the activation of downstream drought-responsive genes that encode for osmoprotectants, late embryogenesis abundant (LEA) proteins, and heat shock proteins (HSPs) (Nakashima et al., 2007). Additionally, rice plants utilize microRNAs (miRNAs) to fine-tune gene expression during drought stress. For example, miR169 and miR393 have been shown to regulate genes involved in stress responses and hormone signaling pathways (Zhao et al., 2007). In response to drought, rice plants generate ROS, which act as signaling molecules in stress adaptation. Low to moderate ROS levels trigger the activation of stress-responsive TFs and antioxidant defenses. ROS interact with other signaling pathways, such as ABA and MAPK, to mediate drought responses (Mittler et al., 2011). The integration of these physiological and molecular responses enables rice plants to survive and adapt to drought conditions. Understanding these mechanisms provides valuable insights for developing drought-resistant rice varieties through genetic engineering and molecular breeding approaches.

3 Identification of Drought Resistance Genes in Rice

3.1 Methods for identifying drought resistance genes

Identifying drought resistance genes in rice involves a combination of traditional and modern molecular techniques. GWAS have been instrumental in identifying loci associated with drought resistance traits. A study utilized a non-destructive phenotyping facility to extract 51 image-based traits (i-traits) from 507 rice accessions, leading to the identification of 470 association loci, some containing known drought resistance (DR)-related genes (Guo et al., 2018). Additionally, genetic linkage maps and QTL mapping have been used to dissect the genetic basis of drought resistance. A comprehensive study mapped QTLs for osmotic adjustment and root traits in a doubled-haploid rice population, identifying 41 QTLs that explained 8%~38% of the phenotypic variance (Zhang et al., 2022). Transcriptomic analyses and gene co-expression networks also play a crucial role in identifying differentially expressed genes (DEGs) under drought conditions, as demonstrated by the identification of key modules and hub genes associated with drought sensitivity in rice (Yu et al., 2020).

3.2 Key drought resistance genes discovered in rice

Several key drought resistance genes have been discovered in rice through various studies. The *OsPP15* gene, identified through GWAS and confirmed by genetic transformation experiments, plays a significant role in drought resistance (Guo et al., 2018). Another study highlighted the role of the AP2/ERF TF family member *OsERF71*, which, when overexpressed, conferred a drought-resistant phenotype by modulating global gene expression to prioritize survival-critical mechanisms (Ahn et al., 2017). Additionally, a meta-analysis of QTLs identified stable QTLs across different genetic backgrounds and environments, pinpointing genes such as ABA-Insensitive Protein 5 (ABI5) and G-box binding factor 4 (*GBF4*) as crucial for drought response (Selamat and Nadarajah, 2021). *DREB1* and *DREB2* have been extensively studied for their role in drought tolerance. These genes bind to dehydration-responsive elements (DRE) in the promoter regions of stress-inducible genes and activate their expression, leading to improved drought tolerance (Lata and Prasad, 2011). Furthermore, genes like WRKYs and PR family proteins have been identified as differentially expressed hub genes involved in ROS scavenging, contributing to drought resistance (Yu et al., 2020).

Successful drought-resistant advantages of upland rice have motivated researchers to explore related genetic mechanisms. Sun et al. (2022) found that the elite haplotype of *DROUGHT1* (*DROT1)* exists in upland rice, and the key SNP variation in the promoter region results in higher expression of *DROT1*, thereby enhancing drought resistance in upland rice. Recently, Wang et al. (2024) evaluated the drought resistance of 541 rice accessions in the field and identified 25 upland rice varieties, identified 80 key candidate genes, and validated that the *qRT9* gene in selective regions can positively regulate drought resistance in rice. Similarly, Wu et al. (2019) characterized *ENHANCED DROUGHT TOLERANCE 1* (*EDT1*), a member of rice's bZIP transcription factor family, which positively regulates drought tolerance. This gene offers promising targets for breeding drought-resistant rice varieties. Lou et al. (2023) reported that *OsSAPK3* is significant in both ABA-dependent and ABA-independent drought stress responses. Furthermore, *OsSAPK3* has the potential to enhance rice yield by indirectly regulating tiller number and grain size. These findings offer valuable insights for developing drought-resistant rice varieties.

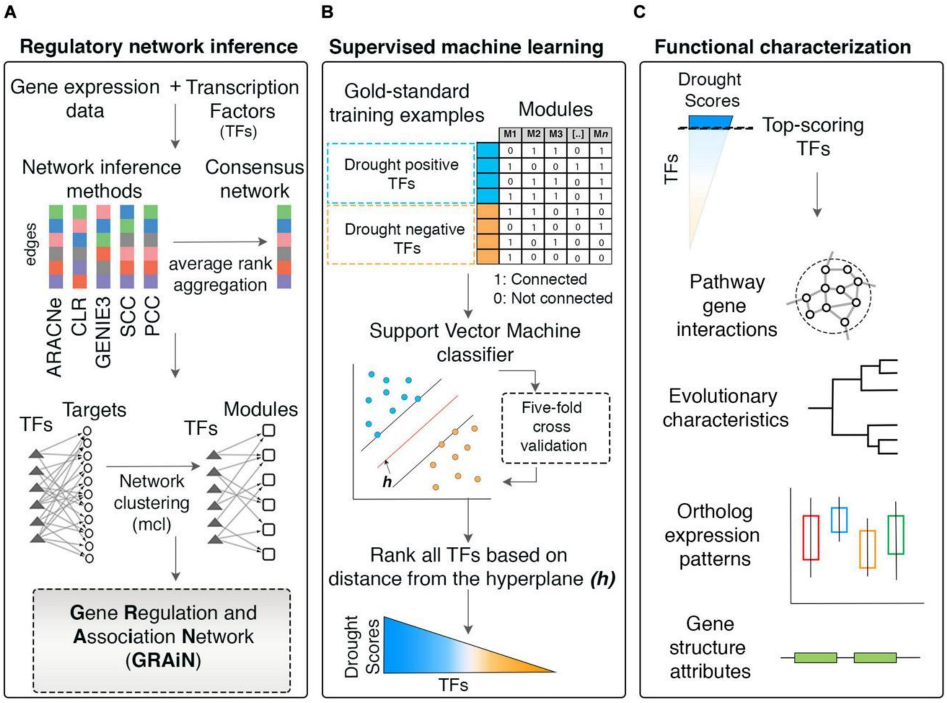
3.3 Comparative genomics and cross-species analysis

Comparative genomics and cross-species analysis have provided insights into the conservation of drought resistance mechanisms across different species. A study on comparative mapping within and across species identified three conserved genomic regions associated with various physiological responses to drought in several grass species, suggesting that these regions have been conserved during genome evolution and could be applied across species for improving drought resistance in cereal crops (Zhang et al., 2001). Another study conducted a comparative transcriptome analysis between drought-tolerant and drought-susceptible rice genotypes, revealing genotype-dependent genes responsible for drought tolerance. This analysis identified specific pathways, such as the α-linolenic acid metabolic pathway, which were significantly up-regulated in drought-tolerant genotypes (Lenka et al., 2011). These findings underscore the potential of leveraging conserved genetic regions and pathways for breeding drought-resistant rice varieties.

4 Functional Mechanisms of Drought Resistance Genes

4.1 Gene regulation and expression under drought stress

Drought stress triggers a complex network of gene regulation and expression in rice with DEGs identified under drought conditions through various studies. A meta-analysis of microarray data revealed 643 upregulated and 677 downregulated genes in rice under drought stress. These genes are associated with responses to abiotic stimuli, water deprivation, and ABA signaling (Figure 1) (Gupta et al., 2021; Soltanpour et al., 2022).



M1	M2	M3	[..]	M*n*
0	1	1	0	1
1	0	0	1	1
0	1	1	0	1
1	1	1	0	1
1	1	0	1	0
0	1	0	0	1
1	0	1	0	0
1	0	0	0	0

Figure 1 Workflow of the network-based machine learning framework (Adopted from Gupta et al., 2021)

4.2 Role of TFs in drought resistance

TFs play a crucial role in mediating the plant's response to drought stress. Several TF families, including bHLH, bZIP, NAC, and MYB, have been implicated in drought resistance. The bHLH TFs are significantly upregulated under drought conditions, enhancing stress tolerance (Soltanpour et al., 2022). *OsbHLH148*, in particular, interacts with JAZ proteins to activate jasmonic acid signaling, contributing to drought adaptation (Seo et al., 2011). The NF-YA TF *OsNF-YA7* has been shown to confer drought tolerance in an ABA-independent manner by regulating downstream genes involved in drought response (Lee et al., 2015). Additionally, *OsNF-YB1* positively affects drought tolerance by enhancing root architecture and promoting the expression of stress-responsive genes (Nelson et al., 2007). The TF, C2H2-type regulates stomatal closure in response to water deficit stress and is also responsible for inducing gene expression to quench ROS and H_2O_2, thereby maintaining their dynamic balance during drought stress (Huang et al., 2009). Moreover, Cominelli et al. (2005) reported that AtMYB60, a TF primarily expressed in guard cells, plays a key role in controlling the opening and closing of stomatal apertures as part of the plant's drought tolerance responses. Similarly, the AP2/ERF TF *OsERF71* alters root structure to enhance drought resistance by promoting cell wall loosening and lignin biosynthesis (Lee et al., 2016). The NAC TF *ONAC022* and the MYB TF *OsMYB6* also contribute to drought and salt stress tolerance by modulating ABA-mediated pathways and enhancing the expression of stress-responsive genes (Hong et al., 2016; Oladosu et al., 2019). Furthermore, *OsMYB2* enhances proline accumulation and ROS scavenging, further improving rice drought resilience (Yang et al., 2012).

Using an integrative approach combining a genome-wide association study with analyses of introgression lines and transcriptomic profiles, Sun et al. (2022) identified a gene *DROT1*, encoding a COBRA-like protein that confers drought resistance in upland rice. A C-to-T single-nucleotide variation in the promoter increases *DROT1* expression and drought resistance in upland rice. *DROT1* is specifically expressed in vascular bundles and is directly repressed by ERF3 and activated by ERF71, both drought-responsive TFs.

4.3 Signal transduction pathways involved in drought response

Signal transduction pathways are essential for the activation of drought-responsive genes and for regulating rice's adaptive mechanisms under water-limited conditions. The ABA signaling pathway is a key regulator of drought response in rice. The bZIP TF *OsbZIP23* is activated by SAPK2, a SnRK2 protein kinase, and regulates a large number of genes involved in stress response and ABA biosynthesis and signaling (Zong et al., 2016). Other bZIP TFs, such as *OsbZIP46*, also regulate drought stress through ABA-dependent pathways (Tang et al., 2012). The AREB/ABF TFs, including *AREB1*, *AREB2*, and *ABF3*, are master regulators of ABA-dependent gene expression and are crucial for drought tolerance. These TFs require ABA for full activation and regulate the expression of *LEA* and *PP2C* genes, which are involved in stress response (Yoshida et al., 2010). Additionally, network-based machine-learning approaches have identified key TFs, such as *OsbHLH148*, that regulate stress signal transduction and modulate gene expression under drought conditions (Gupta et al., 2021). The molecular mechanisms of drought resistance in rice involve a complex interaction of gene regulation, TFs, and signal transduction pathways. Understanding these mechanisms provides a foundation for developing drought-resistant rice varieties through molecular breeding.

5 Genomic Approaches to Enhance Drought Resistance

5.1 GWAS

GWAS has emerged as a powerful tool for dissecting the genetic architecture of complex traits, including drought resistance in rice. By analyzing genetic variants across diverse rice populations, GWAS can identify loci associated with drought resistance traits. A study identified 470 association loci related to drought resistance, with 443 loci identified using image-based traits (i-traits) and 437 loci co-localizing with previously reported drought-related quantitative trait loci (QTLs) (Guo et al., 2018). Another study highlighted the identification of loci underlying tens of rice traits, including drought resistance, and emphasized the importance of functional characterization of candidate genes discovered through GWAS (Wang et al., 2011). Additionally, GWAS has been used to identify significant associations for root traits under drought stress, which are crucial for drought avoidance (Li et al., 2017).

5.2 QTL mapping

QTL mapping is another genomic approach that has been extensively used to identify regions of the genome associated with drought resistance traits in rice. QTL mapping involves the use of molecular markers to link phenotypic traits with specific genomic regions. Price and Courtois (1999) highlighted the importance of QTL mapping in revealing the complex genetic architecture of drought tolerance traits. Using mapping populations like recombinant inbred lines (RILs) and doubled haploids, researchers can identify QTLs associated with specific drought-related phenotypes, such as root depth, leaf water retention, and osmotic adjustment. Babu et al. (2003) identified 47 QTLs associated with plant water stress indicators, phenology, and production traits under both irrigated and drought stress conditions. Another study mapped QTLs for various drought-related traits in a panel of Vietnamese rice landraces, identifying 17 different QTLs with potential pleiotropic effects on drought tolerance (Figure 2) (Hoang et al., 2019).

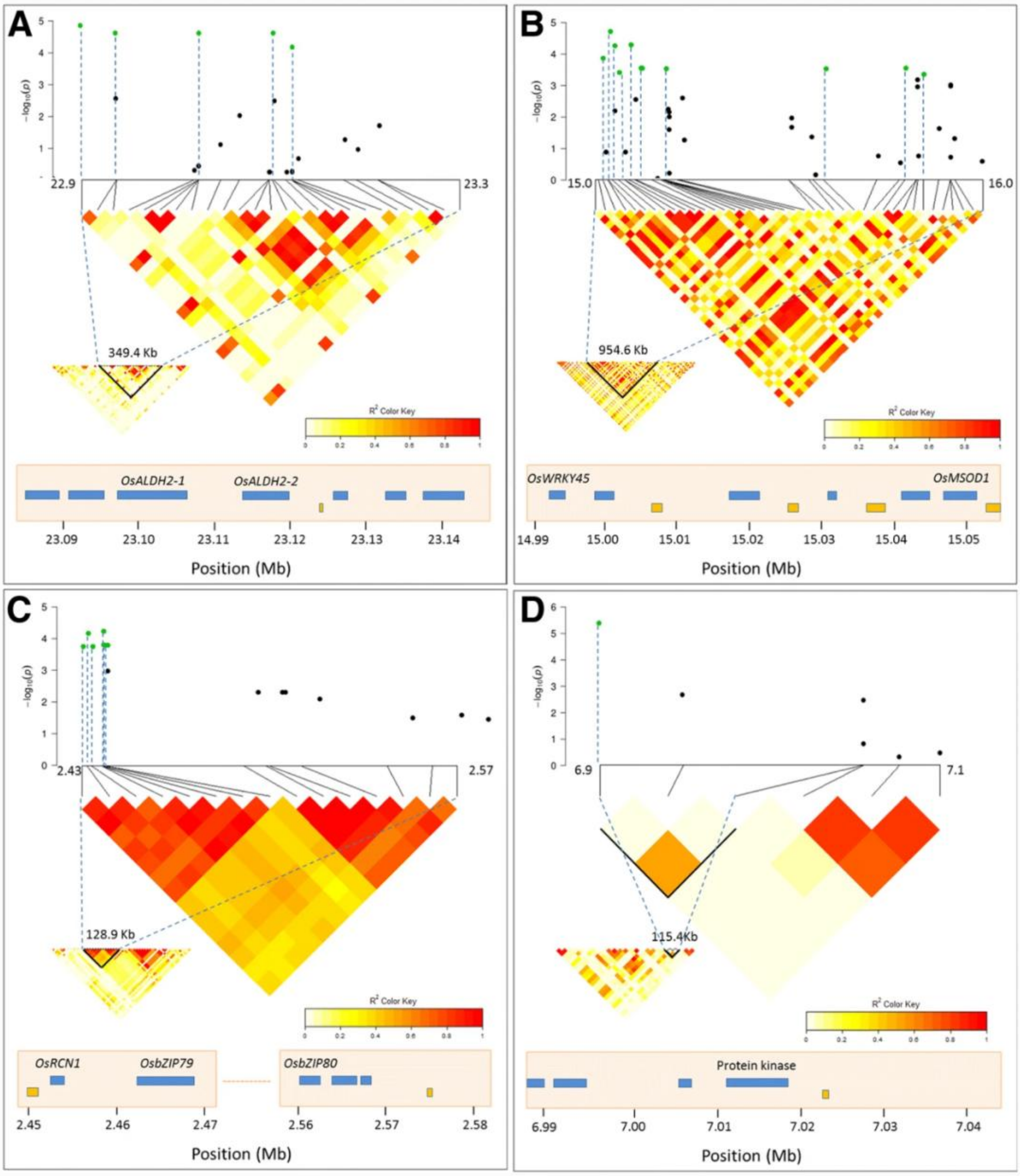


Figure 2 Manhattan plots and Linkage Disequilibrium (LD) heatmaps for some strong QTLs (Adopted from Hoang et al., 2019)

Another study conducted on rice at the germination stage identified multiple QTLs linked to germination percentage (GP), mean germination time (MGT), and seedling percentage (SP). These QTLs are associated with drought tolerance, with genes such as *LOC_Os03g14990* and *LOC_Os03g16050* playing critical roles in metabolic and drought response pathways (Nyasulu et al., 2024). Recently, a study used GWAS and linkage mapping to identify drought tolerance genes in *japonica* rice. The key SNP, C8_28933410, was located on chromosome 8 within the qLRS-8-1 region, validating its role in drought tolerance (Liu et al., 2024). These findings underscore the potential of GWAS in identifying key genetic determinants of drought resistance, which can be leveraged in breeding programs to develop drought-resistant rice varieties.

5.3 CRISPR/Cas9 and other gene editing techniques

CRISPR/Cas9 and other gene editing techniques offer precise and efficient tools for modifying specific genes associated with drought resistance in rice. These techniques allow for targeted modifications, such as gene knockouts or insertions, to improve drought tolerance. The role of the *OsPP15* gene in drought resistance was validated through genetic transformation experiments, demonstrating the potential of gene editing in validating candidate genes identified through GWAS (Guo et al., 2018). Additionally, transgenic rice plants with enhanced tolerance to water deficit and osmotic stresses have been developed, highlighting the potential of genetic engineering in improving drought resistance. The application of CRISPR/Cas9 and other gene editing techniques in rice breeding holds great promise for accelerating the development of drought-resistant varieties by enabling precise manipulation of key genes involved in drought response mechanisms. Genomic approaches such as GWAS, QTL mapping, and gene editing techniques provide powerful tools for enhancing drought resistance in rice. These approaches enable the identification and validation of key genetic determinants of drought tolerance, which can be leveraged in breeding programs to develop rice varieties with improved resilience to drought stress. The integration of these genomic approaches with traditional breeding methods holds great potential for addressing the challenges of drought in rice cultivation and ensuring food security in the face of climate change.

6 Case Studies of Successful Breeding for Drought Resistance

6.1 Traditional breeding approaches

Traditional breeding approaches for drought resistance in rice have primarily focused on selecting for yield stability across various environments and years. Traditional breeding programs often involved participatory approaches, where farmers' knowledge and preferences were integrated into the breeding process. This led to the development of varieties better suited to local environmental conditions (Oladosu et al., 2019). This method, although effective, is often slow and expensive due to the low heritability of yield under stress and the inherent variability in field conditions. Oladosu et al. (2019) highlight several successful varieties developed through conventional breeding, including IR64 and Swarna, which have been enhanced for drought tolerance through the incorporation of traits from local landraces. Selecting for traits such as deep root systems and osmotic adjustment has been a key focus, but these traits require extensive field or greenhouse facilities and are prone to environmental variability. Despite these challenges, traditional breeding has laid the groundwork for understanding the complex nature of drought resistance and has provided a baseline for more advanced techniques.

6.2 MAS

MAS has revolutionized the breeding of drought-resistant rice by allowing for the precise identification and selection of genes associated with drought tolerance. MAS involves the use of molecular markers linked to specific traits, enabling breeders to monitor the presence or absence of these genes in breeding populations (Jena and Mackill, 2008). The successful pyramidization of multiple genes/QTLs for resistance to various stresses, including drought, has been demonstrated in rice varieties such as improved Lalat (Das and Rao, 2015). This approach has significantly accelerated the development of drought-resistant cultivars by reducing the number of generations required and increasing the precision of gene transfer (Figure 3) (Das et al., 2017). Additionally, MAS has been used to integrate major genes or QTLs with large effects into widely grown varieties, providing broad-spectrum resistance to multiple stresses (Jena and Mackill, 2008).

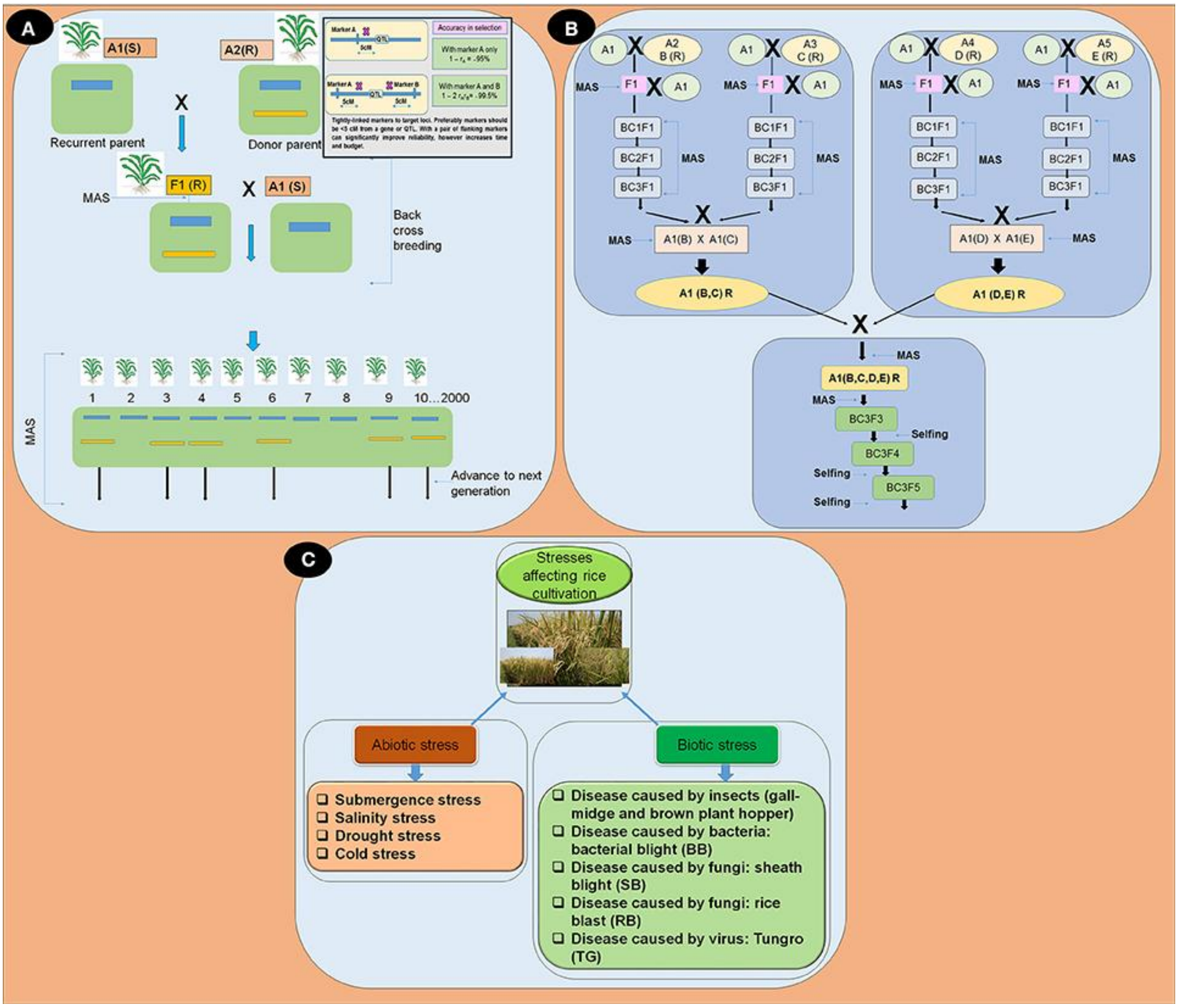


Figure 3 A: Overview of marker assisted backcross breeding program; B: Flow diagram depicting the gene pyramiding of multiple stress resistance (R) genes into a single line using marker assisted backcross breeding; C: Flow diagram of stresses affecting rice productivity (Adopted from Das et al., 2017)

Recently, Mohanavel et al. (2024) indicated that MAS facilitated the identification and development of inter-mated F_1 progenies harboring eight target QTLs/genes for drought tolerance. Genotyping revealed 14 homozygous progenies, which showed enhanced dehydration tolerance through better chlorophyll retention and RWC. This approach underscores the effectiveness of MAS in breeding multiple-stress-tolerant rice varieties. Liu et al. (2024) introduced the *Pi9* gene into the drought-resistant rice variety Hanhui 3 through backcrossing and MAS, producing Hanhui 8200, which exhibited equivalent drought resistance and enhanced resistance to rice blast.

6.3 Genomic selection and precision breeding

Genomic selection (GS) and precision breeding represent the latest advancements in the development of drought-resistant rice. These approaches leverage the complete rice genome sequence, genome-wide molecular markers, and low-cost genotyping platforms to improve grain yield under drought conditions (Swamy and Kumar, 2013). GS involves the use of genome-wide markers to predict the performance of breeding lines, allowing for the selection of the best candidates even before field trials (Swamy and Kumar, 2013). Precision breeding, on the other hand, integrates various "omics" technologies to identify candidate genes and pathways involved in drought tolerance, facilitating the development of transgenic rice plants with enhanced drought resistance (Swamy and Kumar, 2013). These methods hold great promise for the future of rice breeding, offering the potential for more rapid and accurate development of drought-resistant varieties. Recently, Zhang et al. (2023) analyzed 459 rice varieties and found that the reproducing kernel Hilbert space (RKHS) model had the highest predictive accuracy for drought tolerance. By integrating GS with GWAS, they enhanced GS application, significantly improving the precision and efficiency of breeding drought-resistant rice varieties. Similarly, Wang et al. (2024) conducted a comprehensive study integrating genome, transcriptome, and population analyses of rice, identifying key candidate genes for drought adaptation in upland rice. They developed a genomic navigation map for drought-resistant rice breeding, highlighting the pivotal role of highland-specific variations in improving drought tolerance.

7 Prospects and Challenges in Breeding Drought-resistant Rice

7.1 Integrating molecular and breeding approaches

Breeding drought-resistant rice is a multifaceted challenge that requires the integration of various scientific disciplines and methodologies. This section explores the prospects and challenges in this field, focusing on integrating molecular and breeding approaches, the potential and limitations of current techniques, and future directions and innovations. The integration of molecular genetics with traditional breeding methods holds significant promise for developing drought-resistant rice varieties. Molecular markers linked to drought resistance traits, such as root characteristics and osmotic adjustment, have been identified and are being used in MAS (Oladosu et al., 2019). For example, QTLs associated with root architecture, such as *Deeper Rooting 1 (DRO1)*, have been incorporated into elite rice cultivars, enhancing drought tolerance by promoting water uptake from deeper soil layers (Uga et al., 2013). The development of molecular linkage maps and the identification of QTLs associated with drought resistance traits have provided new tools for breeders. Transgenic approaches, including the introduction of genes responsible for osmoprotectants like proline and glycine betaine, have shown potential in enhancing drought tolerance (Hadiarto and Tran, 2011). However, the success of these approaches depends on close collaboration between molecular geneticists, plant physiologists, and breeders to ensure the practical application of these genetic tools in breeding programs. The challenge lies in combining these advanced technologies with field-based breeding practices to ensure that drought-resistant varieties perform well in farmers' fields under real-world conditions.

7.2 Potential and limitations of current techniques

Current techniques in breeding drought-resistant rice include conventional breeding, MAS, and genetic engineering. Conventional breeding has been foundational in the development of drought-resistant varieties, but it is often slow and resource-intensive due to the low heritability of yield under stress and environmental variability (Panda et al., 2021). Despite these limitations, conventional breeding remains essential for selecting traits from landraces and wild rice varieties that have naturally adapted to drought-prone environments. MAS offers a more efficient alternative by allowing the selection of specific traits linked to drought resistance, but it still requires extensive field testing to confirm the effectiveness of selected markers. Additionally, many QTLs associated with drought tolerance have only small effects, necessitating the combination of multiple QTLs to achieve significant improvements in yield stability under drought (Bernier et al., 2007). Genetic engineering provides a direct approach to introducing drought-resistant genes, but it faces regulatory hurdles and public acceptance issues (Hadiarto and Tran, 2011; Hu and Xiong, 2014). Additionally, the complexity of drought resistance, which involves multiple genes and environmental interactions, poses a significant challenge to all these techniques (Sahebi et al., 2018).

7.3 Future directions and innovations

Future research in breeding drought resistant rice should focus on a multidisciplinary approach, integrating advanced genetic techniques, precise phenotyping, and an understanding of plant physiology under drought conditions (Sahebi et al., 2018). Emerging innovations like high-throughput phenotyping, genome editing technologies like CRISPR/Cas9, and systems biology approaches can provide deeper insights into the molecular mechanisms of drought resistance and identify new targets for breeding (Price et al., 2002; Sircar and Parekh, 2019). Systems biology approaches, combining transcriptomics, proteomics, and metabolomics, can offer comprehensive insights into the molecular mechanisms governing drought responses, enabling researchers to identify new genetic targets and improve the drought tolerance of rice at multiple levels (Sircar and Parekh, 2019). The use of computational models and network-based approaches to analyze gene expression and protein interactions under drought stress can also help in identifying key regulatory networks and potential candidate genes for improving drought tolerance (Sircar and Parekh, 2019). Furthermore, integrating knowledge from different environmental stress responses, such as heat and salinity, can lead to the development of rice varieties with broad-spectrum stress resistance (Hadiarto and Tran, 2011). While significant progress has been made in understanding and breeding for drought resistance in rice, the complexity of the trait and the need for interdisciplinary collaboration remain major challenges. Advancing innovation and integration of molecular and breeding approaches will be essential for developing resilient rice varieties that can withstand the increasing threat of drought due to climate change.

8 Implications for Global Rice Production

8.1 Economic and food security implications

Drought stress is a significant constraint to rice production, particularly in rainfed regions of Asia, Africa, and South America, leading to substantial economic losses and threatening food security (Oladosu et al., 2019; Panda et al., 2021). The potential elite haplotype of *DROT1* in upland rice could originate in wild rice (*O. rufipogon*) and may be beneficial for breeding upland rice varieties (Sun et al, 2022). The development of drought-resistant rice varieties through molecular breeding and genetic engineering can mitigate these losses by stabilizing yields under water-deficit conditions (Hadiarto and Tran, 2011; Wang et al., 2022). Enhanced drought tolerance in rice can ensure a more reliable food supply, which is crucial for more than half of the world's population that relies on rice as a staple food (Hadiarto and Tran, 2011; Wang et al., 2022). Economically, the adoption of drought resistant varieties can reduce reliance on irrigation, lower production costs, and boost the resilience of rice farming communities against climate variability (Serraj et al., 2011; Zhang et al., 2022). These advancements not only enhance food security but also provide economic benefits to vulnerable rice-growing regions, strengthening their capacity to withstand future climatic challenges.

8.2 Environmental and ecological considerations

The introduction of drought-resistant rice varieties can have significant environmental benefits, particularly in regions facing water scarcity. By reducing the need for irrigation, these varieties can help conserve water resources, mitigating the pressure on overexploited aquifers and rivers (Farooq et al., 2009; Serraj et al., 2011). Additionally, drought-resistant rice can contribute to maintaining soil health and preventing land degradation by promoting sustainable agricultural practices (Farooq et al., 2009; Zhang et al., 2022). Molecular breeding techniques used to develop these varieties also minimize the need for chemical inputs like fertilizers and pesticides, thereby reducing the environmental footprint of rice production (Wang et al., 2022; Zhang et al., 2022). Furthermore, the ability of drought resistant varieties to thrive under stress conditions can enhance biodiversity in agricultural ecosystems by allowing a broader range of species to coexist in the farming ecosystem (Farooq et al., 2009; Hadiarto and Tran, 2011; Oladosu et al., 2019). By fostering a more diverse and resilient agricultural system, drought-resistant varieties contribute to ecological stability and environmental sustainability.

8.3 Policy and agricultural practice recommendations

To fully leverage the advantages of drought-resistant rice varieties, it is essential to incorporate these advancements into both national and international agricultural policies. Governments should support research and development in molecular breeding and provide incentives for the adoption of drought-resistant varieties by farmers (Serraj et al., 2011; Oladosu et al., 2019). Policy frameworks should also focus on improving infrastructure for efficient water management and irrigation to complement the use of drought-resistant crops (Farooq et al., 2009; Serraj et al., 2011). Extension services and farmer education programs are crucial for widespread adoption of these new varieties. Comprehensive training and dissemination of knowledge on drought-resistant rice cultivation techniques will empower farmers to maximize yield and sustainability (Farooq et al., 2009; Oladosu et al., 2019). Additionally, international collaboration and funding can accelerate the development and distribution of drought-resistant rice, ensuring that these innovations reach the regions most vulnerable to water stress and food insecurity (Babu et al., 2003; Serraj et al., 2011).

9 Concluding Remarks

The study on the molecular mechanisms of rice drought resistance genes and their prospects in breeding has highlighted several critical aspects. Drought stress significantly impacts rice production, particularly in rainfed regions, necessitating the development of drought-resistant varieties. Traditional breeding methods, while useful, are often slow and resource-intensive due to the low heritability of yield under stress and environmental variability. Advances in molecular genetics, such as the identification of QTLs and the use of MAS have provided new avenues for improving drought resistance in rice. Transgenic approaches have also shown considerable potential. Overexpression of specific genes like *OsERF71* and the knockout of genes such as *OsNAC092*, have shown promise in enhancing drought tolerance by modulating various physiological and biochemical pathways. Additionally, GWAS and weighted gene coexpression network analysis (WGCNA) have been instrumental in identifying key genetic loci and hub genes associated with drought resistance. Future research should focus on integrating traditional breeding methods with modern biotechnological tools to develop rice varieties with enhanced drought resistance. This includes the continued identification and characterization of drought-responsive genes and QTLs, as well as the development of robust molecular markers for MAS. Advanced phenotyping techniques, such as image-based traits (i-traits), can provide more accurate and high-throughput assessments of drought responses, facilitating the identification of novel drought resistance genes. Moreover, the application of multi-omics approaches, including transcriptomics, proteomics, and metabolomics, can offer comprehensive insights into the molecular mechanisms underlying drought tolerance. Collaborative efforts between molecular geneticists, plant physiologists, and breeders are essential to translate these findings into practical breeding programs. The integration of molecular genetics and traditional breeding methods holds great promise for developing drought-resistant rice varieties. Identification of key genetic loci and the use of transgenic approaches have provided valuable insights into the complex mechanisms of drought tolerance. Continued research and collaboration are crucial to harness these advancements and improve rice production in drought-prone regions. The prospects for breeding drought-resistant rice are promising, with the considerable potential to significantly enhance food security and agricultural sustainability in the face of climate change.

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Conflict of Interest Disclosure

The authors affirm that this research was conducted without any commercial or financial relationships that could be construed as a potential conflict of interest.

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