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Techniques against Distinct Abiotic Stress of Rice

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Abstract

Plants cannot physically escape environmental stresses because they are sessile organisms, which can stunt their growth. As a result, plants have had to evolve distinct strategies to deal with abiotic stress. Indeed, responding to and eventually adapting to abiotic stress may be a driving force in speciation. Because of the complexity of stress, multiple sensors, rather than a single sensor, are more likely to be responsible for stress perception. Stress-induced gene issues can be divided into two categories: those involved in stress tolerance and those involved in signal transduction. Stress-tolerance genes help plants cope with stress in both short- and long-term responses. These can include the synthesis of chaperones and enzymes for osmolyte biosynthesis. And, as with cold stress, detoxification causes a change in the composition of membrane lipids. Gene products can also function as transcription regulators, controlling groups of stress-related genes, or as components in the production of regulatory molecules. It has been shown that multiple signaling pathways can be activated during stress, resulting in similar responses to different triggers.

Keywords: stemless, abiotic stress, resistance, membrane lipid, enzymes, defense, tolerance, toxicity

1. Introduction

Land plants have evolved to thrive in harsh environments since their inception. To address the various environmental constraints that affect their growth and development as stemless organisms, plants have evolved a variety of complex and efficient molecular and physiological mechanisms [1]. They are physically and chemically hostile to cold and heat, for example. Stress can be caused by a lack of or an excess of water, high salt levels, heavy metals, ultraviolet (UV) radiation, and other factors. These pressures, known as biological stress, pose a significant threat to agriculture and ecosystems, resulting in significant crop losses [2, 3]. Plants must adapt to their ever-changing environment because they lack stems. During development, plants are subjected to a variety of environmental influences, which can limit productivity. A yield gap is observed when the crop is grown under suboptimal environmental conditions, so the average yield achieved is much lower than the maximum potential yield of a particular crop [4]. Yield gaps for the three major grains: wheat, rice, and corn account for 40, 75, and 30% of the world's major growing regions, respectively [5]. The primary causes of crop yield gaps can be classified as some abiotic factors such as

temperature, water, or minerals, or (ii) biological factors such as bacteria, fungi, or insect invasion [6, 7].

Rice cultivation and productivity are water-intensive, making them highly vulnerable to drought and flooding. Due to drought impairment, Asia's most pertinent rice-producing belts most pertinent rice-producing belts in Asia produce only 40% of total production efficiency [8, 9]. The overwhelming majority of strain-related studies in rice, as in other plant species, have primarily focused on single stresses, either abiotic or biotic. Despite undeniable progress in the overall field, this approach provides an oversimplified and unrealistic picture. Furthermore, changes in the global environment (GEC) endanger crop production. Droughts, floods, soil acidification, soil salt content, frigid and hot temperatures, and other harmful environmental conditions are all caused by GEC. All of these stressors have an impact on crop yield and quality, either directly or indirectly. Furthermore, with the world's population expected to reach 9 billion by 2050, crop production must be increased to feed an additional 2 billion people over the next 40 years. Rice (23%), wheat (17%), and corn account for roughly half of total human calories (10%).

Despite their immobility, plants must simply respond to and endure a variety of environmental and biotic stresses in the field. A biotic and abiotic factor contends both cause crop yield losses [10]. As a result, many crop improvement programs prioritize the development of stress-tolerant plant varieties [11–13]. Plants respond differently to different or concurrent stresses, and breeding for single stress (e.g., drought, salinity, pathogen) rather than multiple stresses (e.g., abiotic or biotic) may be risky. It is worth noting that increasing tolerance to one type of stress may reduce tolerance to another [14, 15]. Climate change is increasing the frequency of extreme weather events, and plants are subjected to a variety of stresses in the field, including additional pressure from plant diseases [16].

As a result, recognizing the similarities and differences among stress response pathways is essential for optimizing targeted crop improvement. Stomatal closure, reduced photosynthesis, increased reactive oxygen scavenging activity, reduced leaf growth, and increased root length are all indications of plant responses to abiotic stresses [17]. Plant pathogens, for example, cause stomata to close, reducing photosynthesis [18, 19]. The production of toxic compounds such as phytoalexins and reactive oxygen species, as well as the induction of localized cell death, are other pathogen-induced plant responses [20]. Many of these responses are governed by phytohormones [21, 22].

Hormones like abscisic acid (ABA) and jasmonic (JA) play a key role in regulating inanimate stress tolerance. For pathogen immunity, plants primarily rely on salicylic acid (SA), JA, and ethylene signaling. The abiotic stress response is regulated by many transcription factor (TF) families, both ABA-dependent and ABA-independent. ABA-induced basic leucine zipper (bZIP) transcription factors are among the aforementioned [23, 24]. These TFs are responsible for stoma closure, dehydration resistance gene expression, and other adaptive physiological responses [25–27]. ABA, on the other hand, frequently increases plant sensitivity to biological interactions [28–32] and frequently interacts detrimentally with SA [28–32] [33–35]. As a result, plants must have evolved the ability to detect and respond to multiple environmental cues in varying combinations. Developing stress-tolerant plants and testing their performance against individually imposed stresses, according to this viewpoint, may be insufficient. Furthermore, plants exposed to multiple stresses activate a single response that is not simply additive but results from synergistic and antagonistic interactions, resulting in unpredictable effects when each stress is taken into account

[11]. The presence of secondary stress, according to this theory, can either aggravate the negative consequences of primary stress or, on the other hand, contribute to a better response.

2. Defenses against abiotic stresses in general

2.1 Cuticle

The cuticle is a fine translucent lipid structure that seals the aerial surfaces of land plants' organs on the outside. The thin hydrophobic layer is essentially a cutin matrix filled with cuticular waxes and encapsulated with them. As the plant's primary interface with the environment, the cuticle, as the plant's primary interface with the environment, is critical for controlling liquid and gas fluxes, defending against pathogen and bug attacks, and resisting abiotic stresses. The ability of land plants to deploy an outer shield made of simple molecules is a brilliant innovation that is critical to their success in terrestrial colonization [36–38]. The cell wall, the second barrier that actively remodels in response to abiotic stresses [39, 40], is far more complex and poorly understood to order to counteract this [41, 42]. The cuticle is macromolecular polyester of C16 or C18 oxygenated fatty acids (FAs), which are exclusively produced by epidermal cells. Waxes, on the other hand, are a high-end blend of C24 to C34 FA derivatives such as alcohols, aldehydes, alkanes, esters, and ketones. The biosynthetic pathways of these organisms are nearly complete and well documented [10, 37, 43–45]. In a nutshell, C24 and C34 are constituted from acetyl coenzyme A (CoA) in plastids via de novo FA synthesis, adding the addition of two carbons in each recurring cycle. Until C16/C18 products emerge, they are transported to the endoplasmic reticulum (ER), they are oxidized and incorporated to form cutin precursors (monoacylglycerols) or elongated modified to include wax components. The alcohol-forming (or acyl-reduction) pathway for primary alcohols and esters and the alkane-forming (or decarbonylation) pathway for aldehydes, alkanes, secondary alcohols, and ketones, are two distinct modification pathways. These materials must be transported from the ER to the cytomembrane (PM), where cutin monomers polymerize and wax members crystallize, to form the apoplastic cuticle on the outer surface. Membrane vesicle trafficking [46] is one of the systems involved in intracellular shipments to the ATP-binding cassette (ABC) transporters that channel the PM [38, 43, 47].

2.2 Unsaturated fatty acids

C16/C18 FAs are not only important components of the cuticle, but also of membranes, which serve as basic biological barriers. Phospholipids and glycolipids with a glycerol core and two FA-derived “tails” are the primary components of botanic membranes. Membrane properties are greatly influenced by FAs. Their degree of unsaturation, in particular, is an important determinant of membrane fluidity. The UFA chain will kink at a cis-double bond, which will act as a steric hindrance in the intermolecular package, causing the intermolecular package to become more fluid [48, 49]. Membrane fluidity is vulnerable to abiotic stresses, particularly extreme temperatures. Cold-driven rigidification and heat-driven fluidization can cause biomembrane dysfunction, as exemplified by protein deactivation and ion leakage [50]. Cytoskeleton destabilization is also a direct consequence [51, 52].

C18 UFAs are used as a raw material in the production of a variety of aliphatic compounds in plants, including membrane glycerolipids, TAG, cutin/suberin, jasmonates, and nitroalkenes (NO₂-FAs). All of these products, as well as C18 UFAs, help plants; defend themselves against biotic and abiotic stresses. Multiple mechanisms implicate C18 UFAs in stress defense, either directly and indirectly. Biomembranes are a functional platform for many cellular processes, including substance exchange, signal transduction, and many metabolic reactions, in addition to being a structural barrier for cells and intracellular organelles [53]. The signaling of Ca²⁺, a versatile second messenger involved in virtually every stress response in plants, is based on membrane isolation and transportation. With the help of its channels, such as the PM cyclic nucleotide-gated channels (CNGCs) and the tonoplast TWO PORE CHANNEL 1 (TPC1), the sharp influx of the cation ignites Ca²⁺ signaling into the cytosol [51, 54, 55]. Furthermore, efflux through Ca²⁺-ATPases and Ca²⁺/H⁺ exchangers has quickly rinsed it [56, 57]. Other ion transporters, such as the K⁺ rectifier ARABIDOPSIS K⁺ TRANSPORTER 1 (AKT1) [54] and the Na⁺/H⁺ antiporter SALT OVERLY SENSITIVE 1 (SOS1) [26, 34], preserve a sufficient K⁺/Na⁺ ratio in the cytoplasm, which is necessary for salt tolerance [58, 59]. The electrochemical gradient created by transmembrane proton pumps, such as PM H⁺-ATPase, vacuolar H⁺-ATPase (V-ATPase), and vacuolar H⁺-translocating inorganic pyrophosphatase (V-PPase), energizes these secondary transporters [60–62]. The PM H⁺-ATPase, in particular, is a critical site that responds to salt and other stresses such as cold and heavy metals, as well as active transport across the PM [63].

Membrane fluidity is vulnerable to a variety of stresses, including extreme temperatures. Cold-induced rigidification and thermal fluidization, on the other hand, are harmful to membrane function, causing protein deactivation, electrolyte leakage, and perhaps even cytoskeleton destabilization [51, 52]. As a thermodynamic property, membrane fluidity could be used as a sensor in heat flux signaling. Interestingly, dimethylsulfoxide (DMSO) and benzyl alcohol (BA) can both mimic the effects of cold and heat at 25°C. Plants are poikilothermic organisms, emphasizing the significance of membrane remodeling, as well as the threat of climate change.

2.3 Scavengers of reactive species

The endless generation of noxious RS, particularly reactive oxygen species (ROS) such as superoxide (O₂⁻), oxide (H₂O₂), hydroxyl (OH), and singlet oxygen (O₂¹), as well as reactive carbonyl species (RCS) such as malondialdehyde and methylglyoxal, is an inherent paradox in aerobic organisms' normal metabolism (MG; CH₃COCHO). The two types of RS are inextricably linked. RCS can be caused by ROS-induced lipid peroxidation, while ROS are frequently raised by RCS activities. Almost all abiotic stresses can cause a surge of ROS and RCS, transforming their scavengers into particular defenses. Nonetheless, ROS and MG have been shown to perform a signaling role at low levels, which is tactically exploited to aid stress perception and elicitor retention [64, 65]. As a result, it's critical to maintain the delicate RS homeostasis, which must be taken into account when trying to manipulate RS scavengers for multi-stress tolerance.

2.4 Reactive oxygen species

The active transport of chloroplasts imposes a greater burden of ROS on plant cells. When these small chemicals are overproduced, they attack a variety of

biomolecules such as carbohydrates, lipids, proteins, and nucleic acids, causing oxidative catastrophes such as increased photoinhibition inhibition and membrane damage, which can be measured by the amount of MDA generated per oxidation of UFA [64, 66, 67]. MDA is a potential RCS that attacks under acidic conditions, forming covalent adducts known as advanced lipoxidation end products (ALEs), usually causes protein dysfunction and its consequences. Plants have evolved sophisticated ROS scavenging systems that employ both non-enzymatic and enzymatic methods. Many metabolites, such as betalain, carotenoids, flavonoids, and vitamin E, have antioxidant properties [68, 69]. Superoxide dismutase (SOD), catalase (CAT), and various peroxidases are examples of special enzymes (POD). SOD converts oxygen to hydrogen peroxide (H₂O₂), which is then reduced to water by CAT and POD. Dehydroascorbic acid reductase (DHAR), monodehydroascorbic acid reductase (MDHAR), and glutathione reductase are all core component of the ascorbate glutathione (ASAGSH) cycle, which is required for ascorbic acid peroxidase (APX) (GR). The intervention of detoxifying enzymes can undoubtedly be used to achieve multiple stress tolerance. Transgenic plants have used APX, an important enzyme that makes sure the removal of H₂O₂, to combat drought, salt, and intense light [70–72]. It also revealed glutathione peroxidase (GPX) activity, as well as cold air, heat, ultraviolet light, and heavy metals [73–75].

2.5 Carbonyl reactive species

Methylglyoxal, a substantial type of RCS, is attracting more attention in stressful situations. Because of the non-enzymatic dephosphorylation of two intermediates, glyceraldehyde3-phosphate, and dihydroxyacetone phosphate, glycolysis is the primary source of this cytotoxin in plant cells. Even before MG increases to a dangerous level, it can harm a variety of biomolecules, particularly because of its aldehyde group. Plant defenses against abiotic stresses ALEs, MG can help accelerate the photo-reduction of O₂ to O₂ in chloroplasts and consume GSH via spontaneous combination into hemithioacetal, actually results in a vicious cycle and eventual cell death.

2.6 Chaperones at the molecular level

Heat shock proteins (HSPs) are molecular chaperones that are articulated either induced or constitutively to assisted protein folding, assembly, transport, and degradation. HSPs' anti-stress role isn't limited to their definition. This large family of proteins is a universal rescue system used by nearly all living organisms to combat all dangerous factors can trigger protein damage. They work to prevent denatured proteins from accumulating, assist in their refolding, or present them to lysosomes or proteasomes for proteolysis, restoring cellular homeostasis [76, 77]. Furthermore, some unusual hydrophilic proteins, such as members of the late embryogenesis abundant (LEA) and cold-regulated (COR) families, may act as chaperones to protect proteins and membranes from stress injury [78, 79]. The five conserved HSP classes based on molecular weight are HSP100/Clp, HSP90, HSP70/DnaK, HSP60/Chaperonin, and small HSP (smHSP). The most widely conserved among species is HSP70, which consists of an N-terminal ATPase domain and a C-terminal substrate-binding domain. In response to stress, smHSPs accumulate quickly and are more likely to seize non-native proteins and transfer them to ATP-dependent chaperones like the HSP70 system for re-naturation [80, 81]. According to a new study, *Arabidopsis* transformed with HSP16.4 from pepper (*Capsicum annuum*) was less

susceptible to drought, heat, and their combination, and ROS scavenging enzymes were more active under stressful conditions [82].

2.7 Compatible solutes

Conformance solutes are small organic compounds with electrical neutrality, high solubility, and low toxicity that can cause some problems when present in high concentrations in cells. Qualified molecules include sugar and amino acid derivatives, as well as their derivatives, such as ash, trehalose, inoside, mannitol, proline (PRO), and glycine betaine (GB). Except for the protein and membrane RS and stabilizer, these metabolites begin under stressful conditions for dehydration and can be started. A compatible dissolved compatible lysis solute is a small organic connection with electrical neutrality, high solubility, and low toxicity that really can cause a variety of problems in a significant cell concentration. Qualified molecules include sugar and amino acid derivatives, as well as their derivatives, such as ash, trehalose, inoside, mannitol, proline (PRO), and glycine betaine (GB).

3. Plant responses by signal transduction

Plant response to environmental changes has been related to changes in signaling molecules [e.g., sugars, hormones, calcium, reactive oxygen species (ROS), nitrous oxide (NO)] [54, 83], along with large-scale genomic restructuring, including transposon activation [84, 85], and rapid changes in gene expression patterns (e.g., genes encoding transcription factors [86, 87]). A percentage of transcription factors (TFs) from different crops have been discovered to play critical roles in abiotic stress responses. The ability of transcriptional regulators to act as master regulators has been hailed as a long-term solution for modifying complex traits in crop plants [85, 88]. Several transcription factor families, including AP2/ERF, bZIP, Zn-finger, NAC, MYB, and WRKY, have been implicated in abiotic stresses in past few decades [88–90]. Three major methodologies have been used to identify TFs associated with abiotic stress responses in rice: comparative genomics—abiotic stress-responsive genes from *Arabidopsis* and maize have been used to identify rice orthologs; forward genetics—genes related to traits like drought or hypoxia tolerance were identified through association mapping; genome-wide expression profiles—transcriptome analysis using microarrays was used to identify novel abiotic stress-response genes. Plant stress responses have also been interconnected to chromatin remodeling and nuclear organization. Salinity and heat-shock stresses, for example, caused decondensation of interphase ribosomal chromatin in rice and wheat [91, 92]. Heterochromatin maintenance mechanisms may repress transcription in normal circumstances, but they may fail to cause chromatin remodeling and novel gene expression profile in stressful situations [93, 94].

Changes in signaling pathways molecules for example, B. sugar, hormone, calcium, reactive oxygen species (ROS), basic oxide (NO)] are linked to plant response to the environmental changes. [83] only Not even with the most thorough genomic reconstruction, which included transposon activation (for example, gene encoding transcription factor) (e.g., transcription factor) [75, 87]. Many transcription factors (TFS) derived from various plants were found to play a key role in their stress responses. TFS's ability was viewed as a long-term solution for reconfiguring different dynamics in crops, as well as a long-term solution as a master regulatory authority

[88]. TF families such as AP2 / ERF, BZIP, Zn-finger, NAC, MYB, BZIP, Zn-finger, NAC, MyB, WRY, and others have been implicated in the rise in stress resistance in recent decades [13, 88–90]. In rice, three effective interventions were used to identify TFS. By assigning associations, the forward genetics gene associated with characteristics like drought or hypoxia resistance was discovered. Microarrays were used to identify new and assistant voltage attractive genes using genomic effect expression profile transcript analysis. The plant's response to stress also involves chromatin remodeling and nuclear organization [95]. Salt and heat shock stress, for example, caused decondensation of interphase ribosomal chromatin in rice and wheat [91, 92]. Heterochromatin maintenance mechanisms can suppress transcription under normal conditions, but under stress, these mechanisms can disrupt, leading to chromatin remodeling and new genetic patterns [93, 94].

4. Abiotic stress responses: epigenetic mechanisms and gene expression regulation

The effects of stress on genomic epigenetic marks, which affect gene expression regulation, are referred to as environmental epigenetics [96, 97]. Epigenetic memory is achieved by interacting with a variety of molecular mechanisms, including DNA methylation, post-translational modification of the nucleosome core histone protein's N-terminal region, and chromatin remodeling [98, 99]. Many proteins, known as transcription factor-interacting proteins (TFIPs), have been found to regulate epigenetic responses to environmental stress, but only a few have been found in rice. Rice underlying genetic factors were discovered primarily through comparative genomics. Plant plasticity responses to unpredictable abiotic stresses rely heavily on epigenetic mechanisms.

4.1 DNA methylation and abiotic stress

Cytosine methylation is a conserved epigenetic mark that plays a role in genome defense against endogenous transposable elements and viral DNA, as well as gene regulation throughout plant development. Methyltransferases catalyze the addition of a methyl group to cytosine residues (MTases). Furthermore, in plants, this can happen in both asymmetric (CHH) and symmetric (CG and CHG) situations. DOMAINS REARRANGED METHYLTRANSFERASE TFS AND EPIGENETIC MECHANISMS IN ABIOTIC STRESS RESPONSES 847 (DRM), METHYLASE 1 (MET1), CHROMOMETHYLTRANSFERASE (CMT), and DNA methyltransferase homolog 2 (Dnmt2) are four key families of plant MTases that seem to have distinct functions in de novo and/or maintenance methylation [100]. While methylated cytosines are replaced with unmethylated ones during DNA replication, active demethylation occurs without DNA replication throughout a base excision repair mechanism mediated by DNA glycosylases [101]. Other frameworks, such as the RNA-directed DNA methylation (RdDM) pathway, mediated by siRNAs [102], and chromatin remodeling factors, also impact DNA methylation [78, 103]. Overall, these regulatory pathways provide a dynamic platform for establishing DNA methylation patterns, which may be critical for epigenomic plasticity and rapidly respond to developmental cues and environmental stress. The technique of DNA methylation's implication on transcription is still unidentified. Several lines of evidence suggest that cytosine methylation has a broad array of functions that are likely individualized for different

genes [100, 104]. Methylated cytosines may attract methyl binding proteins, which in turn may attract histone modifiers and chromatin remodeling proteins, resulting in a complex that can disrupt transcription factor linkage [36, 104].

On either hand, high-resolution DNA methylation mapping has demonstrated some common aspects related to the H3K9me3 and H3K27me3 are infused in genes of euchromatic regions [105]. Biotinylation and sumoylation, two other histone modifications, have been interconnected to gene repression [106]. Large and powerful histone lysine acetylation has been linked toward a more open chromatin structure and thus enhanced transcription, whereas weak acetylation has been linked to chromatin compaction and gene silencing [107]. Histone acetyltransferases (HAT) and histone deacetylases enforce histone lysine acetylation (HDAC). In plants, there have been four major classes of HDAC encoding genes [108], also with HD2 class being the only one that exists [109, 110]. In hybrid rice, the OsHDT1 gene is involved in regulation of gene expression [111]. There are at least 19 HDAC genetic traits in the nucleotide sequence, and most of them are differentially regulated by different abiotic stress conditions [12, 112]. Most rice HDAC genes were exceptionally responsive to drought or salt stresses, primarily through transcriptional repression, as according microarray data [112]. As a result, abiotic stresses may start regulating the transcription of chromatin modifier enzymes. Down regulation of HDAC may be required in this case to allow the induction of stress-responsive genes [12, 113].

The highest density of methylated cytosines is reported in transcriptionally inactive heterochromatic regions, which contain countless transposable elements (TEs) and repetitive sequences. Lower but still significant cytosine methylation levels were observed in euchromatic regions. Surprisingly, DNA methylation related to active genes was more abundant in transcribed regions than in promoters in both *Arabidopsis* [114] and rice. The magnitude of methylation within the gene body was negatively correlated with transcript elongation performance in *Arabidopsis* [114]. It's reasonable to assume that rice has a similar principle. Abiotic stresses may end up causing changes in DNA methylation levels, which may be posted a link to chromatin remodeling and stress-responsive gene transcription regulation. Genome-wide analyses in several plant species reveal a global methylation readjustment in response to stress, owing primarily to demethylation [115–117]. Because conserved patterns were observed between different genotypes or tissues, the AFLP-based methylation-sensitive approach (MSAP) demonstrated that some of these improvements (methylation/demethylation) are site-specific. This method is best suited to CG methylation analysis. Other studies, on the other hand, have found that stress induces transcriptional induction of silent loci without a loss of DNA methylation, but instead a decrease in nucleosome occupancy [118, 119]. Elevated expression of the *AtHKT1* gene, which encodes for a vacuolar Na⁺/H⁺ transporter, was also linked to lower DNA methylation in the *Arabidopsis* met1-3 mutant. The methylation pattern of a putative small RNA target region in the *AtHKT1* promoter is required for the differential expression of this gene in roots and leaves, which may influence salt sensitivity and response [120]. Two *Laguncularia racemosa* species that grow in salt marsh and riverside habitats had different global DNA methylation patterns [121]. It's possible that epigenetic variation plays a role in helping plants adapt to different environments under natural conditions. It's possible that epigenetic variation plays a role in helping plants adjust to different environments under natural circumstances. Several MTases have been defined in rice, with such microarray data indicating that some are found to be elevated preferentially even during the commencement of floral organs [81, 122].

Furthermore, during the booting and heading stages, increased levels of methylation in rice leaves were detected (as ascertained by MSAP) than during the tillering stage [116]. As a result, drought-induced demethylation levels were higher at the tillering stage than it is at the booting and heading stages [116]. Changes in DNA methylation may differentially modulate response of plants to abiotic stress across the whole of development, according to these studies.

4.2 Abiotic stress and histone modifications

Nuclear DNA is packed and organized in eukaryotic cells in affiliations with a histone protein core-forming nucleosome, is also one of the chromatin's structural units. Combinations of histone variants and covalent modifications of histone tails, also including acetylation, methylation, phosphorylation, ubiquitination, biotinylation, or SUMOylation, resulted in changes in nucleosome structure. Assemble an integrated histone code that has been linked to gene expression regulation [106, 123, 124]. Depending on which lysine is methylated and how many methyl groups are added, the methylation process of lysine residues on histone H3 has been linked to transcription activation or repression [96, 105, 106]. Histone H3 lysine four trimethylation (H3K4me₃), for example, has been linked to euchromatin and gene activation in maize, revealing inactive gene sequences not found in transposons [125]. Histone H3 lysine 9 dimethylation (H3K9me₂) has been accompanied with transposons in Arabidopsis as an indication for heterochromatin and repressed transcription [105, 126]. H3K9me₃ and H3K27me₃ are, on the other hand, abundant in euchromatic genes [105]. Biotinylation and sumoylation, two other histone modifications, have been linked to gene repression [106]. In terms of histone lysine acetylation, strong acetylation has been linked toward a more relaxed chromatin structure that promotes transcription, so even though weak acetylation has been linked to chromatin densification and gene silencing [107, 127].

Histone acetyltransferases (HAT) and histone deacetylases enforce histone lysine acetylation (HDAC). In plants, there are four major classes of HDAC encoding genes [128, 129], with the HD2 class being the only one [109]. In hybrid rice, the OsHDT1 gene is involved in genetic variations [111]. There are at least 19 HDAC genes in the rice genome, and most of them are differentially regulated by different abiotic stress conditions [12, 112]. Most rice HDAC genes were exceptionally responsive to drought or salt stresses, pretty much exclusively through transcriptional repression, thus according microarray data [112]. As a result, abiotic stresses may regulate the transcription of chromatin modifier enzymes. Down regulation of HDAC may be taken into account to allow the induction of stress-responsive genes [12, 130]. Gene expression regulation has been coupled to histone modifications and DNA methylation crosstalks. In Arabidopsis, for example, the loss of DNA methylation in the *ddm1* mutants was associated with low levels of dimethylation of histone H3 at lysine 9 (H3K9me₂) [127, 131, 132]. A SUVH [Su(var)3-9 homologs] protein that plays in H3K9 methylation has been discovered to directly bind to methylated DNA, revealing the existence of a self-reinforcing feedback loop for DNA and histone methylation preservation in this species [133]. Recently, several rice SUVH genes with a deduced role in heterochromatin formation were revealed [134]. Through DNA methylation and H3K9me₃, some of these have been shown how to resolve retrotransposon repression [74, 135].

Furthermore, most protein-coding genes with methylated DNA in rice are associated with H3K4me₂ and/or H3K4me₃, and when H3K4me₃ is present, the repressive impact of DNA methylation on gene expression is reduced. Due to the rapid

technological advances such as chromatin immunoprecipitation (ChIP) and genome-wide sequencing, the consequence of abiotic stresses on the genome-wide landscape of histone modifications is beginning to be deciphered (ChIP-Seq). Submergence stress in rice resulted in a decline in H3K4me2 levels, an increase in H3K4me3 levels, and a gradual increase in H3 acetylation at the ALCOHOL DEHYDROGENASE 1 (ADH1) and PYRUVATE DECARBOXYLASE 1 (PDC1) genes' 5- and 3-coding regions [136]. These changes were associated with increased ADH1 and PDC1 expression as a result of stress [136]. Cold stress, on the other hand, lessened H3K27me3 in the promoters of two cold-responsive genes, COLD REGULATED 15A (COR15A) and GALACTINOL SYNTHASE 3 (ATGOLS3), whereas salt stress increased H3K9ac, H3K14ac, and H3K4me3, while depleting H3K9me2 at stress-responsive genes [60]. These observations show the importance of histone code plasticity in transcriptional regulation during plant responses to various abiotic stresses when taken together.

5. Drought tolerance's molecular mechanism

Drought stress could severely limit rice production, leading to significant financial losses. It has become a more serious issue as the world's temperature rises. In light of current and projected global food demand, it is critical to prioritize increasing crop productivity on drought-prone rainfed lands. Drought-tolerant rice varieties are intended to address the assembly target in rainfed areas, and genetic improvement of rice for drought tolerance should also be a high priority theme of research in the next two decades. Breeding for drought tolerance could be an interesting challenge. The present study would be severely hampered by the complex nature and multigenic control of drought-tolerant traits.

Environmental drought impulses are intercepted by membrane sensors, which are still heavily portrayed. The signals are then transmitted via various signal transduction pathways, resulting in the outflow of drought-responsive attributes with effective gene functions and drought tolerance [98, 137]. Drought is a complex phenomenon, making it difficult to comprehend [73, 138]. As a result, hybridization and selection strategies could not provide precise drought tolerance results. Using DNA markers in molecular studies, at the other hand, can append the procedure by providing precise outcomes. These molecular markers are also useful for identifying drought-tolerant germplasm in a mass and using it to improve crops. Many studies have been conducted in order to identify some qualitative trait loci (QTL) linked to various traits [139, 140]. DNA studies based on marker-based phenotyping were the very first methodologies used to distinguish genes associated in rice drought resilience. Despite the progress, only a few traits have been officially approved for drought resistance [138, 141]. Molecular breeding can improve crop varieties, and yield assortments, produce productive, safe harvests, and also have high agronomic credibility in this way.

6. Rice drought tolerance genes and transgenic approaches

Many remarkable genes are highly expressed in rice after exposure to drought varieties, with approximately 5000 genes upregulated and 6000 genes downregulated [142, 143]. These genes can be divided into three categories: membrane transport, signaling, and transcriptional regulation [140, 144]. Many important genes/transcription factors are expressed differently in rice and are used to create transgenic plants

for drought strains [73, 140]. The majority of the genes regulated by drought are ABA-independent, as are the ABA-independent regulatory requirements that manage rice's drought tolerance mechanisms [131, 145]. OsJAZ1 has also been shown to mitigate drought tolerance in rice by impairing ABA signaling, which synchronizes plant responses to expansion and success under drought stress [12]. Osmoregulation and late embryogenesis abundant (LEA) proteins, which confer terminal drought tolerance in rice, are also linked with a number of genes [137, 140]. In transgenic rice, the gene DRO1 causes root elongation and deeper rooting. In rice under water deficit conditions, other genes like as OsPYL/RCAR5 and EcNAC67 induced leaf water content, delayed leaf rolling, improved growth parameters mass, and stomatal regulation [146, 147]. Over expression of OsDREB2B, CYP735A, and OsDREB1F [82, 148] pronounced the DREB2-like gene OsDRAP1 conferring drought tolerance in rice accelerated root morphological diversifications in rice under drought strain. Increased grain yield in rice under drought is critical, and it can be achieved by using transgenic approaches to start introducing genes like OsNAC5 [112], OsbZIP71 [51], OsWRKY47 [149], OsbZIP46 [150], and OsNAC10 into the crops. The WRKY genes play an important role in plant improvement by responding to drought strains and can be used to create drought-tolerant transgenic plants [151, 152]. Several genes were investigated using transgenic approaches to confer drought tolerance in rice grown in a research lab or glasshouse conditions. However, those genes must be investigated further.

7. The role of micro RNA in rice drought tolerance

Micro RNAs (miRNAs) are small noncoding regulatory RNAs that modulate gene expression during abiotic stress, as has been acknowledged [151, 153]. These 20–24 nucleotide long proteins control gene expression at the post-translational level [140]. Several miRNAs have also been found to alter gene expression in rice by up- up-and down-regulation, which confers drought tolerance [134, 154, 155]. Arabidopsis [156] was the first to reveal the expression of miR393, miR319, and miR397 in response to drought, and rice control transcriptional factors OsAUX1 and OsTIR1 confer tiller number increment, early flowering, and auxin increased sensitivity [157].

Rice does have 30 miRNAs, 11 of which are down-regulated and eight of which are up-regulated under drought stress [126]. Under drought stress, MiR160 and MiR167 regulate the expression of the ARFs gene, that further regulates early auxin response [140]. Through ROS homeostatic genes, DST- amiRNA enhances drought resistance by increasing stomatal closure and decreasing stomatal density [155, 158]. Over expression of the UDP-glucose-4-epimerase gene, facilitated by OSA-miR169-3p and Osa-miR166e-3p, regulated root development and cell wall biogenesis, along with carbohydrate metabolism [154, 159]. Ten miRNAs (miR531, miR827, miR8175, miR977, miR6300, miR1861, miR440, miR9773, miR3982, and miR1876) were recently discovered to be regulated under drought stress and confer tolerance attributes in traditional rice land races [160]. Drought tolerance can be accomplished by gene manipulation of these miRNAs. As a consequence, miRNAs regulate many drought tolerance responses, potentially enhancing the development of drought-tolerant rice genotypes.

Natural rice genotypic variation could be investigated to seek novel genotypes with a drought-tolerant trait of interest and a gene/locus affiliated with them. Drought-tolerant rice varieties can be developed and use these novel genotypes in traditional breeding programs using marker-assisted selection. The breeding program's aim is to create high-yield lines with improved performance parameters, as well as to

commercialize the cultivars. Numerous researchers have investigated the progeny of drought-tolerant genotypes in the past [139, 161, 162], but the overall performance has been far lower than expected due to the difficulty in finding suitable donors with a higher tolerance level, as well as the environment-specific nature of the genotypes. The majority of marker-assisted breeding approaches for improving drought-tolerant rice varieties have always been carried out at the International Rice Research Institute in the last decade [163]. In India [145, 160], the Philippines [159, 161], and Malaysia, several works on marker-assisted progression of popular varieties were carried out [164]. Several QTLs for drought tolerance in rice have been incorporated into leading cultivars using marker-assisted breeding techniques [162]. By using a marker-assisted backcrossing approach, they were able to successfully incorporate QTLs such as qDTY9.1, qDTY2.2, qDTY10.1, and qDTY4.1 in the high yielding IR64 variety [27]. They also developed the drought-tolerant elite Malaysian rice cultivar MR219 by pyramiding three QTLs, qDTY2.2, qDTY3.1, and qDTY12.1. They created TDK1 rice varieties with three QTLs for high yield in drought conditions (qDTY3.1, qDTY6.1, and qDTY6.2). Drought has only received attention as a constraint, and no effective methods for developing drought-tolerant rice varieties have yet been successful. Farmers prefer to grow high-yielding cultivars with better grain quality but are drought-prone, or traditional drought-tolerant varieties with low yield. As a result, more effort will be needed in the future to develop unique rice varieties that can produce high yields in drought and acclimate to a range of adverse climatic conditions.

8. Salt tolerance

Salt stress may cause progress in multiple physiological and metabolic pathways depending on the severity and duration of the stress, leading to a reduction in rice productivity [50, 120, 165, 166]. To estimate the phenotypic coefficient of variation (PCV), genotypic variance (GCV), broad-sense heritability, and genetic Advance, genetic characterization of salt tolerance-related traits is required (GA). Assume there is sufficient variation in the germplasm for salt tolerance-related attributes with greater heritability and genetic advance. As a result, by utilizing salt-tolerant landraces/germplasm in breeding programs, it may be possible to improve the personality characteristics associated to salt tolerance in rice. The low Na-K ratio was controlled by both additive and dominance gene effects, according to a genetic component analysis (GCA) study [89, 167]. The results of the amalgamating ability analysis show that both general combining ability (GCA) and specific combining ability (SCA) effects are important in understanding salt tolerance genetics. They also revealed that selection for common heritable traits like the Na-K ratio could have been built in subsequent generations under controlled conditions to reduce environmental effects. Additive gene action is linked to narrow-sense heritability [168, 169], and additive gene action may enhance or fix the action of the desired combination of genes. As a result, early generation preference for salinity tolerance is possible. Recognizing the gene action in rice that generates salt tolerance will support future breeding efforts [112, 170].

9. Submergence

Submergence is among the most important abiotic stresses in rice-growing areas prone to flash floods [171]. Submergence tolerance is a necessary trait for rice in

rain-fed lowland conditions (*Oryza sativa*). A significant gene known as Sub1 is mainly accountable for this trait. Indica cultivar FR13A is a highly tolerant rice variety that can withstand complete submersion for up to two weeks. Near the centromere of chromosome 9, they have a substantial quantitative trait locus known as submergence1 (Sub1) [157, 172, 173]. Background genetic information for submergence tolerance was well documented out of some research using QTL mapping and map-based cloning techniques [172, 174, 175]. Because of the great specificity of contemporary rice varieties, salt stress is a significant constraint in many rice-producing areas. One of the most severe abiotic stresses restricts rice growth and development of plants, resulting in yield reduction of more than 50% [176, 177]. Salinity tolerance is multifaceted, involving a range of biological mechanisms such as sodium exclusion from root system. Salinity is estimated to affect over 150 million hectares of current and potential rice land in tropical and subtropical regions of the world [176, 178]. Despite the fact that rice is the source of nutrition for half of the world's population, it is more susceptible to salt stress than other cereals [179, 180].

If rice plants are immersed in water for even more than five days resulting from environmental or abiotic stress, they become the deepest submergence-tolerant contributors and are widely used by rice breeders. The pyramiding of submergence and salinity tolerance is especially important in coastal areas where floodwaters are frequently saline. On chromosome 1, a major salinity QTL has recently been introduced and characterized [79, 170]. Although many QTLs may be necessary to accomplish adequate salinity tolerance in the field, additional QTLs for vegetative growth and reproductive-stage salinity tolerance may be compelled to provide salinity stress defense during in the rainy season. Using molecular marker technologies to stack multiple tolerance genes/QTLs into single rice varieties provides breeders with a once-in-a-lifetime chance to advance tolerant cultivars more faster for specific environments [172, 181]. There are various types of biotic stresses. The Sub1 gene, which is managed to find on chromosome 9 of rice, is well-known for conferring submergence tolerance intolerant rice cultivar FR13A and its progenies [157, 173, 175].

10. Modern breeding techniques

Using a variety of innovative tools, genomic assisted breeding (GAB) is routinely used to improve the genetics of salt-tolerant rice. Genomic breeding, forward breeding, rapid breeding, and haplotype-based breeding are all examples of genomic breeding [115, 182]. 5G breeding methods are used to improve genotype productivity by improving genome sequence availability (genome assembly), characterization of germplasm at the genomic and morpho-agronomic level, genomic detection and understanding function, genomic breeding, and genome editing [118, 183, 184]. These could be used to improve efficiency and accuracy of breeding for complex abiotic stress tolerance traits. Through SNP-based speed breeding, SNP-assisted introgression of the *hst1* (Salt-tolerant 1) gene enhanced salt tolerance in a high-yielding rice variety [41]. The emphasis in contemporary breeding is on data-driven parent selection. Genetic technique, trait categorization through diagnostic trait markers, genomic screening, and breeding value estimation are all applied to local and exotic germplasms. Native germplasm with low yield potential may contain traits of interest (ToI) like salinity and submergence tolerance, aroma, and resistance to disease. Then, in order to develop pre-breeding materials, ToI is first transferred to a privileged

background with a higher yield. The elite line with the desired traits is then used to accomplish the product profile for breeding [185].

11. Underpinning defense systems is a regulatory network

The five general defense mechanisms are coordinated by a delicate regulatory network composed of numerous signaling molecules and gene regulation indicators in the face of abiotic stresses. We'll look at some of the more well-known ones here. Stress hormones (ABA), reactive oxygen species (ROS), hydrogen sulfide (H₂S), nitrogen oxides (NO), polyamines (PAs), phytochrome B (PHYB), and calcium interplay with others at various levels, synergistically or antagonistically, to establish a specific directive for downstream effectors, especially transcription factors (TFs), to alter gene expression and protein/enzyme activities in a specific pattern, thereby launching a proper response. Hormones of Stress Phytohormones like ABA, ethylene (ET), jasmonic acid (JA), and salicylic acid (SA) are important organizers of systemic stress defense, and they work together in the complex hormonal signalosome [3]. S Notably, melatonin, a universal multi-regulatory molecule across all life forms, is increasingly recognized as a potent stimulator against stress in the plant. One notable aspect of this yet-to-be-licensed phytohormone is that it operates as if a commander of other phytohormones [28, 186]. Nevertheless, ABA is the main stress hormone, which not only extensively interplays with other phytohormones but with all following signaling molecules. Particularly, components of all biochemical defenses remarked above can be mobilized by ABA, including cuticular waxes [187, 188], HSPs [95], Pro [120], antioxidants [189, 190], and RS detoxifying enzymes [137, 191]. Stress stimuli can rapidly trigger de novo synthesis of ABA from oxidative cleavage of β -carotene, with 9-cisepoxycarotenoid dioxygenase (NCED) is the rate-limiting enzyme.

ABA can also end up causing organic changes in order to cope with stressful situations. Probably one of the best is the closing of stomata, tiny pores formed by paired guard cells that allow gas exchange and thus minimize water loss from transpiration and thus mitigate dehydration. The activity of ion channels and aquaporins is modulated to achieve this movement. As a result, the outflow of K⁺ and anions pulls water out through osmosis, causing guard cell shrinkage, which is ensured by actin filament reshuffling [48, 192, 193]. Another unique feature is seed dormancy, which enables seeds to avoid existing stresses and wait for ideal germination conditions [194–197]. Endogenous ABA elevation and exogenous ABA addition both help plants cope with a wide assortment of stresses. For in-field applications, the development of ABA analogs with greater security is promising. Overloaded ABA signaling, such as that caused by over expressed NCED or constitutively active PYLs, can cause vegetative growth retardation and grain yield reduction [81, 198], while foliar ABA spraying can cause leaf senescence in rice (*Oryza sativa*) and maize (*Zea mays*). As a result, it's critical to gain a better understanding of ABA homeostasis, its wide range of biological effects, and crosstalk with other pathways in order to create crop stress tolerance strategies that don't sacrifice economic traits. ROS are continuously produced in plant cells as byproducts of aerobic metabolism in chloroplasts, mitochondria, and peroxisomes, among other cytoplasmic organelles. However, as noted previously, it is not only toxins that can only be removed but also signaling molecules that are required for a variety of physiological processes, including stress resistance. A ROS signal is shaped by a variety of factors, including dose, duration, source, and type

[199, 200]. The extensive crosstalk between H₂O₂ and other signaling molecules has been reviewed, including ABA, ET, JA, SA, NO, and Ca²⁺ [136]. Ca²⁺ influx, in particular, is a notable event in H₂O₂ signaling, which modulates H₂O₂ levels by activating producing (e.g., RBOHs) or scavenging enzymes. Because of the degradation of PAs, H₂O₂ is strongly intertwined to them [189]. Numerous enzymes in the apoplast can produce ROS on their own in response to increases stimuli. Respiratory burst oxidase homologs are the most common (RBOHs). These PM-localized NADPH oxidases are activated by Ca²⁺ binding to the EF-hand motifs in the N-terminal cytosolic region, in combination with phosphorylation by receptor-like cytoplasmic protein kinases, for example (RLCKs). The MAPK signalosome plays a key role in H₂O₂ intracellular signaling, which is triggered by metabolic disturbance and/or apoplastic discharge. It is a pertinent stress signaling divergent node. MAPK kinase (MAPKKK), MAPK kinase (MAPKK), and MAPK make up each phosphorylation cascade. Many MAPKs and cascades have been discovered to decode the H₂O₂ signal in different ways, but how the precision is determined is still unspecified. The MAPK pathway, on the other hand, functions upstream of ROS by modulating the activities of RBOHs, either positively or negatively [201, 202]. Two MAPKs, MPK3 and MPK6, are aligned in defensive response in Arabidopsis, and can eventually elevate the levels of defending factors such as GSTs and HSPs. H₂O₂ can activate them through the ANP1, a MAPKKK, and other kinases such as oxidative signal-inducible 1 (OXI1), which is required for full activation of MPK3/6, and NUCLEOTIDE DIPHOSPHATE KINASE 2 (NDPK2), which can interact with MPK3/6 and potentiate its activities. NPK1 (tobacco ANP1 ortholog) and AtNDPK2 imparted tolerance to a variety of stresses, which would include salt and extreme temperatures, on transgenic plants. MKK2, a MAPKK in another anti-stress cascade, MEKK1-MKK2-MPK4/6, did this very same [44, 203].

12. Nitric oxide and hydrogen sulfide

At low concentrations, toxic secondary gaseous molecules, H₂S and NO, show impressive powers in providing protection against a wide range of stresses, just like H₂O₂. Many anti-stress mechanisms are shared by the two. Both, for example, can reduce salt toxicity by increasing Na⁺ exclusion by unlocking SALT OVERLY SENSITIVE 1 (SOS1), a PM Na⁺/H⁺ antiporter [155, 204]. The ability to combat oxidative stress should be their most prominent role, as both of them not only act as antioxidants in their own right but can also repress ROS production and activate ROS elimination. H₂S can be assimilated into GSH as a source of sulfur, resulting in an increase in this important R.S. scavenger [20, 205]. The first recognized gasotransmitter, carbon monoxide (CO), is also an elicitor. CO research on this topic, however, is still in its infancy [114]. During various stresses, the three R.S., H₂O₂, H₂S, and NO, are typically available and together demonstrate intricate interactions depending on the context. It can ablate NO accumulation and aid stomata opening with the antagonist's face [176]. NO, on the other hand, is a mediator of H₂S in the promotion of adventitious root development [103, 206], which can boost O₂ uptake and thus reduce hypoxia stress caused by waterlogging [33, 173]. H₂S, on the other hand, is a NO mediator in maize heat tolerance and bermudagrass (*Cynodon dactylon*) cadmium resistance [116]. Furthermore, with the addition of another R.S. player, MG, the situation will become even more complicated. Their chemical reactions add to the complexity, blocking one another while also forming new compounds with physiological implications, such as

peroxynitrite (ONOO) formation by NO and O₂ nitrosothiol formation by NO and H₂S. There is even a competition between M.G. and GSH participants. Thiol modification, such as oxidation by H₂O₂, sulfhydration by H₂S, nitrosylation by NO, glycation by M.G., and glutathionylation by GSH, can directly modulate protein function [152, 176]. Even though GSH is a derivative of H₂S but a cocktail mixer of the other three, it provides additional pathway for their crosstalk. Besides this, the MAPK pathway is likely to be a point of convergence for the four signaling RS. Two gasotransmitters originate from various sources and are natural products of botanic metabolism. Cysteine desulfhydrases (DES) and sulfite reductase (SIR) for H₂S, along with nitrate reductase (NR) and a nitric oxide synthase (NOS)-like a pathway for NO, though a truthful NOS has yet to be discovered in plants. PAs have long been acknowledged for their protective role in plant response to a variety of stresses [75, 165, 189]. Indeed, protein expression of every PA biosynthetic enzyme, such as arginine decarboxylase (ADC), spermidine synthase (SPDS), and S-adenosylmethionine synthase (SAMS), simultaneously breakthroughs stress tolerance mechanisms in various plant species, seeking to make exogenous PA application unnecessary [8, 75, 207]. Dissecting the mechanisms underlying PAs' anti-stress effects is complicated. Because of their polycationic nature, RS-scavenging property, and signaling function, it's conceivable that these multifaceted substances contribute to stress defense in a multitude of ways. Protonated PAs, for instance, not only take an active part in ion homeostasis at the physiological PH, but they can also bind to negatively charged molecules such as membrane lipids and integral proteins, which helps mitigate stress-induced membrane damage. PAs not only convey with ABA in stress signaling, but they can also induce rapid NO production. PAs are linked to other stress-related metabolites, such as Pro and ET, which are linked to PA anabolism and H₂O₂. Furthermore, GABA is produced as a result of PA catabolism [8, 75]. PAs also fall into the Janus category [168], which must be taken into account in their practical implementation due to the obvious specific link with H₂O₂. Phytochromes PHYB, a modest family of chromophore-containing proteins that serve as photoreceptors to perceive red (R) and far-red (FR) light, is emerging as a negative regulator in stress tolerance. PHYB's signaling activity undergoes reversible photoconversion, that also involves R activation and FR deactivation in response to protein aggregation. The Pr (R-absorbing) form of nascent PHYB is inactive. Dimeric PHYB will translocate into the nucleus once converted to the bioactive Pfr (FR-absorbing) form, where it can interact with and trigger the proteasomal degradation of phytochrome interacting factors (PIFs), a subfamily of basic helix-loop-helix (bHLH) TFs, to remodel the expression profile of thousands of light-responsive genes, guiding photomorphogenesis [131, 208–210].

PHYB was discovered recently to be a thermosensor [46, 71]. Warm ambient temperatures can effectively induce elongation development, which is phenocopied by shade avoidance and is controlled by the PHY-PIF cascade. Indeed, thermal (or dark) reversion, which is independent of light but sensitive to temperature, can end up causing to spontaneously revert to warm temperatures, especially at night, can relieve PIF4 repression by fastly unplugging PHYB and increasing PIF4 transcription, resulting in thermo morphogenesis. Because active PHYB was discovered to interact with PIF-binding sites (G-boxes) at PIF4-targeted promoters, it was tried to suggest that it could play a co-repressor or competitor role in gene regulation with PIF4 [211].

In case of light and temperature-induced growth, another cascade downstream of PHYB involves the RING E3 ligase CONSTITUTIVE PHOTOMORPHOG for degradation to depress the growth genes. ENIC 1 (COP1), and the TF ELONGATED HYPOCOTYL 5 (HY5), with COP1 ubiquitinating. Notably, COP1 can indirectly potentiate the activity of PIF4, thereby connecting the two branches [211, 212]. Plant

Defenses against diverse abiotic stresses, ROS and GOLS are essential for raffinose synthesis via binding upon oligomerization to the heat shock elements (HSEs) located in their promoter regions. Therefore, HSFs are capable of launching three general defensive systems. Surprisingly, plants have a powerful and relatively variable number of HSFs. Nonetheless, genetic manipulation of HSFs remains a viable option for conferring multiplex sensitivity to plants [83, 89]. It's also worth noting that HSFA6b and HSFA3 allow ABA to play a legitimate role in HS response. The former is stimulated directly by AREB1, whereas the latter is activated downstream of DREB2A, a destination that both AREB1 and HSFA6b share [95]. Another member of the class 2 DREB family, DREB2C, is also an HSFA3 activator [96]. It can also work against salt toxicity by trying to target chaperones like COR15A and DESICCATION-RESPONSIVE PROTEIN 29A (RD29A) [173, 213]. Interestingly, DREB2C from *Ammopiptanthus mongolicus* and evergreen broadleaf shrubs living in the desert was newly reported to up-regulate 11-pyrroline-5-carboxylate synthetase initiates Pro biosynthesis, as well as FADs that catalyze 18:3 production, thereby promoting Arabidopsis endurance to drought, freezing, and heat [188]. A safe conclusion can be drawn that this single TF governs all four cellular general defenses. Furthermore, a computational analysis of the Arabidopsis DREB2C promoter revealed a variety of elements that are sensitive to ABA (ABRE), MeJA, SA (TCA), heat (HSE), low thermal conductivity (LTR), and stress (TC rich) [206, 214], implying that TF is a central point in stress signaling. It is an ABA-inducible transcription factor that can delay seed germination by exerting good feedback on ABA biosynthesis by trans-activating NCED9. The enzyme genes in Arabidopsis are primarily controlled by TFs from two families: the AP2/ERF superfamily's SHINE 1 (SHN1), -2, -3, and DEWAX, as well as the R2R3-MYB family's MYB16, MYB30, and MYB106. MYB96, on the other hand, is a repressor of cutin synthesis, whereas MYB41 is an inducer of wax manufacturing [187]. MYB96, in specific, is a key player in ABA signaling, which helps regulate the whole of wax metabolism. Not only elongation and modification enzymes, but also ABC transporters and nsLTPs are directly or indirectly targeted by at least one isoform gene [103, 215]. MYB96 transgenesis continued to improve Arabidopsis drought and freezing tolerance, but it also caused significant dwarfism [99, 215]. Wax production 1 (WXP1), an ERF member from *Medicago truncatula*, may be a better candidate, as it was the one responsible for the previously mentioned observation that higher n-alkane and predominant alcohol contents results in improved viability under drought and freezing without interfering with transgenic Arabidopsis growth [99].

12.1 E3-Ubiquitin ligases, water stress responses

At some point during the plant growth cycle, climate change is threatening more than 20 million ha of rain-fed lowland rice (12 percent of total rice area and about 20% of global production) [216–218]. As extreme events become more familiar, water scarcity is expected to worsen, with yield losses of up to 81 percent [161, 216]. Drought has a particularly negative impact on seedlings (2 to 3 weeks old) and reproductive tiers (pollen-development stage) [207, 211], delaying flowering and lowering yields [186, 219]. Drought leads to inefficient water use, stomatal closure, photosynthesis impairment, and decelerated cell division and expansion [186]. As a proactive approach to cope with water deficit, plants directly influence divergent genetic and metabolic methodologies, such as cellular osmotic potential, stomatal aperture, impaired antioxidant, phytohormones, and chlorophyll content. This really is likely to result in the adaptation and maintenance of their physiological activity under drought

conditions [220]. As a result, it's critical to comprehend the molecular mechanisms underpinning rice drought response, particularly the role of ubiquitination, and to apply these skills to the development of drought-tolerant crop varieties. Over the last two decades, several rice E3-ubiquitin ligases and their interacting proteins have been linked to drought response in plants. To fully comprehend their interactome and function, however, more research is required.

12.2 E3-Ubiquitin ligases in salinity responses

High salinity, drought, and ABA induce *Oryza sativa* salt-induced RING finger protein 2 (OsSIRP2), which encodes a RING-type E3-ubiquitin ligase that binds specifically to the nucleus of rice protoplasts for both control and high-salinity conditions. OsSIRP2 has been shown to confer tolerance to salinity and osmotic stresses in *Arabidopsis* when overexpressed [221]. OsSIRP2 has been shown to interact with the rice transketolase 1 (OsTKL1) in the cytoplasm, causing it to be targeted for degradation by the UPS. OsTKL1 is a member of the transketolase family, which is involved in the Calvin cycle's oxidative pentose phosphate pathway. It is observed in the chloroplast and is considered necessary for the regeneration of ribulose 1,5-bisphosphate [189, 191]. In tobacco, reduced TKL1 activity causes photosynthesis to be inhibited [165]. The enzymatic activity of transketolase is also compelled for the stress-induced manufacturing of cytosolic NADPH, which is an important component of a plant's defense against ROS-induced damage [214]. It is critical to perform functional characterization of these two proteins in rice to stronger understand the mechanism of OsSIRP2 and the physiological implying of the OsSIRP2–OsTKL1 interaction in salt (and drought) stress responses, which include photosynthesis performance. It's crucial to figure out if and how OsSIRP2's deleterious regulation of OsTKL1 promotes stress tolerance. Finally, because OsSIRP2 did not change specificity under salt stress, the translocation of OsSIRP2 from the nucleus to the cytoplasm to ubiquitinate OsTKL1 raises a question of the underlying mechanism driving this export.

12.3 Response to low temperature

OsPUB2 and OsPUB3 are homologous U-box type E3-ubiquitin ligases that have recently been identified as positive regulators of rice's cold stress response [222]. Minimum temperature, drought, and salt stress upregulate OsPUB2, whereas OsPUB3 expression is unaffected by any of the aforementioned stresses. Overexpression of OsPUB2 or OsPUB3 in rice plants, on the other hand, confers a cold-tolerance phenotype in the result of enhanced survival rates, total chlorophyll, and diminished ion leakage. Furthermore, gene expression analysis reveals that under both control and cold conditions, overexpression of the two OsPUB genes is linked to upregulation of cold stress-inducible genes also including glutamate decarboxylase (GAD), WRKY77, and multidrug resistance protein 4 (MRP4). Furthermore, both were crafted more stable by the cold. Both E3-ligases are found in small cytosolic punctate bodies in *Nicotiana benthamiana* leaf protoplasts' subcellular localization. However, it remains to see whether those two homologous E3-ubiquitin ligases collaborate to confer cold tolerance to rice plants and, if so, which target protein(s) are used to achieve this tolerance. Furthermore, the OsPUB2 mutants should really be studied for phenotypic analysis under a variety of stresses. The RING-type upregulation of osmotically responsive gene 1 (OsHOS1) is another E3-ubiquitin ligase that modulates rice plant response to cold stress [204]. OsHOS1 proteins bind to the nucleus's Inducer of CBF

Expression 1 (OsICE1) and direct it to be broken down by the UPS. Stress-responsive transcription factor dehydration responsive element (DRE)-binding protein 1A (OsDREB1A) transcript thresholds and protein levels of OsICE1, a master integrator of cold stress, are higher in OsHOS1-silenced (RNAi) lines.

13. Conclusion

Plants are tough and have evolved strategies accordingly to a variety of environments over the course of their evolution. As a result, understanding the molecular mechanisms that underlie stress tolerance is essential for improving crop stress tolerance as the impact of abiotic stresses grows as a result of global climate change. Distinctive cutting-edge/modern breeding strategies are aggregated in the holistic breeding approach. Genotypes could help the farmers cope with rising temperatures, increase varietal turnover, and help meet the challenges of abiotic stress-prone ecosystems by increasing productivity and ensuring food security. In addition, rice cultivation areas in slightly elevated abiotic stress-prone areas under which salt stress is extremely crucial for rice production during pre- monsoon season will be decided to expand in various rice-growing countries, including Bangladesh. Furthermore, the stress associated with HNT must be highlighted because this stress could pose a threat to food security in areas where rice is a staple food.

Conflict of interest

No conflict of interest.

Author details


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