



REVIEW ARTICLE

Drought responses in rice (*Oryza sativa* L.): An integrated review of morphological, physiological, biochemical, phenological and genetic perspectives

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Abstract

Rice (*Oryza sativa* L.) production is severely affected by drought, which reduces yield, growth and physiological functions in various environments. This review integrates the morphological, physiological, biochemical, phenological and genetic responses of rice to drought, focusing on both common and environment-specific responses. Rice plants respond to water deficit by reducing leaf area and stomatal opening and modifying osmotic potential; roots may deepen or alter their architecture and flowering time may be delayed as an escape mechanism. Biochemically, osmolytes, antioxidants and hormones, especially abscisic acid (ABA), are key players in stress tolerance. Genetic mapping has identified several quantitative trait loci (QTLs) and candidate genes associated with root architecture, osmotic adjustment and flowering time, while transcriptomic studies have revealed the regulatory mechanisms underlying these traits under drought conditions. However, several challenges remain, including the lack of root phenotyping under field conditions, the instability of QTL effects across environments and the limited translation of pot-based findings to field performance. Integrated approaches that involve high-throughput field phenotyping, multi-environment trials to assess genotype × environment interactions and better integration of genomics with physiological traits across a variety of genetic backgrounds will be essential for future advances. These integrated approaches are pivotal in bridging the gap between field performance and the underlying physiological and molecular mechanisms, thereby facilitating the development of drought-resilient rice cultivars.

Keywords: drought tolerance; flowering time; genotype × environment interaction; *Oryza sativa*; osmotic adjustment; phenology; qDTY loci; reactive oxygen species; root architecture

Introduction

Rice (*Oryza sativa* L.) is a staple food and a primary energy and protein source in Asia and is vital for the food security of billions of people (1). However, rice production is water-intensive, requiring approximately 2500–3000 L of water to produce 1 kg of grain under traditional rice cultivation systems, making it highly susceptible to drought (2, 3). Changing climate variability and unpredictable rainfall have also exacerbated the impact of drought stress in rice producing areas.

In Asian rice ecosystems, drought and drought-heat compound events are occurring more frequently, particularly during critical growth stages such as panicle initiation, booting and grain filling, resulting in significant yield losses (4, 5). In irrigated farms, the spread of drought hotspots has been reported (6). Drought stress in rice occurs at various levels of organisation. It affects the architecture

of plants by reducing tillering, leaf area, biomass production and promoting premature senescence; it can also influence flowering patterns and spikelet sterility (7, 8); and physiologically, it closes stomata, impairs photosynthesis, promotes oxidative stress and activates osmolyte responses and antioxidant pathways (9, 10). Overall, these effects constrain rice yield potential, especially in water-limited and marginal conditions.

Several recent reviews have addressed individual aspects of drought tolerance in rice, including root system architecture, physiological adaptation, molecular regulation and breeding strategies (11, 12). However, these reviews generally emphasise specific components rather than providing an integrated analysis across morphological, physiological, biochemical, phenological and genetic responses. Furthermore, few reviews critically evaluate conflicting findings, methodological limitations and the translation of controlled-environment studies to field conditions. This review

was prepared through a comprehensive literature search conducted using Web of Science, Scopus, PubMed, ScienceDirect, Google Scholar and AGRICOLA. Peer-reviewed articles published primarily between 2018 and 2025 were retrieved using combinations of keywords including rice, drought stress, phenology, root architecture, physiology, biochemistry, genetics, quantitative trait locus (QTL), genome-wide association study (GWAS), multi-omics and drought breeding. Additional landmark studies published before 2018 were included where necessary to provide historical context. Relevant original research articles and recent review papers were critically evaluated to synthesise current knowledge, identify methodological limitations and highlight future research priorities.

Phenological responses of rice to drought

Importance of phenology in drought adaptation

Rice responses to drought are greatly affected by phenology, which affects the timing of radiation interception, canopy development and assimilate allocation under water scarcity (13). Phenological matching of vegetative and reproductive growth with rainfall may enhance carbon assimilation and ensure sufficient assimilates for panicle development and grain filling. However, phenological asynchrony may result in drought during sink development and early grain filling, when spikelet fertility and source-sink relationships are critical (14, 15).

Early flowering, a shorter reproductive period and mid-day anthesis are common drought-escape strategies. However, these characteristics may be associated with a yield penalty and may not always maximise productivity under variable or prolonged drought conditions (16, 17). Therefore, drought adaptation should be evaluated within an integrated framework encompassing whole-plant carbon assimilation, root system function and the regulation of source-sink dynamics and their genetic control (18, 19). Although early flowering is widely recognised as an effective drought-escape mechanism, its benefits are highly dependent on drought timing, severity and genotype. Under mild or intermittent drought, premature flowering may reduce biomass accumulation and sink capacity, ultimately limiting yield despite successful stress escape. Furthermore, many conclusions regarding phenological adaptation are derived from controlled-environment experiments, emphasising the need for multi-environment field validation before these traits are incorporated into breeding programs.

Phenological shifts under drought

Drought affects rice phenology in a complex manner that depends on the timing, severity and duration of the stress and the rice genotype (20). Depending on the timing and severity of drought stress, heading may occur either earlier or later than under well-watered conditions. For example, pre-flowering mid-season drought can accelerate panicle initiation and flowering due to increased abscisic acid (ABA) signalling and associated changes in source-sink relationships, which may improve temporary drought avoidance. However, this shift is generally accompanied by smaller panicles, reduced biomass accumulation and lower grain yield (21).

Conversely, severe or prolonged drought generally delays heading, disrupts anthesis, shortens the grain-filling period and ultimately reduces grain yield. It decreases photosynthesis and assimilates transport, closes stomata, hastens maturity and increases the sterility of spikelets (17). These effects are influenced by genotypic differences in hormone sensitivity, water status and

photosynthetic assimilate storage and remobilisation. In addition, heading date is also affected by environmental and management factors and genotype $\times$ environment interactions play an important role (22). Although drought-induced shifts in heading date are generally considered adaptive, their effectiveness is highly context dependent. Early heading may facilitate drought escape when terminal drought predominates, whereas delayed heading can expose reproductive tissues to prolonged water deficits and increase spikelet sterility. Moreover, many studies reporting phenological shifts have been conducted under controlled environments, making it difficult to predict their stability across diverse field conditions and genotype $\times$ environment interactions. These inconsistencies highlight the need for multi-location validation before phenological traits are widely incorporated into breeding programmes.

Sensitive phenological stages

Sensitivity to drought varies across rice developmental stages, with the reproductive phase generally being more susceptible than the vegetative phase (19). During the vegetative stage, drought suppresses tillering and root development; however, these adverse effects can be partially reversed by rewatering, making this stage suitable for evaluating drought avoidance and recovery traits such as early vigour, deep rooting and leaf rolling (13). In contrast, panicle initiation (PI) is highly sensitive because drought disrupts assimilate supply, hormonal balance and panicle development, resulting in smaller panicles and increased spikelet sterility (19). The booting-to-anthesis transition is equally vulnerable, as drought impairs anther dehiscence, pollen viability and stigma receptivity, thereby increasing reproductive failure (23). During grain filling, drought restricts photosynthesis and assimilate translocation, leading to poor grain filling, reduced grain weight and yield loss (24). Although reproductive-stage drought is widely recognised as the most damaging, its effects vary with genotype, stress intensity and duration. Moreover, much of the current evidence is derived from controlled-environment studies, highlighting the need for multi-environment field validation before stage-specific traits are prioritised in breeding programmes.

Important phenology screening traits

Phenology-related traits widely used for screening rice under drought include flowering time (anthesis), days to 50 % flowering (DTF), anthesis synchrony and grain-filling duration (25). Days to 50 % flowering, defined as the interval from sowing or transplanting to the stage when 50 % of the primary tillers have flowered, is commonly used to classify rice genotypes into early-, medium- and late-maturing groups. Although DTF is an important indicator of drought escape, it does not always reflect drought tolerance because early flowering may reduce biomass accumulation and yield potential under prolonged or intermittent stress (21). Anthesis synchrony can reduce spikelet exposure to peak drought stress; however, its effectiveness is strongly influenced by the microenvironment and is difficult to quantify under field conditions (15). Similarly, grain-filling duration plays a key role in assimilate accumulation and remobilisation, but its expression is highly dependent on temperature and post-anthesis environmental conditions (26). Therefore, these phenological traits should be evaluated together with complementary characteristics, including vegetative duration and crop maturity, to improve the reliability of drought screening in both nursery and field environments (27).

Phenology-linked mechanisms of tolerance

Phenology, together with plant physiology and architecture, plays a central role in determining rice adaptation to drought and other water-limited environments (19). Accelerated flowering can improve drought escape by enabling plants to complete reproduction before severe water deficits develop; however, this strategy is effective only when supported by adequate root water uptake and sustained assimilate supply under stress (28). Likewise, efficient carbon allocation, including maintenance of green leaf area and assimilate transport to developing panicles, is essential for sustaining grain filling during drought (14, 29). Reproductive resilience, particularly the maintenance of spikelet fertility, depends on coordinated flowering synchrony and source-sink balance under transient water deficits (19). Although QTL mapping, multi-environment evaluation and root phenotyping have identified several promising traits, most studies continue to examine phenological, physiological and root characteristics independently and often under controlled rather than representative field conditions (30). Consequently, the interactions among these traits remain insufficiently understood, highlighting the need for integrated, multi-environment approaches to identify stable trait combinations for drought-resilient rice breeding.

Morphological responses to drought

Water deficit alters rice growth and morphology in a manner that depends on the developmental stage, stress severity and genetic background (10). During the seedling stage, reduced soil water potential restricts water uptake and suppresses radicle, coleoptile and leaf expansion, thereby causing patchy emergence and reduced seedling vigour (31). Although pot- and Petri dish-based screening methods are convenient for early evaluation, they often overestimate drought responses because of artificial microclimatic conditions and poor representation of soil-root interactions under puddled or residue-covered field soils (32, 33). Under prolonged drought, plant height, leaf area, tillering and biomass decline owing to reduced cell expansion, assimilate production and bud development, processes that are regulated by phytohormones (9, 10). Root growth is also constrained by soil drying; however, container-based studies frequently exaggerate stress intensity because soils dry more rapidly

than under field conditions, limiting the extrapolation of results to aerobic and rainfed environments (21). Leaf rolling initially reduces transpirational water loss, but excessive rolling indicates severe dehydration and impaired recovery, while premature senescence accelerates the loss of photosynthetically active leaf area (34). Furthermore, visual scoring of drought symptoms is influenced by temporal and spatial variability within the canopy, reducing its reliability as a standalone screening criterion (35).

Root architectural modifications contribute substantially to drought avoidance by increasing the root-to-shoot ratio, optimising rooting angle and promoting deeper and more prolific lateral root development (36). However, much of the available evidence is derived from pot experiments, rhizoboxes, or shovelomics, which inadequately capture the three-dimensional complexity of root systems under puddled, cracking, or fluctuating field soil conditions (37). Consequently, breeding programmes should prioritise validation across both controlled and multi-environment field trials to identify stable root ideotypes. Among the proposed drought-adaptive ideotypes, shallow, deep and dense lateral root systems each offer distinct advantages depending on the target production environment, underscoring the importance of environment-specific trait selection (Fig. 1).

Physiological responses to drought

Drought profoundly alters rice water relations by reducing relative water content (RWC), leaf water potential (ψ_{leaf}) and cellular turgor, thereby restricting cell expansion and plant growth (38). Drought-tolerant genotypes generally maintain higher RWC through improved osmotic adjustment and enhanced root development, although these responses vary considerably with stress severity and genotype (19). While RWC remains one of the most widely used indicators of plant water status, its interpretation may be influenced by tissue age, sampling time and rehydration artefacts, limiting direct comparisons among studies (39). Consequently, physiological assessments should integrate multiple water-status indicators rather than relying on a single parameter. The sequence of physiological events linking declining soil moisture to changes in plant water relations, gas exchange and oxidative stress (Fig. 2).

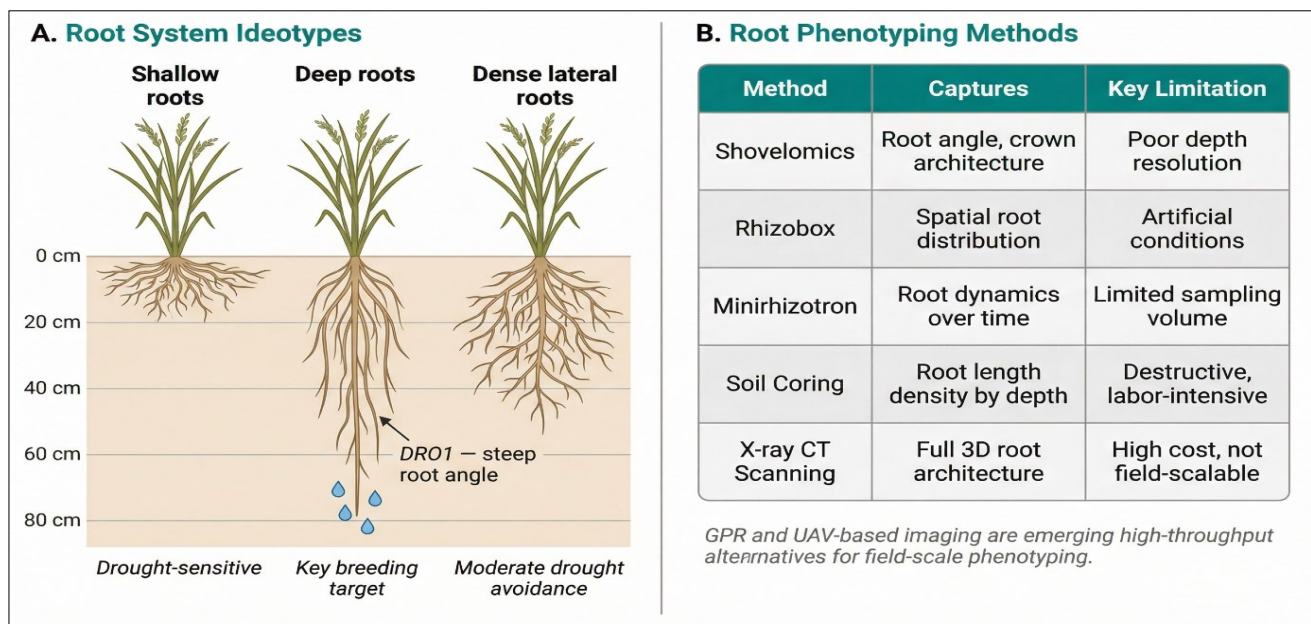


Fig. 1. Root system ideotypes and phenotyping approaches for drought adaptation in rice: (A) root system ideotypes; (B) root phenotyping methods.

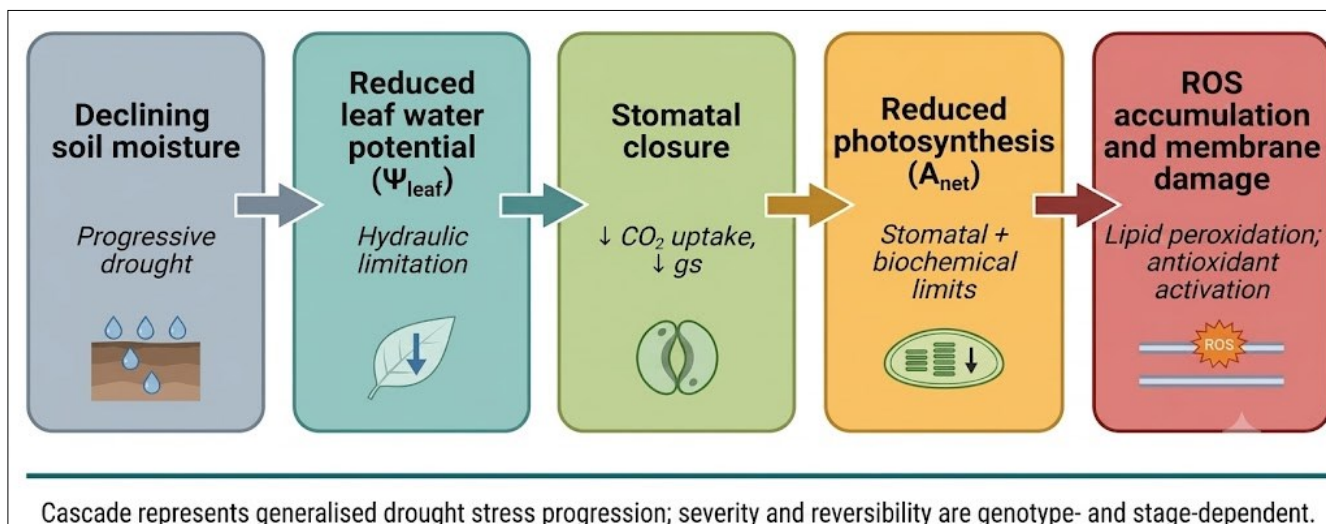


Fig. 2. Physiological cascade linking progressive drought stress to cellular damage in rice.

Stomatal conductance declines under drought to reduce transpirational water loss; however, this response also limits CO_2 uptake and carbon fixation, creating a trade-off between water conservation and photosynthetic productivity (40). Genotypic variation in stomatal density, size and regulation contributes to differences in drought adaptation, yet many short-term pot experiments fail to capture the dynamic effects of diurnal fluctuations, vapour-pressure deficit (VPD) and progressive soil drying observed under field conditions (41). Likewise, gas-exchange measurements may be affected by leaf size, chamber leakage and failure to achieve equilibrium, reducing comparability across experiments (42).

Drought-induced inhibition of photosynthesis results from both stomatal and non-stomatal limitations. Initially, reduced CO_2 availability restricts carbon assimilation, whereas prolonged stress impairs rubisco activity, electron transport (ET), ATP production and PSII function, ultimately leading to photoinhibition (43). Chlorophyll fluorescence parameters, including the PSII operating efficiency (ΦPSII) and the maximum quantum efficiency of PSII (F_v/F_m), are widely used to assess photosynthetic performance under drought (44, 45). However, fluorescence measurements obtained under dark-adapted or constant-light conditions may not accurately represent the fluctuating light environments experienced under field conditions, emphasising the importance of validating these measurements under realistic production environments (46).

Water deficit also compromises membrane integrity by increasing lipid phase transitions, membrane permeability and ion leakage, which are commonly assessed using membrane stability index or electrolyte leakage assays (47). Although greater membrane stability is frequently associated with improved drought tolerance and yield retention, this relationship is influenced by tissue type, growth stage, temperature and sample handling, limiting its universal application as a selection criterion (38). Overall, drought responses progress from impaired water status and stomatal closure to disruptions in photosynthesis, membrane stability and accelerated senescence (48). Despite recent advances in high-resolution imaging, gas-exchange analysis and chlorophyll fluorescence phenotyping, relatively few studies have integrated these physiological traits with membrane stability across multiple environments. This gap limits the identification of robust physiological markers and their effective utilisation in drought-resilient rice breeding programmes (49).

Biochemical responses to drought

Rice responds to drought through coordinated osmotic adjustment, antioxidant defence, hormonal regulation and metabolic reprogramming. Osmolytes, including proline, soluble sugars and sugar alcohols, help maintain cellular osmotic balance, stabilise proteins and membranes and reduce reactive oxygen species (ROS) accumulation (12). Drought-tolerant genotypes generally accumulate higher levels of these osmoprotectants, although proline accumulation may also reflect stress injury rather than drought tolerance, depending on genotype, developmental stage and stress severity (9).

Drought-induced oxidative stress activates both enzymatic antioxidants, including superoxide dismutase (SOD), catalase, peroxidases and ascorbate peroxidase (APX) and non-enzymatic antioxidants such as ascorbate, glutathione and phenolics to minimise lipid peroxidation and maintain membrane stability (50). However, antioxidant responses are highly variable among tissues, developmental stages and stress intensities and differences in assay conditions, sample handling and normalisation procedures often limit direct comparisons among studies (51). The coordinated roles of osmolytes and antioxidant systems in osmotic adjustment and ROS detoxification are summarised in Fig. 3.

Phytohormones further regulate biochemical adaptation under drought. Elevated abscisic acid (ABA) promotes stomatal closure, osmolyte accumulation and stress-responsive gene expression, whereas ethylene primarily regulates senescence and stress signalling. Brassinosteroids, acting alone or in combination with ABA, enhance antioxidant capacity, osmolyte biosynthesis and leaf expansion under water deficit (52–54). Nevertheless, enhanced stress tolerance may involve growth and yield penalties under favourable conditions, emphasising the physiological trade-offs associated with constitutive stress responses (55).

Drought also alters carbohydrate, nitrogen and secondary metabolism to maintain cellular homeostasis and redox balance (56). Recent omics approaches have improved understanding of the regulatory networks underlying these biochemical responses; however, many studies continue to rely on severe pot or hydroponic stress rather than progressive soil drying under field conditions, limiting the translation of laboratory findings into breeding applications.

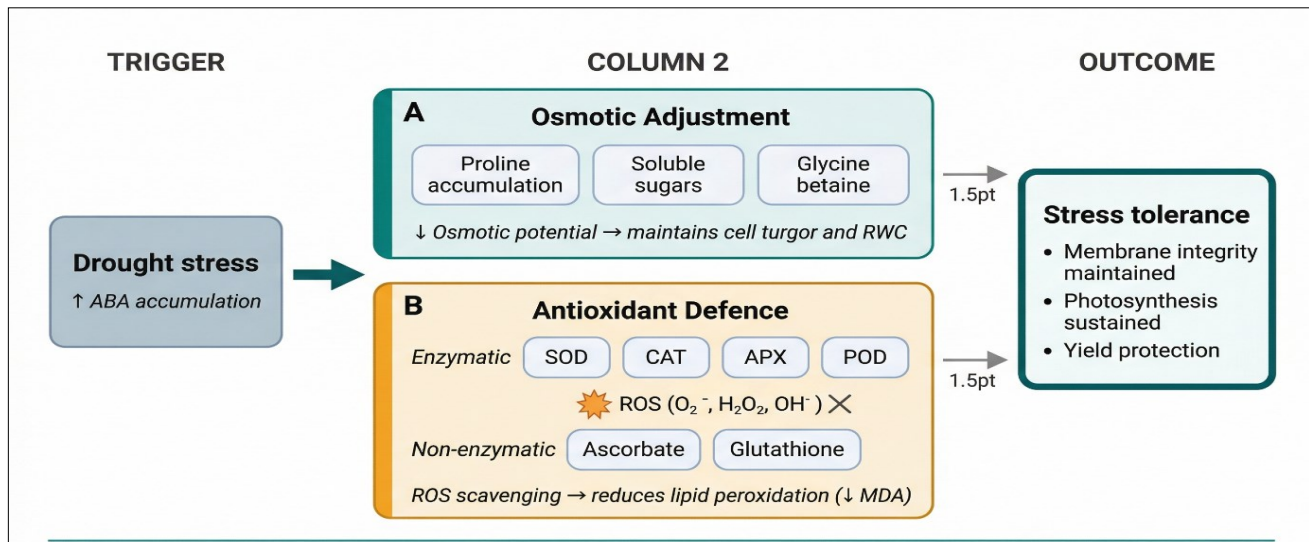


Fig. 3. Biochemical defence network activated under drought stress in rice.

Growth stage sensitivity to drought

Rice is very sensitive to drought at various development stages, owing to stage-specific physiological and biochemical limitations during the vegetative, reproductive and grain-filling stages (10). The significant morpho-physiological and biochemical traits related to drought tolerance at each stage are listed in Table 1. At the vegetative stage, water stress decreases leaf water potential and turgor, stomatal conductance and ultimately leaf growth, tillering and growth. This can be partially alleviated by osmotic adjustment (proline and sugars) and early root development and mild stress may lead to recovery following rewatering (57). Loss in yield currently is primarily due to sink development.

The reproductive phase is most sensitive. Drought affects assimilate supply and hormone balance, spikelet number, pollen fertility and anther dehiscence and greatly enhances spikelet sterility (15, 58). Even a brief period of acute drought stress can disproportionately reduce grain yield, highlighting the importance of maintaining spikelet fertility and photosynthetic stability during reproduction (52, 59). During grain filling, drought accelerates senescence, inhibits photosynthesis and restricts remobilisation of

reserves, as well as reducing grain size. Oxidative stress also limits assimilate supply and grain development (14, 60). Although reproductive-stage drought is generally the most damaging, the relative sensitivity of each developmental stage varies with genotype, stress severity and environmental conditions, emphasising the importance of stage-specific phenotyping in breeding programmes.

Adaptation and tolerance mechanisms in rice

Rice adapts to drought through three complementary strategies: drought escape, drought avoidance and drought tolerance, whose effectiveness depends on the timing, duration and predictability of water deficit (19). Drought escape accelerates panicle initiation and flowering, shortening the crop cycle through the coordinated action of ABA, gibberellins (GA) and flowering-time genes, thereby allowing reproduction before severe soil moisture depletion (19, 61). This strategy is particularly effective under predictable terminal drought; however, it often reduces biomass accumulation and sink capacity, making it less suitable under favourable environments or unpredictable drought scenarios where yield potential may be compromised (19).

Table 1. Growth-stage-wise key morpho-physiological, biochemical traits and breeding implications associated with drought tolerance in rice (*Oryza sativa*)

Growth stage	Important morpho-physiological traits	Important biochemical traits	Breeding implication	References
Seedling	Reduced radicle and coleoptile growth; low germination rate; reduced seedling vigour under low soil water potential	Elevated proline and soluble sugars; early ROS accumulation; low antioxidant activity	Screen for germination index and seedling vigour under PEG-simulated stress; avoid overreliance on pot-based assays	(31, 10)
Vegetative	Reduced plant height, LAI, tillering and biomass; leaf rolling; increased R:S ratio; deeper root growth angle	Proline and soluble sugar accumulation; activation of SOD, CAT, APX; moderate ABA increase; reduced chlorophyll	Select for early root depth, R : S ratio and stay-green under moderate stress; reversible stress recovery is a useful screening criterion.	(9, 19, 10)
Reproductive (PI to anthesis)	Reduced panicle size and spikelet number; impaired anther dehiscence and pollen viability; increased spikelet sterility; reduced gs and Anet.	Strong ABA-mediated stomatal closure; elevated ROS; increased MDA (lipid peroxidation); upregulation of stress-responsive genes	Prioritise spikelet fertility and Fv/Fm under staged reproductive drought; use qDTY-based MAS for yield under stress	(8, 9, 15, 52)
Grain Filling	Accelerated senescence; reduced grain weight; suppressed Anet and remobilisation of NSC; shortened GFD	Oxidative damage (increase MDA); reduced antioxidant capacity; impaired starch synthesis; reduced HI	Select for NSC remobilisation efficiency and longer GFD; combine with membrane stability index screening.	(14, 59, 60)

LAI: leaf area index; R:S: root-to-shoot ratio; gs: stomatal conductance; Anet: net photosynthesis rate; PI: panicle initiation; ABA: abscisic acid; ROS: reactive oxygen species; MDA: malondialdehyde; SOD: superoxide dismutase; CAT: catalase; APX: ascorbate peroxidase; NSC: non-structural carbohydrates; GFD: grain filling duration; HI: harvest index; Fv/Fm: maximum quantum efficiency of PSII; MAS: marker-assisted selection; qDTY: drought yield quantitative trait locus; PEG: polyethylene glycol.

Drought avoidance minimises tissue dehydration through deeper rooting, a higher root-to-shoot ratio, reduced canopy expansion, leaf rolling and stomatal regulation, thereby maintaining water status and photosynthetic activity during intermittent drought (62–64). Nevertheless, prolonged stomatal closure and conservative water use may reduce carbon assimilation and limit recovery following rewatering. In contrast, drought tolerance enables continued metabolic activity at low tissue water potential through osmotic adjustment, enhanced antioxidant defence, maintenance of membrane integrity and protection of the photosynthetic apparatus (19, 65). However, these protective mechanisms are energetically expensive and, under non-stress conditions, may divert resources from growth and yield. Therefore, high-performing rice cultivars generally combine moderate drought escape with efficient avoidance and tolerance mechanisms rather than relying on a single adaptive strategy. Defining the optimal balance among these responses across diverse environments remains a major challenge for drought-resilient rice breeding (19).

Breeding approaches for drought tolerance

Conventional breeding

Conventional breeding approaches, including pedigree, index and recurrent selection, have been widely employed to exploit the polygenic nature of drought tolerance and improve grain yield, adaptation and agronomic performance under field conditions (66). However, progress has been relatively slow because drought tolerance is a complex quantitative trait with low-to-moderate heritability and strong genotype $\times$ environment interactions, which often mask phenotypic expression and reduce selection efficiency (18). Consequently, conventional breeding alone is insufficient for developing climate-resilient cultivars and is increasingly complemented by molecular breeding approaches.

Marker-assisted selection

Marker-assisted selection (MAS) facilitates the introgression of favourable alleles into elite cultivars using drought-yield quantitative trait loci (qDTYs), including qDTY1.1, qDTY2.2, qDTY3.1 and qDTY4.1, thereby accelerating genetic improvement while minimising linkage drag (67). Successful examples include DRR Dhan 42 and near-isogenic lines of IR64, particularly under reproductive-stage drought. Nevertheless, the effectiveness of MAS depends on the genetic background and the stability of QTL effects across environments and loci with small phenotypic effects are often overlooked. Furthermore, the high cost of genotyping and the limited transferability of some QTLs across diverse genetic backgrounds and production environments continue to restrict the broader application of this approach (68).

Quantitative trait locus identification and genomic mapping

Numerous QTLs associated with grain yield, spikelet fertility, root architecture, stay-green characteristics and phenological traits have been identified across diverse rice genetic backgrounds (69). Table 2 summarises the major drought-responsive QTLs and candidate genes with potential breeding applications. At the vegetative stage, several QTLs are associated with root density, leaf rolling and chlorophyll content, whereas candidate genes primarily regulate hormone signalling, stress perception and transcriptional control (70). Genome-wide association studies and SNP-based approaches have further improved the resolution of QTL identification; however, their application in breeding remains constrained by low phenotypic

variance explained, genotype $\times$ environment interactions and the environmental specificity of many loci (30, 71). Consequently, validation of stable QTLs across diverse genetic backgrounds and multi-environment field trials remains essential before their routine deployment in breeding programmes.

Gene/quantitative trait locus pyramiding and advanced lines

Introgression of drought-related qDTYs, root architecture and phenology-associated QTLs into elite cultivars through backcrossing has improved grain yield under drought conditions (72). Pyramided lines carrying multiple qDTYs generally outperform single-QTL near-isogenic lines (NILs), particularly under reproductive-stage drought, while maintaining yield under non-stress conditions (73). Root-related QTLs, such as *DRO1*, further enhance water uptake by promoting deeper rooting (74). However, the effectiveness of gene pyramiding is often constrained by epistatic interactions, linkage drag, marker availability and variable QTL expression across genetic backgrounds. Therefore, successful deployment requires background selection, multi-environment validation and integrated physiological evaluation to identify stable allele combinations.

Bringing phenology into drought breeding

Phenology should be regarded as a central component of drought breeding rather than merely a determinant of flowering time (75). Early flowering facilitates drought escape under predictable terminal drought but may reduce biomass accumulation and yield potential under favourable rainfall conditions. Conversely, later flowering can maximise resource utilisation when moisture is available but increases the risk of exposure to reproductive-stage drought (76). Consequently, ideal drought-resilient ideotypes should combine appropriate maturity duration, deep and efficient root systems, stable spikelet fertility and strong assimilate remobilisation according to the target production environment (77, 78). Selection strategies should therefore integrate multi-stage phenotyping, genotype $\times$ environment evaluation and genetic information on flowering-time genes to optimise adaptation across diverse drought-prone environments (79).

Knowledge gaps and future research directions

Despite significant advances in understanding drought responses in rice, several knowledge gaps continue to limit the development of drought-resilient cultivars for field conditions. Addressing these challenges will require integrated advances in high-throughput phenotyping, multi-omics, genomics and breeding strategies that effectively capture genotype $\times$ environment interactions.

Multi-omics integration gaps

Multi-omics studies have considerably improved our understanding of drought-responsive pathways; however, most investigations analyse transcriptomic, proteomic, or metabolomic datasets independently, limiting the identification of upstream regulatory networks (80). Furthermore, many studies rely on severe pot-imposed drought rather than progressive soil drying under field conditions, reducing their breeding relevance (53). Future research should integrate time-course multi-omics, weighted gene co-expression network analysis (WGCNA), root hydraulic traits and shoot transcriptomics across contrasting genotypes under realistic drought scenarios to identify robust regulatory networks and candidate genes.

Table 2. Major drought-responsive traits and associated quantitative trait loci and candidate genes in rice (*Oryza sativa*) with chromosomal location, phenotypic effect, validation status and breeding relevance

Trait	QTL / Gene	Chr.	Growth Stage	PVE (%)	Validation status	G × E stability	References
Grain yield under drought	<i>qDTY1.1</i>	1	Reproductive	12–31	NIL tested; field validated in indica	Stable across environments	(73, 80)
Grain yield under drought	<i>qDTY2.2</i>	2	Reproductive	8–18	NIL tested; IR64 background	Moderately stable	(73)
Grain yield under drought	<i>qDTY3.1</i>	3	Reproductive	17–35	NIL tested; multi-environment	Stable in indica	(73, 81)
Grain yield under drought	<i>qDTY4.1</i>	4	Reproductive	6–14	NIL tested	Environment-specific	(73)
Root length density	<i>qRT6</i>	6	Vegetative	10–15	Rhizobox and field validated	Moderate	(70)
Steep root angle / deep rooting	<i>DRO1</i>	4	Vegetative	23–35	Field validated; transgenic confirmed	Stable	(70, 69)
ABA signalling/ stress gene expression	<i>OsZIP23</i>	3	All stages	—	Transgenic overexpression lines	Limited + model genotypes only	(52)
Stomatal closure/ stress tolerance	<i>SNAC1</i>	9	Reproductive	—	Transgenic; field performance variable	Environment-specific	(9, 51)
Proline biosynthesis / osmotic adjustment	<i>OsP5CS</i>	1	Vegetative–Reproductive	—	Transgenic overexpression	Limited - controlled conditions	(9, 12)
Late embryogenesis/ desiccation tolerance	<i>OsLEA3</i>	5	All stages	—	Transgenic; improved survival under severe stress	Limited - not field-validated	(10)
Dehydration-responsive transcription	<i>OsDREB2A</i>	1	Vegetative–Reproductive	—	Transgenic; upregulated under drought	Environment-specific	(19)
Flowering time/ drought escape	<i>Hd1</i>	6	Reproductive	20–40	Natural variation; widely validated	Stable across photoperiod environments	(21, 60)
Stay-green / delayed senescence	<i>SGD1</i>	7	Grain filling	8–12	QTL mapping; limited NIL work	Moderate	(69)

Chr.: chromosome; PVE: phenotypic variance explained; G×E: genotype × environment interaction; QTL: quantitative trait locus; NIL: near-isogenic line; ABA: abscisic acid; *DRO1*: DEEPER ROOTING 1; *SNAC1*: stress-responsive NAC 1; *OsZIP23*: OsbasicLeucine Zipper 23; *OsP5CS*: OsDelta1-pyrroline-5-carboxylate synthetase; *OsLEA3*: Os Late Embryogenesis Abundant 3; *OsDREB2A*: Os Dehydration Responsive Element Binding 2A; *Hd1*: Heading date 1; -: not available or not reported in primary mapping studies.

Root phenotyping constraints under field conditions

Root phenotyping remains a major bottleneck in drought breeding because most available techniques, including rhizoboxes, pot experiments and shovelomics, inadequately represent root growth under heterogeneous field conditions (81). Future efforts should prioritise field-based phenotyping using minirhizotrons, ground-penetrating radar and X-ray computed tomography to validate root ideotypes across multiple environments. Integrating root hydraulic traits with whole-plant physiological responses will further improve the identification of drought-adaptive root systems (6, 28).

Limitations in phenology phenotyping

Current phenology phenotyping relies heavily on days to 50 % flowering (DTF), which does not adequately capture flowering synchrony, canopy dynamics, or the timing of drought during reproductive development (82). Integrating UAV-based phenotyping, canopy temperature imaging, stay-green assessment and source-sink dynamics with field observations will provide more reliable indicators for large-scale drought screening across breeding environments (80, 81).

Quantitative trait locus stability and genotype × environment interactions

The practical application of drought-responsive QTLs remains constrained by strong genotype × environment interactions and the environmental specificity of many loci (82, 83). Bayesian genomic prediction, machine-learning models and CRISPR-based functional validation offer promising approaches for identifying stable alleles across diverse environments. However, broader validation in elite germplasm and under-represented rice ecologies remains essential before these loci can be routinely deployed in breeding programmes (83, 84).

Artificial intelligence, genomic prediction and participatory breeding

Artificial intelligence, genomic prediction and participatory breeding provide new opportunities to accelerate drought-resilient rice improvement by integrating multi-environment phenotypic and genomic datasets (84, 85). Nevertheless, current predictive models are limited by small datasets, restricted environmental representation and inadequate integration of physiological and phenological traits. Developing large, standardised multi-trait databases and combining AI-assisted prediction with field validation will substantially improve breeding efficiency and facilitate the deployment of climate-resilient cultivars (84, 86, 87).

Conclusion

Rice drought tolerance is a complex quantitative trait governed by the coordinated interaction of phenological, morphological, physiological, biochemical and genetic mechanisms, which are strongly influenced by genotype $\times$ environment interactions. Rather than selecting individual drought-responsive traits, future breeding programmes should prioritise integrated trait combinations, including optimised flowering time, efficient root architecture, stable spikelet fertility, sustained photosynthetic capacity and effective assimilate remobilisation to achieve consistent performance under diverse drought scenarios. Equally important, breeding strategies should move beyond reliance on single-environment phenotyping, unstable QTLs, or isolated physiological measurements and instead adopt multi-environment validation, systems-level phenotyping and integrated multi-omics approaches. Emerging technologies, including AI-assisted genomic prediction, high-throughput field phenotyping using unmanned aerial vehicles (UAVs), CRISPR-based gene editing and genomic selection, offer unprecedented opportunities to accelerate the identification and deployment of drought-resilient cultivars. Future research should focus on validating stable candidate genes and trait combinations across diverse agroecological conditions to bridge the gap between laboratory discoveries and field performance. Collectively, these integrated approaches will accelerate the development of climate-resilient rice cultivars capable of sustaining productivity under rainfed and water-limited environments.

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Authors' contributions

VBK contributed to conceptualisation, literature search, manuscript writing and original draft preparation. UK contributed to supervision, conceptualisation, critical review and manuscript editing. PM contributed to literature search, data compilation and manuscript writing. AV contributed to literature search and the crop physiology and vegetable science sections. VKK and M contributed to the genetics and plant breeding sections and literature review, while SN contributed to the agronomy-related sections and literature review. All authors read and approved the final manuscript.

Compliance with ethical standards

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

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

During the preparation of this work, the authors used Perplexity Pro (Perplexity AI) and Grammarly Premium to assist with literature exploration, language clarity, structural refinement and editorial improvements. After using these tools, the authors carefully reviewed and edited all content, verified the accuracy of information and take full responsibility for the final version of the manuscript.

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