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RECENT PROGRESS IN PHYSIOLOGICAL RESPONSES AND MOLECULAR STRATEGIES FOR DROUGHT TOLERANCE IN RICE

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ABSTRACT

Rice is highly sensitive to drought, making it essential to enhance its tolerance in order to secure global food supplies. Drought stress adversely affects various physiological and biochemical processes in rice, leading to significant yield losses. Traditional breeding methods have played a role in developing drought-resistant rice varieties; however, molecular approaches such as marker-assisted selection (MAS) and genetic engineering provide more targeted and accurate solutions. This study reviews key molecular mechanisms underlying drought tolerance in rice, including transcriptional regulation, post-translational modifications, and metabolic adjustments. The application of molecular markers, genome-wide association studies (GWAS), and transgenic strategies has led to advancements in drought-tolerant rice breeding. However, challenges such as genotype-environment interactions, phenotyping limitations, and regulatory hurdles need to be addressed. Future research integrating multi-omics approaches, gene-editing technologies, and advanced phenotyping will be essential for enhancing drought resilience in rice.

Keywords**:** Drought stress, rice breeding, molecular breeding, physiological changes.

Introduction

Rice is a primary food source for a significant portion of the global population, especially in the densely populated regions of Asia (Sahebi *et al*., 2018; Panda *et al*., 2021). With the global population projected to rise substantially, particularly in developing nations, a twofold rise in rice production by 2050 is required to cope with future demand. Achieving the required increase in rice production largely relies on enhancing yield per unit area. While certain intensive cultivation systems can attain yields of 10–15 t/ha, average yields on typical farmers' fields remain much lower, at approximately 3–5 t/ha (Miah *et al*., 2013). The yield gap is primarily due to abiotic stresses such as drought, flooding, salinity, high temperatures, and biotic stresses, including diseases and pests. Among these, drought is especially critical, affecting nearly 50% of the world's arable land and representing a major limitation to rice productivity (Singhal *et al*., 2016; Panda *et al*., 2021).

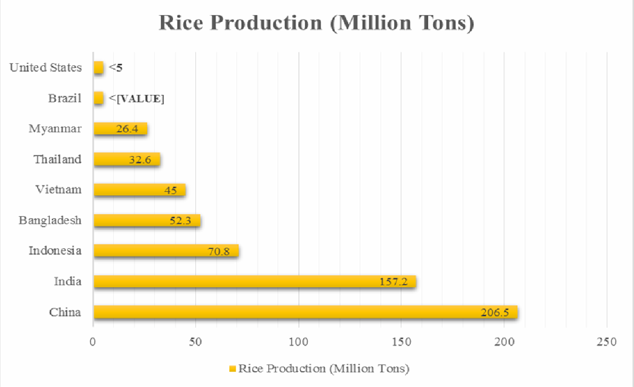

Fig. 1: Rice Production in Major Countries: A Global Comparison.

Source: FAOSTAT (2017, 2018)

Rice is commonly considered one of the most sensitive crops to drought, with severe drought stress severely impacting its growth and development across multiple stages. At present, drought stress impacts more than a third of the world's total cultivated land.

Of the total drought-affected cultivated area, 33% (99 million hectares) lies in developing countries, 25% (60 million hectares) in developed nations, and the remaining 42% (126 million hectares) in underdeveloped countries (Rijsberman, 2006 In the Asian region, drought stress affects an estimated 34 million hectares of rainfed lowland rice and an additional 8 million hectares of upland rice cultivation (Singh *et al.*, 2016).

Rice may suffer yield losses of up to 100% due to drought, depending on the growth stage at which the stress takes place. Drought stress is generally categorized into two main types: terminal and intermittent (Polania *et al.*, 2017; Panda *et al.*, 2021). Terminal drought occurs when the water supply is completely depleted, subjecting plants to extreme stress that ultimately results in their death. In contrast, intermittent drought refers to interruptions in plant growth caused by insufficient rainfall or irrigation, occurring either periodically or unpredictably throughout the growing season. Unlike terminal drought, intermittent drought is generally non-lethal, allowing the plant to survive, although it may hinder growth and development.

The drought tolerance of rice plants depends on their ability to endure and maintain essential physiological processes during water-deficit conditions. lants adapt to drought through coordinated genetic control of molecular, biochemical, physiological, and structural changes at distinct growth stages. These responses are further influenced by the severity, duration, and intensity of the drought stress (Pandey and Shukla, 2015; Bailey *et al.*, 2019; Xia *et al.*, 2022).

When exposed to drought stress, the plant's molecular responses include the upregulation or downregulation of genes across the genome (Yang *et al.*, 2010). Biochemical adaptations include the enhancement of chlorophyll content, a reduction in osmotic potential, and alterations in metabolite levels, all of which assist the plant in managing the stress. Drought-tolerant plants typically exhibit greater stomatal conductance, lower transpiration levels, and other changes in their physiological characteristics. Morphologically, rice plants respond to drought by developing deeper root systems, thicker waxy leaf coatings, smaller and lighter leaves, delayed leaf aging, and an expanded green leaf area. These visible traits help the plant conserve water and enhance its survival under water-limited conditions (Pandey and Shukla, 2015; Sahebi *et al.*, 2018; Panda *et al.*, 2021).

This article aimed to explore physiological and molecular breeding strategies for developing drought-resistant rice, examine the key mechanisms behind drought stress in rice, update the current understanding of drought-resistant genes, review commercially available drought-tolerant rice varieties, discuss traditional breeding approaches for creating drought-resistant varieties, and provide recommendations for rice breeders on improving drought tolerance through molecular techniques.

Responses and mechanisms involved in drought stress

Drought stress, which occurs when there is a shortage of water in the soil, interferes with physiological functions and inhibits normal plant growth (Singhal *et al.*, 2016; Bailey *et al.*, 2019). To assess drought stress, a variety of morphological, physiological, biochemical, and molecular responses are usually considered. This includes a decrease in plant water content, hindered cell growth and elongation, stomatal closure, diminished gas exchange, and interference with enzyme-mediated processes. The combined effect of these factors adversely affects both the growth and yield of the plant.

Phenotypic/morphological response

Rice plants' initial response to drought stress is typically observed through alterations in their phenotypic traits. One of the most common symptoms is leaf wilting, which can affect both above-ground and below-ground tissues. As the drought stress worsens, the plant begins to show more severe effects, such as stunted growth and development, which signal the increasing intensity of the stress.

Physiological responses

Under drought conditions, several physiological functions in plants are negatively impacted, prompting them to activate adaptive responses to survive the stress. Fine-tuning these physiological traits is essential for improving crop yield during drought and is a key consideration before initiating any breeding efforts (Dash *et al.*, 2018; Barik *et al.*, 2019; Gupta *et al.*, 2020). Water shortage influences the physiological characteristics of rice in several ways, leading to declines in net photosynthesis, transpiration, stomatal conductance, water use efficiency, internal CO2 levels, photosystem II (PSII) activity, relative water content, and membrane stability (Farooq *et al.*, 2009; Dash *et al.*, 2018; Mishra *et al.*, 2018; Zhu *et al.*, 2020).

Molecular response

When rice plants experience drought stress, they convert the detection of this stress into molecular and cellular signals. Throughout evolution, rice plants have developed a complex signalling system that conveys stress signals across the plant through various signalling pathways (Oladosu *et al.*, 2019). These pathways involve several signalling molecules, including various hormones. The accumulation of biochemical compounds, such as reactive oxygen species, proteins, and other osmolytes, is often necessary for regulating gene expression. The synthesis of these compounds by the plant or their accumulation due to cellular damage may occur (Yang *et al.*, 2010; Hu and Xiong, 2014). The signalling cascades triggered by the perception of drought function as both the initiator and the response, resulting in downstream changes in gene expression that enhance the plant's drought tolerance. This process is regulated by plant hormone signalling pathways. At the same time, physiological processes such as transpiration, respiration, leaf relative water content, and the accumulation of abscisic acid are disrupted (Yang *et al.*, 2010; Fahad *et al.*, 2017). If the drought stress is intense enough, it can ultimately lead to plant death (Ozga *et al.*, 2017).

Adoptive tolerance mechanisms

Typically, drought tolerance is characterized by a plant's capacity to maintain growth, development, and grain production under water-limited conditions (Rollins *et al.*, 2013; Kumar *et al.*, 2017). This multifaceted trait encompasses a range of adaptive responses-molecular, biochemical, physiological, and morphological-that enable the plant to endure drought stress at various stages of growth. Because of its critical importance in global rice production, the mechanisms underlying drought tolerance have been extensively researched, though several aspects remain unclear. Common strategies used by rice plants include drought avoidance, where the plant reduces water loss or improves water uptake, and drought escape, where the plant finishes its life cycle before severe drought stress occurs (Panda *et al.*, 2021).

Drought escape is the ability of a plant to complete its life cycle ahead of the onset of severe soil moisture stress. This mechanism typically involves entering a dormant state or triggering programmed cell death in most tissues, preserving only the critical parts needed for regrowth or regeneration once favourable conditions, such as after prolonged water stress, are restored (Oladosu *et al.*, 2021). In contrast, drought avoidance is the plant’s ability to sustain a relatively high internal water status, even when soil moisture is limited (Kumar *et al.*, 2017; Panda *et al.*, 2021). This type of tolerance is supported by adaptations such as deeper root systems or leaf rolling, which reduce water loss and delay dehydration. Developing drought-resilient, high-yielding rice varieties depends heavily on understanding these physiological adaptations.

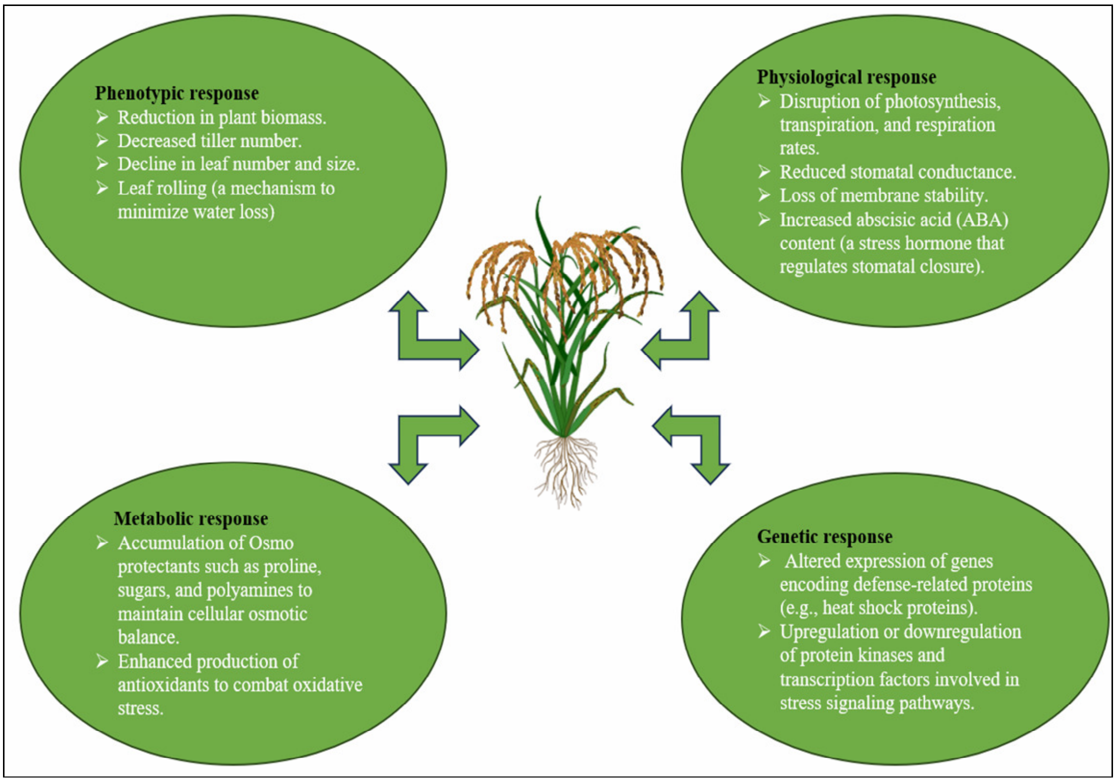

Fig. 1: Responses and mechanism of rice traits under drought condition

Effects of drought at seed and seedling stages

The early morphological development of rice, particularly during germination and seedling stages, is highly vulnerable to drought stress. Ensuring timely and uniform crop establishment is crucial for maximizing yield potential. Under water-deficient conditions, drought mainly results in low germination rates and restricted seedling growth (Farooq *et al.*, 2012; Kadam *et al.*, 2017; Mishra and Panda, 2017). Rice is especially vulnerable to drought at these initial stages, even more so than many other crop species. Effective seed germination depends on sufficient soil moisture and suitable temperatures, both of which are negatively affected during drought. Limited water availability hampers the seed's ability to absorb moisture, resulting in reduced seedling vigor and delayed emergence (Vibhuti *et al.*, 2015). Drought also disturbs the cellular water balance and interferes with essential metabolic processes such as membrane transport, ATP production, and respiration key functions required for successful seed germination (Kadam *et al.*, 2017). Several studies have further shown that drought stress results in decreased plant height, reduced leaf area, and lower biomass accumulation during the early stages of growth (Sarvestani *et al.*, 2008; Mishra and Panda, 2017; Hussain *et al.*, 2018).

Drought stress effects on root traits

Root traits are vital for improving crop performance under drought conditions. In rice, the plant's effectiveness in coping with water scarcity largely depends on the growth, architecture, and functionality of its root system. Root dry weight and length serve as important indicators for predicting rice productivity under drought conditions (Comas *et al.*, 2013). Rice roots respond differently to drought stress; for instance, some studies like Manivannan *et al.* (2007) have observed increased root length, which is attributed to elevated levels of abscisic acid in the root tissues. Under drought conditions, rice plants with extensive and deep root systems tend to show better growth and yield (Mishra *et al.*, 2019). Drought tolerance is commonly observed in genotypes with deeper and thicker roots, prolific branching, and a greater root-to-shoot ratio (Kim *et al.*, 2020). The morphological and physiological traits of rice roots are essential in influencing shoot development and final grain yield under drought stress conditions.

Drought stress effect on leaf photosynthesis

Photosynthesis is integral to crop development and yield, but drought stress can severely hinder its efficiency. In water-stressed environments, the closure of stomata helps retain moisture, but it also limits carbon dioxide uptake and promotes the formation of reactive oxygen species (Farooq *et al.*, 2009; Mishra *et al.*, 2018). Drought causes a drop in turgor pressure, impedes gas exchange in leaves, and limits CO_2 assimilation, resulting in compromised photosynthetic function (Gupta *et al.*, 2020; Zhu *et al.*, 2020). These consequences lower photosynthetic efficiency, particularly in rice genotypes that are more sensitive to drought.

Drought stress disturbs the equilibrium between light absorption and its use, primarily due to decreased Rubisco activity, degradation of pigments, and dysfunction of photosystems I and II (Zlatev, 2009; Mishra and Panda, 2017). Specifically, photosystem II (PSII), which is vital for ATP production, is damaged, disrupting electron transport and energy generation. Under drought conditions, chlorophyll content, which is crucial for light energy absorption, significantly decreases, reducing photosynthetic efficiency (Mishra *et al.*, 2019; Sarwar *et al.*, 2013). Furthermore, the efficiency of PSII, measured by the Fv/Fm ratio, is lower in plants experiencing water stress. Drought stress also affects carotenoids, which are essential for photoprotection and stress signalling. Given their importance, efforts are being made to enhance carotenoid content through breeding or genetic strategies to improve drought tolerance (Ashraf and Harris, 2013).

Effect on water regulation and membrane integrity

The impact of drought stress on plant water relations and membrane stability is evident as leaf water potential and relative water content (RWC) decrease during periods of water deficit (Farooq *et al.*, 2009). Relative water content (RWC) serves as an accurate indicator of plant hydration, reflecting modification in water potential and turgor pressure (Gupta *et al.*, 2020). A decline in RWC and turgor pressure due to drought stress results in compromised transpiration and reduced water use efficiency, both of which are essential for sustaining yield (Mishra *et al.*, 2019; Rao and Chaitanya, 2016).

During the initial stages of drought exposure, osmotic adjustment, including the accumulation of proline, helps temporarily maintain RWC, as seen in rice seedlings (Choudhary *et al.*, 2009). Membrane stability is also a crucial trait for drought tolerance. During water stress, dehydration alters membrane lipid structures, leading to increased membrane permeability and cellular damage (Pandey and Shukla, 2015). The

Membrane Stability Index (MSI) is commonly used to assess drought tolerance, as it correlates with yield performance under stress (Upadhyaya and Panda, 2019).

Effects of drought on biochemical compositions

Plants undergo biochemical changes during drought stress to preserve cell turgor and reduce cellular damage. During drought stress, plants accumulate Osmo protectants like proline, glycine betaine, and soluble sugars to lower osmotic potential and improve water conservation (Kumar *et al.*, 2016; Upadhyaya and Panda, 2019). In response to drought stress, plants boost antioxidant activity, aiding in the removal of reactive oxygen species (ROS) and preserving cellular integrity. Furthermore, alterations in protein content and expression patterns enhance the plant's stress resilience (Pandey and Shukla, 2015). Additionally, drought triggers hormonal responses via abscisic acid (ABA), brassinosteroids, and ethylene signalling pathways. These hormone-driven responses are typically tissue- and time-specific, contributing to drought tolerance while having minimal impact on yield (Gupta *et al.*, 2020).

Breeding for drought stress tolerance in rice

Traditional breeding methods

Rice breeding has traditionally focused on increasing grain yield, and this focus persists, even in the face of drought stress. Drought tolerance breeding, though a more recent focus, mainly follows the same approaches used to develop high-yielding rice varieties (Bolaños and Edmeades, 1993) as depicted in the Fig. 2. Historically, selections for rice breeding have been made under well-watered conditions, assuming that elite lines would perform reasonably well under stress (Dixit *et al.*, 2014). However, using grain yield alone as a selection criterion has proven ineffective because of its low heritability and considerable genotype × environment interactions (Oladosu *et al.*, 2019; Panda *et al.*, 2021).

Advances in plant physiology have improved traditional breeding by allowing selection based on physiological traits, which can be measured at various stages and require less time. Pedigree selection, recurrent selection, backcrossing, and induced mutation are among the methods frequently employed in rice breeding (Khan *et al.*, 2020).

- **Pedigree selection** is a common method, especially when drought tolerance is controlled by one or a few major genes. It allows for the integration of several beneficial alleles but is labour-intensive and requires extended selection periods (Khan *et al.*, 2020).
- **Recurrent selection** aims to accumulate favourable alleles from different parents while preserving genetic diversity. This method enables shorter breeding cycles and greater accuracy in developing high-yielding drought-tolerant varieties (Pang *et al.*, 2017).
- **Backcrossing** is commonly employed to transfer specific drought-tolerant genes from donor lines into elite cultivars, facilitating the creation of near-isogenic lines with enhanced drought resistance (Lafitte *et al.*, 2006).
- **Induced mutation** complements conventional breeding techniques by generating new allelic variations. This method has resulted in the creation of rice mutants with improved yield and grain quality under water-limited conditions (Oladosu *et al.*, 2014, 2015, 2019). For instance, the Super Green Rice mutant in Indonesia showed both drought tolerance and high yield under conditions of low water and fertilizer inputs (Efendi *et al.*, 2017).

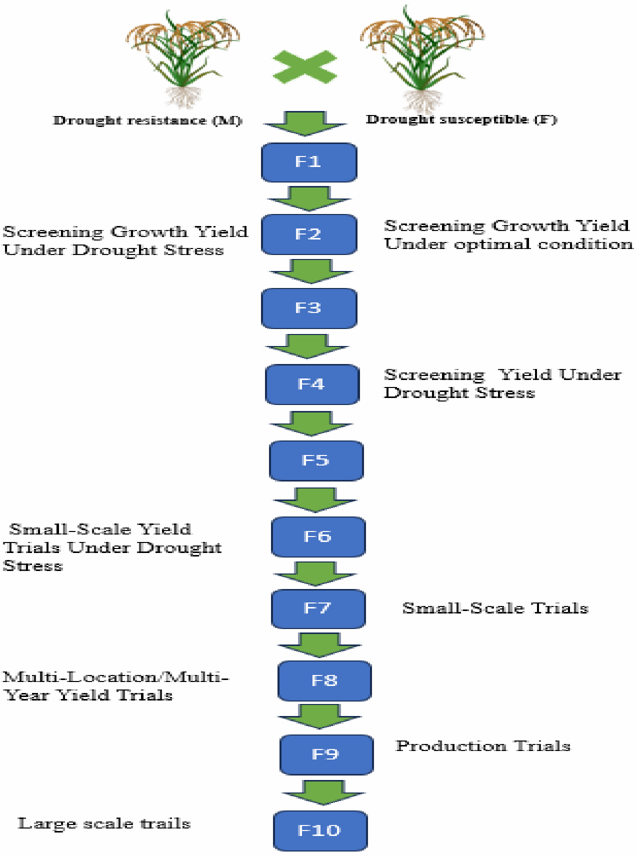

Fig. 2: General approach for breeding rice varieties with drought tolerance

Molecular Marker-Assisted Selection (MAS) for Drought Tolerance

Molecular marker-assisted selection (MAS) is a DNA-based approach utilized by rice breeders to follow specific dominant or recessive alleles over multiple generations. It helps identify individuals with desired traits from a segregating breeding population and enables the integration of beneficial alleles while eliminating undesirable linked loci. MAS is frequently integrated into various contemporary breeding techniques, such as marker-assisted pedigree selection, genomic selection, marker-assisted recurrent selection, and marker-assisted backcrossing (MABC), with MABC being the most widely applied and successful method (Miah *et al.*, 2017; Usman *et al.*, 2018; Chukwu *et al.*, 2019).

If a trait is primarily controlled by one or a few genes, transferring a gene segment from a donor parent to a recipient parent can significantly improve the expression of that trait. If a trait is primarily controlled by one or a few genes, transferring a gene segment from a donor parent to a recipient parent can significantly improve the expression of that trait. This method offers two key advantages: (1) it improves the accuracy of selection for complex phenotypic traits by using markers closely linked to the target gene and (2) it allows the introgression of desirable genes from the donor parent while preserving the essential traits of the recipient parent. MAS, through various techniques like marker-assisted pedigree selection and backcrossing, has proven to be an effective strategy for enhancing drought tolerance in rice by improving the selection gain, especially for phenotypically complex traits (Miah *et al.*, 2017; Usman *et al.*, 2018; Chukwu *et al.*, 2019).

Genes Associated with Drought Tolerance in Rice

Recent developments in molecular biology have greatly expanded our knowledge of the drought responses in rice plants, covering molecular, individual plant, and population levels. A significant number of genes responsive to drought have been discovered, researched, and effectively cloned. Several approaches, such as genetic engineering, are being applied to develop rice varieties with enhanced drought tolerance. Moreover, emerging methods such as genome-wide association studies (GWAS), proteomics, and imaging technologies like fluorescence and thermal imaging are progressively being adopted in contemporary breeding programs.

Transcriptional regulations in response to drought stress

In response to drought stress, transcriptional regulation in rice is controlled by several transcription factors (TFs), including ABA-responsive element binding proteins/factors (AREB/ABF), stress- and ABA-activated NAC proteins, dehydration-responsive element binding proteins (DREB/CBF) that function without ABA, zinc finger proteins, nuclear factors, and WRKY domain-containing TFs. When subjected to drought stress, rice initiates the expression of these essential transcriptional regulators, which leads to the activation of various downstream genes that support the plant in overcoming the stress (Table 1).

A notable example is ABA (abscisic acid), which plays a key role in regulating the drought response. AREB/ABF proteins, belonging to the bZIP TF family, are essential in ABA signalling. As ABA accumulates during drought stress, these transcription factors bind to ABA-responsive elements (ABREs) in the promoters of target genes, which results in the upregulation of their expression. (Mundy *et al.*, 1990; Baker *et al.*, 1994; Yamaguchi-Shinozaki & Shinozaki, 2005; Yang *et al.*, 2010).

Despite their potential, directly using transcriptional regulators to improve drought tolerance presents challenges. Many drought-responsive genes have been primarily studied in Arabidopsis, and while stress signalling mechanisms are generally conserved across plant species, it is essential to validate these gene candidates specifically in crops like rice to fully comprehend their role in drought resilience.

Table 1: Summary of genes involved in transcriptional regulation of drought tolerance in rice

Gene	Transcriptional factors (TF)	Evaluation Condition	Observed regulatory response	Reference
OsDREB1A	AP2/ERF	Greenhouse	Rapid stomatal closure	Hsieh *et al.*, 2002
OsDREB1B, OsDREB1F	AP2/ERF	Field	Rapid closure of stomata	Pellegrineschi *et al.*, 2004
AtHARDY	AP2/ERF	Greenhouse	Improved water use efficiency, reduced transpiration, enhanced photosynthesis	Karaba *et al.*, 2007
AtABF3	bZIP	Greenhouse	Decreased leaf rolling and wilting, increased chlorophyll fluorescence (Fv/Fm)	Oh *et al.*, 2005

AtZat10	Zinc finger (EAR motif)	Greenhouse, Field	Increased fertility of spikelet's	Xiao *et al.*, 2009
AtSNAC1	NAC domainTF	Greenhouse, Field	Increased ABA sensitivity	Rabbani *et al.*, 2003
OsZFP252	Zinc finger (TFIIIA-type)	Greenhouse	Increased proline and sugar content, improved balance of hydrogen peroxide	Xu *et al.*, 2008; Huang *et al.*, 2009
OsWRKY11	WRKY (Zinc finger)	Greenhouse	Reduced wilting of leaves and slower water loss rate	Wu *et al.*, 2009

Post-translational modifications in response to drought stress

The plant's response to drought stress is significantly influenced by post-translational modifications (PTMs) of proteins, including farnesylation, phosphorylation, and poly (ADP-ribosyl) ation. Farnesylation, in particular, is the process of attaching a farnesyl group to target proteins, which impacts several plant growth and developmental processes (Nambara & McCourt, 1999; Galichet & Gruissem, 2003). Plant farnesyltransferase enzymes are composed of FTA and FTB subunits. By utilizing antisense and RNA interference (RNAi) technologies to downregulate FTB and FTA, researchers have successfully enhanced drought tolerance in transgenic canola. Long-term field evaluations showed that plants with modified farnesyltransferase enzymes had higher yields under moderate drought during flowering, compared to the controls grown under irrigated conditions (Wang *et al.*, 2005, 2009; Yang *et al.*, 2010). Protein phosphorylation is another important post-translational modification, in which protein kinases activate target proteins.

Various kinases have demonstrated drought-related responses at the transcriptional level under different environmental conditions (Boudsocq & Laurière, 2005; Chae *et al.*, 2009). Prominent kinases in this context include calcium-dependent protein kinases and SNF1-related kinases such as CIPK and SnRK2, which are crucial for adapting to osmotic stress (Furihata *et al.*, 2006). Environmental changes detected by plants activate poly (ADP-ribosyl) ation. During drought stress, reactive oxygen species (ROS) lead to DNA damage and disrupt cellular energy balance through the activation of poly (ADP-ribose) polymerases. (Amor *et al.*, 1998; Doucet-Chabeaud *et al.*, 2001).

While many drought-responsive genes are first identified through transcriptional induction, most need post-translational modifications to become functionally active (Gong *et al.*, 2002; Sakuma *et al.*, 2006). Some post transcriptional biomolecules and genes identified depicted in Table 2. Hence, altering the activated forms of regulatory proteins offers a promising approach for developing drought-resistant crops. Effective manipulation of genes associated with protein modifications, such as inhibiting farnesylation, has been successfully implemented in both rice and canola (Saijo *et al.*, 2000; Wang *et al.*, 2005; Xiang *et al.*, 2007). One of the major hurdles in stress tolerance research is determining which protein kinases or post-translational regulators to target.

Table 2: Post transcriptional genes and biomolecules for drought tolerance in rice

Gene	Function	Evaluation	Physiological Effect	Reference
AtLOS5	Abscisic acid synthesis	Field	Enhances fertility of spikelets and results in higher crop yield.	Xiao *et al.*, 2009
OsCDPK7	Farnesylation	Greenhouse	Stimulates the expression of genes associated with late-stage embryogenesis.	Saijo *et al.*, 2000
OsHSP17.7	Heat/cold-shock protein	Greenhouse	Offers protective effects for proteins under stress conditions.	Sato and Yokoya, 2008
CspA	Heat/cold-shock protein	Greenhouse, field	Improves the photosynthetic process, leading to a boost in yield.	Castiglioni *et al.*, 2008
HVA1	Late embryogenesis abundant protein	Greenhouse, field	Increases efficiency in water usage, enhances water retention, and strengthens membrane stability.	Xu *et al.*, 1996; Sivamani *et al.*, 2000
OsLEA-3	Late embryogenesis abundant protein	Greenhouse, field	Promotes better spikelet fertility and contributes to higher grain yield.	Xiao *et al.*, 2007
Oatadc	Polyamine	Greenhouse	Builds up spermine/spermidine, improves chlorophyll content, and alleviates leaf wilting.	Capell *et al.*, 1998, 2004

VaP5CS	Proline	Greenhouse	Increases proline levels, helping to reduce leaf wilting.	Zhu *et al.*, 1998; De Ronde *et al.*, 2004
OsCIPK03, OsCIPK12, OsCIPK15	Protein phosphorylation	Greenhouse	Elevates levels of proline and sugar, minimizing leaf rolling.	Xiang *et al.*, 2007
NPK1	Protein phosphorylation	Greenhouse, field	Boosts photosynthesis, improves spikelet fertility, and enhances overall yield.	Shou *et al.*, 2004; Xiao *et al.*, 2009
TPS	Sugar	Greenhouse	Raises trehalose levels, which helps in reducing leaf rolling.	Garg *et al.*, 2002; Jang *et al.*, 2003

Metabolites and Osmo protectants in drought stress response

In plant drought response, metabolites and Osmo protectants play a vital role, covering areas like abscisic acid (ABA) metabolism, phospholipid signalling, late embryogenesis abundant (LEA) proteins, heat/cold shock protein chaperones, amino acids (such as proline), glycine betaine, sugars (like trehalose and mannitol), and polyamines. Although these compounds are diverse, they typically operate through similar mechanisms. One of the initial responses of plants to drought is the rapid buildup of ABA, which subsequently activates ABA-responsive genes. (Yamaguchi-Shinozaki & Shinozaki, 2006) and triggers stomatal closure to reduce water loss through transpiration. Despite the diversity of these compounds, they generally work through similar mechanisms. In response to drought, one of the first plant reactions is the quick buildup of ABA, which triggers ABA-responsive genes and leads to stomatal closure to reduce water loss through transpiration (Schroeder *et al.*, 2001; Hsiao, 1973).

However, successfully improving drought tolerance by enhancing metabolite or Osmo protectant levels has been limited. The reason for this could be that these drought-induced compounds represent a small proportion of total cellular solutes, and increasing their concentration may hinder overall plant growth and development (Holmström *et al.*, 1996; Abebe *et al.*, 2003; Karim *et al.*, 2007). Thus, although approaches targeting metabolites are promising, more comprehensive studies are crucial to identify effective methods for improving drought resistance in rice via metabolic engineering.

Genetic Engineering for Commercial Drought-Tolerant Crops

Although drought tolerance involves complex mechanisms, genetic engineering has led to significant progress in enhancing this trait in major crops such as maize and rice. A significant milestone was achieved with Monsanto's Drought Gard, the first genetically modified (GM) drought-tolerant crop to receive regulatory approval in 2011. The maize hybrid (MON87460) incorporates a cold-shock protein gene (CspB), enhancing RNA stability under drought stress. The CspB protein functions as an RNA chaperone, safeguarding key processes such as photosynthesis, stomatal regulation, and carbon fixation, resulting in higher grain yields. This innovation has gained widespread adoption, particularly within the U.S. Corn Belt region. Some more successful drought tolerant rice commercials are furnished in Table 3.

Corteva Agriscience (formerly DuPont Pioneer), following its development of drought-tolerant Optimum AQUAmax hybrids, created a maize variety that silences the ACC synthase gene via RNA interference (RNAi) to reduce ethylene synthesis. This genetic modification delays ethylene production, which preserves yield during water stress. While field trials across the U.S. and Chile have demonstrated its effectiveness, regulatory approval for commercial use remains pending.

Arcadia Biosciences is developing a drought-tolerant technology based on the regulation of cytokinins, plant hormones that influence stomatal behavior during water stress. They have engineered transgenic rice plants to express isopentenyl transferase (IPT), an enzyme responsible for cytokinin biosynthesis. While the approach has shown potential in enhancing drought resilience, the technology has not yet been commercially released. In India, Performance Plants Inc. has evaluated abscisic acid (ABA)-related drought-tolerant rice varieties that enhance water-use efficiency by modulating stomatal responses. Field trials have demonstrated a 5–10% increase in yield under drought conditions, highlighting the effectiveness of targeting ABA pathways for improving drought resilience in rice.

To improve drought tolerance in rice without negatively impacting plant growth, JIRCAS and RIKEN in Japan have combined constitutive (35S) and drought-inducible (rd29A) promoters with the DREB1A gene. This approach led to the development of rd29A-DREB1A transgenic rice at the University of

Tokyo, which has demonstrated strong drought resistance, offering a promising strategy for genetic improvement under water-limited conditions.

The OsmiR156–OsSPL14 regulatory module, which is essential in shaping the ideal plant architecture in rice, has been investigated by the Chinese Academy of Agricultural Sciences and the China National Rice Research Institute. Pot experiments have shown that manipulating this module enhances resource use efficiency, improves carbon allocation, and increases yield potential under water-limited conditions, making it a promising target for drought-resilient rice breeding.

Table 3: Transgenic drought-tolerant rice in commercial development and market

Developer	Mechanism	Implementation Location and Status	Field Trial Result
Arcadia Biosciences (USA)	Introduction of isopentenyl transferase from Agrobacterium, driven by the stress-responsive SARK promoter, to enhance cytokinin production	Two years of field trials were conducted on rice, with the technology being licensed for use in various crops to enhance tolerance to water, nitrogen, and salt stress.	Extended photosynthetic activity during drought by delaying senescence; improved Osmo protectant accumulation and drought resilience
Chinese Academy of Sciences (China)	Modification of OsSPL14 via OsmiR156 to optimize plant architecture and tiller number	Altered OsSPL14 expression disrupted OsmiR156 regulation, resulting in fewer tillers, improved plant stability, and higher grain yield	Achieved better plant structure and resource use, enhancing drought tolerance and productivity
DuPont Pioneer (USA)	Use of RNAi to express an ACS6 construct that suppresses ACC synthase, reducing ethylene synthesis	Conducted field evaluations in the USA and Chile	Yield increase through reduced ethylene levels during drought stress
Monsanto (USA)	Cold-shock protein B from Bacillus subtilis is expressed to bolster RNA stability in response to stress.	Approved for commercialization in 2011 in the USA, targeting drought-prone regions like the Midwest and western Great Plains	Boosted corn yield by approximately five bushels per acre under drought
Performance Plants (Canada)	RNAi-mediated suppression of farnesyltransferase using conditional promoters to control stomatal behaviours	Licensed to companies including Syngenta, Bayer, DuPont Pioneer, Scotts, and Mahyco	Demonstrated a 26% increase in canola yield and enhanced flowering in petunia under stress
University of Tokyo (Japan)	Expresses DrEB1a transcription factor	In collaboration with the University of Calcutta (India), field trials were conducted.	Transgenic rice lines exhibited a 20–30% increase in sugar accumulation under drought compared to non-transgenic varieties

Challenges and limitations

Although there has been significant progress in improving drought tolerance in rice, challenges and limitations remain that prevent the full realization of these advancements in agricultural practice. One major issue is the complexity of the drought stress response, which involves intricate physiological, biochemical, and molecular mechanisms that vary between genotypes and environmental conditions. Genotype-environment interactions further complicate the development of universally effective drought-resistant varieties, as traits that perform well in controlled environments often fail to do so under field conditions. Additionally, drought tolerance is a polygenic trait, and while key genes have been identified, the incomplete understanding of these multigenic traits limits breeding efforts. Even when drought tolerance traits are identified, their inconsistent performance in the field remains a significant challenge, as environmental variability often impacts the expression of these traits.

The cost and time required for advanced molecular research, such as genome-wide association studies and transcriptomic analyses, pose further barriers, limiting their application in large-scale breeding programs. Furthermore, technological and infrastructure limitations, particularly in developing countries, hinder the use of cutting-edge tools like gene editing, while regulatory challenges surrounding genetically modified organisms (GMOs) add another layer of complexity. Finally, the unpredictability of climate change and the increasing severity of droughts create additional hurdles, as breeding programs must adapt to future climate extremes, requiring novel strategies for improving resilience. Public acceptance and policy issues regarding GMOs also continue to impede the widespread adoption of drought-tolerant rice varieties. These challenges highlight the need for a multifaceted approach to drought tolerance research, combining advanced molecular techniques with practical breeding strategies that account for environmental variability and global climate change.

Conclusion

The ongoing research on drought tolerance in rice has made significant strides in understanding the physiological responses and molecular mechanisms involved in drought stress adaptation. This review highlights the diverse physiological processes, including osmotic adjustment, stomatal regulation, and root architecture modifications, that enable rice plants to cope with water scarcity. Furthermore, the molecular strategies revealed through the identification of key genes, transcription factors, and signalling pathways have opened new avenues for developing drought-resistant rice varieties. In conclusion, recent progress in drought tolerance research has provided a solid foundation for breeding rice varieties with enhanced drought resilience. Despite this progress, tackling the rising global food demand under climate change-induced water stress necessitates a combined approach involving physiological, molecular, and breeding techniques. The continued development of novel molecular strategies and the incorporation of drought-tolerant traits in rice breeding programs hold significant potential for ensuring food security in regions susceptible to drought.

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