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Understanding abscisic acid-mediated stress signaling to affect rice development under stress

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Introduction: Rice is a vital staple food for many countries, and its yield is known to be significantly affected by various abiotic stresses, which are expected to intensify with climate change, posing a threat to global food security. Abscisic acid (ABA), a crucial plant growth regulator, plays a crucial role in plant responses to these abiotic stresses. It influences several processes, such as seed dormancy, leaf gas exchange, reactive oxygen species (ROS) scavenging, ion toxicity reduction, and root elongation, all of which contribute to enhancing plant survival under stress.

Methods: This article reviews recent research on ABA-mediated gene responses and expressions involved in rice plant architecture and its response to abiotic stress.

Results and discussion: Abscisic acid responses were primarily driven by changes in gene expression. Expression analyses of the gene related to ABA biosynthesis or catabolism indicated several changes in plant architecture, such as changes in leaf angle, delayed flowering, and modifications in growth regulators. Additionally, tolerance-related mechanisms, such as increased ROS scavenging, reduced membrane leakage, and vacuolar compartmentation of toxic radicals, were activated under single or multiple stress conditions. While these adaptations may improve plant survival and yield sustainability under stress, they may not necessarily enhance yield potential in environments affected by drought, salinity, or heat stress. ABA expression was also associated with improved pollen viability, grain-filling potential, and seed setting under abiotic stresses such as heat, which could enhance seed yield in such challenging environments.

KEYWORDS

altered gene expression, dormancy, electrolyte leakage, genome editing, ion toxicity, omics, plant architecture, reactive oxygen species

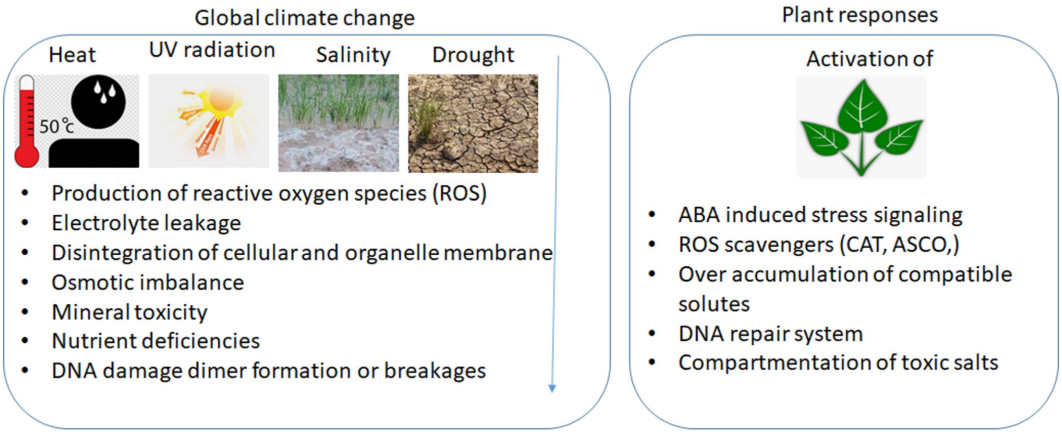

FIGURE 1
Impact of various stresses on plants and cellular responses.

Introduction

Crop species are often exposed to various types of abiotic stresses, such as extreme temperatures, soil salinity, UV light, hypoxia, metal toxicity, and drought. Among these, drought, salinity, and heat are the most widespread globally, affecting large areas (Figure 1). These stresses significantly reduce crop yields by causing harmful effects such as the production of reactive oxygen species (ROS), disruption of electron transport chains, and the disintegration of cellular membranes due to electrolyte leakage (Rauf et al., 2010; Hirayama and Umezawa, 2010).

Physiological responses include the deterioration of leaf gas exchange traits, measured by stomatal conductance, photosynthesis, and transpiration rates. In response to these stresses, plants activate ROS scavengers and produce osmoprotectants such as prolines, trehalose, glycine betaine, and heat shock proteins. These osmoprotectants not only maintain osmotic potential but also help preserve the integrity of cellular structures. Plant defense responses to stress are strongly linked to stress signaling and the activation of various stress-responsive genes. These genes are responsible for transcribing antioxidant enzymes, such as superoxide dismutase (SOD), catalase (CAT), and ascorbate peroxidase (APX), via the mitogen-activated protein kinases (MAPKs) signaling pathway.

Global climate change (CC) poses a significant threat to the production potential of various crops, including rice, in various regions of the world, particularly in South Asia. The rising global temperatures have increased the risk of famine due to food shortages and surging food prices in South Asia. Heat waves and the rapid melting of glaciers, which have led to catastrophic floods, have destroyed standing rice crops. In the 2022 cropping season alone, 10 million people in Pakistan's rice-growing areas were affected by the impacts of climate change. CC has introduced the risk of multiple simultaneous (Sinha et al., 2024), challenging rice production with issues such as UV radiations, weed pressure, supra-optimal temperatures, salinity, high transpiration rates (leading to higher water demands), reduced efficiency of fertilizers due to rapid leaching, and nitrogen loss from volatilization under extreme temperatures of 45–50°C (Hasanuzzaman et al., 2023). Additionally, high temperatures have exacerbated the infestation of insect pests, as well as bacterial and fungal pathogens.

Abscisic acid signal for multi-stress

Abscisic acid (ABA) is a common signal produced in response to various abiotic stresses such as extreme temperature, nutrient deficiency, UV radiation, drought, and salinity (Yoshida et al., 2021; Aslam et al., 2022).

Abscisic acid signals, which are generated at various growth stages of plants, modulate various functions such as seed dormancy, embryo morphogenesis, stomatal closure, and the upregulation of stress-responsive genes (Yoshida et al., 2021; Mizokami et al., 2019). ABA is known to improve stress adaptability and the survival of crop species.

Abscisic acid overexpression is associated with a reduced leaf expansion rate, the overaccumulation of osmolytes such as proline (Pro), and an increase in lateral root length in model species such as maize (Sharp et al., 2004) and *Arabidopsis* (Van Houtte et al., 2013).

An ABA-deficient mutant of *Arabidopsis thaliana* experienced more wilting than the wild-type plant (Ozfidan et al., 2013). The same study revealed that the exogenous application of ABA maintained relative water content but reduced stomatal conductance, while the exogenous application of ABA under non-stressed conditions produced stress-like symptoms (Ozfidan et al., 2013) (Figures 2, 3).

Rice plant architecture and development

Stress significantly affects plant development by modifying the expression of genes involved in normal growth and development.

Stress conditions prioritize root growth, stomata closure, activation of reactive oxygen species scavenger enzymes, overaccumulation of compatible solutes, and the production of stress-related proteins, such as chaperones or dehydrins (Figure 1). Stress responses in rice plants occur at the expense of growth, development, and production.

Genes affecting plant growth have been identified through targeted mutations induced by various molecular methods, such as RNAi or clustered regularly interspaced palindromic region (CRISPR).

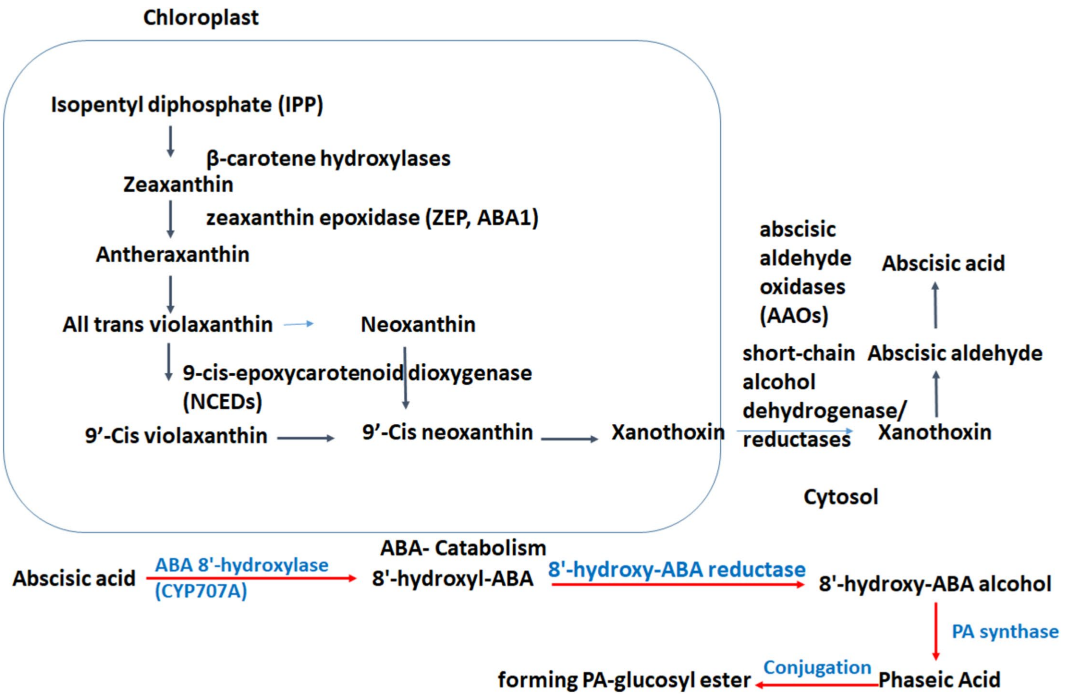

FIGURE 2
Abscisic acid biosynthesis pathways in crop species.

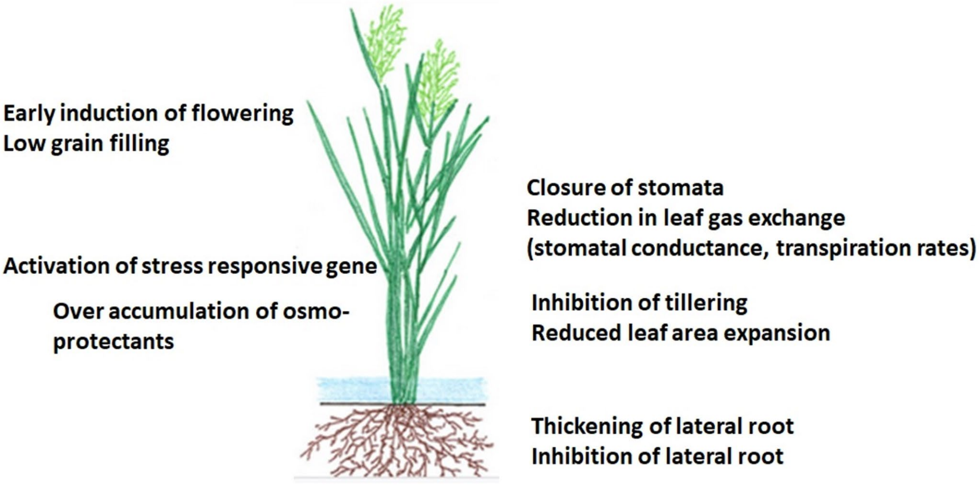

FIGURE 3
ABA-mediated plant signaling and responses.

The Pyrabactin resistance-like (PYL) abscisic acid receptor family has been characterized and is known to induce ABA signaling in response to abiotic stress in *Arabidopsis* and other plant species, including rice (Tian et al., 2015).

Ten orthologs of *PYL* have been isolated in rice, and overexpression of the rice *PYL* orthologs (*Os PYL3* and *Os PYL9*) positively regulated ABA expression and enhanced cold and drought tolerance in rice (Tian et al., 2015).

CRISPR/Cas9-generated mutant lines demonstrated that *PYL* orthologs control stomatal movement, seed dormancy, and growth regulation (Miao et al., 2018). A mutant line for *pyl1/4/6* exhibited increased growth and productivity in rice paddy fields while maintaining seed dormancy (Miao et al., 2018).

The antagonistic relationship between the plant growth regulators

Abscisic acid biosynthesis antagonizes cytokinin- and auxin-related factors, which may affect normal plant architecture and

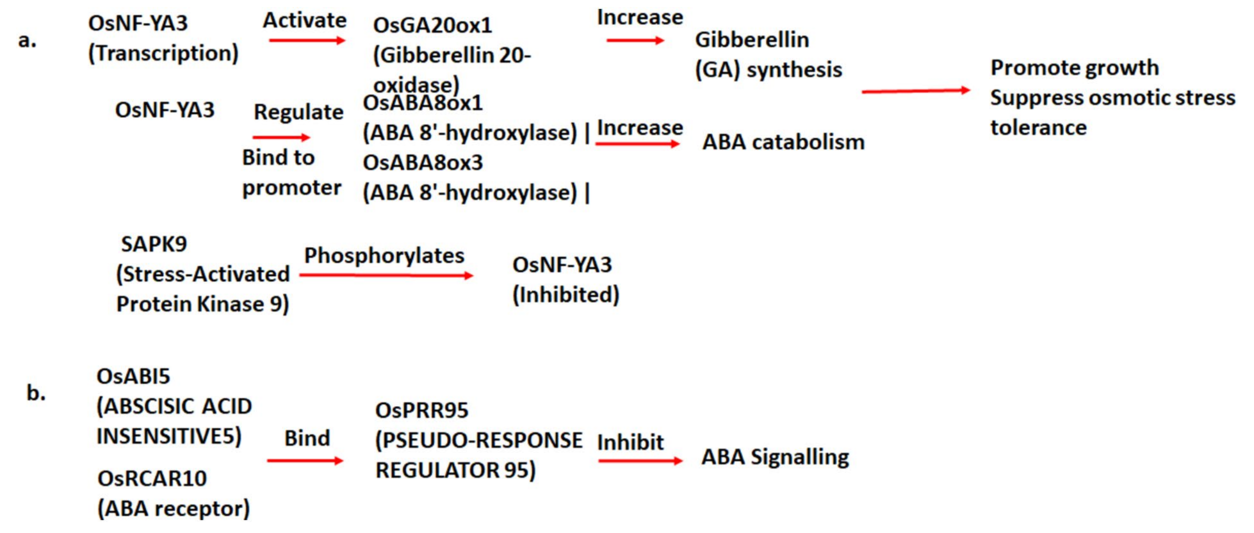

FIGURE 4
Conceptual illustration of inactivation of ABA signal pathways led to the increase of plant growth regulators and loss of osmotic stress tolerance.

development. *OsNF-YA3* is a negative regulator of ABA signaling by regulating the expression of ABA catabolic genes (i.e., *OsABA8ox1* and *OsABA8ox3*) by binding to their promoters (Jin et al., 2023). It positively upregulates gibberellic acid biosynthesis by activating the GA biosynthesis gene (*OsGA20ox1*). Thus, it balances the biosynthesis of GA, the promotion of growth, and the negative regulation of ABA biosynthesis under non-stress conditions (Jin et al., 2023). *SAPK9*m, which is a positive regulator of ABA biosynthesis, is activated under osmotic stress and phosphorylates *OsNF-YA3*, thereby causing its degradation under stress conditions (Jin et al., 2023) (Figure 4).

OsPRR95 (*PSEUDO-RESPONSE REGULATOR 95*) is an inhibitor of ABA signaling and is associated with seed germination, seedling growth, and breaking seed dormancy. It binds to the ABA receptor gene (*OsRCAR10*) DNA to inhibit its expression (Wang et al., 2023). *OsRCAR10* acts downstream of *OsPRR95* in mediating ABA responses. *OsPRR95* expression required a functional OsRCAR10 and the ABA-responsive element-binding factor ABSCISIC ACID INSENSITIVE5 (OsABI5), which bound directly to the promoter of *OsPRR95* (Wang et al., 2023). *OsGA20ox2* requires ABA-responsive proteins ASR5 and ABA receptor PLY5 for the upregulation, and it increases the plant height and gibberellic acid contents under non-stress conditions (Nawaz et al., 2020).

NAC054 activates *OsABI5* and *NYC1* by binding to the mitochondrial dysfunction motifs in their promoters. The activity of *OsNAC054* is regulated by proteolytic processing of the C-terminal transmembrane domain (TMD).

The onaco54 mutant showed downregulation of *ABA INSENSITIVE5* (*OsABI5*) and senescence-associated genes, including *STAY-GREEN* and *NON-YELLOW COLORING1* (*NYC1*). Lines overexpressing *OsNAC054* exhibited early leaf yellowing under dark- and ABA-induced senescence conditions (Sakuraba et al., 2020). Additionally, the *OsGA20ox2* gene was mutated using a guided gRNA sequence. The CRISPR-Cas9-mediated mutagenic line showed the upregulation of abscisic stress-ripening protein 5 (ASR5) and abscisic acid receptor (PYL5). This suppression leads to an increase in gibberellins (GA_1 and GA_4) levels, plant height (28.72%), and flag leaf length. However, other morphological traits remained unchanged (Nawaz et al., 2020).

Leaf senescence

Several genes related to leaf senescence or staying green in rice have been induced by ABA signals and are identified through expression analyses or the development of mutants through CRISPR/Cas9 (Table 1). *OsNAP* is a marker of leaf senescence in rice and is induced by the ABA. It affects chlorophyll degradation and nutrient transport in rice (Liang et al., 2014). The mechanism of leaf senescence has been investigated in the *psf* rice mutant.

Sugar starvation is known to increase ABA concentration and induce premature leaf senescence in rice leaves (Asad et al., 2021).

Knocking down the *OsNAP* gene in the PS1-D mutant reduced leaf senescence and extended the grain-filling period, resulting in a rice yield increase of 6.3 and 10.3% in two independent RNAi-induced mutant lines (Liang et al., 2014).

The *OSMADs-18* gene is known to control plant architecture, unlike its paralogs, *OSMADs-14* and *OSMADs-15*, which induce flowering in rice. Expression of *OSMAS-18* was stimulated by abscisic acid, which helps its translocation from the plasma membrane to the nucleus.

A mutant line induced by CRISPR/Cas9 in the *OsMADS18* gene increased the yield component of rice, such as the number of tillers plant^{-1} and altered panicle size but reduced seed setting, while overexpression lines produced fewer tillers (Yin et al., 2019). Overexpression lines (*nd1*) for cell wall cellulose synthase-like D4 protein (OsCSLD4) had increased grain weight and width in rice (Zhou H. et al., 2022; Zhou Z. et al., 2022). The gene *OsPP2C09* was rapidly induced by exogenous ABA treatments and positively affects rice growth but is a negative regulator of drought tolerance.

Exogenous application of ABA suppressed excessive ABA signaling. The *OsPP2C09* gene may act as a negative regulator of ABA, helping recover from the growth arrest induced by ABA.

OsPP2C09 transcript levels were much higher in the roots than in shoots and rapidly increased with stress treatment (Tian et al.,

TABLE 1 Gene related to plant architecture affected by ABA signaling.

Gene	Plant material	Function	References
OsMADS18 osmads18-cas9	Downregulation of Osmads18 RNAi lines, Overexpression lines	Downregulation caused a number of tillers, altered panicle size, and reduced seed setting	Yin et al. (2019)
Os*ERA1*	Rice *osera1* mutant lines	Increased primary root growth and stomatal regulation	Ogata et al. (2020)
OsCSLD4	*nd1*	The mutant line had lower grain size and weight, while overexpression lines increased grain size and weight	Zhou H. et al. (2022) and Zhou Z. et al. (2022)
IPA1 (*IDEAL PLANT ARCHITECTURE 1*)/*OsSPL14*	*IPA1* and *ipa1*-NILs (near isogenic lines)	A near-isogenic line carrying the ipa1 allele had longer root length with lower stomatal size and density. Upregulation of *OsHOX12* and *OsNAC52* in the *ipa1* plants	Zhu A. et al. (2022) and Zhu M. et al. (2022)
OsPP2C09		Regulate above-ground growth and maintain root-to-shoot ratio, while mutant lines had improved drought tolerance	Miao et al. (2020)
OsMYB102	Transgenic lines (*35S:OsMYB102* and *35S:GFP-OsMYB102*)	Overexpressing lines had reduced leaf senescence as compared to the wild type.	Piao et al. (2019)
OsPMEI12	Ospmei12 mutant lines (LOC_Os03G01020)	Mutants were dwarfed by poor seed setting and lower fresh and dry biomass. Higher pectin contents are present at the seedling and maturity stages.	Li Q. et al. (2022) and Li Z. et al. (2022)
OsGA20ox2	OsGA20ox2	Increased gibberellin (GA_1 and GA_4) levels, plant height (28.72%), and flag leaf length, while all the other traits remained unchanged	Nawaz et al. (2020)
ONAC054	*onac054* knockout mutants	Mutant *onac054* maintained green leaves for a longer period, while *ONAC054*-overexpressing lines had early leaf senescence in the presence of dark- and ABA	Sakuraba et al. (2020)
OsWRKY53	Overexpressing (*OsWRKY53*-oe) plants knockout mutants	Overexpression led to higher leaf senescence, while the mutant line had a contrasting phenotype. Its expression is linked to high ABA biosynthesis	Xie et al. (2022)
Seed dormancy *Oswrky29*	*Oswrky29* mutant	RNAi lines of *OsWRKY29* had higher seed dormancy, while wild types had shorter seed dormancy.	Zhou et al. (2020)
Internodal distance	Overexpressing OsPP2C08 (OsPP2C08-OX)	OsPP2C08 regulates GA biosynthesis. Gibberellin 20-oxidase (OsGA20ox4) and Ent-kaurenoic acid oxidase (OsKAO) were increased in OsPP2C08-OX lines	Song et al. (2023)
Flowering	*abf1* and *sapk8* mutants	The mutant had early flowering while overexpressing lines (*SAPK8* and *ABF1*) had ABA-mediated delayed flowering	Tang et al. (2024)
Leaf angle	Biosynthesis gene *D11* and signaling genes *GSK2* and *DLT*	ABA antagonizes the effect of BR on lamina joint inclination by targeting the BR biosynthesis gene D11 and BR signaling genes GSK2 and DLT	Li et al. (2019)
Seed storability	*OsGH3-2* Overexpression and knock-down lines	Overexpression lines of *OsGH3-2* had lower seed storability activity, while mutant lines had higher seed storability by modulating many genes related to the ABA pathway	Yuan et al. (2021)
ghd7	*Mutant*	*Ghd7* affects the ABA/GA_3 ratio and may inhibit seed germination.	Hu et al. (2021)

2015). This differential expression may control the root-to-shoot ratio.

A CRISPR/Cas9-edited line carrying mutants in *gn1a*, *dep1*, and *gs3* had larger grain size, erect panicles, and a higher number of grains panicle^{-1} (Khan et al., 2020). Another line carrying CRISPR/Cas9-mediated mutants in *dep1* and *gs3* produced a phenotype with long awns, large grains, and semi-dwarf plant architecture (Khan et al., 2020).

Overexpressing *OsWRKY53*-oe lines showed higher leaf senescence, while *OsWRKY53* knockout mutants (*oswrky53*) remained green longer compared to the normal wild type.

OsWRKY53 is a regulatory gene that binds directly to the promoters of *OsABA8ox1* and *OsABA8ox2*, inhibiting their expression and increasing endogenous ABA levels (Figures 5, 6). The genes *OsABA8ox1* and *OsABA8ox2*, which are involved in ABA catabolism, had their ABA 8′-hydroxylase activity reduced by the *OsWRKY53*-oe (Xie et al., 2022).

Moreover, *Oswrky29* controls seed dormancy in rice. RNAi lines of *OsWRKY29* enhanced the seed dormancy, whereas its overexpression lines showed contrasting phenotypes, i.e., lower seed dormancy. *OsWRKY29* could bind to the promoters of *OsABF1* and *OsVP1* to inhibit their expression (Zhou et al., 2020). *OsABA8ox* encodes abscisic acid hydroxylase and is considered a drought stress-responsive gene. Its expression was decreased in roots due to stress treatment. CRISPR/Cas9 was used to develop a mutant for the osaba8ox. The analyses showed that the mutant had higher ABA contents and large vertical root lengths, while overexpression lines had smaller roots (Zhang et al., 2020).

Overexpression transgenic lines (*35S: OsMYB102* and *35S: GFP-OsMYB102*) had longer growth cycles, maintaining green

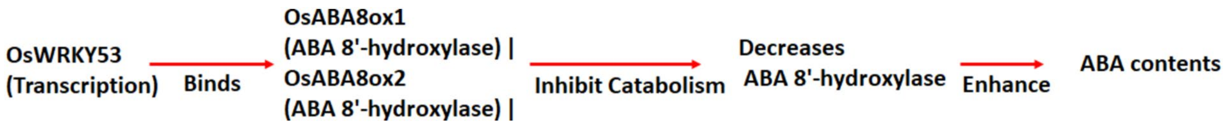

FIGURE 5
Activation of ABA pathway signals by inactivation of ABA catabolism genes to enhance ABA contents.

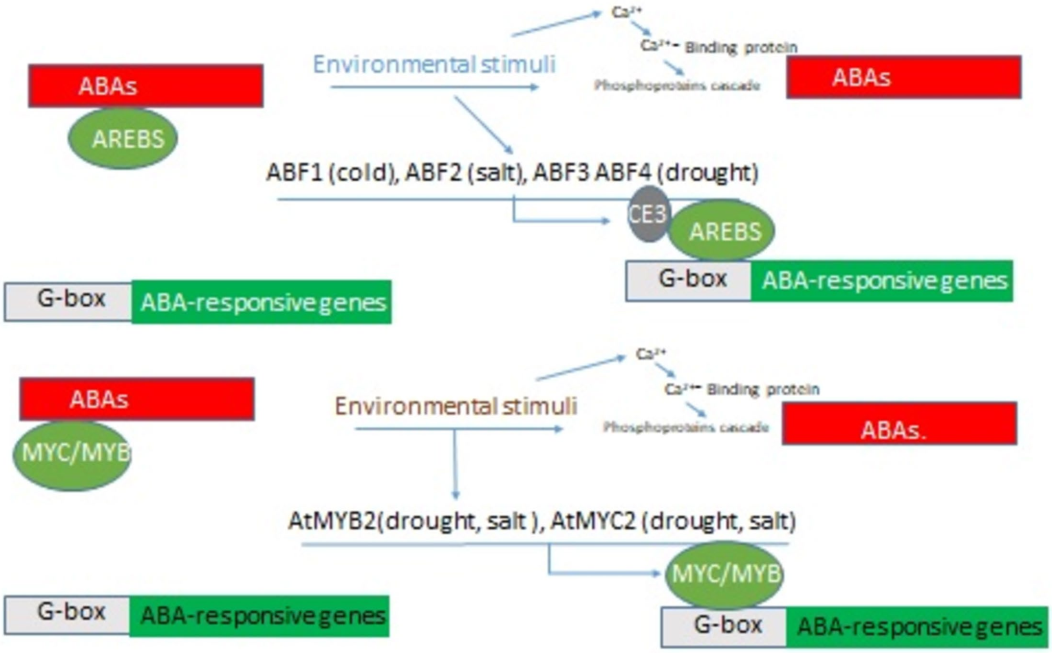

FIGURE 6
Activation of the ABA-responsive gene under various abiotic stress.

leaves longer compared to the wild type. A knockout mutant of *osmyb102*, when treated with ABA, showed senescence at a higher rate in the dark. Near isogenic lines, i.e., *IPA1* (Ideal Plant Architecture 1), controlled the tiller number, and *ipa1* was phenotypically characterized. The iso line *ipa1* had longer root elongation and a smaller leaf aperture, allowing them to show better survival with reduced leaf senescence under water stress conditions (Zhu A. et al., 2022). *IPA1* and *OsSPL14* encode a transcription factor that takes part in plant architecture and abiotic stress response by activating the ABA signaling pathway. An *ipa-1* isogeneic line significantly improves the abiotic stress at the seedling stage. *Ipa1* plants have better root systems and smaller leaf stomatal apertures. Under stress conditions with PEG 8000, *ipa1* shows high ABA content upregulation in mutant type as compared to wild APA1, and by promoter edition and yeast two-hybrid protein interaction and dual luciferase assay find some promoter *OsHOX12* and *OsNAC52* and its activity support the ABA signaling pathway (Zhu A. et al., 2022). Table 1 lists some examples of various genes affected by ABA signaling.

UGT74E2 is involved in the transfer of glucose to the indole butyric acid and controls plant architecture and stress tolerance in *Arabidopsis thaliana*. Overexpression of *UGT74E2* in rice resulted in improved seed germination under multiple treatments and stress conditions (Wang B. et al., 2020; Wang C. et al., 2020; Wang H. et al., 2020; Wang T. et al., 2020). ABA biosynthesis genes, i.e., *OsABI3* and *OsABI5*, were, however, downregulated in overexpression lines (Wang B. et al., 2020; Wang C. et al., 2020; Wang H. et al., 2020; Wang T. et al., 2020).

ABA-regulated rice flowering

The rice SnRK2 comprises 10 members from *SAPK1-10* (Sn-RK2, protein kinase). These proteins are crucial for the ABA pathways inducing drought and salt tolerance (Liu et al., 2024). Simultaneous knockout of *ABF1* and *SAPK8* accelerated the flowering, while the overexpression line delayed the flowering. The ABA signal (SAPK8 stress-activated protein kinase) phosphorylates ABF1, which helps the binding of the promoters related to the flowering regulators (*Ehd1* and *Ehd2*) (Tang et al., 2024). Epigenetic suppression of ABF1 by PRC2 (polycomb repressive complex 2) of flowering regulators (*Ehd1* and *Ehd2*) by trimethylation of histone (H3K27me3 suppressive histone modification) leads to the delayed flowering in rice (Tang et al., 2024). SAPKs are an important component of the ABA signal pathways. *SAPK1-3* may not have any role in the regulatory pathway of rice heading date, while *SAPK4*, *SAPK5*, and *SAPK5* were positive regulators of flowering (Liu et al., 2024). The double mutant of sapk9/sapk10 had delayed flowering. Overexpression of *SAPK10* resulted in the early flowering of rice. The *SAPK10* phosphorylated the *bZIP77*. It was known that *SAPK10* partially regulates the flowering through FAC-MADS15 pathways (Liu X. et al., 2019; Liu X. L. et al., 2019). *SAPK2* helps to transport nitrate and assimilation by regulating the specific promoters, and mutant sapk2 had stunted growth and fewer grains (Lou et al., 2020).

ABA signaling and related genes under drought conditions

When exposed to the water stress condition, several phenotypic changes were noted in the plants. These include the closure of stomata, activation of accumulation of leaf cuticular waxes and compatible solutes, and primary root elongation, among others. Most of these responses are ABA-induced to avoid water loss from the plant organs and increase the chances of plant survival under stress conditions. The general mechanism of any stress tolerance includes the following steps: (i) activation of transcriptional factors under stress conditions; (ii) binding with the ABA signal pathway to direct synthesis of ABA, and (iii) upregulation of ABA-dependent genes. CRISPR/Ca9-directed mutant lines have been developed to study the plant's response under stress and regulation of stress-responsive genes. Gene expression of *SAPK2* was upregulated by stress factors such as drought, salinity, or osmotic (polyethylene glycol). However, a mutant line for *sapk2* showed ABA insensitivity during seed germination and ABA-mediated seed dormancy (Lou et al., 2017).

Moreover, mutant *sapk2* was more sensitive to drought tolerance and ROS, thus showing the role of *SAPK2* in the enhancement of drought tolerance (Lou et al., 2017).

The gene has been shown to assist plant survival by reducing water loss through stomatal closure, activating ROS scavengers, and upregulating the expression of genes such as *OsRab16b*, *OsRab21*, *OsbZIP23*, *OsLEA3*, and *OsOREB1* (Lou et al., 2017). The gene *SAPK9* has a role in osmolyte (sugar and proline) accumulation, which helps to maintain osmotic potential under water stress conditions and retain water content by stomatal closure and reduction in the electrolyte leakage and ion detoxification (Dey et al., 2016a,b).

The gene *SAPK9* was originally cloned from *Oryza rufipogon*, and overexpression lines were developed in *Oryza sativa* (rice crop), which showed higher drought tolerance than wild-type and RNAi lines (Dey et al., 2016a). *SAPK9* physically interacted with the *OsMADS23* for transcriptional activation that upregulated the ABA and proline biosynthesis genes such as *OsNCED2*, *OsNCED3*, *OsNCED4*, and *OsP5CR* (Li et al., 2021). The expression of gene *OsbZIP23* was induced during the reproductive stage and improved the yield component by overaccumulating the osmotica such as sugar proline and decreasing the lipid oxidation when the gene was cloned in the drought-susceptible lines IR20 (Dey et al., 2016b). Overexpression transgenic lines in rice have also been developed to confirm stress tolerance in the rice. Overexpression of the *OsPYL6* gene reduced plant transpiration by 25% compared to the control plant (Santosh Kumar et al., 2021). To cope with water stress and to avoid stress, plants produce several metabolites, i.e., sugars, free amino, heat shock proteins, and acids, to cope with the changing osmotic potential of the cell. These metabolites are collectively called osmolytes, which protect the cellular membrane and organelles at the cost of energy. Metabolites may, however, be utilized during stress recovery of the plant.

BA1 (*ERA1*) plays a role in plants during osmotic stress. It encodes a β-subunit of farnesyltransferase, which regulates the ABA signaling and dehydration response; therefore, ABA1 (ERA1) is an important candidate gene to enhance drought tolerance in numerous crops. Frameshift mutant cas9 line shows a similar phenotype of leaf shape while positively increasing the root growth, which helps the plant to uptake water from deep soil profile and enhance the drought tolerance capacity (Ogata et al., 2020). It also enhances both the ABA sensitivity and drought response through stomatal regulation. As a result, during no-stress conditions, the role is opposite for primary root growth. However, the study of the *ABA1* gene benchmark assists in understanding the role of ABA in osmotic stress, and such knowledge may improve rice drought tolerance for caryopsis yield.

OsPYL/RCAR7 was a novel ABA receptor linked with drought tolerance. It has weak ABA signal activity but a strong dependency on ABA. This receptor-induced drought tolerance with a minimum penalty for yield (Bhatnagar et al., 2020). Overexpression of the ABA receptor (i.e., OsPYL/RCAR3) induced better growth under osmotic stress. Clade A Type 2C protein phosphatases are a negative regulator of ABA signals but activate the ABA-independent pathway via cis-acting drought-responsive elements. Overexpression of the OsPYL/RCAR3 interacting protein, i.e., OsPP2C09, resulted in plant sensitivity to the stress (Min et al., 2021).

SiMYB56 was related to ABA biosynthesis and upregulates drought tolerance genes. Overexpression lines *SiMYB56* had lower monoaldehyde contents and high lignin contents, which may be related to the transpiration reduction without affecting the plant's normal morphology (Xu et al., 2020).

Leaf morphology (such as leaf cuticular waxes and leaf rolling) is also important to avoid dehydration.

Homozygous mutants were developed using CRISPR-mediated targeted gene knockdown of *SRL1* and *SRL2* in rice (Liao et al., 2019).

The mutants exhibited lower chlorophyll content, impaired leaf gas exchange characteristics, and a reduced number of panicles (Liao et al., 2019). However, under drought conditions, the mutants showed lower monoaldehyde contents and a higher panicle-filling percentage compared to wild-type plants. The mutants also demonstrated greater defense against ROS by activating ROS scavenging enzymes, such as superoxide dismutase (SOD), and catalase (CAT), and showed higher ABA content (Liao et al., 2019). Proteomic analysis of the semi-rolled lead mutant showed that LBD proteins were downregulated, while stress-responsive proteins were upregulated under drought conditions (Liao et al., 2019).

Drought drastically changes the expression of genes. It activates genes related to adaptability under water stress (Table 2). Functional genomics and the development of mutant or

TABLE 2 ABA signaling pathways for genes related to drought tolerance in rice identified in overexpression six or knockdown lines.

Gene	Functions	Plant material	References
OsHSFA3	Reduced water loss and reactive oxygen species (ROS) levels. Increased *AtADC1*, *AtADC2*, *SPDS1*, and *SPMS* expression levels.	Overexpression	Zhu et al. (2020)
OsPYL6 along with the *AtRD29A* promoter.	Lower plant transpiration (25% less transpiration) is related to the dehydration avoidance mechanism. It upregulates different 9-*cis* epoxy carotenoid dioxygenase (*NCED*)	Overexpression lines	Santosh Kumar et al. (2021)
Semi-rolled *leaf1,2* (*SRL1* and *SRL2*) genes	Mutants had lower chlorophyll content, transpiration rate, stomatal conductance, vascular bundles (VB), stomatal number, and agronomic traits with increased panicle number and bulliform cells (BCs)	Knock down lines	Liao et al. (2019)
Os3BGlu6	Higher β-glucosidase activity. ABA concentration and expression of drought-responsive genes.	Overexpression lines	Wang B. et al. (2020), Wang C. et al. (2020), Wang H. et al. (2020), and Wang T. et al. (2020)
OsASLRK	Mutant had less sensitivity to the exogenous abscisic acid	*Osaslrk* mutant	Du et al. (2022)
OsSLAC1 and *SAPK10*	*OsPP2C50* and *OsPP2C53* among 9 *OsPP2CAs* related to stomatal closure/opening signaling based on guard cell. *OsPP2C50* and *OsPP2C53* showed significantly higher water loss than the control	Overexpression of both genes	Min et al. (2019)
AAO3	The mutant had increased seedling traits such as germination and seedling growth with lower drought tolerance. Mutant also had higher grain yield due to higher panicle number per plant, spikelet number per panicle, and spikelet fertility	*osao3* mutant. *OsAO3*-overexpressing lines	Shi et al. (2021)
OsPIL15	Increase drought tolerance by reducing stomatal size. *OsPIL15* interacts with the NIGT1/HRS1/HHO family transcription factor rice HRS1 HOMOLOG 3 (OsHHO3)	Overexpression lines	Li Q. et al. (2022) and Li Z. et al. (2022)
BAH1	Stress recovery. It upregulates genes such as *NCED2, NCED3, NCED4,* and *AAO2.*	'BRS-Querência' (lowlands) and 'AN-Cambará' (uplands)	Auler et al. (2021)

overexpression lines resulted in understanding the genes related to water stress tolerance in rice. Genes related to osmotic adjustment and reactive oxygen species (ROS), e.g., *OsHSFA3*, are known to be activated by ABA signals (Zhu et al., 2020). *OsPYL6* upregulated the *epoxy carotenoid* (*NCED*) gene to direct ABA biosynthesis. Disruption of the *Os3BGlu6* gene caused dwarfism and decreased the ABA contents of the cell, lowered the photosynthesis rate, and increased the overall sensitivity to drought (Wang B. et al., 2020; Wang C. et al., 2020; Wang H. et al., 2020; Wang T. et al., 2020). Contrastingly, overexpression lines had higher drought tolerance and maintained higher ABA contents. Overexpression lines also had higher activity of the β-glucosidase enzyme (Wang B. et al., 2020; Wang C. et al., 2020; Wang H. et al., 2020; Wang T. et al., 2020). Similarly, disruption of the *OsASLRK* gene resulted in drought sensitivity and lower ABA contents in the cell (Du et al., 2022). Mutants for gene *Osao3*- had lower drought tolerance with high yield potential due to increased number of panicles, spikelet number, and spikelet fertility.

OsFBX257 is co-expressed in a network of the protein kinases and phosphatases. Its knockdown *oxfbx257* has reduced root growth and depth, panicle size, and survivability under stress (Sharma et al., 2023). Overexpression lines for *OsFBX257*, on the other hand, had deeper root, grain yield, and panicle size (Sharma et al., 2023).

Salt tolerance

Dehydration or osmotic stress and mineral toxicity due to the accumulation of salts in response to brackish water irrigation induce several plant responses, such as vacuolar compartmentation, activation of reactive oxygen species, and osmotic adjustment. Many of the plant defense responses against salt stress are induced by the ABA signaling. The gene *OsMFT1* was involved in the ABA and GA metabolism in rice under salinity stress and also modulates seed germination (Lu et al., 2023). Suppression of catabolic ABA gene *OsABA8ox1*-kd maintained a higher level of ABA, and plants exhibited reduced plasma lemma injury, ROS accumulation, NA$^+$/K$^+$ ratio, and less mortality under mineral stress induced by the various levels of Na2CO3 (Liu et al., 2022a,Liu et al., 2022b).

The structural and functional diversity of OsNHX1-OSNHX5 was investigated in rice, as these genes are involved in Na$^+$/K$^+$ antiporters for the vacuolar compartmentation of ions (Fukuda et al., 2011). The activity of the genes *OSNHX1* was localized in the specialized tissues such as guard cells and trichomes of rice leaf, whereas *OSNHX1* activity was observed in the pollen grains and root tip (Fukuda et al., 2011).

Downregulation of the *miR528* (1-ascorbate oxidase) resulted in the increase of ascorbic acid and ABA contents of the cell, which caused a significant decrease in reactive oxygen species

(ROS), inducing salt tolerance in rice (Wang G. et al., 2021; Wang M. et al., 2021; Wang T. et al., 2021). The regulatory gene *OsJRL40* was known to have higher activity in roots and internodes under salt stress (Gao et al., 2023). It controlled the expression of genes related to the Na^+/K^+ transporter and antioxidant activity of the cell (Gao et al., 2023). Overexpression of OsMADS25 activated the genes *OsGST4* (glutathione *S*–transferase) and *OsP5CR* involved in the biosynthesis of proline by directly binding to the promoter of the respective gene (Xu et al., 2011). It increased the plant sensitivity for the ABA application and promoted the expression of the ABA-dependent gene. The expression of *OsMADS25* also resulted in the scavenging of ROS (Xu et al., 2011). Many other genes (e.g., *SalT*, *OsNAC9*, *OsAKT1*, and *OsHKT*) were involved in the transcription of reactive oxygen scavengers, i.e., superoxide dismutase, catalase, and peroxidase that reduced the damage due to alkalinity (Liu X. et al., 2019; Liu X. L. et al., 2019).

OsNAC genes play an important role in rice development under salt stress, with *OsNAC3* specifically associated with ABA stress signaling and salt tolerance. Knocking out of *OSNAC3* decreased the sensitivity for ABA and increased sensitivity for the salt stress. Knock outline for *osnac3* showed a higher accumulation of Na^+ in the shoot (Zhang A. et al., 2021; Zhang X. et al., 2021). Knock outline also showed downregulation of the *OsHKT1;4, OsHKT1;5, OsLEA3–1, OsPM-1, OsPP2C68,* and *OsRAB-21*, which were related to the ABA pathway and salt tolerance (Zhang A. et al., 2021; Zhang X. et al., 2021). Overexpression lines of *OsERF19* induce salt tolerance and hypersensitivity for the ABA. It was found that the transcriptional factor of *OsERF19* binds with the promoters of *OsOTS1* and *OsNCED5* to induce the synthesis of ABA. *OsERF19* also upregulates the genes *OsLEA3, OsNHX1*, *OsHKT6*, and *OsOTS1* under salinity stress, while genes such as *OsRAB21*, *OsNCED5*, and *OsP5CS1* were upregulated under ABA treatment (Huang et al., 2021). *OsSAPK7* modulates ion homeostasis, redox reaction, and photosynthesis. It increased seedling survival, chlorophyll and proline contents, catalase, and superoxide dismutase activity. The knockout line of *ossapk7* had a lower survival rate, higher Na^+/K^+ uptake, and ion toxicity under salt stress, which showed their role in salinity tolerance (Dan et al., 2021).

In conclusion, it was noticed that suppression of the ABA catabolic gene (i.e., *OsABA8ox1*-kd) increased the ABA contents, which also improved salt tolerance. Gene *OsNHX1-5* may be considered for further research and use in breeding due to their role in the vacuolar compartmentation. The gene *OSNAC3* was related to ABA contents and stress signaling under salinity. Gene *OsSAPK7* and other series kinase proteins within the same group are also of particular interest due to their positive role in stress signaling and other responses under stress (Table 3).

Multi-stress

The ABA is a common stress signal under various abiotic stress conditions. The common stress-responsive genes were identified when cells were exposed to multiple stress factors. Transcriptional factor *OsbZIP72* bonds to the promoter of the *OsHKT1* for the activation of ABA biosynthesis. Overexpression of *OsbZIP72* induced tolerance against water and salinity stress (Baoxiang et al., 2021). *OsbZIP72* binds to the promoters of genes like *OsSWEET13 and OsSWEET15* to activate sugar transport under multiple stressors (Mathan et al., 2021). *OsbZIP86* encodes a transcriptional factor that binds to the ABA biosynthesis gene (e.g., OsNCED3 to mitigate drought tolerance). *OsbZIP86* itself was regulated through *miR2105*, which directs its cleavage (Gao et al., 2023).

Moreover, *OsSAPK10* activates the expression of *OsbZIP86* to increase the expression of *OsNCED3*. Overexpression lines of *OsbZIP86* caused the enhancement of drought tolerance by reducing the water losses from stomata and controlling the transpiration loss (Gao et al., 2023). Similarly, *OsNAC006* induces regulatory transcriptional factors for the activation of abiotic-resistant genes under various treatments, i.e., H_2O_2, cold, heat, abscisic acid (ABA), indole-3-acetic acid (IAA), gibberellin (GA), NaCl, and polyethylene glycol (PEG) 6,000 (Wang B. et al., 2020; Wang C. et al., 2020; Wang H. et al., 2020; Wang T. et al., 2020). *OsMSR2* induced drought and salinity tolerance by modulating the ABA acid pathway (Xu et al., 2011). Overexpression of the *OsSMP1* (stress membrane protein) induced tolerance against drought, cold, and salinity heavy metals and was dependent on the ABA pathways (Zheng et al., 2021). Overexpression of *OsMLP423* increased the sensitivity to the ABA and water use efficiency and reduced the membrane damage and reactive oxygen species under salinity and drought stress (Zhou H. et al., 2022; Zhou Z. et al., 2022). Auxin/IAA genes were induced in response to the drought and other abiotic stresses. RNAi lines for *OsIAA20* showed reduced tolerance to drought and salt tolerance (Zhang A. et al., 2021; Zhang X. et al., 2021). This stress-sensitive line had lower proline content and gradually lost chlorophyll content.

Moreover, the susceptible mutant line for *osiaa20* had a higher monoaldehyde value and Na^+/K^+ ratio. The overexpression line had increased stomatal closure and decreased transpiration loss, helping rice plants to survive under salt and drought stress (Zhang A. et al., 2021; Zhang X. et al., 2021). RNAi line also had downregulated *OsRab21*, which was an ABA-responsive gene. The overall result showed that *OsIAA20* induced salt and drought tolerance via ABA stress signals (Zhang A. et al., 2021; Zhang X. et al., 2021). The overexpression line for the *glycosyltransferase* gene *UGT3* enhanced the salt and drought tolerance in rice. There was high expression of antioxidant enzymes and very low production of reactive oxygen species within the overexpression line of UGT3 (Wang G. et al., 2021; Wang M. et al., 2021; Wang T. et al., 2021).

HDA710 expression levels accumulate in response to multiple stressors and phytohormones, i.e., the jasmonic and abscisic acids. Knock-down line *oshda710* showed enhanced salt tolerance and reduced ABA sensitivity (Sharma et al., 2023). Mutant *hda710* also upregulated the ABA and salt-tolerant genes such as *OsLEA3*, *OsABI5*, *OsbZIP72*, and *OsNHX1* (Sharma et al., 2023). Expression of these genes was epigenetically controlled by acetylation of H4 histones.

OsABAR1 confers drought and salt tolerance in ABA-dependent pathways and is a novel GRAM-encoding gene. Gene expression was highest in roots under drought and salt stress and upregulated by ABA (Zheng et al., 2020). Overexpression

TABLE 3 ABA stress signaling in rice for plant responses and tolerance mechanism under mineral stress.

Gene	Function	Plant material	Reference
OsABA8ox1-kd	Suppression of *OsABA8ox1*-kd seedlings accumulated 25.9–55.7% higher levels of endogenous ABA. They had lower cell membrane injury, reactive oxygen species accumulation, and Na^+/K^+ with high survival under stress (10, 15, and 20 mmol L^{-1} of Na_2CO_3).	*OsABA8ox1*-kd lines in two different *japonica* cultivars, Dongdao 4 and Nipponbare.	Liu et al. (2022a,b)
miR528	Downregulating l-ascorbate oxidase (AO) miR528 induced a high concentration of ascorbic acid (AsA) and ABA contents. Reduction in ROS accumulation	Downregulation of miR528	Wang G. et al. (2021), Wang M. et al. (2021), and Wang T. et al. (2021)
SalT and *OsWsi18*, *OsJRL*, *OsPEX11*, *OsNAC9*, *OsAKT1* and *OsHKT1*	There was a higher activity of antioxidant enzymes, including superoxide dismutase, catalase, peroxidase, and ascorbate peroxidase, which contributed to a lower accumulation of reactive oxygen species (ROS), specifically $O_2·-$ and H_2O_2. As a result, seedling injury and mortality were reduced.	Expression analysis	Liu X. et al. (2019) and Liu X. L. et al. (2019)
OsRLCK241-	*OsRLCK241* overexpression decreased ABA sensitivity and ABA content under salt stress	Overexpressing rice lines	Wang K. et al. (2022)
osmft1	ABA and GA metabolism and their signaling pathways are regulated by *OsMFT1*, modulating seed germination in rice under salt stress	Overexpressing rice lines	Lu et al. (2023)
OsWRKY28	*Mutant lines carrying oswrky28* had higher susceptibility to salt stress when compared with the wilt type. Wild type binds to the promoter of *OsDREB1B* to improve plant performance under stress conditions.	Mutant and overexpression lines	Zhang et al. (2023)
OsVDE	Mutant lines showed a lower plant height, a small panicle, and less seed setting under stress conditions. Overexpression lines had higher ABA levels, stomatal closure percentage, and survival rate than wild-type ones. *OsVDE* negatively regulates the *OsNECD2/4/5* expressions	Overexpressing and CRISPR-Cas9-mediated gene editing	Wang X. et al. (2022)
OsJRL40	High expression in root enhances antioxidant enzyme activities and regulates Na^+-K^+ homeostasis under salt stress	Mutant and high expression lines	Gao et al. (2023)
OsERF106MZ	Overexpression led to the accumulation of monoaldehyde, ROS, and accumulation of Na^+ and K^+, while catalase activity was reduced. The gene was a negative regulator of salt tolerance.	Overexpression	Chen et al. (2021)
OsZFP213 and *OsMADS25*	Enhanced primary root length and lateral root density with low accumulation of ROS. It activated the ABA pathways and abiotic stress-related genes	RNAi silencing	Xu et al. (2011)
OsNHX1	Antiporter Na^+/H^+ compartmentation into vacuole. The expression of OsNHX1 through OsNHX5 increased under salt stress and was positively related to ABA.	Mutant	Fukuda et al. (2011)

lines of *OsABAR1* had a high tolerance to salinity and drought, while knock-out mutant lines had the opposite phenotype (Zheng et al., 2020).

OsRF1-OE is a small ring-type E3 ligase that is involved in the increased endogenous level of the ABA and confers tolerance to salt and drought stress. Overexpression lines of *OsRF1*-OE had enhanced ABA level, salt, and drought tolerance. Overexpression lines showed faster transcriptional activation of genes related to ABA biosynthesis, e.g., *ZEP, NCED3*, and *ABA4*. OsRF1 exhibited E3 ligase activity and was involved in the ubiquitination and degradation of the OsPP2C09 protein. It was identified that the OsRF1 facilitates ABA biosynthesis by modifying and degrading the clade A PP2C proteins (Kim et al., 2022). OsDIP1 and ZFP36 activated the ABA-induced antioxidative defense system in rice. Overexpression lines had a high activity of superoxide dismutase and catalase enzyme, i.e., there was a decrease in monoaldehyde contents. In contrast, mutant lines *OsDIP1* had decreased expression of genes such as *SODCc2* and *CatB* and increased levels of monoaldehyde contents (Min et al., 2021) (Table 4).

ABA-mediated responses under heat stress

Heat stress causes significant damage to rice plant development by increasing respiration, accelerating senescence, causing membrane leakage, and generating reactive oxygen species (ROS). High pollen sterility has been associated with elevated ROS levels (Zhao et al., 2023). ABA-induced gene responses under heat stress have been shown to improve plant tolerance (Wang B. et al., 2020; Wang C. et al., 2020; Wang H. et al., 2020; Wang T. et al., 2020). Direct foliar application of ABA at 40°C also increases heat tolerance and boosts yield due to increased pollen viability (Rezaul et al., 2019).

Increases of 14 and 22% in seed setting were observed in heat-resistant and heat-susceptible rice lines, respectively, following exogenous application under heat stress (Zhou et al., 2019). ABA application under stress conditions induced heat shock proteins (*HSP24.1* and *HSP71.1*) and triggered the expression of sucrose transporter (*SUT*) genes, sucrose synthase (*SUS*) genes, and invertase (*INV*) genes (Rezaul et al., 2019). Several ABA-associated genes, such as *OsIAA13*, *OsIAA20*, *ILL8*, *OsbZIP12*, *OsPP2C51*, *OsDi19-1*, and

TABLE 4 ABA-modulated genes under a multi-stress environment in rice.

Gene	Stress	Functions	Plant material	References
OsCAT, *OsSOD*, *OsGR2* and *OsAPX8*	Salinity, dehydration, and cold, and exogenous ABA treatment	Higher expression of transcriptional factors and LEA family genes (*TRAB1* and *Osem*), osmolyte-related genes (*OsBADH1* and *OsP5CS*), and polyamine metabolic genes (*SAMDC*) observed in the salt-tolerant cultivar. In contrast, higher expression of proline (*ProDH*) and polyamine (*DAO* and *PAO*) was found in the salt-sensitive cultivar.	IR-64 (moderately salt-sensitive) and Nonabokra (salt-tolerant)	Paul and Roychoudhury (2019)
OsbZIP72	Salinity and drought	Over-expressing lines for *OsbZIP72* had higher tolerance to drought and salinity stresses.	CRISPR-Cas9 knock-out and overexpressing *OsbZIP72* transgenic rice	Baoxiang et al. (2021)
OsNAC006	H_2O_2, cold, heat, NaCl, and polyethylene glycol (PEG) 6,000 treatments	Knock-out mutants had increased sensitivity to the heat and drought stress conditions.	Kock out mutant	Wang B. et al. (2020), Wang C. et al. (2020), Wang H. et al. (2020), and Wang T. et al. (2020)
OsSMP1	Cold, salt, and heavy metals	Higher tolerance for the multiple stress condition	Source accessions Pei'ai 64S	Zheng et al. (2021)
OsMLP423	Drought and salt	Expressed in the cell membrane and nucleus. Higher water use and increased expression of ABA-responsive genes related to various abiotic stress	Overexpression lines	Zhou H. et al. (2022) and Zhou Z. et al. (2022)
Os4BGlu12 and *Os4BGlu13*	Salt and drought	β-glucosidase, activities on ABA-GE and gibberellin A_4 glucose ester (GA_4-GE). β-glucosidase expression lines had deeper roots and longer shoots under salt and drought stress	Transgenic *Arabidopsis*	Kongdin et al. (2021)
OsGF14b	Drought and osmotic stress	The mutant exhibited improved resistance to drought and osmotic stress while contrasting effects in *OsGF14b*-overexpression lines.	Mutant	Liu X. et al. (2019) and Liu X. L. et al. (2019)
CIRCADIAN CLOCK ASSOCIATED1 (*OsCCA1*)	Drought osmotic and salt stress	Binds to the promoters of the genes *OsPP108* and *OsbZIP46* involved in the ABA signaling	Wild type	Wei et al. (2022)
OsSWEET13 and OsSWEET15	Multi stress tolerance	OsbZIP72 binds to the promoters of OsSWEET13 and OsSWEET15 and activates their expression under stress conditions for the transport of sugar	Wild types	Mathan et al. (2021)

OsHOX24, were validated under high temperatures of 37 and 42°C during the seedling stage (Sharma et al., 2021).

The ABA pretreatment reduced cell injury, monoaldehyde, ROS, and the expression of programmed cell death genes such as *OsKOD1*, *OsCP1*, and *OsNAC4* while upregulating *OsBI1*, a suppressor of programmed cell death (Liu et al., 2020). Additionally, ABA pretreatment increased the antioxidant capacity of cells by reducing ROS and monoaldehyde levels (Liu et al., 2020). Overexpression of OsNCED1, a key factor in ABA biosynthesis, increased pollen viability, grain filling, and ROS scavenger activity (catalase, superoxide

TABLE 5 ABA-mediated genes under heat stress.

Gene	Plant material	ABA signal pathways	Function	References
OsTPP1	*tpp1* mutant Higher ABA content	OsGAMYB Activator of OSTTP1	*OsGAMYB* decreased by both the exogenous and endogenous ABA	Wang G. et al. (2021), Wang M. et al. (2021), and Wang T. et al. (2021)
ub1A quantitative trait loci	cv. Swarna	Synthetic gene in *nine-cis-epoxy carotenoid dioxygenase 3* (*NCED3*)	–	Saha et al. (2019)
HSP71.1 and *HSP24.1*	Nipponbare (wild-type) with flat leaves Mutant high-temperature susceptibility (hts)		Carbohydrate content, ATP, NAD (H), and biomass were higher in wild-type	Li et al. (2020)
OsNCED1	Overexpression	Involved in ABA biosynthetic pathway	Improve pollen viability, seed setting, and ROS scavengers	Zhou et al. (2019)
OsPYL9	Mutant through CRISPR/Cas9	ABA activates proteins GIGANTEA, adagio-like, and pseudo-response regulator proteins	Mutant lines had higher drought-related traits.	Usman et al. (2020)
florigen *FLOWERING LOCUS T* (*FT*)	Rice lines	FD interacts with FT-like proteins to regulate ABA responses	Related to flowering genes	Martignago et al. (2020)
OsGLP2-1	Artificial microRNA and CRISPR/CAS9 approaches	*OsGLP2-1* is antagonistically controlled by *ABA INSENSITIVE5* and GAMYB factors.	Suppression of *OsGLP2-1*. Organ-specific expression increased by exogenous abscisic acid	Wang B. et al. (2020), Wang C. et al. (2020), Wang H. et al. (2020), and Wang T. et al. (2020)
OsIAGLU	*OsIAGLU* was cloned in rice	Higher expressions of *ABA-INSENSITIVE 3* (*OsABI3*) and *OsABI5 osiaglu* mutants	Disruption of *OsIAGLU* resulted in reduced seed vigor	He et al. (2020)
H2Bub1		H2Bub1 interacted with OsbZIP46	Regulate ABA signaling and drought response in rice	Ma et al. (2019)
OsPL6 gene	Rice mutant having purple leaf blade (pl6)	Elevated levels of OsCHS, OsPAL, OsF3H, and OsF3′H	Mutant with high accumulation of abscisic acid (ABA), cytokinin (CK), and anthocyanins	Khan et al. (2020)

dismutase, and peroxidase) compared to controls while reducing relative electrolyte leakage and monoaldehyde content in transgenic plants carrying the *OsNCED1* gene (Zhou et al., 2019) (Table 5).

Author contributions

RG: Writing – review & editing, Writing – original draft, Conceptualization. SR: Writing – review & editing, Writing – original draft, Supervision, Project administration, Conceptualization. RO: Writing – review & editing, Resources, Project administration. MK: Writing – review & editing. YK: Writing – review & editing.

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