



REVIEW ARTICLE

# Integrative strategies for enhancing drought tolerance in rice (*Oryza sativa* L.): From breeding to biotechnology

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## Abstract

Drought stress is a critical abiotic factor limiting rice (*Oryza sativa* L.) productivity, posing a significant challenge to global food security. Given the increasing frequency and severity of drought events due to climate change, developing drought-tolerant rice varieties has become a major research priority. Conventional breeding strategies and marker assisted selection (MAS) have been widely used to improve drought resilience in rice. These approaches focus on incorporating key traits like deep rooting, osmotic adjustment and efficient water use. Advances in molecular techniques, such as genomic selection, quantitative trait loci (QTL) mapping and CRISPR/Cas-based gene editing, allow precise genetic modifications to improve drought tolerance. Omics technologies such as genomics, proteomics and metabolomics have facilitated the identification of drought-responsive genes, regulatory pathways and adaptation mechanisms. Agronomic practices such as alternate wetting and drying (AWD), in combination with nanotechnology-based interventions, contribute to sustainable drought stress mitigation and water management. Additionally, multi-omics approaches and big-data analytics accelerate trait discovery and deployment, enabling the development of climate-resilient rice varieties. Addressing the complexity of drought tolerance requires an integrative approach that combines advanced breeding, genetics, plant physiology and sustainable agronomic practices to ensure food security and mitigate the impact of drought on rice production.

**Keywords:** climate resilience; CRISPR/Cas; drought stress; marker-assisted selection (MAS); nanotechnology; omics

## Introduction

Rice (*Oryza sativa* L.), a member of the Poaceae family ( $2n = 2x = 24$ ), has long served as a staple food grain for over half of the global population. This crop originated in the tropical regions of Southern and Southwest Asia with its domestication taking place in India and China (1). Following maize, rice is the second most significant cereal crop globally because of its vast diversity of over 40000 cultivated varieties. In recent years, global production of milled rice has exceeded 513 million metric tonnes. In India alone, rice is cultivated over an area of 47.8 million hectares with a production of 135 million tonnes and achieving a productivity rate of 2838 kilograms per hectare. These figures underscore rice's pivotal role in global food security and the need for ongoing research and innovation to enhance its productivity, resilience and sustainability.

With shifting dietary preferences and an increasing population, it is imperative to enhance rice production to meet the rising demand for food grains. Projections suggest that global rice output will reach 567 million tonnes by 2030 and through enhanced productivity, crop intensity and diversity, production could exceed 1035 million tonnes by 2050 (2, 3). In economically poor countries, where rice serves as a staple food, addressing food security is of utmost importance (4). Notably, rice constitutes 76 % of Southeast Asians' calorific intake,

making it a crucial crop for the world economy (5). The Food and Agriculture Organization (FAO) projects that food production must double to sustain the rapidly growing population which is expected to reach nine billion people by the year 2050. Consequently, the challenge of increasing grain output while conserving water is critical for rice cultivation. Additionally, rice production faces threats from diminishing arable land, depleting natural resources, erratic rainfall patterns and abrupt climate change, compounded by the world's largest population. To develop strategies for enhancing crop resilience, it is essential to understand the physiological challenges in root architecture during drought stress. By identifying key traits and mechanisms that contribute to drought tolerance, the latest breeding techniques are essential. Recognizing the implications of increasingly unpredictable weather patterns is essential for promoting sustainable agricultural practices.

Abiotic stresses including heat, salinity and drought can significantly diminish crop yield, which is of considerable importance to the agro-economic sector (6). Drought, occurs almost in every climatic zone adversely affecting ecosystems, natural habitats, society and the economy (7). Various environmentally induced abiotic stresses considerably lower the overall yield in rice (8). Drought represents the most challenging abiotic factor impacting rice production globally. To achieve and maximize high yield potential with water conservation, one

effective strategy is the development of innovation to rice genotypes that exhibit resistance to water scarcity (9). Drought happens when there's not enough water for the plant, causing changes in its structure and growth. As shown in Fig. 1, these conditions disrupt cellular processes, hinder nutrient uptake and affect overall plant growth. Understanding these impacts is crucial for developing drought-resilient crops.

Satellite images have revealed that vegetation across all continents is experiencing stress. Numerous agriculture areas worldwide are facing challenges related to insufficient soil moisture and declining groundwater levels, particularly in America, Africa and Australia. The GEOGLAM Crop Monitor highlights that the most significant threats to agriculture are found in the regions of Africa, Europe, Southern Asia and Central and South America. Furthermore, the Famine Early Warning System Network (FEWSNet) reports that many regions of Africa, Southwest Asia and Central and South America continue to experience considerable food insecurity. Irregular rainfall patterns exacerbated by climate change pose a serious threat to agricultural productivity and often lead to drought during critical phases of rice cultivation. This also leads to drought during the critical stages of rice. Drought severity varies across different regions of India due to climatic and geographical factors. Fig. 2 illustrates the spatial distribution of drought intensity across the country, highlighting the most vulnerable regions and underlining the urgent need for region-specific mitigation strategies.

Producing one kilogram of rice requires approximately 3000 L of water, making it a highly water-sensitive crop. Drought conditions significantly affect rice's physiological functions, leading to reduced tillering, fewer panicles and a higher number of sterile spikelets. Notably, drought stress during the reproductive phase has a profound effect on lowland rice. Extended periods of drought can severely impair the crops' capacity to recover. Many high-yielding varieties face complete loss of yield during severe drought conditions (10).

Efforts are underway to identify key genes essential for drought tolerance in order to develop rice varieties with improved resilience to drought (11). Through a combination of techniques, including genetic engineering and marker assisted selection (MAS), interdisciplinary researchers have unravelled the intricate mechanism of plant tolerance, leading to the creation of novel cultivar with enhanced drought resistance (12). The application of modern biotechnological breeding techniques aims to develop rice varieties that not only yield more but also exhibit enhanced tolerance to drought and improved grain quality, thereby addressing these critical challenges (13).

### Growth stages of rice and its response to drought

Drought stress impacts crop growth at different phases. The most drought-sensitive stages in rice are the reproductive phases, including panicle initiation and flowering. This is due to a decline in the assimilation and translocation of reproductive components (14). Table 1 shows the effect of drought on different stages of rice. Stem and leaf growth have a major influence on the development of the plant during the vegetative stage. Plant degeneration, poor seed germination and seedling stand established during the vegetative stage. Furthermore, the moisture levels in the soil play a crucial role in determining plant

**Table 1.** Drought stages and drought effects

Stages	Effects	References
Flowering	Moderate	(81)
Water use efficiency	39 %	(15)
Plant height	49.31 %	(45)
Shoot length	Mild	(82)
1000 grain weight	13.7 %	(83)
Photosynthesis	Decreased	(84)
Panicle development	Reduced	(85)
Leaf area and biomass	Reduced	(80)

height during the booting, flowering and grain-filling stages (15). Table 2 shows the landrace donors of drought tolerance.

### Mechanism of drought stress

Plant growth and development are regulated by a combination of biochemical processes, environmental conditions and genetic factors (16). Conditions of drought, whether permanent or sporadic, can adversely affect growth and overall productivity. Drought tolerant mechanisms encompass physiological adaptations, morphological changes driven by genetic factors and cellular modifications. Increased harvest index, decreased osmotic potential and higher chlorophyll content are some of the indicators for cellular modifications. Signs of physiological adaptation are characterized by higher stomatal density, decreased transpiration rates and improved yield. Morphological responses to drought involve increased leaf weight, waxy leaf coatings and enhanced root thickness for better water uptake (17). Crop production is becoming increasingly concerned with drought tolerance as research responses are difficult due to its quantitative and complicated character. The genetic heterogeneity in drought tolerance exhibited by various cultivars, subspecies and species emphasizes the significance of diversity in drought tolerance and it's critical to comprehend how plants react to drought stress (18). The multilevel plant responses to drought stress are illustrated in Fig. 3.

### Morphological response

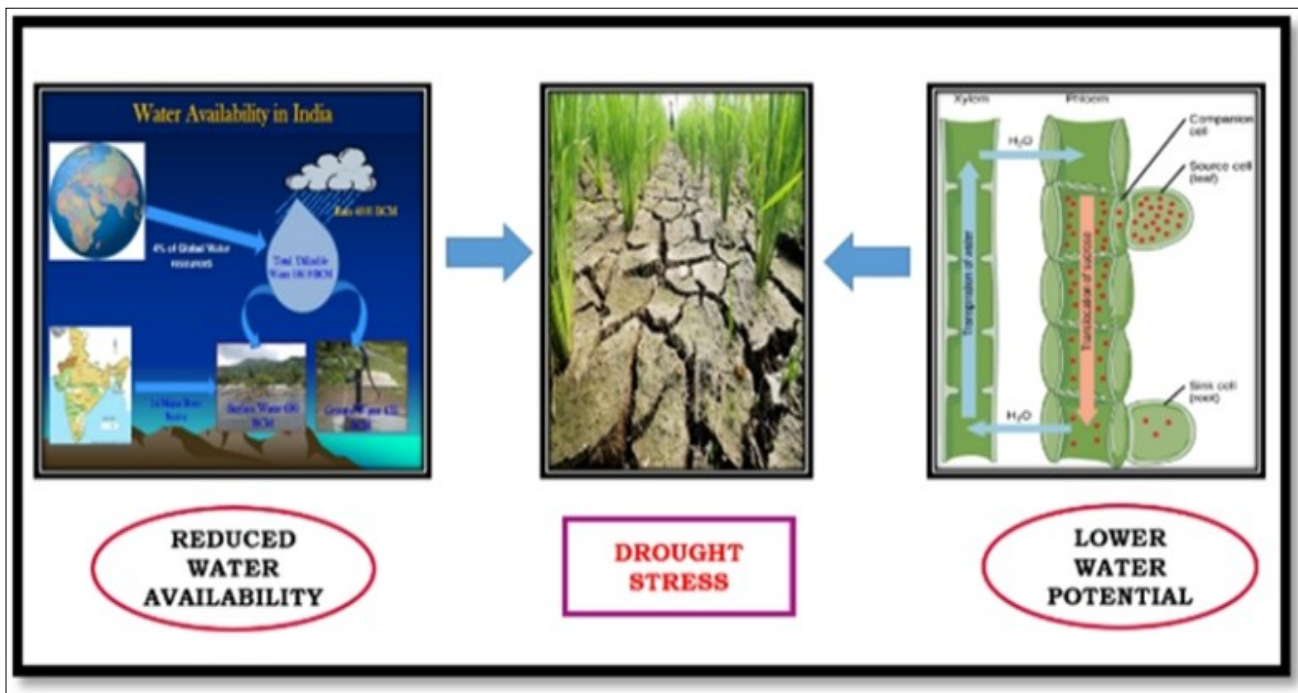
The morphology of rice plants, encompassing aspects viz., plant growth, biomass and yield, roots and grain formation, is adversely affected by drought stress. Insufficient water flow to the xylem or adjacent cell, in diminished germination rates, reduced leaf size, leaf area, leaf number, biomass and cell growth (19). Various studies have indicated that drought stress causes a reduction in plant height, biomass and leaf area (20).

### Unveiling the impact of drought stress on seed germination and seedling growth

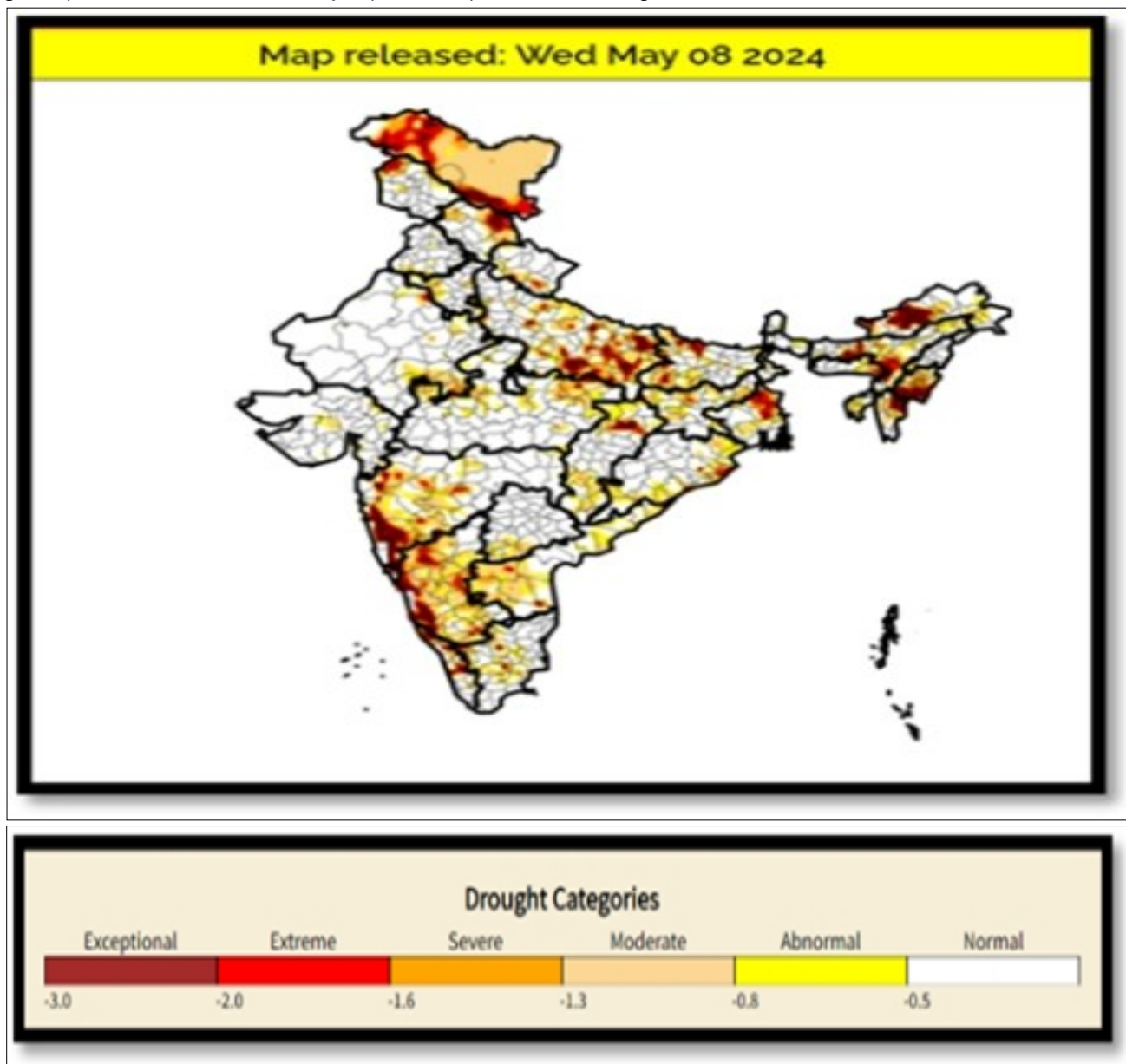
Timely and optimal seed germination, supported by appropriate soil temperature and moisture, is critical for ensuring crop productivity. Drought stress negatively impacts germination and early seedling growth, leading to stunted development (21). Drought stress is significantly associated with seedling germination, ultimately results in diminished growth. Drought condition impairs respiration and ATP synthesis, disrupts the water balance, affects metabolic processes at the cell level and

**Table 2.** Landrace donors for drought tolerance

Landraces	References
<i>O. rufipogon</i>	(86)
<i>O. nivara</i>	(87)
<i>O. glaberrima</i>	(88)
<i>O. longistaminata</i>	(89)
<i>O. meridionalis</i>	(90)
<i>O. punctata</i>	(91)

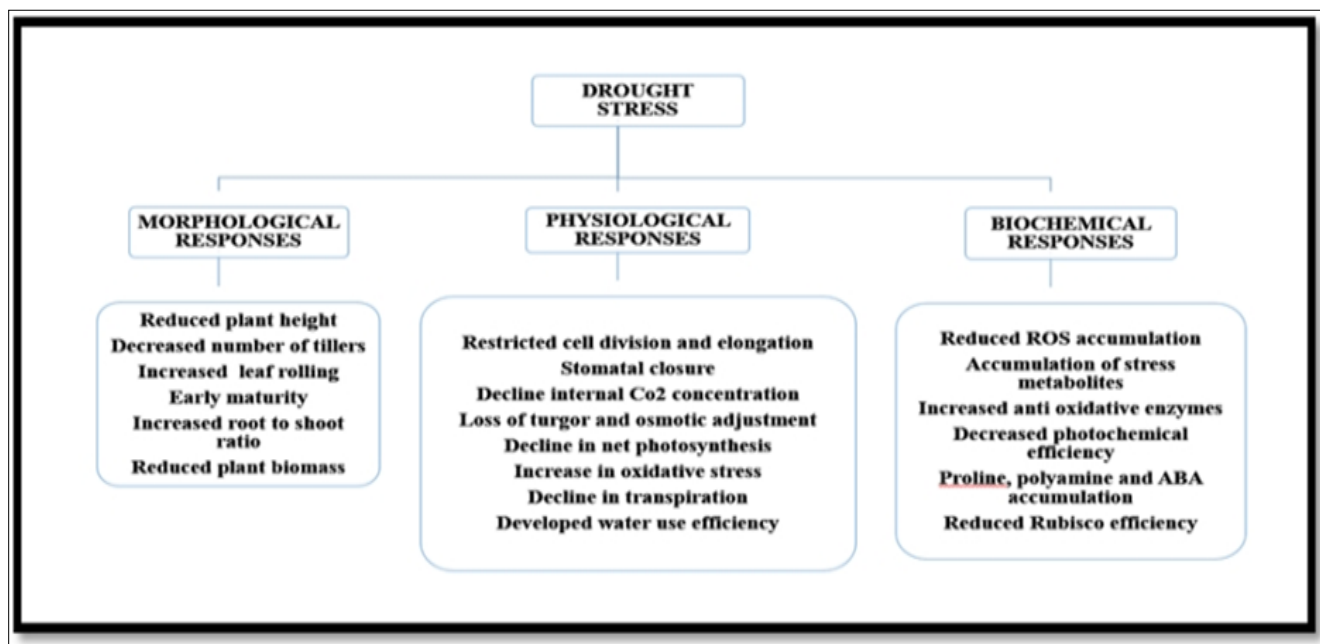


**Fig. 1.** Impact of reduced water availability on plant water potential cause drought stress.



**Fig. 2.** Spatial distribution of drought severity across India (Source: India Drought Monitor, 2024).





**Fig. 3.** Multilevel plant responses to drought stress.

reduces membrane transport. These factors collectively lead to insufficient seed germination (22). Studies indicate that water stress adversely affects plant height, leaf area and biomass (19). The impact of water stress on rice varies with its intensity and the plant's growth stage. Mild stress allows better recovery and compensatory growth compared to severe stress. Stress during booting reduces effective panicles, grains per panicle and seed setting rate, lowering yield. At flowering, it significantly reduces 1000-grain weight and seed setting, further affecting yield.

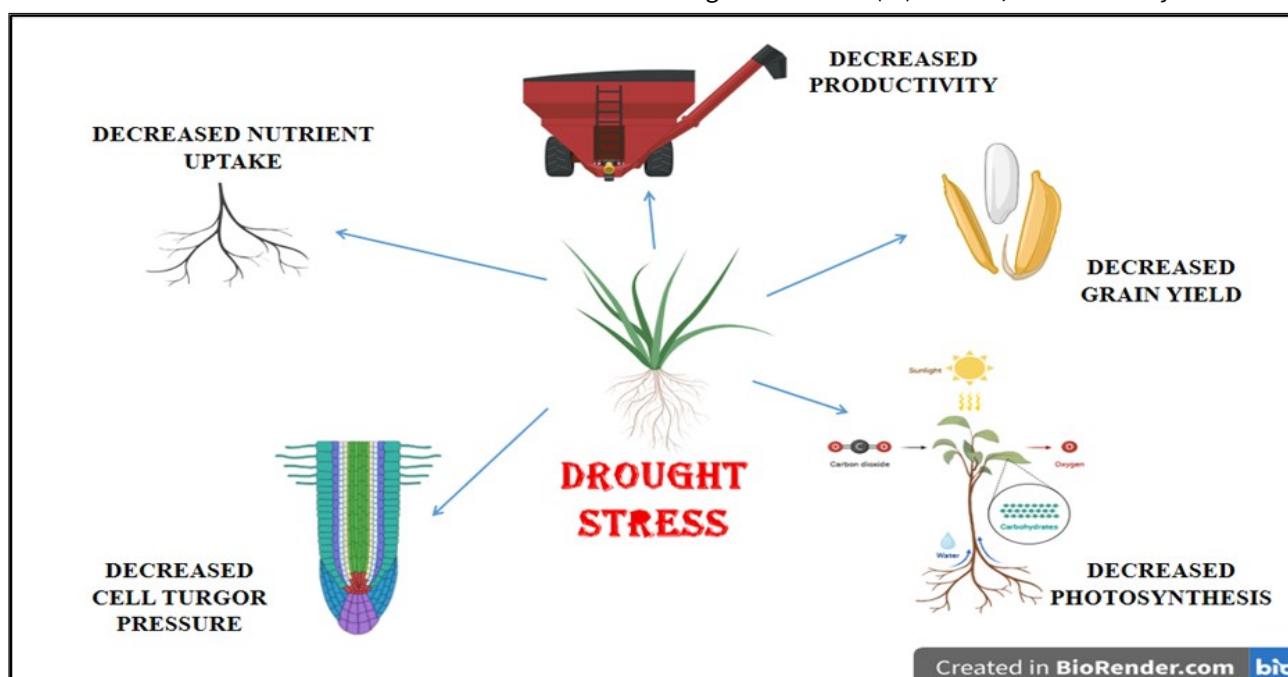
#### Root resilience on drought stress

Enhanced root characteristics of plants are crucial for improved production (23). The attributes of plant roots significantly influence agricultural productivity, particularly under drought conditions. Crop function is largely determined by the development of root system (24). Roots are the initial plant tissues to experience drought stress (25). By modifying root architecture and hydraulic conductivity, roots are vital for the

plant adaptation to drought (26). However, in contrast to other cereals, rice possesses a shallow root system, rendering it more susceptible to drought (27). An increase in ABA concentration leads to an elongation of roots (28). Drought stress has a profound effect on the morpho-physiological traits of rice roots, which in turn impacts shoot growth and total grain yield. The impact of drought impairs the root functionality by reducing cell water permeability and influencing the growth of root system. Root dry matter drops by 5 % during vegetative stage dryness (23). The consequences of drought stress in rice was depicted in Fig. 4.

#### Physiological response

Drought stress exerts a variety of adverse physiological effects on plants, leading to diminished production level. Previous breeding initiatives have shown that the necessity of enhancing physiological components and processes to boost yield under drought conditions (29). In rice, water scarcity results in a



**Fig. 4.** Consequences of drought stress in rice.

decrease in the membrane stability index, internal carbon dioxide concentration, stomatal conductance, net photosynthetic rate, transpiration rate and water use efficiency (30). Physiological responses to drought include an increase in osmoprotectants and membrane stability. The closure of stomata restricts the entry of CO<sub>2</sub> into the plant, thereby lowering photosynthetic activity and subsequently reducing the plant's overall metabolic processes (31). Plants use various natural compounds to tolerate stress. In rice, glycine betaine, trehalose and proline are especially important as they help the crop hold onto water and keep its cells stable in drought.

#### **Impact of drought stress on leaf photosynthesis**

Drought stress reduces water potential in plant tissues, leading to impaired leaf development and diminished leaf expansion (31). In agriculture crops, inadequate cell development and a reduction in leaf area results from impaired water transport from the xylem to other cells, which is exacerbated by decreased turgor pressure owing to water scarcity. Structural changes in drought-stressed leaves include reduced leaf size, fewer stomata, thickened cell walls, increased cutinisation of the leaf surface and underdeveloped vascular tissues (32, 33). Additionally, leaf rolling and premature senescence are prominent features observed in drought-stressed plants (34).

Several leaf traits-such as increased flag leaf area, higher leaf area index (LAI), greater relative water content and higher pigment concentrations-are associated with drought tolerance and can be used to screen for resilient cultivars (35). Water stress also disrupts the functionality of Photosystem II (PSII), which plays a vital role in ATP synthesis and the light-dependent reactions of photosynthesis. Water stress disrupts Photosystem II (PSII), which is crucial for ATP synthesis and reduction, by reducing mesophyll cells' ability to use CO<sub>2</sub> under water-limited conditions, leading to decreased chlorophyll. This results in increased PSII quantum generations, the energy transfer processes that convert light into chemical energy and determine photosynthetic efficiency (29, 36). In extreme environments, carotenoids are critical for photoprotection and plant growth (37).

#### **Biochemical response**

Plants respond to drought stress by synthesizing osmoprotectants, increasing protein content and enhancing antioxidant activity to maintain cell turgor. Additionally, they develop mechanisms to counteract oxidative stress, like scavenging reactive oxygen species (ROS) (32). In upland or drought-resistant cultivars, the accumulation of proline and the activity of antioxidant enzymes are linked to drought resistance. These plants establish a sophisticated antioxidant defense system, enabling them to survive and maintain function under drought conditions (38).

#### **Osmolyte accumulation amid drought stress**

In plants, osmoregulation serves as a critical mechanism that leads to the accumulation of osmoprotectants in response to reduced turgor pressure. Osmolytes such as proline, soluble sugar, phenolic and total free amino acids increases in concentration during water stress period and playing a vital role in enhancing drought tolerance (39). When the plants faced with water stress it can regulate the osmotic regulation in three ways: by reducing intracellular water content, by decreasing cell

volume, or by increasing cell contents. Plants have all three of these routes, although not all of them are osmotically regulated. The active control of cells to lower osmotic potential by adding solute is commonly understood to constitute osmotic regulation. First, it lowers the free energy of water bound inside the cell, keeps the water potential inside and outside the cell different and allows the cell to take in water when the external water potential is lower (40). In rice, proline levels were observed to rise significantly at a 30 % PEG-induced water stress (41). Proline accumulation is associated with the maintenance of stomatal conductance and leaf turgor, thereby contributing to drought resistance (42).

#### **Conventional approach for drought tolerance**

Conventional breeding approaches for improving drought tolerance in rice primarily involve utilizing the genetic diversity found in rice germplasm and employing rigorous screening protocols across multiple field locations. Through pure line selection from traditional drought-resistant landraces such as PTB10, N22 and BR19, several resilient rice varieties have been developed (43). Pedigree breeding has further advanced drought tolerance by combining beneficial traits, leading to the creation of varieties like 'Sahbhagidhan' (44). Recurrent selection has also been effective in increasing the frequency of favourable alleles for drought tolerance, though it requires more time and resources compared to pure line selection (45). While conventional breeding has yielded significant success in developing drought-tolerant rice varieties, incorporating genomic tools can enhance precision and efficiency.

#### **Molecular approach for drought tolerance**

Plant drought tolerance is complicated and necessitates a thorough examination of the physiological and genetic foundation. It is ineffective to improve drought tolerance in rice using conventional breeding methods (46). Recent developments in phenotyping, genetics and physiology have produced new insights into drought tolerance (47). Molecular tools, including quantitative trait loci (QTL) mapping and genome-wide association studies (GWAS), have been instrumental in identifying key drought-responsive genes. MAS and genetic engineering approaches enable the development of transgenic or gene-edited varieties with enhanced drought resilience (48). On the other hand, molecular research using DNA markers, can yield precise results and help identify drought-tolerant germplasms for crop modification. Numerous investigations have concentrated on discovering QTLs associated with different qualities; the main techniques for identifying drought-resilient genes in rice are DNA studies based on marker-based phenotyping (49). Enhanced yield assortments, safe, high-agronomic harvests and improved crop types are all possible outcomes of molecular breeding. A summary of varieties developed through various breeding approaches has been presented in Table 3.

#### **Marker assisted selection**

Plant breeders utilize MAS to introgress favourable alleles, identify suitable individuals from segregated breeding lines and accumulate desired alleles (50). MAS is the most successful approach in plant breeding. It offers several benefits, including improved precision and efficacy in selecting challenging phenotypic traits, the ability to introgress desired genes while

**Table 3.** Varieties released through various breeding process

Pure line selection (varieties developed from traditional landrace)			
Varieties	Parents	References	
PTB 10 N 22 BR 19	Thavalakkannan Raj Bhog Brown Gora	(43)	
Shuttle breeding			
Sahbhagidhan	IR 55419*2/Way Rarem	(44)	
Interspecific hybridisation			
Nerica rice CO 31	<i>O. sativa</i> × African rice GEB 24 × <i>O. perennis</i>	(92)	
Mutantion breeding			
Varieties	Mutagen	Parent	References
MR 219 – 9	Gamma rays	MR 219	(93)
MR 219 – 4	Gamma rays		
MK – D – 2	Gamma rays	Manawthukha	(94)
MK – D – 3	Gamma rays		
Taromhali	Gamma rays	Iranian landrace	(95)

preserving essential features and the elimination of the need for additional selfings in backcrossing. When selection intensity is high, the application of MAS can greatly reduce the time and resources needed to attain selection goals for heritability characteristics of low to moderate values. The most precise, rapid, cost-effective, eco-friendly and accurate technology for creating improved rice varieties with drought tolerance or resistance is provided by MAS (51). Fig 5 shows marker-assisted backcross breeding (MABB) integrated with pedigree selection for developing improved lines.

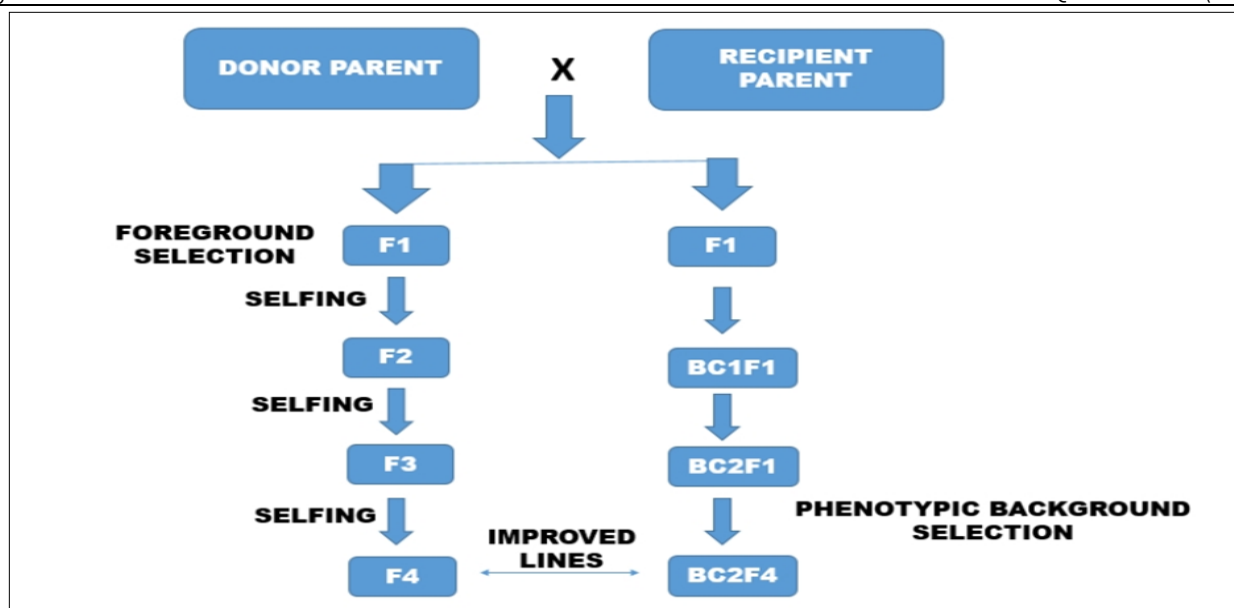
#### Drought linked QTLs

QTLs are specific genomic regions that contain genes associated with the inheritance of quantitative traits. Previous molecular genetic studies have identified numerous QTLs linked to various physiological and biochemical characteristics (49). However, due to low mapping resolution and weak phenotypic effect, these studies were unable to identify the genes that regulate

these traits (52). Mapping populations, locating polymorphic markers, genotyping, constructing genetic maps, precise phenotyping and mapping QTL based on genotypic and phenotypic data are all necessary steps in determining the QTL governing drought-related variables. Thus, breeders must uncover QTLs related to drought stress. Numerous QTLs associated with grain yield (GY) and its constituent parts have been found through studies; some of these QTLs have favourable effects on alleles, while others have negative effects. A population of 436 random F<sub>3</sub> lines from a hybrid between 'Vandana' and 'Way Rarem' highland rice cultivars revealed the first QTL, qDTY12.1, for GY under drought stress (53). Under drought stress, QTLs qDTY3.1 and qDTY6.1 show complementary effects (54). In a pyramided population, discovered a yield QTL, qDTY7-1, under drought stress (55). Two yield QTL, qDTY8-1 and qDTY3-1, were reported to contribute to enhanced population yields (56). Table 4 shows drought tolerance linked QTL in various crosses.

**Table 4.** Drought linked QTLs of rice in various crosses

Parents	Total number of lines	Marker used	Number of QTLs	References
Kaybonnet × ZHE733	198 RILs	SNP Marker	41 QTLs	(96)
CT 9993 × Samba Masuri	150 RILs	Polymorphic Microsatellite Markers	8 QTLs	(97)
Lvhan 1 × Aixian 1	120 RILs	SNP Marker	9 QTLs	(98)
Miyang 23 × Jileng 1	253 RILs	SNP Marker	28 QTLs	(9)
IR64 × Hawara	90 RILs (F <sub>3</sub> )	SNP Marker	154 QTLs	(100)
HHZ × 9311 (conventional <i>indica</i> rice varieties)	365 F <sub>2:3</sub> LINES	SNP Marker	50 QTLs	(101)
<i>O. longistaminata</i>	143 BC2F <sub>20</sub> LINES	SNP Marker	28 QTLs	(102)

**Fig. 5.** Marker-assisted backcross breeding (MABB) integrated with pedigree selection for developing improved lines.

## Improving drought-tolerance in rice through plant genome editing

The CRISPR/Cas system is a popular, effective and precise genome editing technique. TALENs, CRISPR-Cas9, CRISPR-Cpf1 and base editing techniques have been used to edit a large number of these genes for resistance to biotic and abiotic challenges. Genome editing in rice targets drought-responsive genes like OsPYL, OsDREB1A, OsbZIP46 and OsNACs to enhance ABA signaling, root growth and stress tolerance. Genomic edits improve water-use efficiency, reduce transpiration and stabilize yield under drought conditions (57). CRISPR-dCas9/nCas9 base-editing techniques and DSB-dependent CRISPR-Cas9 technology have been standardized for rice and other crops. For inducing precise point mutations, adenine base editors (ABEs) and cytosine base editors (CBEs) are employed to generate A-to-G and C-to-T conversions, respectively, through enzymatic deamination reactions involving dCas9/nCas9 fusion proteins (58). For functional genomics and agricultural advancement, genome editing is a precision mutagenesis technique.

These technologies have revolutionized crop breeding by enhancing genetic gains and speeding up crop breeding (59). Since CRISPR allows for targeted genome editing, its specificity and accuracy have allowed it to surpass other systems (60). To repair DNA double-strand breaks (DSBs) through homologous recombination (HR) or non-homologous end joining (NHEJ), SSNs break the target DNA sequence at specified points and make use of the plant's native DNA repair mechanism (61).

Tolerance to abiotic stresses, including drought, involves complex regulatory networks governed by multiple genes that maintain cellular homeostasis under adverse conditions (62). However, the application of genome editing technologies to improve rice under drought stress has been the subject of very few studies. Research on rice's ability to withstand drought has focused on the ethylene response factor (ERF) family, particularly OsERF109, whose target editing has been found to aid in the development of water stress tolerance (30). By selectively changing candidate genes for drought responses across the plant genome, genome editing has emerged as a powerful strategy for targeted rice improvement under drought-stress circumstances (63). Achieving consistent and accurate gene editing can be challenging due to factors like off-target effects and the complexity of controlling gene expression. Furthermore, there are ongoing ethical concerns regarding the potential misuse of CRISPR, especially in human germline editing, where changes can be passed down to future generations. Therefore, while CRISPR is revolutionary, a more cautious and nuanced understanding of its capabilities and limitations is essential.

## Omics in drought tolerance

Omics-based approaches comprising genomics, transcriptomics, proteomics and metabolomics have become indispensable in modern plant breeding and biotechnology. The identification of genes responsive to drought, the regulatory network that governs their expression, the functional proteins involved and alterations in plant metabolism have all been accomplished through the application of omics techniques. Such integrative analyses offer insights into potential candidate genes and loci for targeted breeding interventions (64). Understanding the rice plant's complex molecular responses under drought stress is

crucial for developing effective drought-tolerant varieties, thus contributing to sustainable food security.

## Genomics in enhancing drought tolerance in rice

To comprehend the genetic foundation of crop plant drought resistance, genomics has become a potent bioinformatics tool. Until the molecular mechanisms underlying grain yield stability are fully understood, current breeding techniques for drought-tolerant crop plants are ineffective (65). The complete genome sequencing of *indica* and *japonica* rice subspecies has greatly expanded the availability of genetic resources for trait improvement. Large germplasm sets of rice may have breeding signatures, such as loci linked to significant agronomic traits and essential functional genes when their genomics-based alterations are analysed. Combining genetic advancements with genomics, breeding techniques and accurate phenotyping offers a reliable approach to identifying potential genes. It enables an understanding of the networks that regulate their expression and helps in mapping the metabolic pathways involved in drought tolerance. Genomics-assisted breeding approaches have proven beneficial for improving drought tolerance in rice by identifying stress-associated loci that can be further utilized in breeding programs (17). Key genes in abscisic acid (ABA)-mediated signaling, such as *PYR/PYL/PP2C* and *SnRK*, have been identified and functionally validated for their role in enhancing drought resistance (66).

## Proteomics in enhancing drought tolerance in rice

Proteomics is an effective tool for identifying and characterizing the proteins that are changed in response to stress conditions and their role in drought tolerance. Plant responses to drought stress conditions are accompanied by changes in the expression of various proteins (67). About thirty-one drought-responsive proteins have been discovered (68). The Rice Proteome Database, developed by the National Institute of Agrobiological Sciences, facilitates comparative proteomic analysis between drought-tolerant and sensitive genotypes (59). For instance, the ClpD1 protease is significantly upregulated in drought-tolerant cultivars. Notably, the drought-tolerant variety alone showed upregulation of the ClpD1 protease multiple times, while the pathways involved in the manufacture of porphyrin and chlorophyll were downregulated. A comparative proteomic analysis of a susceptible rice cultivar and its stress-resistant somaclonal mutant line identified a significant number of drought-associated proteins (DAPs). These DAPs are primarily related to retrotransposons, sequences of DNA in a plant's genome that can copy themselves and move to different parts of the genome. This finding suggests that gene expression linked to drought tolerance mechanisms is heavily regulated by epigenetic factors. Four isoforms of LEA proteins and an 18.6 kDa class III small heat shock protein (HSP18.6) were found in all cultivars in a comparative proteome profiling of eight rice genotypes, including both *japonica* and *indica* sp. This drought-induced protein was identified. The N22 genotype, which is exceptionally resilient to drought stress, showed the highest levels of HSP18.6 and four LEA proteins, indicating the critical functions that these proteins play in resistance to drought stress (64).

## Metabolomics in enhancing drought tolerance in rice

Since it measures the total or groups of metabolites expressed in a small number of samples over a certain period, metabolomics



analysis in plant systems is advancing quickly. Drought triggers changes in primary and secondary metabolites such as amino acids, organic acids, soluble sugars, fatty acids, phenolics and osmolytes, which aid in osmotic regulation and reactive oxygen species (ROS) scavenging (69-71). During drought changes in metabolite responses in plant species are essential to acquire adaptations (72). Research on primary and secondary metabolites and their varying expression patterns under biotic and abiotic stress conditions might be aided by both quantitative and qualitative rice metabolomics investigations (73). To facilitate molecular breeding under stressful circumstances, metabolomics techniques are a promising set of technical interventions that act as frameworks for obtaining a comprehensive biochemical and genetic image of organisms. Rice transcriptome and metabolome analyses have shown metabolic markers linked to reproductive characteristics under conditions of heat and drought. The most significant metabolic component is sugar metabolism, with increased expression of sugar transporter and cell wall invertase in sensitive and tolerant cultivars respectively (74). While ROS detoxifying enzyme activities rise during drought stress, soluble sugar levels and net photosynthetic rate fall (75). Understanding these metabolic shifts offers a pathway to develop stress-resilient rice varieties through metabolomics-assisted breeding.

Data integration and environmental variability are major bottlenecks in applying omics data to real-world agriculture. Integrating complex datasets to generate actionable insights is challenging, especially when interpreting them under variable field conditions. Additionally, factors like soil type, climate and microclimates can make it difficult to translate lab-based omics data effectively to diverse field environments.

#### **Drought tolerance-gene and transgenic approach**

Drought stress in rice leads to differential expression of around 5000 genes, with 6000 downregulated (76). These genes are categorized into three major categories: membrane transport, signalling and transcriptional control (23). They control most biochemical, physiological and molecular mechanisms under drought stress in rice. Most genes are ABA-independent or ABA-independent regulatory systems (29). Some genes are associated with osmoregulation and late embryogenesis abundant proteins, which impart tolerance to water deficit in rice (32). Transgenic approaches increase grain yield, water use efficiency, antioxidant enzyme activity and photosynthesis. Overexpression of OsDREB2A enhances survival of transgenic plants under severe drought and saline conditions (77). CDPK7 and CIPK03/CIPK12 control regulatory proteins, signal transduction pathways and protein kinases in rice (78). OsITPK2 reduces levels of inositol triphosphate and ROS homeostasis under drought stress. WRKY genes play crucial roles in plant development by responding to drought stress.

#### **Management of drought stress through nanoparticles**

In agriculture, nanoparticles have demonstrated great promise, especially in the management of drought and abiotic stress. According to studies, using nanomaterials can increase crop output while using less money and energy. Research has demonstrated that silicon nanoparticles can reduce drought stress in crops like rice. It has also been discovered that other nanomaterials, such as composite micronutrients, zinc oxide

nanoparticles and sodium silicate, lessen the impacts of drought stress. It has been discovered that iron nanoparticles can lessen the negative impacts of drought stress on yield components and oil percentages (79). Plant physiological and biochemical responses have been demonstrated to be modulated by zinc and zinc oxide nanoparticles (80). By creating nanoparticles with certain properties, nano biotechnological interventions, especially in rice, can control drought stress responses. Nanotechnology shows potential for drought stress management, but its high cost and the need for scalable production are challenges. Safety concerns arise from nanoparticles' potential effects on plants, soil and water, requiring thorough testing. While lab results are promising, large-scale application demands efficient delivery systems and stability in diverse climates. Regulatory hurdles also exist, with ongoing development of safety standards that could delay widespread adoption.

### **Conclusion**

Climate change is projected to exacerbate water scarcity, posing a significant challenge to the long-term sustainability of rice cultivation. The anticipated increase in the frequency, duration and severity of droughts threatens global food security and stable rice production systems. As drought tolerance is a complex and quantitative trait influenced by multiple genes and environmental factors, understanding its genetic and physiological basis is essential. Moreover, heat and salinity stresses further intensify drought effects in rice-growing regions. While conventional breeding has contributed to some progress, integrating modern approaches such as molecular breeding with drought-linked QTLs, MAS, nanotechnology and multi-omics techniques targeting candidate genes offers a more precise and efficient path toward developing drought-resilient rice varieties. A multidisciplinary approach is vital to ensure rice productivity under future climate uncertainties. The main challenges of biotechnology accessibility in low-income regions are lack of infrastructure, high costs and limited expertise, hindering the development and adoption of biotechnological solutions. Similarly, QTL mapping and MAS rely on high-quality genotypic data, which can be costly and variable. Inaccurate data reduces their effectiveness and these methods face challenges due to complex trait inheritance and the limited availability of reliable molecular markers, further restricting their practical application.

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## Authors' contributions

NKR searched, collected and wrote the first draft. MU and PS analyzed the manuscript, provided the regular assistance to revise and finalize it. RS along with RR review and edited the manuscript. SM critically reviewed and edited the same. SRM has corrected the grammatical and typographical errors in the manuscript. All authors read and approved the final manuscript.

## Compliance with ethical standards

**Conflict of interest:** Authors do not have any conflict of interest to declare.

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