



REVIEW ARTICLE

Drought stress tolerance in rice: a critical insight

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Abstract

Drought is currently a serious threat for farming especially in rice cultivation, due to its substantial water requirements throughout its lifecycle. Drought is one of the major environmental constraints disrupting the growth and yield of rice plants, affecting them at physiological, morphological, biochemical, and molecular levels. Global climate change exacerbates this issue, leading to substantial economic losses. As rice is a major food crop worldwide, the demand for rice production is increasing in tandem with the expanding human population. Consequently, it has become imperative to utilize drought-prone areas for agriculture and develop drought-tolerant rice genotypes. In addition to conventional breeding methods, the application of multi-omics approaches proves most effective in meeting the need to enhance drought tolerance in rice plants. Protective mechanisms, such as morphological adaptation, physiological acclimatization, cellular adjustments, and antioxidant defense, play pivotal roles in helping plants overcome drought stress. Plant-microbial interactions are important for plants to overcome drought-induced adversities. Furthermore, applications of conventional approaches, omics approaches and nanotechnology are very promising for generating climate smart agriculture. Our aim in this review is to focus on drought stress tolerance in rice including drought-tolerant rice genotypes, their adaptation mechanisms, the unveiling the genes, transcription factors, microRNAs (miRNA) involved, microbial assistance, and exploring approaches to mitigate drought stress in rice plants. The present review might throw some light on understanding the mechanism of drought stress tolerance in rice, including its molecular crosstalk and biochemical dynamics, for future researchers.

Keywords

Drought; rice; multi-omics; microbial interactions; adaptation mechanisms; mitigate drought stress

Introduction

The global population is projected to increase from the current 7.6 billion to 9.8 billion by 2050 (1). Food production needs to increase by 70% by 2050 to keep pace with the population explosion (2). It has been observed that population growth is much higher in poorest country compared to rich country. According to a report, increment of population density from 1950-2010 in a poorest country was 330% whereas it was only 50% in wealthier countries (3). In the context of the present day, drought is one of the major constraints on agriculture (4). Drought is a natural phenomenon

resulting from the combined effect of climatic, environmental, and hydrological forces, leading to insufficient rainfall for agricultural production over long periods of time (5). Irregular, inadequate, and unpredictable rainfall significantly reduces the yield of rainfed lowland rice (6). Drought stress causes cell dehydration, resulting in osmotic stress and electrolyte imbalance (7). Drought cell also leads to a significant decrease in relative water content, plant growth, chlorophyll, and carotenoid contents while increasing the production of reactive oxygen species (ROS), which can cause oxidative damage (7, 8).

Typically, water is absorbed from the soil by the roots, maintaining the soil-plant-atmosphere continuum, as depicted in Fig. 1.

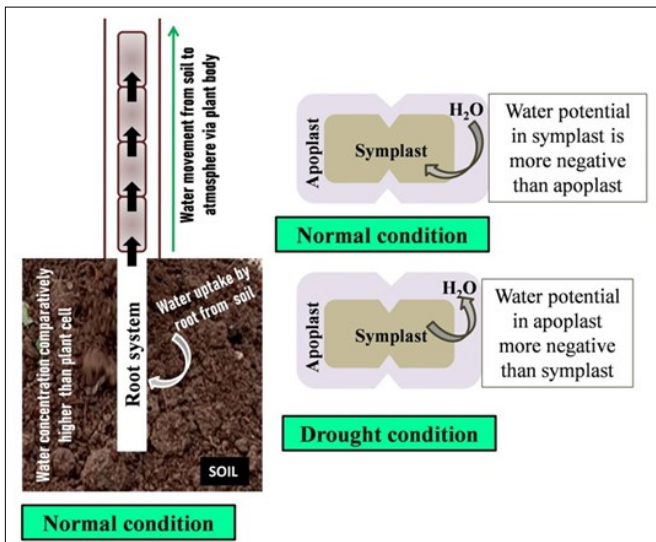


Fig. 1. Soil-plant-atmosphere continuum during normal condition and direction of water movement within plant cell under normal and drought stress conditions.

During drought stress, soil water potential is relatively low compared to the plant body, which is the primary cause of plant cell dehydration. Drought stress triggers numerous changes in plants, including morphological, physiological, and biochemical dynamics, and also leads economic losses (9, 10). An overall understanding of morphological-physiological-biochemical changes and metabolic pathways in plants in response to drought stress, along with drought stress coping strategies (9-11), is diagrammatically presented in Fig. 2.

In response to drought stress, plants are categorized into three broad groups: tolerant, avoiders, and sensitive, as stated in Fig. 3. Avoiders encompass three classes: water savers, water spenders, and drought escapers.

Globally, more than one-third of the total cultivated area is under drought stress (12). In Asia approximately 8.0×10^6 hm^2 of upland and 3.4×10^7 hm^2 of rainfed lowland rice have been reported to be affected by drought stress (13).

Rice plants due to their limited ability to absorb soil water beyond a depth of 60 cm, generally exhibit lesser resilience to water-scarce environments compared to other cereals (14). Drought stress is a significant factor hampering the overall plant growth and development,

affecting plant physiology, biochemistry, reproduction, and crop yield (15). Drought stress can severely hinder rice plants growth, resulting in substantial economic losses during the reproductive stage (48-94%) and grain-filling stage (90%) (13, 16). For instance, the application of 30% polyethylene glycol-6000 (PEG6000) for 120h has been reported to reduce heading rate by 85-97% of rice plants (17). Prolonged drought stress has been reported to hamper crop yield by affecting stages like flowering and grain filling (15).

Drought stress significantly impacts plant nutrient availability (18). Both nitrogen (N) and phosphorus (P) are crucial for plant growth, and drought stress (18) has the potential to disrupt ecosystem N and P cycles. Studies have shown that drought stress can hinder plant growth by affecting the uptake, transport, and redistribution of N and P (19). As soil moisture levels decrease, there is a notable decline in N and P uptake by plants (18). Additionally, under drought stress conditions, plants can experience increased N loss, although there have been reports of a positive induction of the N:P ratio in plants (18). N and P are very important macronutrients to alleviate the adverse effects of drought stress. Application of P has also been reported to decrease drought stress effects by enhancing water uptake through roots, net photosynthetic rate, and leaf water content (20). Recovery of P is very important for plant nutrition. Regeneration of nutrients by biochar is a widely used and promising method (21). Biochar activated with divalent cations has been demonstrated as an important agent for producing phosphorous compound useable for plant nutrition (22, 23). In agriculture, biochar is an important agent to promote overall farming productivity by improving soil fertility, plant nutrition, and plant growth (24). Moreover, application of raw biochar to soil has been proven to ameliorate drought stress (15% roughly) (24).

Undoubtedly, rice is one of the world's most vital food crops (25). More than 50% of the global population solely relies heavily on rice to extenuate their daily caloric requirements (26).

Therefore, the development of drought-tolerant rice varieties is of paramount importance to ensure food security (27). Over the past two decades, scientists from Bangladesh, India, and the Philippines have made significant strides in creating drought-tolerant rice accessions. Bangladesh has produced the highest number of drought-tolerant 'Aus' accessions, while India leads in 'Indica' accessions (12). Table 1 highlights some of the key drought-tolerant rice genotypes.

In response to drought stress, various physiological, biochemical, and molecular changes are activated in plants to lead to drought stress tolerance (15). Different regulatory factors, including genes, proteins, and transcription factors (12, 36-56) have been reported to play drought tolerance roles in rice (Table 2).

Moreover, studies have revealed the investment of plant growth-promoting microbes (PGPMs) in drought stress tolerance in rice (57).

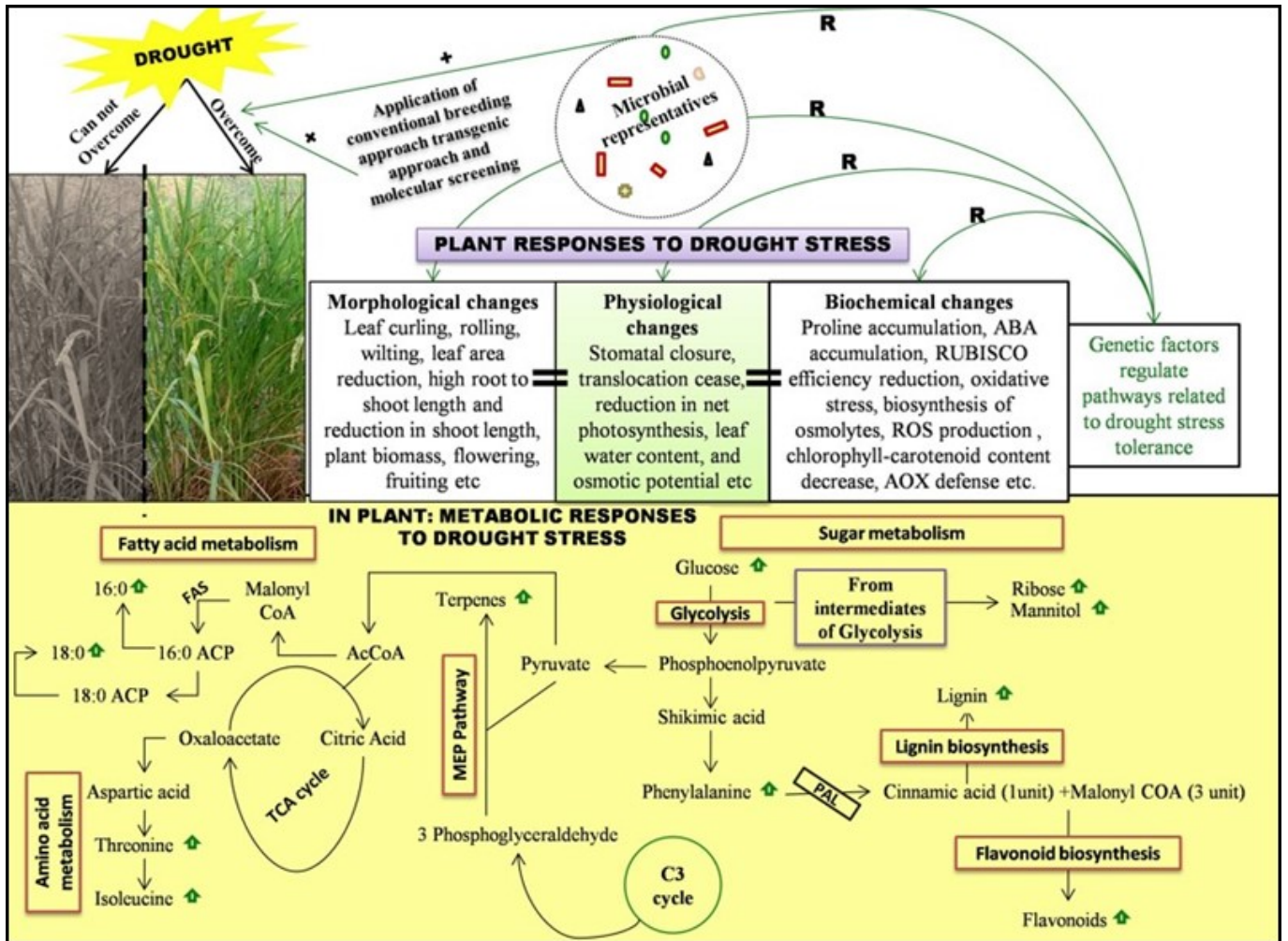


Fig. 2. Morphological-physiological-biochemical changes and metabolic pathways in plants in response to drought stress along with drought stress coping strategies (FAS, R AcCoA and ACP represent fatty acid synthesis, regulate, acetyl CoA and acyl carrier protein respectively. ‘=’ sign indicates interrelationship between each other. Genetic factors regulate biochemical, physiological and morphological changes in plants in response to drought stress. Integrated action of genetic, biochemical, physiological and morphological traits help to promote drought stress tolerance in plants. To overcome drought stress, secondary metabolites (Flavonoids, Terpenes, Phenylalanine), sugar (Ribose, Glucose), sugar alcohol (Mannitol), amino acid (Threonine, Isoleucine) and fatty acid (16:0, 18:0) enhance in plants. Green upright arrows indicate increased level).

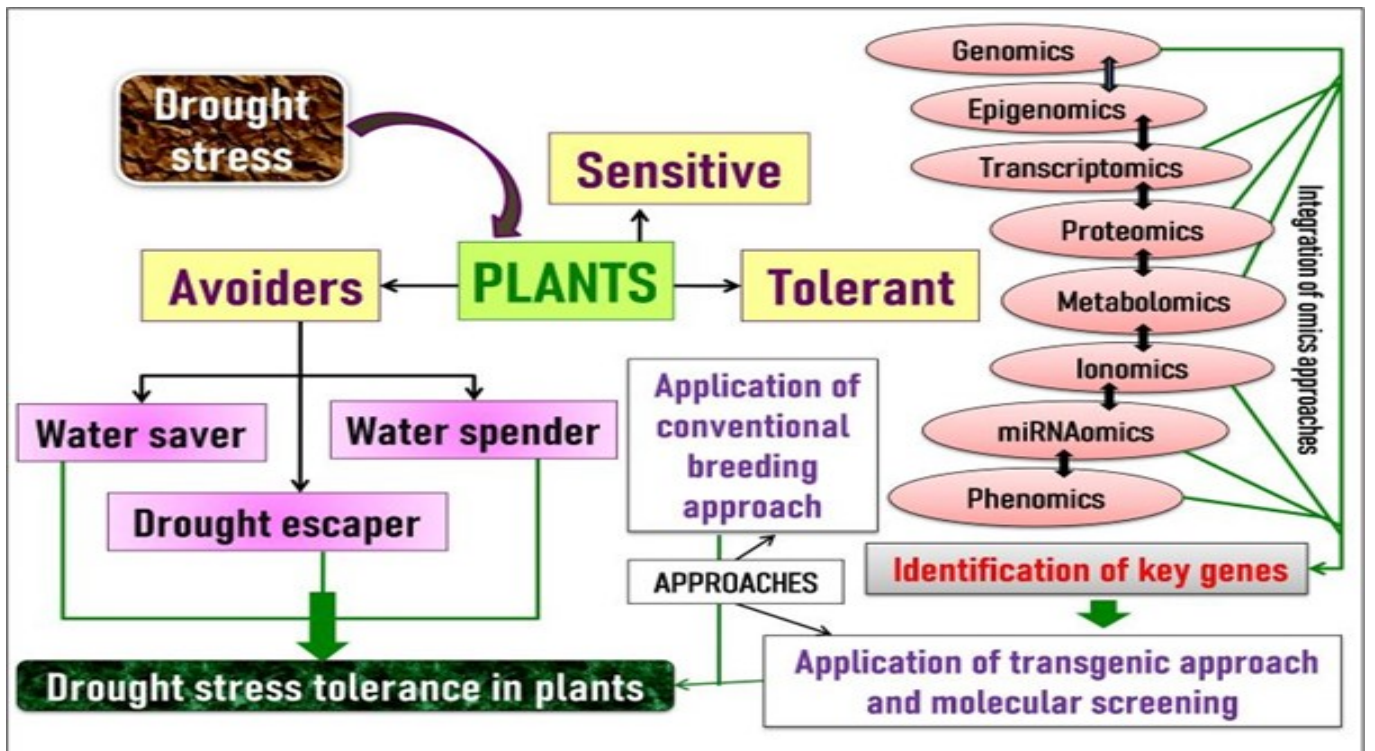


Fig. 3. Classification of plants on the basis of drought stress tolerance and approaches of promoting drought stress tolerance in plants.

Table 1. Important drought tolerant rice plants (28-35).

Drought tolerant rice plants	Reported from
Champavu, Chuvannamodan, Eravapandi, Karavala, Karnellu, Kallele, Kalladiyaran, Karuthapandi, Karuthamodan, Kettamodan, Kochuvithu, Mundon, Parapilarppan, Parambuvattan, Pookulathari, Thondi, Veliyan, Vellathan, Vykatharayan	Reported from Kerala
Sukhadhan-1, Sukhadhan-2, Sukhadhan-3, Sukhadhan-4	Reported from Nepal
Sahbhagi Dhan	Developed by IRRI- collaboration with different Indian institutions
CR Dhan 801	Developed by ICAR-NRRI
Bahuguni dhan-1,2	Reported from Nepal
BRR1 Dhan 56	Reported from Bangladesh
Swarna Shreya	Developed by ICAR-collaboration with IRRI, Phillipines
CR Dhan 40, Anjali, Vandana	Developed by CRURRS, Hazaribag
IR 64 Drt 1	Developed by DRR, Hyderabad- collaboration with BAU, Ranchi and IRRI, Phillipines
Shusk Samrat	Developed by NDUAT, Uttar Pradesh

Table 2. List of some regulatory factors involved in drought stress tolerance in rice (12, 36-56).

Regulatory factors	Functions
OsITPK2	ROS homeostasis and reduction of the levels of inositol triphosphate.
OsNAC5, OsNAC10 OsLEA3-1, OsbZIP46, OsbZIP71, OsWRKY47	Enhancement of grain yield in rice under drought.
OsDREB1E, OsDREB1G, OsDREB2B	Overexpression- significantly improves drought tolerance in rice.
OsAHL1	Contributes drought avoidance and drought tolerance capacity in rice, overexpression of it provides multiple stress tolerance in rice.
SNAC1	Overexpression- significantly improves drought tolerance in transgenic rice lines.
OsAL	Significantly associated with drought resistance in rice.
OsPYL2, OsPYL10	Provide drought tolerance in rice through stomatal closure.
OsNAC17	Provides drought tolerance in rice promoting lignin biosynthesis in roots and leaves.
NOG1-1, NOG1-2	Minimize transpirational water loss and confer drought stress tolerance in rice.
OsERF83	Confers drought tolerance in rice, establishes cross talk between abiotic and biotic stress.
OsMFT1	Promotes drought tolerance in rice.
OsZIP66, osbMYB26	Overexpression- significantly improves drought tolerance in rice.
OsP5CS	Under osmotic stress, expression of it increases in drought tolerant rice lines.
OsHSFA3	Provide drought tolerance by decreasing ROS level, water loss and modulating polyamine biosynthesis.
ALM1, OsAPX2, OsCATC, OsPOX1	Confer drought stress tolerance by enhancing antioxidant enzymes activity.
OsSPS1, OsSUS7	Enhance fructose, sucrose content to maintain osmotic balance during drought stress.
TDC2, ASMT1	Under drought stress, enhance melatonin synthesis to promote drought tolerance in rice.
MSRB2	Provides drought tolerance in rice by defending chloroplast targeted genes.
CaMsrB2	Maintains subsequent quantum yield, boosts photosynthetic pigments and improve relative water content to confer drought tolerance in rice.
HVA1	Through cell membrane protection provides dehydration tolerance in rice.
OsEm1	Enhance drought tolerance and ABA sensitivity.
OsLEA3-1	Overexpression- exerts drought tolerance in transgenic rice lines.
OsABA8ox3	Controls ABA level and provides drought stress resistance in rice.

Several studies have been conducted to explore rice drought tolerance comprehensively. This review aims to delve into topics including drought-tolerant rice genotypes, strategies involving microfloral assistance in enhancing plant drought stress tolerance, and approaches for inducing drought tolerance in rice plants, as depicted in Fig. 2.

Strategies: conferring drought stress tolerance

Plant tolerance to minimum moisture levels in the cytoplasm (water content ~23% of fresh tissue) is defined as drought tolerance (58). Plant defense against water scarcity stress includes some subsequent stages like reduction in turgor-dependent activities, differential allocation of photosynthates towards the root, abscission of leaves due

to ethylene (C₂H₄), and closure of stomata due to abscisic acid (ABA). Various morphological, physiological, and molecular mechanisms have been found to impart drought stress tolerance in rice (12).

Drought stress tolerance: morphological adaptations, physiological acclimatization and cellular adjustments

Plants employ a range of protective mechanisms to overcome drought stress, including morphological adaptations, physiological acclimatization, and cellular adjustments (58). Morphological adaptation involves delaying leaf senescence, enhancing green leaf area, decreasing leaf weight and size, promoting root length, thickness, and leaf covering with waxy material (59). Physiological acclimatization is another critical strategy, which includes reducing transpiration rates, enhancing plant storage and assimilation, decreasing stomatal conductance, improving soil water uptake by modifying root growth, and maintaining osmotic balance (60). Essential plant traits encompassing root, shoot and inflorescence traits, play a vital role in inducing physiological adjustments in crop plants against drought stress (12). Furthermore, an augmented harvest index, improved chlorophyll content, and lessened osmotic potential invoke cellular adjustments for drought tolerance in plants (59).

Under drought stress, changes in the morphological and physiological traits of the roots maintain the absorption of water and nutrients from the soil and regulate the normal physiology, growth, and metabolism of crop plants (61). Important root traits, including enhanced root depth, root density, small fine root diameters, increased root-to-shoot ratio, and long specific root length, have been reported to adjust proper water balance in rice crops and sustain crop productivity under water scarcity (14, 62).

Certain tolerant rice cultivars, such as Chuanguyou208 and Deyou4727, have demonstrated higher root number, root weight, and greater root length, along with increased expression of important enzymatic antioxidants such as superoxide dismutase (SOD) and peroxidase (POD) under drought stress conditions (63). Studies have indicated that the promotion of root length in rice is associated with an increase in ABA concentration in roots during drought stress (64). Rice genotypes with profound and prolific root systems, along with the ability to sprout many branches, show better adaptability in drought stress tolerance (14). Sometimes, plants maintain growth under severe water deficit conditions by increasing turgor pressure in root cells (65). An increase in root hydraulic properties under drought stress in rice has been reported to be due to the development of a denser and deeper root system that improves water transport from the soil to the plant shoot (66). Furthermore, ammonium (NH₄⁺) supplementation has been shown to promote water uptake during drought stress by increasing root tip number and root length in rice seedlings (67). In addition to growth and metabolism, the initiation of new aerial organs is hampered by drought stress (68). Some important shoot traits, such as a significant reduction in leaf elongation rate, leaf rolling, reduced stomatal number, reduced leaf

size, poor conduction system, and leaf surface cutinization, have been observed under drought stress (69-71).

Reducing the rate of leaf expansion and leaf size induces physiological adaptations in crop plants that limit water loss from the plant body through respiration. Leaf surface cutinization also prevents excessive water loss from the plant body under drought conditions. Moreover, leaf rolling has been considered an important adaptive trait to overcome water deficit stress by maintaining water balance in crop plants (72).

Stomatal closure under water-limited conditions prevents excessive water loss from plants, inhibits the flow of carbon dioxide into leaves, and leads to the generation of excess electrons that produce reactive oxygen species. Reduction of photosynthesis during drought stress is attributed to limited gaseous exchange, stomatal closure, low carbon dioxide (CO₂) uptake, and reduced turgor pressure (73). Furthermore, it has been reported that the loss of photosynthesis under drought stress results from the weakening of the photosynthetic machinery (73).

In response to drought, factors such as water availability in the root zone and the photosynthetic capacity of the leaves are the main causes of yield reduction in susceptible rice varieties (73). Certain genotypes with higher photosynthetic capacity delay senescence during stress periods and optimize photosynthetic capacity and nitrogen assimilation under water deficit conditions (74). Early-morning flowering is an important inflorescence trait to improve spikelet fertility under water-deficit conditions. *qEMF3*, an important quantitative trait locus of *Oryza officinalis*, has been reported to enhance the fertility of spikelets in rice (75). The proliferation of drought-tolerant rice requires in-depth investigation to develop important flowering traits, although DST (drought and salt tolerance) proteins in rice facilitate flowering under stress (75).

Another important trait is the role of phytohormones in enhancing drought tolerance in rice cultivars. The regulation of phytohormones such as auxin (AUX), abscisic acid (ABA), cytokinin (CK), ethylene (C₂H₄), jasmonic acid (JA), and salicylic acid (SA) is directly or indirectly involved in abiotic stress tolerance in rice (14). Auxin plays a critical role in root development. Overexpression of the AUX/IAA genes, *OsIAA6* and *YUC* genes has been reported to overcome drought stress in rice and sustain plants in harsh environments (76, 77). ABA-dependent signaling pathways invoke Ca⁺⁺ dependent signaling pathways, enhancing drought stress tolerance by modulating downstream drought-responsive transcription factors like NF-Y, NACs, MYB/MYC, and WRKYs (78), as illustrated in Fig. 4. Overexpression of *JERF1*, an ethylene response factor, has been shown to promote drought stress tolerance in rice seedlings, reduce water loss in transgenic rice, increase proline content in rice, and activate stress-responsive genes (79). The exogenous application of JA has been reported to promote drought stress tolerance in crops by increasing the activity of antioxidant enzymes (80).

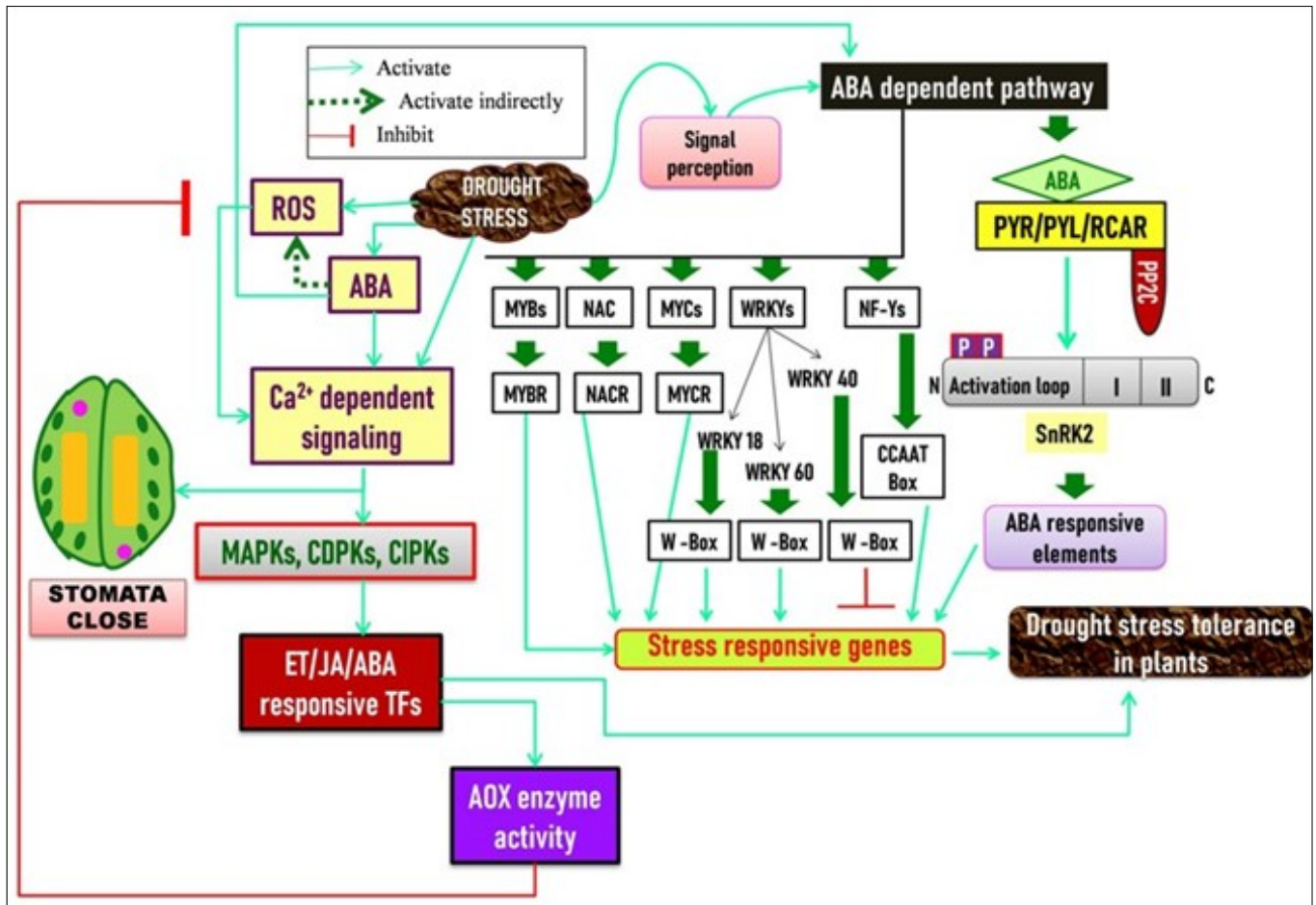


Fig. 4. ABA dependent and Calcium (Ca²⁺) signaling pathway to enhance drought stress tolerance in plants (Drought signal perception activates Abscisic acid (ABA) dependent pathway. ABA binds to its receptor PYR/PYL/RCAR and interferes Protein Phosphatase (PP2C) - Snrk2 Kinase binding. ABA binding with its receptor activates ABA responsive elements to regulate downstream stress responsive genes. ABA also modulates the activities of different transcription factors (TFs) like, MYBs, NAC, MYCs, WRKYs and NF-Ys. In addition to that, drought stress produces Reactive oxygen species (ROS), ABA and activates Ca²⁺ dependent signaling. Ca²⁺ dependent signaling is also activated by ROS and ABA. ABA induced Ca²⁺ dependent signaling induces stomatal closure. ABA again indirectly activates ROS generation. Moreover, Ca²⁺ dependent signaling promote Ethylene/Jasmonic acid/ABA (ET/JA/ABA) responsive TFs by activating Mitogen activated protein kinases (MAPKs), Calcium dependent protein kinases (CDPKs) and CBL interacting protein kinases (CIPKs). ET/JA/ABA responsive TFs modulate AOX enzyme activity and inhibit ROS activity).

In plants, osmoregulation is one of the essential processes to cope with stressful conditions. Osmoregulatory substances are organic or inorganic compounds that maintain osmotic adjustment without interfering with enzymatic activity in the plant body, thereby preventing a decrease in somatic potential. Osmolytes include proline, betaine, total free amino acids, sorbitol, mannitol, trehalose, phenolics, and soluble sugars, plays an important role in drought stress tolerance in plants (70). Proline, a non-protein amino acid, serves as a vital biochemical marker in response to drought stress by regulating

stomatal conductance and leaf turgor (13, 81). Higher accumulation of proline has been reported to contribute to drought stress tolerance in rice under water deficit conditions (81, 82). Carbohydrates especially fructans, oligosaccharides, and disaccharides provide energy to plants for biomass retention and stress management (12). Additionally, macro and micronutrients (83, 84) also play a pivotal role in drought stress tolerance in crops (Table 3).

Drought stress tolerance: molecular mechanisms

To cope with environmental constraints, plants express various stress-responsive genes and synthesize functional

Table 3. Macro and micronutrients involved in drought stress tolerance in crops (83, 84).

Nutrients		Functions
Macronutrients	Nitrogen	Improves water use efficiency, improves nitrate reductase activity, enhances nitrate uptake and improves plant growth and yield.
	Phosphorus	Enhances stomatal conductance, improves photosynthesis, maintains higher water relation, cell membrane stability maintenance, improves plant root growth, maintains water potential in leaf, improves nr activity, enhances nitrate assimilation, enhances nutrient uptake and improves plant growth and yield.
	Potassium	Maintains osmotic potential, maintains cell turgor, regulates stomatal conductance, improves photosynthesis and improves plant root growth.
	Calcium	Maintains cell structure, activates plasma membrane ATPase enzyme, plays role as Calmodulin to control plant metabolic pathway and improves plant growth and yield.
	Magnesium	Increases root growth, increases root surface area, improves water and nutrient uptake, improves sucrose translocation from leaves to roots, interferes photo-oxidative damage and ROS generation.

Micronutrients	Boron	Reduces hollowing of stem, improves sugar transport, improves pollen formation and germination, reduces stunted appearance and improves floral retention.
	Copper	Reduces leaves yellowing, overcomes stunted growth, enhances nitrogen metabolism and reduces dieback of twigs and stem.
	Zinc	Enhances IAA production, enhances root growth, regulates hormonal level, interferes ROS generation by reducing the membrane bound NADPH oxidase, enhances AOX (CAT, POD and SOD) activity.

proteins (85). Different quantitative trait loci (QTL) are important in this regard. Notably, PUP1, DRO1 (DEEPER ROOTING 1), and important root QTLs are associated with phosphorus uptake, and root depth, respectively (86, 87). Several significant QTLs related to drought stress tolerance (12, 88, 89) have been identified in rice, and they are detailed in Table 4.

Table 4. Some important rice QTLs related to drought stress tolerance (12, 88, 89).

QTLs	Associated traits
<i>qDTY1.1, qDTY12.1, qDTY9.1A, qDTY6.1, qDTY2.2, DTY2.1, qDTH12.3</i>	Grain yield
<i>qDLR8.1, qLR9.1</i>	Leaf rolling
<i>qDTR8</i>	Transpiration
<i>qRWC9.1</i>	Relative water content
<i>qLD9.1</i>	Leaf drying
<i>qSF9.1</i>	Spikelet fertility
<i>qHI9.1</i>	Harvest index

About 5000 and 6000 genes have been reported to be upregulated and downregulated, respectively, in rice after exposure to drought (90). They regulate biochemical, physiological, and molecular processes that enables plants to cope with water scarcity. Various regulatory factors like genes, proteins, and transcription factors, contribute to drought stress tolerance in rice by facilitating osmotic adjustment, hormone regulation, lignin synthesis, AOX defense, photosynthesis improvement, quantum yield maintenance, relative water content improvement, and cell membrane protection, as listed in Table 2.

ABA-dependent (Fig. 4) and ABA-independent (Fig. 5) regulatory systems for drought stress management include numerous gene and transcription factors (78).

The ABA-independent regulatory systems also invoke hormonal regulation to overcome drought stress (78). EcNAC67, the OsPYL/RCAR5 genes of the ABA-dependent regulatory system, has been reported to interfere with leaf rolling and promote higher root and shoot mass when exposed to drought (91).

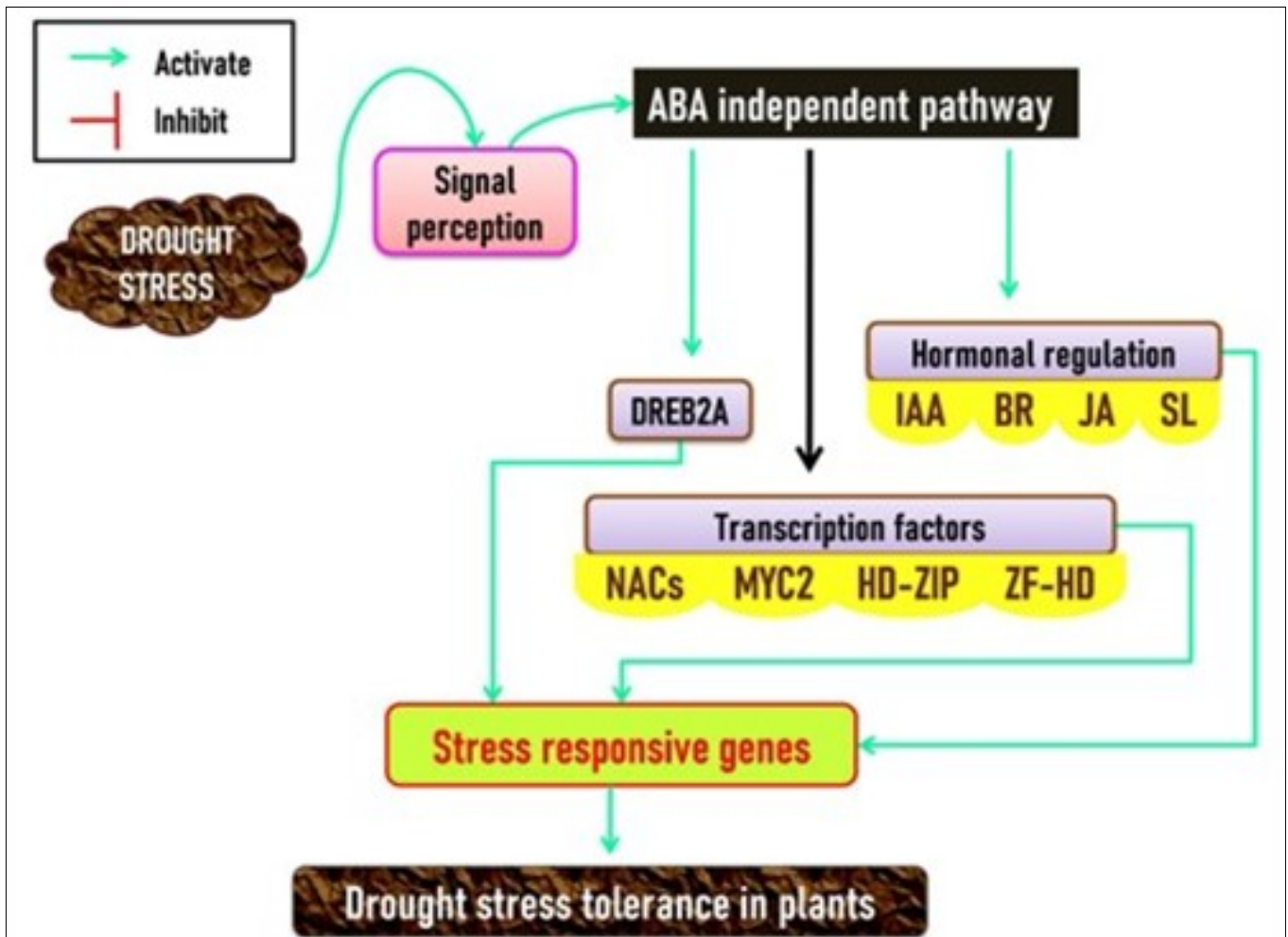


Fig. 5. ABA independent signaling pathway to enhance drought stress tolerance in plants.

To combat drought stress, root morphological adaptations in rice have been linked to significant genes like OsDREB1F, OsDREB2B, and CYP735A (14). The investigation of genes like AtDREB1A, OsDREB2A, EDT1/HDG11, OsMIOX, OsCPK9, and OsTPS1 has shown promising results in promoting the survival of transgenic rice by enhancing osmoregulation, stomatal regulation, enhanced photosynthesis, improved antioxidant enzyme activity and higher water use efficiency (12). miRNA, a type of small non-coding RNA, plays a crucial role in regulating gene expression at the post-transcriptional level during abiotic stress (92). The mechanism of miRNA is illustrated in Fig. 6.

Upregulation and downregulation of miRNAs have been observed in rice under drought stress (93). Several miRNAs involved in drought stress tolerance in rice have been reported to date, and some of them are listed in Table 5.

Drought stress tolerance: antioxidant (AOX) defense

Reactive oxygen species (ROS), a natural by-product of aerobic metabolism, can cause cellular damage and cell death in plants. Various abiotic and biotic stresses have been reported to stimulate ROS production (12). Drought stress, in particular, has been shown to lead to the

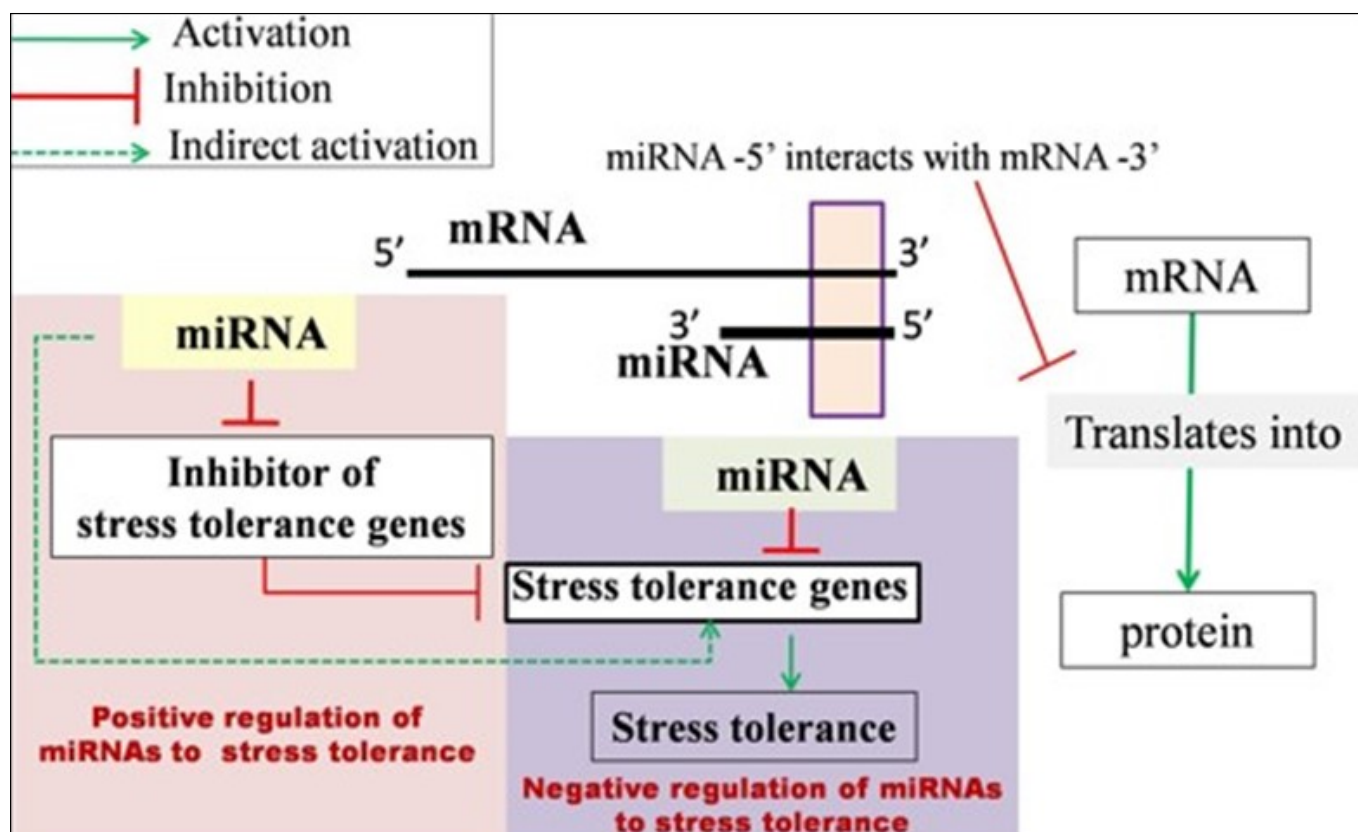


Fig. 6. Diagrammatic representation of miRNA mechanism and its positive and negative regulations to stress tolerance in plants.

Table 5. A list of *Oryza* miRNAs, involved in drought stress tolerance in rice (43).

miRNA	Sequence	miRNA	Sequence
osa-MIR1317	TATGGGAATAAGGGTCCCTTA	osa-MIR167a	GAAGCTGCCAGCATGATCT
osa-MIR1318	GACACCGACATCGCCGAATT	osa-MIR167b	ATCATGCTGTGACAGTTT
osa-MIR1319	TAATATATTATAGGTGTCGGT	osa-MIR167c	GAAGCTGCCAGCATGATCT
osa-MIR1320	GGAACGGAGGAATTTATA	osa-MIR167d	GAAGCTGCCAGCATGATCTGA
osa-MIR1423	TATTTGGGAGGCAACTACACGTT	osa-MIR167e	GAAGCTGCCAGCATGATCT
osa-MIR1427	TCCGCAGCAGGGACATGCGCC	osa-MIR167f	GAAGCTGCCAGCATGATCTGA
osa-MIR1428a	TGAACTGAGTACGCGATGAT	osa-MIR167g	GAAGCTGCCAGCATGATCTGA
osa-MIR1428d	TGAACTGAGTACGCGATGAT	osa-MIR167h	GAAGCTGCCAGCATGATCT
osa-MIR1428g	TGAACTGAGTACGCGATGAT	osa-MIR167i	GAAGCTGCCAGCATGATCT
osa-MIR1431	AGGCAAAATTAGTAGGTAACCCGT	osa-MIR168a	GATCCCGCCTTGACCAA
osa-MIR1432	GACACCGACATCGCCGAATT	osa-MIR169a	AGGATGACTTGCCGATCGATCG
osa-MIR1436	TTATGGGACGGAGGGAGT	osa-MIR166b	GAGATGAGAGTAGATGTCTGTAGA
osa-MIR1437	CGGGGAGGGAGGGAACGG	osa-MIR166c	TTTCGGACCAGGCTTCAT
osa-MIR1440	GTGGTATTTGAGCACTGGCAT	osa-MIR166d	CTGATCTCGGACCAGGCTTC
osa-MIR1441	GTCACATCGGACGTTAACCGGAT	osa-MIR166f	GTCTCGGACCAGGCTTCATTC

osa-MIR156a	GTGACAGAAGAGAGTGAGCA	osa-MIR166g	CGGACCAGGCTTCATTCCCT
osa-MIR156b	GCTCACTCTCTATCTGTGACCC	osa-MIR166h	CGGACCAGGCTTCATTCCCT
osa-MIR156c	ACATGGTGACTTTCTTGCATGCTGAA	osa-MIR166j	CTTGTGATATGGGGATATGCAAC
osa-MIR156d	ATCCCGTCTCGCCGCGTG	osa-MIR166k	GGACCAGGCTTCAATCCCT
osa-MIR156e	GTGACAGAAGAGAGTGAGCA	osa-MIR166l	GGACCAGGCTTCAATCCCT
osa-MIR156f	GCGGCCAGACTGCATCGATCATCA	osa-MIR166n	GAATGACGTCCGGTCTGA
osa-MIR156g	GCTCACTCTCTCTGTGCA	osa-MIR164d	TGGAGAAGCAGGGCACGTGCTCGACG
osa-MIR156h	TGCTCGCTCCTTTCTGTGACG	osa-MIR164e	AGGGCACGTGAGCGGCCATCC
osa-MIR156i	TCACTGCTGTGCTGTGCATC	osa-MIR166a	GCGGTTTTGAGGATGATTTGTGCA
osa-MIR156j	TGCTCGCTCCTTTCTGTGACG	osa-MIR160d	CTGGCTCCCTGTATGCCA

overproduction of ROS, including hydroxyl radicals (OH•), hydrogen peroxide (H₂O₂), and superoxide radicals (O₂•⁻), resulting in membrane and protein damage, lipid peroxidation, and cellular death (94). In rice, an imbalance between ROS production and ROS quenching due to drought stress has been reported (12).

Plants have developed antioxidant (AOX) defense mechanisms to mitigate the harmful effects of ROS. AOX includes non-enzymatic components such as ascorbate (AsA), glutathione (GSH), phenolic compounds, flavonoids, alkaloids, carotenoids etc., and enzymatic AOX such as ascorbate peroxidase (APX), catalase (CAT), glutathione reductase (GR), glutathion-S-transferase (GST), guaiacol

peroxidase (GPX), dehydroascorbate reductase (DHAR), monodehydroascorbate reductase (MDHAR), and superoxide dismutase (SOD). In rice, increased activity of the ASA-GSH pathway (Halliwell-Asada pathway) and increased production of GPX, GSH, and ascorbic acid are considered vital defense mechanisms for managing stress under drought stress conditions (94, 95).

Drought stress tolerance: Through plant-microbe interactions

Plant-microbial interactions enhance plant growth and development and also mitigate environmental stresses (12) as illustrated in Fig. 7.

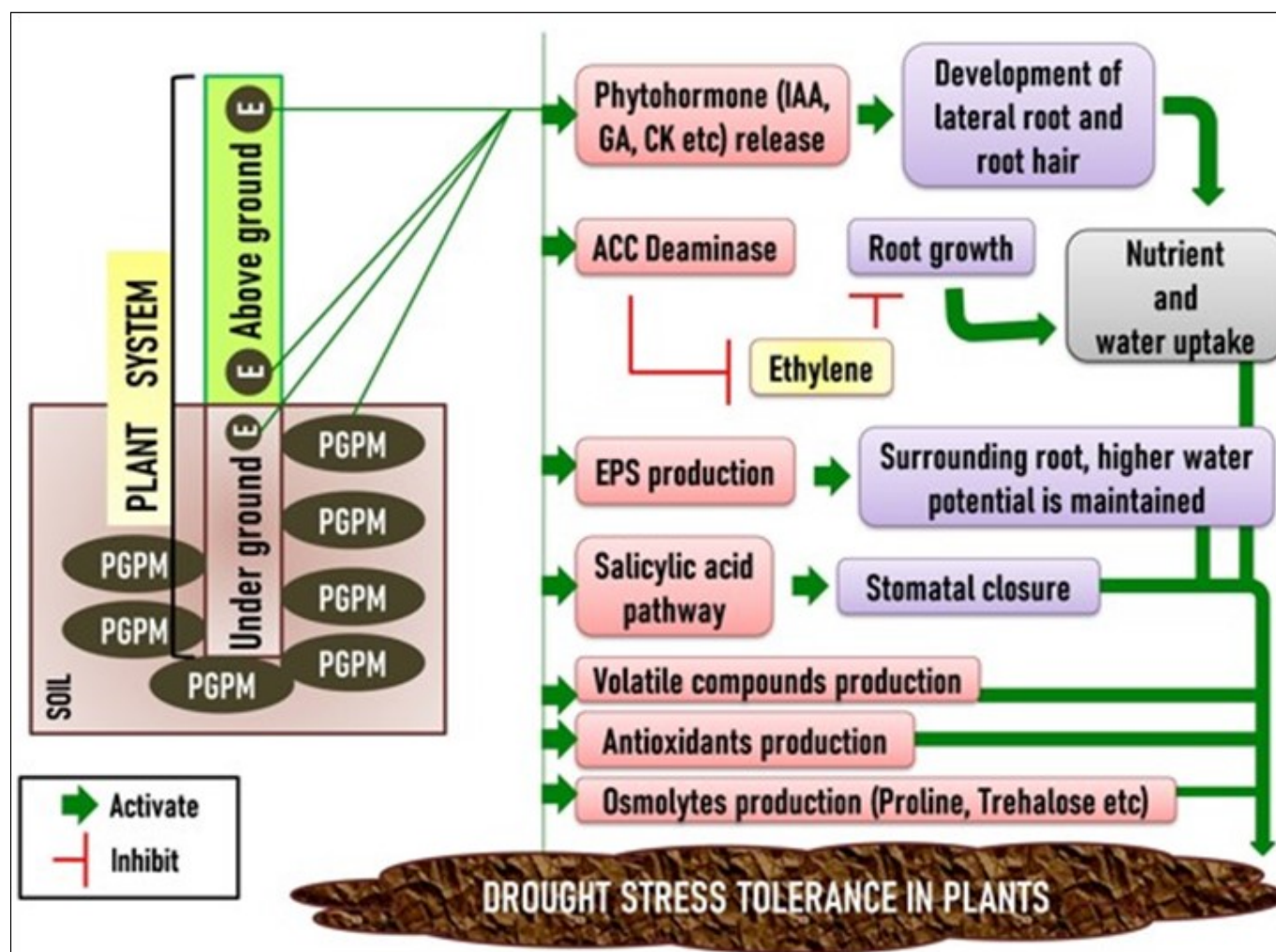


Fig. 7. Plant microbial interaction-important to improve plant growth and development and ameliorate drought stress (PGPM, E, ACC, EPS, IAA, GA and CK represent plant growth promoting microbes, endophytes, 1- aminocyclopropane 1 carboxylic acid, exopolysaccharide, indole acetic acid, gibberellic acid and cytokinin respectively).

Soil microflora plays a significant role in influencing plant biodiversity (96). The colonization of arbuscular mycorrhizae in plant roots contributes to water stress management within plant tissues (97, 98). Extreme drought stress can lead to a decrease in the soil carbon to nitrogen ratio (99), but soil microbes help maintain soil fertility and nutrient cycles. Inoculation of rice with *Trichoderma asperellum* (T42) and *Pseudomonas fluorescens* has been reported to protect rice plants from drought stress by strengthening intrinsic biochemical and molecular mechanisms in rice that help in ROS amelioration (99). Microbial inoculation has been confirmed to induce enzyme activity and activity of *PAL* gene expression leading to promote polyphenolics accumulation in plants (100). *Piriformospora indica*, a root endophytic fungus, has been reported to confer drought tolerance in rice (101). In addition, the inoculation of drought-tolerant rhizobacteria improves the drought tolerance of sensitive rice genotypes by altering the expression levels of genes responsive to growth and stress (102). *Bacillus*, a Gram-positive plant growth-promoting rhizobacteria (PGPR), can capable to alleviate drought stress by reducing oxidative stress levels, and promoting grain yield and higher biomass accumulation (90). A PGPR consortium containing *P. synxantha* R81, *Arthrobacter nitroguajacolicus* strain YB3, and YB5, and *P. jessenii* R62 has been reported to enhance plant growth by inducing enzymatic AOXs such as ascorbate peroxidase (APX), catalase (CAT), peroxidase (PX), superoxide dismutase (SOD) and lowering malondialdehyde (MDA) and hydrogen peroxide (H₂O₂) in drought tolerance (Sahbhagi) and drought-sensitive (IR-64) rice plants (103). Moreover, rhizospheric microbes are important sources of enzymes such as 1-aminocyclopropane-1-carboxylate deaminase (ACC deaminase), phytohormones such as auxin (AUX), cytokinin (CK), and ethylene (ET) and metabolites such as exopolysaccharide (EPS) that induce systemic tolerance against drought (104). However, extreme water scarcity has been observed to decrease the activity of microorganisms (105).

Approaches for developing drought tolerance in rice plants

Conventional breeding is an important approach to developing novel genetic traits that include crosses of interspecific and inter-generic types, induced mutation, recurrent selection, and pedigree selection, but these are all time-consuming approaches (58). The international rice research institute (IRRI) has been reported to carry out marker-assisted breeding approaches for developing a vast range of elite drought-tolerant rice cultivars (58). The drought-tolerant rice variety MR219 has been successfully developed by incorporating QTLs such as qDTY12.1, qDTY3.1, and qDTY2.2 (106). TDK1, a drought-tolerant rice variety developed by the incorporation of qDTY3.1, qDTY6.1, and qDTY6.2, is capable of high yields under drought stress (107).

Advanced research has improved our knowledge of how plants cope with water deficit conditions at the molecular level. Several genes, TFs, miRNAs, and QTLs related to drought stress tolerance have been identified

(Tables 2, 4, 5). Generally, biotechnological methods are applied to develop genetic resistance to drought stress in plants (58). Furthermore, for a more comprehensive understanding of the mechanisms underlying drought stress tolerance in plants, omics approaches, including phenomics, genomics, transcriptomics, proteomics, ionomics, and metabolomics, have proven to be invaluable, as depicted in Fig. 3.

In modern biology, phenomics is a screening method that focuses on the study of plant activities in response to genetic mutation or environmental influences. High-throughput phenotyping methods, including red-blue-green, near-infrared, infrared, and fluorescence imaging systems, have proven valuable for distinguishing between drought-tolerant and susceptible rice crops (108). Evaluation of photosynthetic efficiency, plant temperature, and water content of rice has been done using fluorescence, infrared, and near-infrared images respectively (108). Drought spotter, a high-throughput phenotyping technology, has been reported to determine plants' transpiration rate, water use efficiency, and the rate of water loss by plants (108).

Other advanced technical approaches like zinc finger nucleases (ZFNs), transcription activator-like effector nucleases (TALENs), CRISPER/Cas, MAS selection, and identification of QTLs are included in genomics useful for investigating the gene structure and functional dynamics of non-coding, and coding sequences of genes applicable to crop improvement (58). In rice plants, applications of genomics methods have been reported to identify critical drought-responsive mechanisms of QTL, genes including OsCPK9, OsCPK10, RD22, SNAC1, CBF2, PP2C, and transcription factors such as OsZIP46, DST, DREB, etc. (58). Innovative genomic breeding strategies (IGBS) are promising opportunities for developing drought-adapted crops worldwide (60). IGBS includes various methods such as, haplotype-based breeding, genome editing, systems biology based breeding, genomic selection and speed breeding (60). Haplotype based breeding is promising with low financial investment to identify superior haplotypes for breeding programs and to design future crops with desirable adaptive characters (60, 109). Genome editing is a highly efficient technique for creating desired changes in crops (60). CRISPR-Cas 9 mediated editing has been reported to develop drought tolerant traits in crop plants (60). The application of systems biology-based breeding methods is crucial for developing ideotypes of crops with complex genomes. Adaptation to drought stress involves a complex regulatory network composed of transcription factors, phytohormones, and kinases. Systems biology helps identify specific biological phenomena that indicate suitable candidates for breeding programs (60). In crop improvement, the combined strategy of speed breeding and genomic selection, referred to as Speed GS, holds the potential to accelerate the genetic gain rate (60). Haplo-GS, another combined technique involving superior haplotype and genomic selection, aids in uncovering multifaceted relationships between phenotypes and genotypes and is useful in the rapid generation of new breeding lines (60, 110). Transcriptomic studies have revealed the

TFs (58) involved in ABA-dependent and independent drought responsive pathways, as stated in Fig. 4, 5. Transcriptomic studies provide information about the total transcripts present in organisms. Some important modern technologies, such as microarrays, RNA-sequencing, quantitative real-time PCR, serial analysis of gene expression (SAGE), SAGE-sequencing, and differential display reverse transcription PCR are applicable to transcriptomic studies (58). Transcriptomic analysis based on RNA sequencing is a promising technology to analyze gene, gene networks governing plant regulatory mechanisms during drought stress (15). Microarray-based RNA profiling, affymetrix gene technology, and expressed sequence tags are important technologies that provide new insights to elucidate multiple gene functions during drought stress (15).

Moreover, proteomics, an omics approach is used to unravel the proteomes of a cell or organism. Because environmental conditions affect the proteome on a large scale, the study of proteomes helps to uncover differences in plant responses to stress at the molecular level (111). Under drought stress conditions, plant's regulatory systems (antioxidant mechanism, redox homeostasis, and signal transduction) are regulated by multiple proteins. Differential protein expression helps to reveal upregulating and downregulating proteins under environmental stress conditions (15).

Proteomics studies can be done with gel-based and gel-free techniques. Gel-based technique includes: difference gel electrophoresis (DIGE), mass spectrometry (MS) and two-dimensional gel electrophoresis (2-DE) and the techniques like the isotope-coded affinity tag (ICAT), isobaric tags for relative and absolute quantitation (iTRAQ), matrix-assisted laser desorption ionization-time of flight mass spectrometry (MALDI-TOF MS), stable isotope labelling by amino acids in cell culture (SILAC), multi-dimensional capillary liquid chromatography, sequential windowed acquisition of all theoretical fragment ion mass spectra (SWATH-MS) and liquid chromatography-electrospray ionization/multi-stage mass spectrometry (LC-ESI/MS/MSⁿ) are important gel-free techniques for proteomics study (75). In rice, 32 up-regulated proteins have been identified under drought stress conditions using iTRAQ and LC-MS/MS (112). BGI seq-500 has been reported to be used to reveal the role of OsmIOX in drought stress tolerance by identifying up-regulating and down-regulating genes under drought stress conditions (113).

Ionomics is an important approach for enhancing plant resilience to abiotic stress. Important tools for studying ionomics in plant science like nuclear magnetic resonance (NMR) spectroscopy, liquid chromatography coupled to mass spectrometry (LC-MS), Fourier transform-ion cyclotron resonance mass spectrometry (FT-ICR/MS), liquid chromatography coupled to photodiode array/mass spectrometry (LC-PDA/MS), X-ray fluorescence (XRF), gas chromatography coupled to mass spectrometry (GC-MS), capillary electrophoresis mass spectrometry (CE-MS) and plasma optical emission spectroscopy (ICP-OES) have been reported to be used to study homeostasis between different ions (114).

Metabolomics studies in plant systems help to measure changes in the expression of primary and secondary metabolites in response to drought stress (75). Higher accumulation of carbohydrates in drought-tolerant rice cultivars compared to susceptible cultivars under water deficit conditions has been validated by metabolomics analysis (115). Major techniques for metabolomic studies include 2D chromatography and capillary electrophoresis-mass spectrometry (CE-MS), mass spectrometry (MS), gas chromatography (GC), high performance liquid chromatography (HPLC), ultra HPLC, gas chromatography-mass spectrometry (GC-MS), LC/MS and fourier transform ion cyclotron resonance (FT-ICR).

Epigenomics, an another omics-based approach, plays a vital role in the analysis of epigenetic changes throughout entire plant genome in response to drought stress. It is very crucial to understand the epigenetic modifications under drought stress conditions for developing drought smart crop plants (15). In rice, the percentage of cytosine methylation has also been shown to be a good indicator of drought stress tolerance. Cytosine hypermethylation and hypo-methylation have been reported as indicators of drought sensitive and drought tolerant rice cultivars, respectively (116).

Moreover, databases like MetaCyc, RiceCyc, Kyoto encyclopedia of genes and genomes (KEGG), DrDMassPlus, KNApSACK, OryzaCYC, MetaboLights and Plant Reactome are important for metabolomic study including the snapshot of plant metabolic pathways, enzymes, substrate, reactions and chemical compounds (117-123).

Since omics-based approaches are interdependent and overlapping, the integration of multi-omics approaches is undoubtedly a powerful strategy for studying plant cellular dynamics under water-deficit conditions (75).

The estimation of grain yield in drought tolerant rice, produced through a combination of conventional and modern technologies, holds significant economic importance. It's crucial to employ efficient technologies with low financial investment to develop drought-tolerant, high-yielding rice varieties. Several reports have been published regarding the grain yield of drought-tolerant rice under drought conditions.

Based on field trials, IRRI has suggested that the average productivity of drought tolerant rice varieties such as DRR dhan 42, DRR dhan 43, DRR dhan 44, and Sahbhagi dhan under drought stress conditions typically ranges from 1.0-1.5 t ha⁻¹ (124). Notably, the yield of the tolerant rice variety B15231-MR-10-1 was found to be higher (4.81 t ha⁻¹) compared to the popular rice variety Situ Bagendit (4.56 t ha⁻¹) but slightly lower than another popular rice line Ciherang (5.09 t ha⁻¹) (125).

According to another report the grain yield of Sahbhagi dhan is 3.8-4.5 t ha⁻¹ under normal growing conditions and 2.0-2.5 t ha⁻¹ under drought stress conditions (35). According to Rai *et al.*, the yield of Sahbhagi dhan is reported to be 36.5 q ha⁻¹ (126). Drought-tolerant rice varieties like Khandagiri and Satyabhama have grain yields of 28.3 q ha⁻¹ and 34.3 q ha⁻¹, respectively (126). Furthermore,

drought tolerant rice cultivars developed through conventional breeding methods and marker assisted methods have been reported to maintain grain quality and quantity with grain yield of 0.8-1.2 t ha⁻¹ under drought stress at breeding stage (127).

The Bangladesh Rice Research Institute (BRRI) has developed drought tolerant rice varieties viz., BRRI Paddy 56, BRRI Paddy 66 and BRRI Paddy 71. It has been estimated that the yield of drought tolerant paddy varieties can be 5-3.3 ha⁻¹ without the need for water application during the reproductive stage (128).

In modern agriculture, the use of nanotechnology holds great promise for sustaining agriculture (129). Nanoparticles are effective agents to enhance abiotic stress tolerance in plants and improve grain quality and quantity (130). Application of zinc nanoparticles has been reported to increase grain yield and antioxidant activity under drought stress conditions (129, 131). Silica is one of the most important compounds for increasing environmental stress tolerance in crops. Silica nanoparticles have wide applications in agriculture. The application of silicon nanoparticles at low concentrations has been found to increase seedling germination. Synthesis of silica nanoparticles using tetra ethyl ortho silicate and lignin has been reported as a low-cost strategy for mass production of silica nanoparticles (132). Nanoparticles have also been reported to enhance drought stress tolerance in plants by maintaining membrane stability, promoting nutrient and water uptake, and improving photosynthesis, grain production, and harvest index (133). Soil composition plays an important role in agriculture. Soil organic matter is very important for maintaining soil water holding capacity. Drought stress has the adverse effect of inhibiting the accessibility and activity of soil microbes, crucial components of soil organic matter (134). Nanotechnology has proven to be a valuable tool in enhancing soil fertility, as it facilitates interactions between nanoparticles and rhizospheric bacteria, ultimately leading to improvements in both plant growth and soil health (135). In addition, biochar emerges as a potential agent for improving soil quality. Biochar serves as a valuable source of nutrients and organic matter, and its application results in increased soil N, soil P, organic carbon, soil pH, cation exchange capacity, and soil EC (136). Moreover, biochar application not only improves soil quality but also promotes plant nutrient uptake (137).

Besides breeding and omics methods, some biochemical and mechanical methods, including exogenous application of phytohormones (AUX, BR, C₂H₄, GA, and ABA), nutrient management, water management, and maintenance of perfect sowing times, have also been reported as promising opportunities to mitigate drought stress or enhance drought stress tolerance in crop plants (15).

Conclusion

Drought stress possess a significant challenge to rice plant growth and yield worldwide. Scientists are continuously

exploring strategies to help rice plant adapt to drought stress and enhance growth and production under adverse conditions. Developing drought stress tolerance in rice is a complex task that necessitates a comprehensive approach, encompassing of biochemical, physiological, and molecular aspects. The emergence of innovative omics-based approaches has revealed some molecular factors, including important genes, TFs, miRNAs, proteins, and metabolites related to drought stress tolerance in rice. Although significant progress has been achieved through marker-assisted breeding, we still have several critical issues in molecular breeding to improve drought stress tolerance in rice. Furthermore, plant-associated beneficial microbes are good agents for improving drought stress tolerance in plants in an environmentally friendly manner. Transgenic approaches show a promising role in improving plant traits and productivity. Therefore, it would be an efficient technology for producing rice plants with drought-tolerant high yielding capacity. In this review, we have focused on various strategies, including morphological adaptation, physiological acclimatization, cellular adjustments, molecular mechanisms, metabolic pathways, antioxidant defense, and plant-microbial interactions, all of which contribute to drought stress tolerance in plants. Furthermore, we have outlined approaches for developing drought tolerance in rice plants. Although ongoing research continues to expand our understanding of whole-plant stress management, our knowledge remains incomplete. The application of advanced technologies in crop breeding, crop physiology, and molecular genetics enhances our comprehension of rice drought stress tolerance and facilitates genetic improvements in drought-tolerant rice varieties. Therefore, leveraging advanced technologies, further research is essential to develop climate-smart rice and maintain sustainable rice production under drought-stress conditions.

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Authors contributions

SD conceived the main concept of the review and provided valuable suggestions. Literature study was done by DC. The topic was discussed among the all authors (DC, CM, ShD and SD) and finally DC prepared the manuscript. CM and ShD helped DC in formatting. Finally, all authors read and approved the manuscript.

Compliance with ethical standards

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