



Iron Toxicity in Rice: Mechanisms of Tolerance and Prospects for Genetic Improvement

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Authors' contributions

This work was carried out in collaboration between both authors. Both authors read and approved the final manuscript.

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Abstract

Iron toxicity is an important abiotic constraint to rice production, particularly in flooded and acid sulphate soils where high concentrations of soluble ferrous iron can accumulate. This review synthesises current knowledge of iron acquisition, toxicity symptoms, tolerance mechanisms, and opportunities for the genetic improvement of rice under iron-toxic conditions. Rice possesses a distinctive iron-acquisition system that combines phytosiderophore-mediated uptake with the direct absorption of ferrous iron. Although this system supports iron nutrition under flooded conditions, excessive iron uptake can promote reactive oxygen species formation and cause leaf bronzing, impaired growth, nutrient imbalance, reduced photosynthetic performance, and yield loss. Rice plants respond through multiple anatomical, physiological, biochemical, and molecular defence mechanisms. These include rhizospheric iron oxidation and plaque formation, restriction of iron movement from roots to shoots, tissue compartmentalisation, ferritin-mediated sequestration, chelation, and enzymatic and non-enzymatic antioxidant responses. Iron transporters, regulatory proteins, chelators, and stress-responsive genes contribute to maintaining cellular iron homeostasis and reducing oxidative injury. Considerable genotypic variation in tolerance provides opportunities for breeding through conventional selection, marker-assisted approaches, quantitative trait locus analysis, genome-wide association studies, and other genomic tools. Integrating physiological screening with molecular and genetic approaches can improve understanding of the complex basis of iron-toxicity tolerance and support the development of rice varieties better adapted to iron-toxic environments.

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1. Introduction

Rice (*Oryza sativa* L.) is a principal staple crop supporting more than half of the global population. Globally it accounts for over 21% of human caloric requirements and up to 76% of the caloric intake of Southeast Asian people (Fitzgerald *et al.*, 2009). Apart from its nutritional value, rice is essential for maintaining food security and the livelihoods of millions of smallholder farmers in developing nations. The global demand for rice is expected to rise markedly with the world population projected to reach approximately 9.1 billion by 2050 (Jaggard *et al.*, 2010). Meeting this demand will require an estimated 35% increase in rice production compared to levels around 2000, presenting a major challenge to global food security (Sonu *et al.*, 2024). However, sustained increases in productivity are constrained by various environmental factors that negatively affect both yield and grain quality.

Rice production is significantly constrained by a range of abiotic stresses, including drought, salinity, acidity, submergence, temperature extremes, and nutrient imbalances, all of which adversely affect growth, yield and grain quality. Among these, iron toxicity is a major limitation in lowland rice ecosystems, particularly in acid and waterlogged soils prevalent in Asia and sub-Saharan Africa, where it represents a significant and quantifiable threat to yield stability (Dobermann & Fairhurst, 2000; Audebert & Sahrawat, 2000; Chérif *et al.*, 2009). Owing to the impacts of climate change, the incidence of iron (Fe) toxicity has expanded over time. It has been reported that approximately 18% of the global rice-cultivated area is affected by Fe toxicity (Mahender *et al.*, 2019), and in India, about 11.7 million hectares of rice-growing land are reported to be impacted (Onaga *et al.*, 2016).

Iron toxicity management in rice requires an integrated approach combining genetic improvement, physiological insights, and agronomic practices. Integrating iron-tolerant varieties, selected for their adaptive responses to iron toxicity, with soil management strategies that restrict Fe^{2+} availability offers a sustainable approach to maintaining productivity under iron-stressed conditions. Recent evidence further indicates that iron-toxicity tolerance in rice is governed by multiple genetic and physiological processes. Meta-QTL and association analyses have identified genomic regions and candidate genes linked to iron-toxicity tolerance, reinforcing the value of integrating molecular evidence with conventional breeding (Jaiswal *et al.*, 2026). Field-based studies have also shown that tissue-level tolerance can contribute to performance under elevated leaf Fe, underscoring the need to evaluate multiple physiological mechanisms (Rosdianti *et al.*, 2025). Transcriptomic analyses have identified distinct regulatory responses in rice roots under excess Fe, highlighting the value of molecular approaches for clarifying tolerance mechanisms (Ueda *et al.*, 2025). Hydroponic screening of diverse rice germplasm continues to reveal substantial genotypic variation and potential donor lines for breeding programmes (Nikhil *et al.*, 2026). In parallel, genetic-diversity analyses of rice germplasm can support the identification of distinct genetic material for breeding programmes (Nandedkar *et al.*, 2025).

Despite substantial progress in describing the physiological, biochemical, and molecular responses of rice to excess iron, the available evidence remains fragmented across individual tolerance mechanisms, developmental stages, and screening environments. A consolidated synthesis is therefore needed to connect iron acquisition, toxicity symptoms, defence responses, and breeding prospects within a single framework.

1.1 Objective of the Review

This review aims to synthesise current knowledge on the role and acquisition of iron in rice, the mechanisms and symptoms of iron toxicity, anatomical, physiological, biochemical, and molecular defence responses, and breeding approaches for improving iron-toxicity tolerance, while identifying priorities for future research and genetic improvement.

2. Role of Iron in Plants

Iron (Fe) is an essential micronutrient required in relatively higher amounts than other trace elements, and it is vital for plant growth, development and reproduction (Kobayashi & Nishizawa, 2012; Harish *et al.*, 2023). Its ability to reversibly cycle between Fe^{2+} and Fe^{3+} enables it to function as both an electron donor and acceptor in key metabolic processes (Zhai *et al.*, 2014).

Iron is involved in critical functions such as photosynthesis, respiration, and enzyme activity, acting as a cofactor in heme and iron-sulfur proteins that regulate electron transport and redox balance (Li & Lan, 2017). Its deficiency disrupts chloroplast development and photosynthesis, thereby reducing plant productivity.

Despite its essential role, iron's redox activity also makes it potentially toxic when present in excess concentrations. Elevated levels of ferrous iron (Fe^{2+}) promote Fenton-type reactions, leading to the generation of reactive oxygen species (ROS) that damage lipids, proteins, and nucleic acids (Wu *et al.*, 2014). To mitigate this, plants have evolved tight regulatory mechanisms controlling iron uptake, transport, and storage to maintain cellular homeostasis (Jeong & Guerinot, 2009). This balance is particularly critical in rice under flooded conditions, where high external Fe^{2+} concentrations often exceed physiological tolerance limits. (Ponnamperuma, 1972; Colombo *et al.*, 2014)

3. Iron Acquisition Strategies in Rice

Plants have evolved distinct strategies for iron acquisition, with rice exhibiting a unique combination of two major systems. Non-graminaceous plants (Strategy I) acquire iron through rhizosphere acidification, reduction of Fe^{3+} to Fe^{2+} at the root surface and subsequent uptake via specific transporters. In contrast, graminaceous species (Strategy II) utilise a chelation-based mechanism, releasing mugineic acid family phytosiderophores (MAs) to solubilize Fe^{3+} and transport Fe(III) -phytosiderophore complexes into root cells via specific transporters such as *OsYSL15* (Inoue *et al.*, 2009).

In rice, iron acquisition entails a modified Strategy II augmented by direct (Fe^{2+}) absorption. Rice predominantly produces the phytosiderophore, 2'-deoxymugineic acid (DMA) through enzymes including nicotianamine synthase (NAS), nicotianamine aminotransferase (NAAT), and deoxymugineic acid synthase (DMAS), which are upregulated in response to iron deficiency (Kobayashi & Nishizawa, 2012). DMA is released into the rhizosphere via transporter TOM1 in a diurnal manner (Nozoye *et al.*, 2011). Moreover, rice expresses the ferrous iron transporter *OsIRT1*, facilitating the direct absorption of Fe^{2+} from the soil solution, despite exhibiting relatively low ferric-chelate reductase activity at the root surface (Ishimaru *et al.*, 2006). Although this dual uptake system represents an adaptation to inundated paddy environments where Fe^{2+} is predominant and more accessible than Fe^{3+} , it also poses a risk during prolonged flooding. Transporters such as *OsIRT1* may facilitate excessive uptake of Fe^{2+} , which can build up in root and shoot tissues and make them more likely to become toxic to iron.

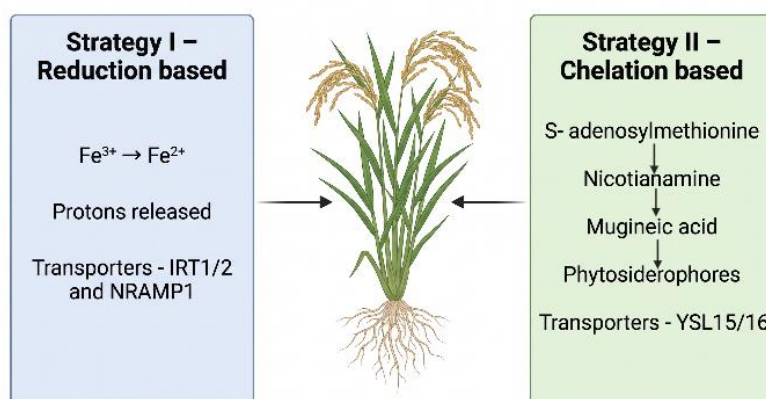


Fig. 1. Iron acquisition strategies in rice. Strategy I (Reduction-based uptake) and Strategy II (Chelation-based uptake)

4. Symptoms of Iron Toxicity in Rice

Excess iron accumulation in rice leads to visible toxicity symptoms, most notably leaf bronzing, in which leaves develop a reddish-brown discoloration that begins at the tips and can progress to necrosis under severe stress (Ponnamperuma *et al.*, 1955; Sahrawat *et al.*, 1996). As toxicity intensifies, plant growth is adversely affected, with reduced tillering, increased spikelet sterility, and consequent yield loss. Plants often appear stunted, with chlorophyll degradation leading to reduced photosynthetic efficiency and lower biomass (Fageria *et al.*, 2008; Sahrawat, 2004).

Root systems are also affected, becoming short, coarse, and darkened, although some recovery may occur if stress conditions improve. At the cellular level, excess Fe^{2+} triggers the formation of reactive oxygen species (ROS) through Fenton reactions, resulting in oxidative damage to key cellular components and further impairing physiological processes. In addition, high iron levels interfere with the uptake of essential nutrients such as phosphorus, potassium, calcium, magnesium, and zinc, compounding the overall stress on the plant (Mandal *et al.*, 2004).

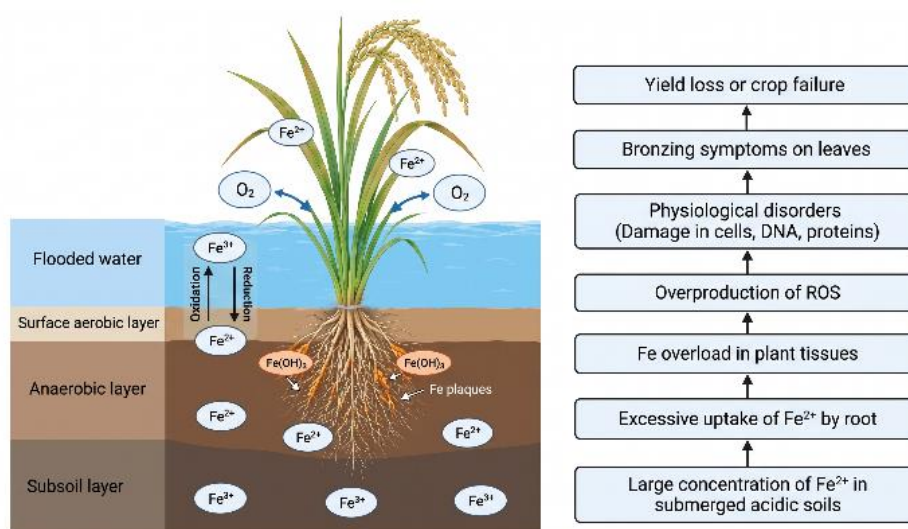


Fig. 2. Effects of iron toxicity in plants

5. Defence Mechanisms Against Iron Toxicity in Rice

Rice has developed a hierarchical, multi-layered defense system against iron toxicity, with sequential lines of protection operating from the root surface inward to the shoot tissues. Each defense layer acts to progressively reduce the quantity of iron that reaches sensitive cellular compartments, and together they constitute an integrated homeostatic network. Iron-tolerant rice genotypes are able to maintain growth under high iron conditions due to a combination of adaptive structural, physiological, biochemical, and molecular traits. Understanding these traits is important for developing improved tolerant varieties (Onyango *et al.*, 2018).

5.1 Anatomical Adaptations

Tolerant plants limit iron entry by promoting rhizospheric oxidation, where oxygen released from roots converts Fe^{2+} into Fe^{3+} , forming protective iron plaques on root surfaces (Green & Etherington, 1977). This ability is stronger in tolerant genotypes due to better internal oxygen transport supported by their root structure, with larger pith cavity diameters and higher lateral root densities (Colmer, 2003). After entry into root cells, rice restricts iron movement to shoots by retaining it in roots. Tolerant genotypes sequester more iron in roots, while the discrimination centre located at the base of the shoot, which serves as a regulatory checkpoint that controls mineral distribution to different plant organs, directs excess iron to older leaves, thereby protecting younger tissues (Stein *et al.*, 2014; Aung & Masuda, 2020).

5.2 Physiological Adaptation

At the physiological level, tolerant rice varieties regulate iron uptake and transport more effectively than susceptible ones. They generally accumulate less iron in shoots due to controlled uptake and translocation (Stein *et al.*, 2009). Enhanced root oxidising capacity helps convert Fe^{2+} to less available Fe^{3+} , limiting iron entry to the plant (Wu *et al.*, 2014). Additionally, tolerant genotypes maintain higher chlorophyll content and photosynthetic efficiency under stress, reflecting better protection of the photosynthetic system.

5.3 Biochemical Adaptation

Rice cells mount a comprehensive antioxidant response involving both enzymatic and non-enzymatic components. Superoxide dismutase, peroxidase, and catalase are upregulated to convert the superoxide radical and hydrogen peroxide, which are primary ROS products of Fenton reactions into harmless water and molecular oxygen (Bode *et al.*, 1995; Fang & Kao, 2000). They also accumulate non-enzymatic antioxidants such as proline and flavonoids that aid in iron chelation and stress mitigation. In addition, increased ferritin levels enable safe storage of excess iron in a non-toxic form, reducing free iron and limiting oxidative damage (Silveira *et al.*, 2009). Cytochrome P450 family genes are also induced under iron excess, suggesting additional enzymatic detoxification pathways (Quinet *et al.*, 2012; Aung *et al.*, 2018).

5.4 Excess Iron Transport Defence Mechanisms in Rice

The first line of defence against iron toxicity in rice occurs at the root level due to anatomical adaptations. When root defences fail, rice compartmentalises excess iron in shoots (shoot compartmentalization), directing it to older leaves. Detoxification is achieved through transport, sequestration, and chelation mechanisms, minimising oxidative damage (Lapaz *et al.*, 2022). The final layer of defence is the direct detoxification of ROS that have already been generated by iron-catalyzed Fenton chemistry.

5.5 Molecular Adaptation

At the molecular level, tolerant genotypes show stronger and more coordinated gene expression responses to iron toxicity by downregulating transporters such as *OsIRT1*, *OsIRT2*, *OsYSL2*, *OsYSL15*, and *OsNRAMP1* to limit uptake and xylem loading under excess iron conditions (Aung & Masuda, 2020). This process is regulated by the hemerythrin motif-containing ubiquitin ligases *OsHRZ1* and *OsHRZ2*, which help maintain iron homeostasis (Kobayashi *et al.*, 2013). Excess iron is detoxified through ferritin sequestration, vacuolar sequestration, and chelation by nicotianamine, reducing oxidative stress (von Wirén *et al.*, 1999). Citrate efflux transporters *OsFRDL1* and *OsFRDL2* facilitate iron movement within shoot tissues, enabling its redistribution from the vasculature to appropriate storage compartments, including nodes involved in grain loading (Yokosho *et al.*, 2016). Ferritin proteins continue their protective sequestration role in shoot cells, and *OsVIT2*-mediated vacuolar compartmentalization operates alongside these mechanisms to isolate iron from the cytoplasm (Zhang *et al.*, 2012). *OsNAS3* upregulation in shoots further enhances nicotianamine-mediated chelation of iron, safeguarding the photosynthetic apparatus and other sensitive organelles from iron-induced oxidative attack (Aung *et al.*, 2018).

6. Breeding for Iron Toxicity Tolerance in Rice

The leaf bronzing score (LBS) serves as the visual assessment of the severity and extent of characteristic bronzing symptoms and is the most widely used field indicator of iron toxicity stress. The visual score is complemented by quantitative measurements of shoot and root biomass, root length, and grain yield, evaluated under both controlled settings (hydroponic and agar-based systems) and natural field conditions (Rout *et al.*, 2014; Nugraha *et al.*, 2016). Controlled environments allow for precise and reproducible genotypic comparisons under defined iron stress levels, while field evaluations capture the complexity of real-world soil variability and assess whether tolerance traits are expressed consistently across diverse agroecological contexts (Mahender *et al.*, 2019).

Developing iron toxicity-tolerant rice requires an integrated breeding strategy combining phenotypic selection with molecular tools. Tolerant germplasm from landraces, wild relatives, and adapted cultivars is used as donor parents and crossed with high-yielding but susceptible varieties. The resulting populations, such as doubled haploids (DH), recombinant inbred lines (RILs), backcross recombinant inbred lines (BRILs), and chromosome segment substitution lines (CSSLs), each offer specific advantages for genetic analysis and selection efficiency (Chrisnawati *et al.*, 2021; Sikirou *et al.*, 2025). The integration of wild relatives of rice as gene sources has broadened the genetic base available for breeding, introducing novel alleles that do not exist in the cultivated gene pool (Rasheed *et al.*, 2020).

Marker-assisted selection (MAS) helps breeders quickly identify important genes linked to iron tolerance, such as *OsIRT1*, *OsIRT2*, *OsFRO2*, *OsNRAMP5*, and *OsbHLH11*, (Wu *et al.*, 2014; Rasheed *et al.*, 2020; Chrisnawati *et al.*, 2021) without having to wait for plants to grow under stressful conditions. At the same time, genome-wide association studies (GWAS) and SNP-based tools have revealed key QTLs across chromosomes 1, 2, 3, 4, 6, and 10 that influence traits like plant growth and biomass under iron stress (Zhang *et al.*, 2017; Kaewcheenchai *et al.*, 2021; Pawar *et al.*, 2021). These molecular approaches make it possible to combine multiple tolerance traits such as limiting iron uptake, storing excess iron safely, and reducing oxidative damage into a single rice variety, leading to stronger and more stable resistance (Gupta *et al.*, 2025; Sikirou *et al.*, 2025). The convergence of approaches such as classical phenotyping, advanced genomics, and mechanistic physiology represents the most promising path toward developing high-yielding rice cultivars capable of sustaining productivity in iron-toxic environments (Mahender *et al.*, 2019; Pawar *et al.*, 2021; Miao *et al.*, 2024).

Overall, the greatest progress is being achieved by combining traditional selection, modern genomics, and physiological understanding to develop high-yielding rice that can withstand iron-rich, stress-prone soils.

7. Conclusion

Iron toxicity is one of the most complex and frequently overlooked abiotic constraints in global rice production. This review illustrates that iron toxicity arises from a network of overlapping factors rather than a single source. It is driven by the dynamic relationship between soil chemistry, plant biology, and environmental changes, and requires a broad and integrated scientific strategy to address it effectively. Rice plants face a fundamental biological challenge in flooded paddy fields due to the dual role of iron: it is an essential micronutrient necessary for growth, yet it can become a toxic threat to cells when present in excessive amounts. Rice employs a hybrid system for iron acquisition that integrates elements of both strategies, facilitated by the synchronised function of *OsIRT1* and phytosiderophore-mediated uptake. This dual approach provides rice with a competitive advantage in environments where Fe is scarce. However, it also makes the plant vulnerable to iron toxicity when there is an increase in soil ferrous iron levels due to extended anaerobic conditions.

The spectrum of toxicity symptoms, ranging from typical leaf bronzing and reduced tillering to root damage and widespread oxidative stress driven by Fenton chemistry, leads to significant and sometimes complete yield loss. Tolerant rice genotypes mitigate this threat through a hierarchical, multi-layered defense system that operates sequentially from the rhizosphere, involving oxidation in the rhizosphere and iron plaque formation on the root surface, active retention and vacuolar sequestration within root tissues, shoot compartmentalization targeting older leaves, and enzymatic and non-enzymatic ROS detoxification as the final cellular defense. The molecular basis of these mechanisms involves regulation by iron transporters, ferritin proteins, nicotianamine chelators, and stress-responsive transcription factors. The regulatory networks that govern stage-specific shifts in tolerance mechanisms throughout the crop life cycle are not fully understood, and the functional characterization of several candidate genes and QTLs identified through GWAS and marker-assisted studies still requires rigorous validation under real field conditions.

8. Future Prospects

Future research must prioritise a comprehensive and mechanistic understanding of tolerance pathways. Comprehensive characterisation of the molecular and physiological mechanisms regulating Fe uptake and transport, in relation to key morpho-physiological traits, is needed to enhance their integration into rice breeding programmes (Mahender *et al.*, 2019). Genome-wide association studies (GWAS) performed on diverse rice populations have effectively identified several quantitative trait loci (QTLs) and candidate genes linked to enzymes that neutralise reactive oxygen species (ROS) and ensure Fe balance. Notably, genes involved in vacuolar iron transport and ferritin regulation have been identified as promising candidates for marker-assisted selection (Miao *et al.*, 2024). However, a significant challenge lies in the fact that various tolerance mechanisms, such as Fe exclusion, compartmentalization in older tissues, and tissue tolerance shift, have different relative importance depending on growth stage and environmental conditions. Using visible phenotypic traits, particularly the expression of symptoms in early seedlings, as the only criterion for identifying Fe-tolerant genotypes is a restrictive approach that overlooks the complexity of tolerance during later stages of growth. Additionally, traditional screening techniques that utilise controlled nutrient solution environments do not adequately reflect the ecological and physiological realities necessary to fully understand the dynamic and complex nature of Fe toxicity tolerance throughout the entire life cycle of rice crops under field conditions (Rajonandraina *et al.*, 2023). Therefore, future breeding efforts should focus on the use of specific molecular markers and customised screening for individual traits, particularly for underground mechanisms such as root iron oxidation and retention.

In plant breeding, combining different tolerance traits with high-yielding backgrounds through marker-assisted selection and genomic tools can help develop promising rice varieties. Further improvement can be achieved by integrating transcriptomic, metabolomic, and proteomic approaches with conventional and molecular breeding methods. These approaches can help identify key regulatory mechanisms, improve marker efficiency, and accelerate the development of iron-toxicity-tolerant varieties. In addition to genetic improvement, management practices such as alternate wetting and drying, organic matter application, and

balanced nutrient management can help reduce iron toxicity. The combined use of tolerant varieties and appropriate management practices can provide more effective control. Future efforts should focus on integrating genomics, systems biology, and improved crop management to promote sustainable rice production in areas affected by iron toxicity.

9. Limitations

This review is limited by the heterogeneity of published studies in experimental conditions, rice genotypes, developmental stages, iron concentrations, and screening methods. Results obtained from hydroponic or other controlled systems may not fully represent field conditions, where soil chemistry and environmental factors interact dynamically. In addition, several candidate genes, QTLs, and proposed tolerance mechanisms still require validation across diverse genetic backgrounds and agroecological environments. Direct comparisons among studies should therefore be interpreted cautiously.

Declaration of AI Use

This manuscript was prepared through the intellectual contributions of the author(s) to the study design, data analysis, interpretation of results, and scholarly content. Grammarly and ChatGPT were used solely to assist with grammatical refinement and reference formatting during manuscript revision. The author(s) accept full responsibility for the accuracy, integrity, and final content of the manuscript.

Competing Interests

Authors have declared that no competing interests exist.

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