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Comparative responses of rice (*Oryza sativa* L.) to iron toxicity, drought and salinity stress: Morphological, physiological, biochemical and molecular regulation mechanisms

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ABSTRACT

Rice (*Oryza sativa* L.) is one of the world's most important staple crops, ensuring food security for more than half of the global population. However, rice productivity is increasingly threatened by major abiotic stresses, particularly drought stress, salinity stress, and iron toxicity, whose severity is intensified by climate change and soil degradation. This review provides a comparative analysis of the morphological, physiological, biochemical, and molecular responses of rice to these constraints. Although these stresses arise from distinct environmental conditions, they converge toward common physiological disturbances, including growth inhibition, impaired photosynthesis, altered water relations, and excessive accumulation of reactive oxygen species (ROS). Drought stress mainly induces water deficit and stomatal closure, whereas salinity stress combines osmotic stress with ionic toxicity caused by excessive Na^+ accumulation. In contrast, iron toxicity is characterized by excessive Fe^{2+} accumulation and enhanced ROS production through Fenton reactions. To maintain redox regulation and cellular homeostasis, rice activates antioxidant systems involving superoxide dismutase, catalase, ascorbate peroxidase, and the ascorbate-glutathione cycle. However, these defenses are often insufficient under severe iron toxicity because of the high reactivity of redox-active iron. At the molecular level, drought and salinity responses are largely regulated through ABA-dependent pathways and transcription factors such as OsDREB, OsNAC, and OsbZIP, whereas iron toxicity specifically mobilizes genes involved in iron uptake, transport, sequestration, and detoxification. This review highlights both the convergence and specificity of stress-response mechanisms and emphasizes the integration of redox regulation, antioxidant systems, ion homeostasis, and molecular responses into breeding strategies for developing multi-stress tolerant rice varieties.

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INTRODUCTION

Rice (*Oryza sativa* L.) is one of the most important food crops worldwide, providing the primary caloric intake for more than half of the global population. Rice production plays a central role in food security, particularly in tropical and subtropical regions where population growth and environmental constraints are increasing pressure on agricultural systems. However, the sustainability of rice production is currently threatened by the intensification of abiotic stresses, whose frequency, severity, and variability are exacerbated by climate change, soil degradation, and inappropriate agricultural practices (Munns and Gilliham, 2020).

Among these constraints, drought stress, salinity stress, and iron toxicity are major factors limiting rice productivity, especially in rice-growing systems of West Africa and Asia. Drought stress reduces plant water potential, leading to stomatal closure and decreased photosynthesis (Todaka *et al.*, 2017). Salinity stress combines osmotic stress and ionic toxicity associated with the accumulation of Na^+ and Cl^-, thereby disrupting nutrient balance and cellular functions (El Mahi *et al.*, 2019). In contrast, iron toxicity, which is specific to flooded environments, results from the accumulation of soluble Fe^{2+}, causing severe physiological disorders and characteristic symptoms such as leaf bronzing (Wairich *et al.*, 2024).

Despite their distinct origins, these stresses converge toward a disruption of redox homeostasis characterized by excessive accumulation of reactive oxygen species (ROS), including superoxide anion, hydrogen peroxide, and hydroxyl radicals. These molecules play a central role in stress responses, acting both as toxic agents and molecular signals (Xu *et al.*, 2018). However, their mechanisms of production differ: ROS mainly result from metabolic imbalances under drought and salinity stress, whereas they are directly amplified by Fenton reactions under iron toxicity.

In addition, these stresses affect key physiological processes such as photosynthesis, transpiration, and nutrient uptake. Under natural conditions, plants are often exposed to combinations of stresses whose effects may be additive, synergistic, or antagonistic, highlighting the need for integrative approaches.

In this context, a comparative analysis of rice responses to these constraints is essential to better understand the underlying adaptation mechanisms. This review aims to (i) analyze the effects of drought stress, salinity stress, and iron toxicity on the morphological, physiological, biochemical, and molecular responses of rice; (ii) identify their common and distinct mechanisms, particularly those associated with redox regulation; and (iii) provide perspectives for the development of rice varieties tolerant to multiple abiotic stresses.

Morphological and agronomic responses of rice to drought, salinity, and iron toxicity

Characteristic morphological symptoms of different stresses

Drought, salinity, and iron toxicity induce distinct morphological symptoms in rice that reflect specific physiological mechanisms and may serve as diagnostic indicators under field conditions.

Under drought stress, the most common symptoms include leaf rolling, reduced leaf expansion, and inhibition of stem elongation. These responses help limit water loss and maintain cellular turgor under water-deficit conditions (Dixit *et al.*, 2014).

Salinity stress is mainly characterized by progressive chlorosis followed by marginal leaf necrosis resulting from the toxic accumulation of Na^+ and Cl^- ions in plant tissues. Reduced tillering and delayed vegetative development are also frequently observed (Razzaque *et al.*, 2019).

Iron toxicity exhibits a particularly characteristic symptom known as leaf bronzing. This symptom results from excessive Fe^{2+} accumulation and associated oxidative damage. Under severe conditions, necrotic lesions and rapid degradation of photosynthetic tissues may occur (Turhadi *et al.*, 2019).

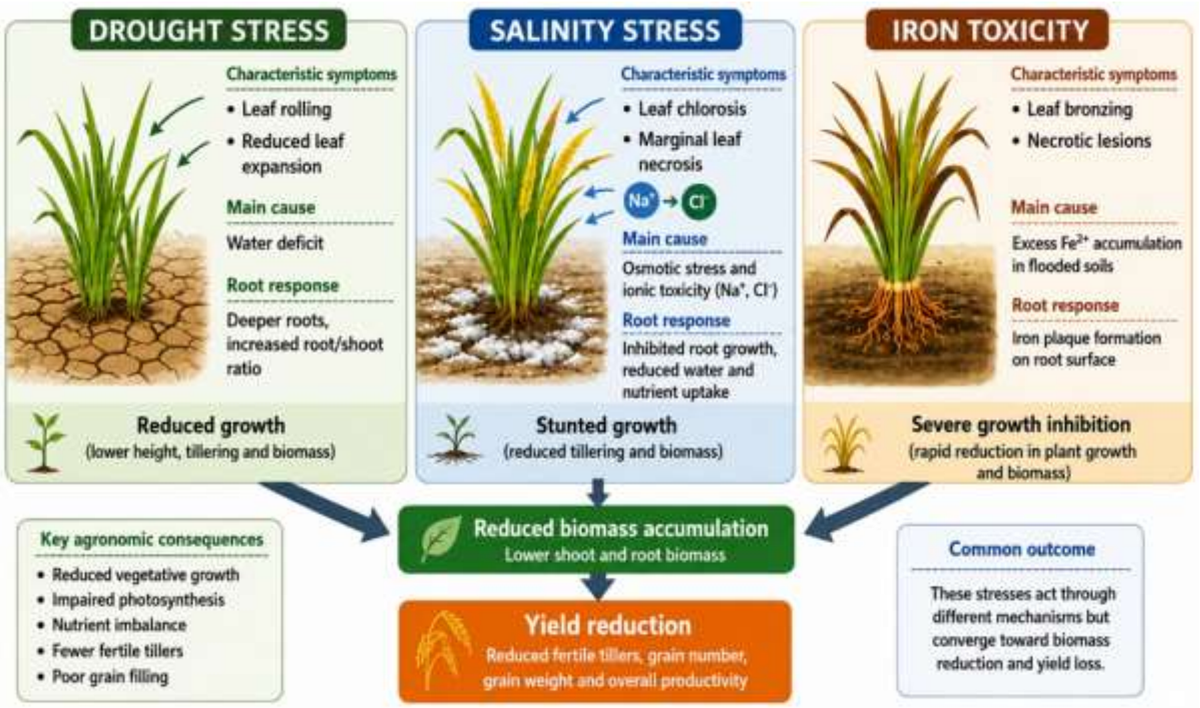

Fig 1. Comparative morphological and agronomic effects of drought, salinity, and iron toxicity in rice
Drought stress induces leaf rolling and reduced growth due to water deficit; salinity stress causes chlorosis and stunted growth because of osmotic and ionic stress; iron toxicity results in leaf bronzing and severe growth inhibition caused by excess Fe^{2+} accumulation. These stresses ultimately converge toward biomass reduction and yield loss.

Effects of abiotic stresses on vegetative growth of rice

Drought, salinity, and iron toxicity significantly reduce vegetative growth in rice, although the underlying mechanisms differ depending on the nature of the stress.

Under drought conditions, reduced cell expansion and division lead to decreases in plant height, leaf area, and biomass accumulation. However, some tolerant genotypes develop deeper root systems that enhance water uptake from deeper soil layers (Korgaonker and Bhandari, 2023).

Salinity stress affects vegetative growth through a combination of osmotic stress and ionic toxicity. Excessive Na^+ accumulation disrupts cellular metabolism and reduces leaf development, tillering, and biomass production (El Mahi *et al.*, 2019; Xu *et al.*, 2024). Inhibition of root growth also limits water and mineral uptake.

Under iron toxicity conditions, excessive Fe^{2+} accumulation rapidly inhibits vegetative growth because of metabolic disturbances and oxidative damage associated with redox-active iron. These effects are particularly severe in flooded rice-growing systems (Turhadi *et al.*, 2019).

Impacts of abiotic stresses on yield and yield components

Drought, salinity, and iron toxicity strongly affect rice yield components, with consequences varying according to stress intensity and developmental stage at stress occurrence.

Under drought stress, yield losses are mainly associated with reduced numbers of fertile tillers, decreased spikelet fertility, and poor grain filling, particularly when water deficit occurs during the flowering stage (Dixit *et al.*, 2014; Sandhu *et al.*, 2017).

Salinity stress causes substantial reductions in the number of fertile panicles, grains per panicle, and grain weight. These effects result from ionic imbalance, disruption of energy metabolism, and reduced photosynthetic activity (Xu *et al.*, 2024).

Iron toxicity generally induces more rapid and severe yield losses in lowland rice systems. Under extreme conditions, yield reductions may exceed 30%. The formation of iron plaques on root surfaces constitutes a tolerance mechanism that limits Fe^{2+} entry into internal tissues. However, these deposits may also reduce the uptake of essential nutrients such as phosphorus and potassium (Wu *et al.*, 2014).

A comparative overview of the morphological and agronomic effects of drought, salinity, and iron toxicity in rice is presented in Fig. 1.

Physiological responses of rice to drought, salinity and iron toxicity

Root responses and specific physiological adaptations

The root system constitutes the primary interface between the plant and the soil and plays a crucial role in rice adaptation to abiotic stresses. Root modifications directly influence water and nutrient uptake as well as the maintenance of plant physiological homeostasis.

Under drought stress, some rice varieties develop deeper root systems and an increased root-to-shoot ratio, enhancing access to soil water reserves. This root plasticity improves drought tolerance, particularly in rainfed rice systems (Sandhu *et al.*, 2017).

Salinity stress generally inhibits root growth because of osmotic stress and toxic Na^+ accumulation in root tissues. This inhibition restricts water and nutrient uptake and exacerbates physiological disturbances associated with ionic homeostasis (Kitomi *et al.*, 2020).

Under iron toxicity conditions, rice develops specific adaptive mechanisms related to its adaptation to flooded environments. The formation of iron plaques on root surfaces limits Fe^{2+} entry into internal tissues and thereby contributes to iron toxicity tolerance. However, these ferric deposits may also reduce the uptake of essential nutrients such as phosphorus, zinc, and manganese (Wu *et al.*, 2014; Zhang *et al.*, 2012).

Disturbance of water relations and gas exchange

Drought, salinity, and iron toxicity strongly disrupt rice water relations and reduce gas exchange, although the underlying mechanisms differ depending on the type of stress.

Under drought stress, reduced leaf water potential and relative water content trigger rapid stomatal closure aimed at limiting water loss. However, this response also restricts CO_2 uptake and decreases photosynthetic activity (Li *et al.*, 2017).

Salinity stress induces osmotic stress that reduces water uptake by roots and decreases cellular turgor. This disturbance also causes stomatal closure, thereby limiting gas exchange and carbon assimilation (Siddiqui *et al.*, 2014; El Mahi *et al.*, 2019).

Under iron toxicity conditions, excess Fe^{2+} disrupts root function and indirectly reduces water uptake, resulting in decreased stomatal conductance and gas exchange (Wu *et al.*, 2014).

Thus, despite distinct mechanisms, these three stresses converge toward reduced CO_2 assimilation and lower photosynthetic efficiency.

Ionic imbalance and nutritional disturbances

Abiotic stresses strongly affect ionic and nutritional homeostasis in rice, with consequences varying according to the nature of the stress.

Under drought stress, nutritional disturbances mainly result from reduced transpiration flow and decreased mineral uptake, without specific accumulation of toxic ions.

Salinity stress causes excessive accumulation of Na^+ and Cl^- in plant tissues. This accumulation disrupts ionic balance, particularly through competition with potassium, and affects several enzymatic and metabolic processes. Therefore, maintaining a high K^+/Na^+ ratio is considered a key mechanism of salt tolerance in rice (El Mahi *et al.*, 2019).

Iron toxicity is characterized by excessive Fe^{2+} accumulation, which may interfere with the uptake and transport of other essential mineral elements. Iron overload severely disrupts cellular metabolism and aggravates nutritional imbalances (Wu *et al.*, 2014).

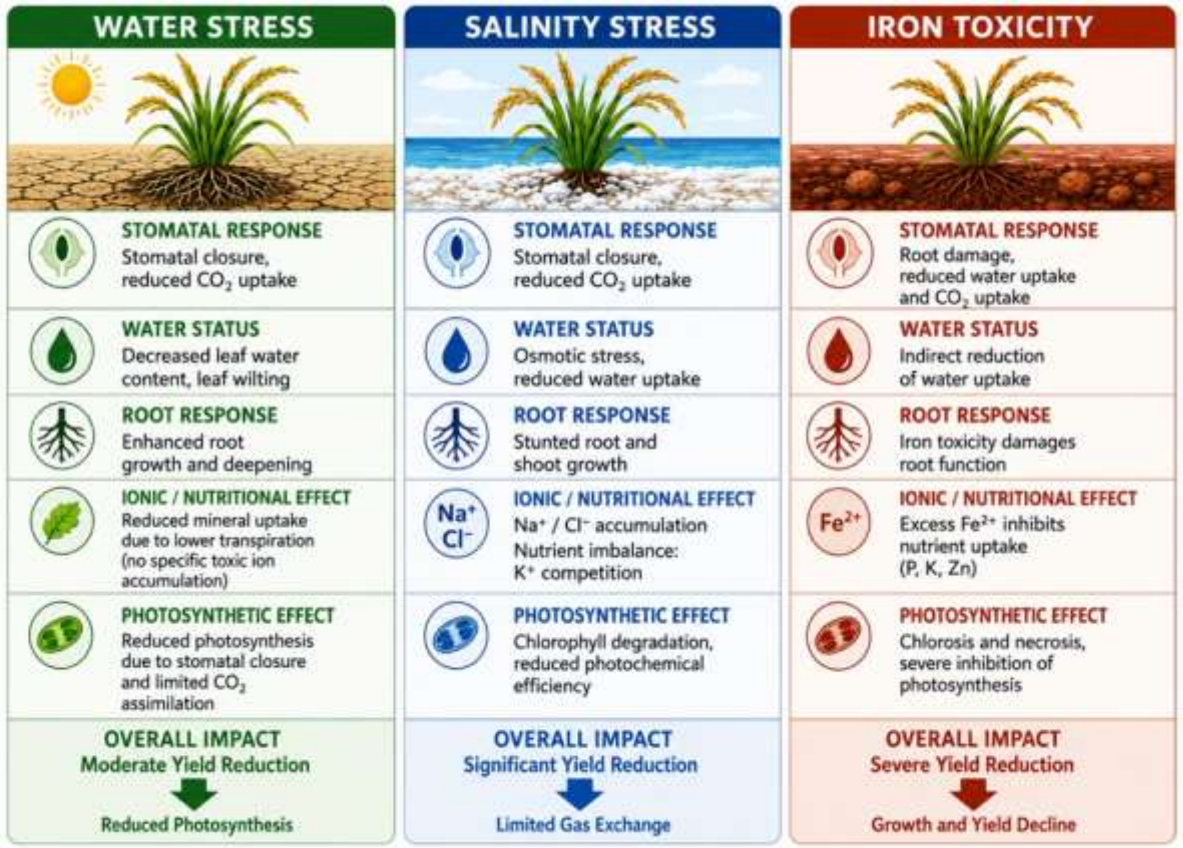

Fig 2. Comparative physiological responses of rice to drought, salinity and iron toxicity stresses

Comparative physiological responses of rice to drought, salinity and iron toxicity. Although these stresses involve distinct mechanisms, they collectively impair water relations, photosynthesis, nutrient balance and ultimately reduce growth and yield.

Overall, ionic disturbances remain relatively limited under drought stress, become severe under salinity stress, and take a specific form associated with excess iron under iron toxicity conditions.

Alteration of photosynthetic activity and chloroplast structures

Photosynthesis is one of the physiological processes most sensitive to abiotic stresses in rice.

Under drought stress, photosynthetic limitation is initially associated with stomatal closure and later progresses toward metabolic impairments affecting photosystem II and energy conversion efficiency (Li *et al.*, 2017).

Salinity stress causes degradation of chlorophyll pigments, disorganization of chloroplast structures, and reduced photochemical efficiency. These disturbances decrease energy production and carbon fixation, thereby contributing to reduced growth and yield in sensitive genotypes (Cha-um *et al.*, 2009; Siddiqui *et al.*, 2014).

Iron toxicity generally induces more rapid and severe damage. Excess Fe^{2+} promotes the generation of reactive oxygen species capable of damaging chloroplast membranes and photosynthetic pigments, leading to strong inhibition of photosynthetic activity (Wu *et al.*, 2014).

Overall, photosynthetic alterations appear more severe under iron toxicity than under salinity or drought stress.

A comparative synthesis of the main physiological responses of rice to drought, salinity, and iron toxicity is presented in Fig. 2.

Biochemical responses and redox regulation of rice under drought, salinity and iron toxicity

Oxidative stress and cellular damage

Despite their distinct origins, drought, salinity, and iron toxicity converge toward a disruption of redox homeostasis characterized by excessive accumulation of reactive oxygen species (ROS), including superoxide anion (O_2^-), hydrogen peroxide (H_2O_2), and hydroxyl radicals (•OH). In rice, this overproduction of ROS constitutes a central mechanism underlying cellular damage induced by abiotic stresses (Ding *et al.*, 2023; Xu *et al.*, 2018).

Under drought stress, stomatal closure and disruption of photosynthetic electron transport promote ROS generation in chloroplasts (Todaka *et al.*, 2017). Salinity stress combines osmotic stress and ionic toxicity, thereby intensifying ROS production in several cellular compartments, including chloroplasts, mitochondria, and peroxisomes (Ren *et al.*, 2005). In contrast, iron toxicity is distinguished by direct and massive ROS production through Fenton reactions catalyzed by redox-active Fe^{2+}, generating highly reactive hydroxyl radicals (Zhang *et al.*, 2012; Wairich *et al.*, 2024).

ROS accumulation leads to cellular damage mainly affecting membranes, proteins, and nucleic acids. Under drought stress, oxidative damage is generally progressive and moderate because of the action of antioxidant defense systems (Xu *et al.*, 2018; Todaka *et al.*, 2017). Salinity stress induces more severe damage due to the combined effects of osmotic stress and ionic toxicity, promoting oxidation of proteins, membranes, and photosynthetic pigments (El Mahi *et al.*, 2019). Iron toxicity causes the most severe damage, as hydroxyl radicals directly attack cellular membranes, enzymatic proteins, and DNA (Zhang *et al.*, 2012).

Antioxidant systems and redox regulation

To limit oxidative damage, rice activates a coordinated network of enzymatic antioxidant systems involved in ROS detoxification and maintenance of cellular redox balance.

Superoxide dismutase (SOD) constitutes the first line of defense by catalyzing the conversion of superoxide anion into H_2O_2. Hydrogen peroxide is subsequently detoxified by several enzymes, including catalase (CAT), ascorbate peroxidase (APX), and peroxidases (POD) (Ding *et al.*, 2023). The ascorbate–glutathione cycle also plays an essential role through the coordinated activities of glutathione reductase (GR), monodehydroascorbate reductase (MDHAR), and dehydroascorbate reductase (DHAR), which regenerate the reduced forms of ascorbate and glutathione required for redox homeostasis (Yin *et al.*, 2014). Other enzymes, such as glutathione peroxidase (GPX), glutathione S-transferase (GST), and peroxiredoxins (Prx), also contribute to membrane protection and lipid peroxide detoxification (Zhou *et al.*, 2022).

Under drought stress, increased activities of SOD, CAT, APX, GR, and POD generally help limit photo-oxidative damage associated with stomatal restriction and disruption of photosynthetic electron transport (Todaka *et al.*, 2017; Bhattacharjee *et al.*, 2023). Salinity stress induces a broader activation of the antioxidant system, reflecting the complexity of osmotic, ionic, and metabolic disturbances associated with salinity (El Mahi *et al.*, 2019).

Under iron toxicity, antioxidant enzymes are strongly activated in response to massive ROS production generated by Fenton reactions. However, despite this induction, their effectiveness often remains insufficient to counterbalance the intensity of oxidative stress, resulting in rapid accumulation of cellular damage (Turhadi *et al.*, 2019).

Thus, antioxidant systems provide relatively efficient regulation under moderate drought and salinity stress but appear more vulnerable under severe iron toxicity.

Osmolyte accumulation and metabolic adjustment

Accumulation of osmolytes represents an important biochemical strategy enabling rice plants to maintain osmotic balance and reduce cellular damage induced by abiotic stresses.

Under drought stress, proline and soluble sugars contribute to the maintenance of cellular turgor, membrane stabilization, and protection of proteins against dehydration-induced damage. Soluble sugars also function as energy reserves that support metabolic recovery after stress relief (Todaka *et al.*, 2017). Under salinity stress, osmolyte accumulation is generally more pronounced because of the combined osmotic and ionic components of the stress. In addition to proline and soluble sugars, glycine betaine contributes to the stabilization of proteins, membranes, and the photosynthetic apparatus while also helping alleviate oxidative stress (Ren *et al.*, 2005; Lamlom *et al.*, 2025). In contrast, osmotic adjustment appears to play a secondary role under iron toxicity conditions. Adaptive mechanisms mainly rely on regulation of redox-active iron and limitation of oxidative damage (Zhang *et al.*, 2012).

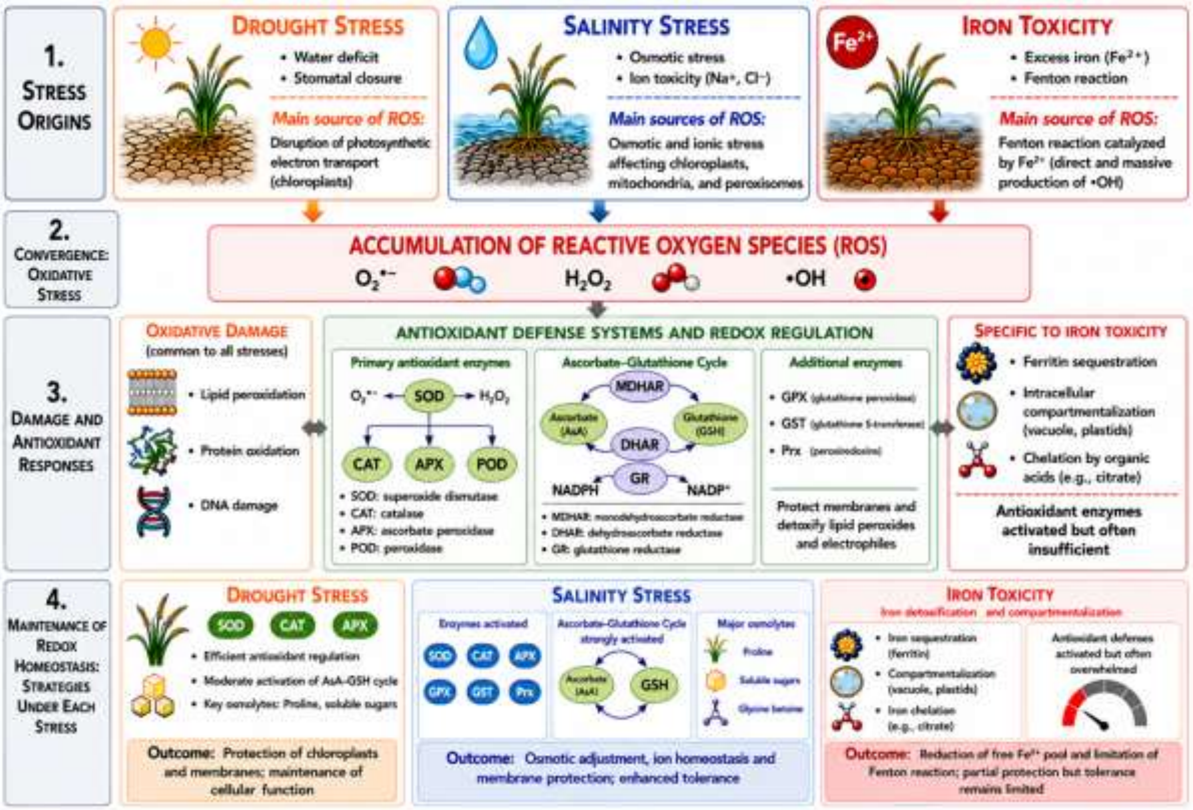

Fig 3. Comparative oxidative stress and antioxidant defense mechanisms in rice under drought, salinity and iron toxicity

Schematic overview of oxidative stress generation and antioxidant defense responses in rice exposed to drought, salinity and iron toxicity. Although these stresses originate from distinct environmental constraints, they converge toward reactive oxygen species (ROS) accumulation and oxidative damage. Rice activates antioxidant enzymes, redox regulation pathways and stress-specific adaptive mechanisms to maintain cellular homeostasis and limit growth reduction

Specific mechanisms of iron detoxification

Iron toxicity differs from other abiotic stresses by activating specific mechanisms aimed at reducing the availability of free Fe^{2+} and limiting Fenton reactions.

Iron sequestration by ferritins constitutes a major cellular protection mechanism. These proteins store iron in its non-reactive ferric (Fe^{3+}) form, thereby limiting hydroxyl radical formation (Paul *et al.*, 2012). Rice also develops subcellular compartmentalization mechanisms involving vacuoles and plastids. VIT-type transporters contribute to this regulation by restricting the accumulation of redox-active iron in the cytosol (Zhang *et al.*, 2012).

In addition, certain metabolites such as organic acids, particularly citrate, can chelate iron and reduce its chemical reactivity. Although classical antioxidant systems are also activated, regulation of the free iron pool remains the primary protective mechanism under iron toxicity conditions (Turhadi *et al.*, 2019; Rajonandraina *et al.*, 2023).

An integrative representation of redox regulation and iron detoxification mechanisms in rice under abiotic stresses is presented in Fig. 3.

Molecular responses of rice to drought, salinity, and iron toxicity

Redox signaling and transcriptional regulation

Despite their distinct origins, drought, salinity, and iron toxicity activate integrated molecular signaling networks in rice involving reactive oxygen species (ROS), phytohormones, and transcriptional regulation. ROS play a central role as early signaling molecules capable of modulating the expression of numerous stress-responsive genes (Ding *et al.*, 2023; Xu *et al.*, 2018; Kobayashi *et al.*, 2007). Under drought and salinity stress, ROS mainly function as secondary messengers activating abscisic acid (ABA)-dependent pathways, leading to transcriptional reprogramming involved in stomatal regulation, osmotic adjustment, and cellular protection (Sun *et al.*, 2020; Li *et al.*, 2017). This regulation involves several transcription factor families, including OsDREB, OsbZIP, OsNAC, and OsMYB, which control the expression of genes associated with osmolyte synthesis, antioxidant defense, and ionic homeostasis (Cui *et al.*, 2011; Tang *et al.*, 2012; Lu *et al.*, 2009; Nakashima *et al.*, 2007; Xiong *et al.*, 2014). Salinity stress also activates more complex transcriptional networks associated with K^+/Na^+ regulation and maintenance of cellular ionic balance (Matsukura *et al.*, 2010). Specialized transporters such as OsHKT1;5, OsSOS1, and OsNHX1 play crucial roles in sodium exclusion, extrusion, and compartmentalization to limit cellular toxicity (Ren *et al.*, 2005; Fukuda *et al.*, 2011; El Mahi *et al.*, 2019).

Under iron toxicity conditions, the molecular response is distinguished by activation of pathways specialized in iron homeostasis. Transcription factors such as OsIRO2 and OsIDEF1 regulate the expression of genes involved in iron uptake, transport, and intracellular storage (Kobayashi *et al.*, 2007; Ogo *et al.*, 2006). However, excessive accumulation of redox-active Fe^{2+} disrupts redox signaling balance and may impair intracellular signal transduction, thereby limiting the efficiency of adaptive responses (Rajonandraina *et al.*, 2023).

Thus, molecular responses appear mainly adaptive under drought stress, integrative under salinity stress, and highly specialized under iron toxicity.

Ionic homeostasis and membrane transporters

Regulation of ionic fluxes constitutes a central mechanism of abiotic stress tolerance in rice, although its importance varies depending on the nature of the stress.

Under drought stress, ionic disturbances generally remain limited and mainly result from reduced transpiration flow affecting mineral uptake. In contrast, salinity stress causes excessive accumulation of Na^+ and Cl^- in plant tissues, requiring strict regulation of the K^+/Na^+ ratio to maintain enzymatic and membrane functions (Ren *et al.*, 2005; El Mahi *et al.*, 2019).

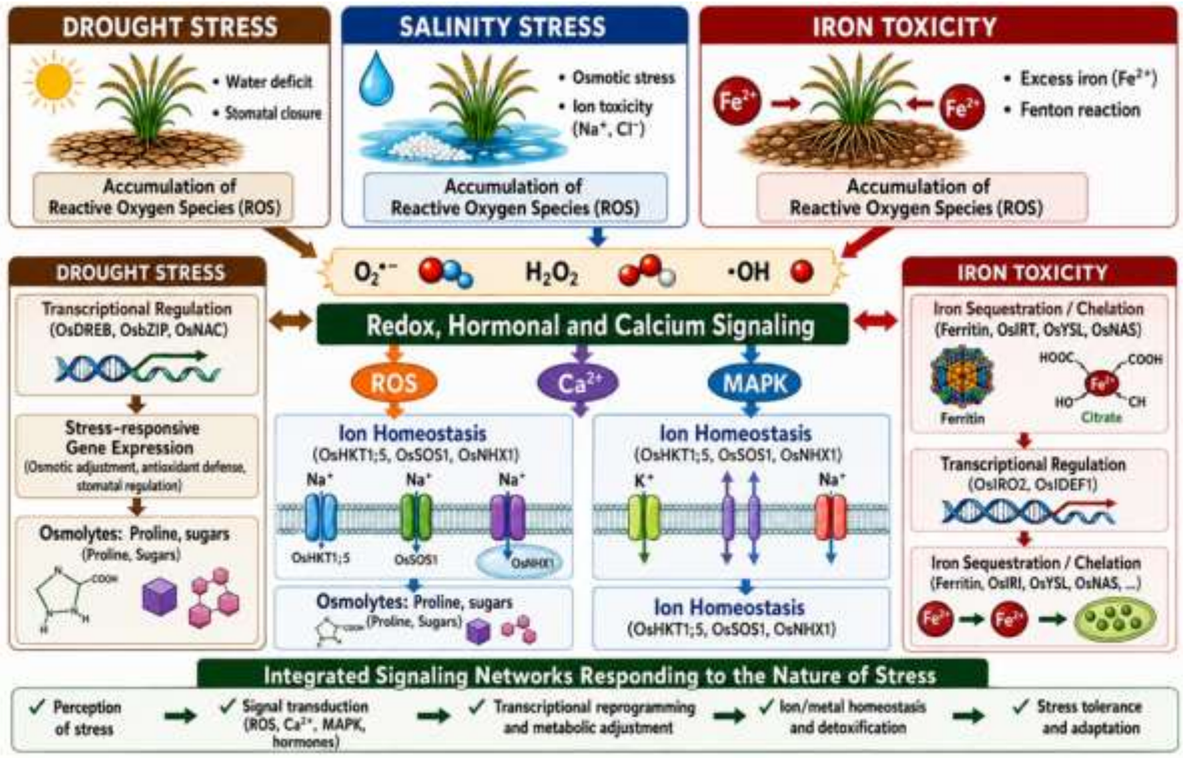

Fig 4. Integrative molecular signaling networks involved in rice responses to drought, salinity, and iron toxicity
Drought, salinity, and iron toxicity activate interconnected signaling pathways in rice involving ROS, Ca^{2+}, MAPK cascades, hormonal signaling, and transcriptional regulation. While drought mainly induces ABA-dependent responses and osmolyte accumulation, salinity primarily affects ion homeostasis through transporters such as OsHKT1;5, OsSOS1, and OsNHX1. Iron toxicity activates specific iron sequestration, chelation, and detoxification mechanisms involving ferritins and iron-related transporters.
ROS, reactive oxygen species; $O_2\bullet^-$, superoxide anion; H2O2, hydrogen peroxide; •OH, hydroxyl radical; Ca^{2+}, calcium ion; MAPK, mitogen-activated protein kinase.

This regulation relies on the coordinated activity of several specialized membrane transporters, particularly OsHKT1;5, involved in sodium exclusion from shoots; OsSOS1, responsible for Na^+ extrusion from cells; and OsNHX1, which mediates vacuolar sodium compartmentalization (Fukuda *et al.*, 2011).

Under iron toxicity conditions, the major constraint is not associated with classical ionic imbalance but rather with the accumulation of a redox-active metal. The molecular response therefore involves iron-specific transporters such as OsIRT1, OsIRT2, OsYSL, and OsNAS, which regulate iron uptake, chelated transport, and intracellular distribution, respectively (Ishimaru *et al.*, 2006; Koike *et al.*, 2004; Inoue *et al.*, 2003).

Iron sequestration and detoxification

Unlike drought and salinity stress, iron toxicity induces specialized molecular mechanisms aimed at limiting the accumulation of free redox-active iron within cells.

In rice, iron sequestration mainly involves ferritin proteins encoded by OsFER1 and OsFER2, which enable iron storage in a non-toxic ferric form. In addition, nicotianamine synthesis mediated by OsNAS facilitates iron chelation, whereas OsYSL transporters ensure iron redistribution within plant tissues (Paul *et al.*, 2012; Koike *et al.*, 2004; Zhang *et al.*, 2012).

Intracellular compartmentalization of iron into organelles such as vacuoles and plastids also contributes to reducing Fenton reactions and oxidative damage associated with excess Fe^{2+} (Zhang *et al.*, 2012). These mechanisms represent a specific molecular signature of rice responses to iron toxicity.

Crosstalk among hormonal, redox, and calcium signaling pathways

Molecular responses of rice to abiotic stresses rely on complex interactions among redox, hormonal, and calcium signaling pathways.

Under drought and salinity stress, ROS act as early signaling molecules, whereas calcium (Ca^{2+}) functions as a second messenger modulating the activity of protein kinases, transcription factors, and MAPK cascades involved in stress responses (Asano *et al.*, 2012; Huang *et al.*, 2009). These interactions enable efficient coordination between stress perception, transcriptional activation, and metabolic adjustment. Under iron toxicity conditions, excess iron partially disrupts these signaling networks by altering intracellular redox balance and MAPK-dependent phosphorylation cascades. This disorganization may reduce the effectiveness of adaptive responses and contribute to the intensification of cellular damage (Pereira *et al.*, 2013; Wu *et al.*, 2014; Rajonandraina *et al.*, 2023). An integrative overview of molecular signaling pathways and regulatory networks involved in rice responses to drought, salinity, and iron toxicity is presented in Fig. 4.

Integrative perspectives and future research directions

Limitations of single-stress approaches

The comparative analysis presented in this review highlights the limitations of conventional approaches based on the study of individual stresses. Under natural conditions, rice is frequently exposed to combinations of abiotic constraints, particularly salinity and iron toxicity in irrigated lowlands, as well as drought and salinity in coastal regions. These interactions may act in additive, synergistic, or antagonistic ways, profoundly modifying plant physiological, biochemical, and molecular responses. Consequently, mechanisms identified under controlled single-stress conditions do not always accurately reflect plant behavior under field conditions.

Future research should therefore prioritize multi-stress approaches integrating physiological, biochemical, and molecular analyses under environments that more closely resemble actual cultivation conditions. Such approaches are essential for improving our understanding of stress interactions and the mechanisms underlying overall rice tolerance to abiotic constraints.

Redox regulation as a central component of multi-stress tolerance

One of the major findings of this comparative review is the identification of redox regulation as a central component of rice responses to drought, salinity, and iron toxicity. Despite their distinct origins, these three constraints converge toward oxidative stress associated with excessive accumulation of reactive oxygen species (ROS). Enhancement of antioxidant systems, stabilization of the ascorbate–glutathione cycle, and fine regulation of redox signaling appear to be key determinants of tolerance to multiple abiotic stresses. However, iron toxicity differs from drought and salinity stress because of the direct involvement of redox-active Fe^{2+} in ROS production through Fenton reactions. Under such conditions, antioxidant defenses alone are often insufficient, and tolerance also depends on efficient mechanisms of iron sequestration, chelation, and intracellular compartmentalization. These observations suggest that future breeding strategies should simultaneously integrate enhancement of antioxidant capacity, maintenance of redox homeostasis, and regulation of redox-active iron to improve rice adaptation to environments exposed to multiple stresses.

Multi-omics approaches and genetic improvement

The integration of transcriptomics, proteomics, metabolomics, and ionomics represents a promising strategy for deciphering the complex regulatory networks involved in rice responses to multiple abiotic stresses. Combined with systems biology and regulatory network modeling approaches, these technologies could facilitate the identification of conserved molecular modules associated with multi-stress tolerance. Recent advances in genome-editing technologies, particularly CRISPR/Cas systems, also provide promising opportunities for developing rice varieties with improved tolerance to combined stresses. Targeted manipulation of genes involved in ionic homeostasis, antioxidant regulation, stress signaling, and iron detoxification may contribute to the development of climate-resilient cultivars. In addition, exploiting natural genetic diversity and identifying tolerant genotypes adapted to different agroecosystems remain important priorities for future breeding programs.

Agronomic implications and climate resilience

Beyond molecular and genetic approaches, improving rice tolerance to abiotic stresses also requires the integration of physiological knowledge into appropriate agronomic strategies. Water management, improved drainage, optimization of fertilization practices, and the use of organic or mineral amendments may significantly reduce the impacts of drought, salinity, and iron toxicity in rice-growing systems. Under climate change conditions, the frequency and severity of abiotic stresses are expected to increase, particularly in lowland rice ecosystems and coastal areas. The development of integrated strategies combining tolerant varieties, improved agronomic practices, and sustainable soil management will therefore be essential to maintain rice productivity and food security in vulnerable regions. Overall, future research should move toward integrative and multi-scale approaches linking physiology, redox biology, molecular regulation, genetics, and agronomy to improve rice adaptation to increasingly complex abiotic stress environments.

CONCLUSION

This comparative review demonstrates that drought, salinity, and iron toxicity induce convergent responses in rice characterized by disruption of redox homeostasis, excessive accumulation of reactive oxygen species, and reduced physiological and agronomic performance. However, the adaptive mechanisms involved differ according to the nature of the stress. While drought and salinity stress mainly involve osmotic, physiological, and ionic adjustments, iron toxicity is distinguished by the necessity to control the accumulation of redox-active iron and the associated oxidative damage. This synthesis highlights the central role of antioxidant systems, redox signaling, and molecular regulatory mechanisms in rice tolerance to abiotic stresses. It also emphasizes the importance of integrative approaches combining physiology, molecular biology, genetics, and agronomy to improve rice resilience to increasing environmental constraints associated with climate change. Future studies should prioritize multi-stress approaches conducted under conditions close to natural environments in order to better understand interactions among abiotic constraints and to develop rice varieties with enhanced tolerance adapted to vulnerable production systems.

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