

Meta-analysis of drought and iron excess stress-responsive gene expression profiles in rice

Divya Gupta, Hans-Jörg Mai, Petra Bauer, Sanjib Kumar Panda

Article - Version of Record

Suggested Citation:

Gupta, D., Mai, H.-J., Bauer, P., & Panda, S. K. (2026). Meta-analysis of drought and iron excess stress-responsive gene expression profiles in rice. *Plant Stress*, 20, Article 101297.
<https://doi.org/10.1016/j.stress.2026.101297>

Wissen, wo das Wissen ist.



UNIVERSITÄTS-UND
LANDESBIBLIOTHEK
DÜSSELDORF

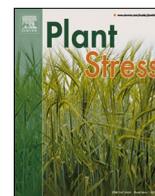
This version is available at:

URN: <https://nbn-resolving.org/urn:nbn:de:hbz:061-20260309-125232-7>

Terms of Use:

This work is licensed under the Creative Commons Attribution 4.0 International License.

For more information see: <https://creativecommons.org/licenses/by/4.0>



Meta-analysis of drought and iron excess stress-responsive gene expression profiles in rice

Divya Gupta^{a,b}, Hans-Jörg Mai^a, Petra Bauer^{a,c,*}, Sanjib Kumar Panda^{b,*}

^a Institute of Botany, Heinrich Heine University, 40225 Düsseldorf, Germany

^b Plant Functional Genomics and Molecular Biology Laboratory, Department of Biochemistry, Central University of Rajasthan, Ajmer, Bandarsindri, 305817 Rajasthan, India

^c Center of Excellence on Plant Sciences (CEPLAS), Düsseldorf, Germany

ARTICLE INFO

Keywords:

Keteki Joha
Drought
Iron
miRNA
Transcriptomics

ABSTRACT

Drought and iron (Fe) toxicity are major abiotic stresses that significantly limit rice productivity. While drought reduces water availability and thereby restricts Fe uptake, waterlogged or rainfed conditions increase soluble Fe levels. Despite these contrasting environments, both stresses trigger oxidative damage caused by reactive oxygen species (ROS). This raises key questions on how plants adjust to such distinct conditions, what responses are shared, and which are stress-specific. To address this, we performed a meta-analysis of transcriptome datasets for drought and Fe excess in the lowland aromatic rice variety Keteki Joha at two developmental stages. Common responses included upregulation of ROS scavenging systems, transcriptional regulation, and hormonal signaling pathways. In contrast, stress-specific responses showed distinct patterns. Under Fe toxicity, unique DEGs were enriched in antioxidant activity, peroxidase function, and ROS metabolism, highlighting the importance of redox defense. In parallel, several genes regulating Fe acquisition and homeostasis, including *OsNAS1/2*, *OsHRZ2*, and *IMAI*, were consistently downregulated, indicating a transcriptional shift to suppress further Fe uptake while enhancing compartmentalization and detoxification to maintain internal balance. Under drought, DEGs were mainly involved in RNA metabolism, protein folding, and vesicle-mediated transport, pointing to post-transcriptional and post-translational regulation as adaptive mechanisms. Additionally, 26 microRNAs (miRNAs) were identified as regulators of transcription factors under both stresses, suggesting an integrated miRNA-TF-target gene regulatory network. Together, these findings provide insights into the molecular basis of stress resilience and identify potential gene targets for crop improvement.

1. Introduction

Global climate change has intensified the frequency and duration of abiotic stresses such as drought, posing a long-term threat to global food security. One major challenge in this context is how to sustain rice productivity under threat for exposure to various stresses, such as drought and/or iron (Fe) toxicity (Oladosu et al., 2019; Gupta et al., 2025). This is particularly critical for aromatic rice cultivars like Keteki Joha—an indigenous variety from Assam, India—prized for its fragrance and high market value but known for its sensitivity to environmental stressors (Das et al., 2010; Sahoo et al., 2019). While its aromatic quality makes it an economically valuable target for genetic improvement, its stress susceptibility limits its performance in rainfed and marginal

ecosystems (Bordoloi et al., 2024).

Within the broader field of plant stress physiology, advances have been made in understanding responses to individual stresses. For instance, drought stress impairs physiological processes in rice, manifesting in leaf rolling, reduced growth, and tissue necrosis (Zampieri et al., 2023; Regon et al., 2024). Similarly, Fe—though essential for photosynthesis, respiration, and redox reactions (Kobayashi and Nishizawa, 2014; Zhai et al., 2014)—becomes toxic under flooded, acidic soil conditions typical of rice cultivation, where Fe²⁺ accumulates, induces oxidative damage and similar morphological responses such as leaf rolling and reduced growth (Becker and Asch, 2005; Kar et al., 2021). Clearly, there remains a critical knowledge gap regarding how rice plants respond similarly or differently to drought and Fe toxicity,

* Corresponding authors.

E-mail addresses: gupta.divya.biotech20@gmail.com (D. Gupta), hans-joerg.mai@hhu.de (H.-J. Mai), petra.bauer@hhu.de (P. Bauer), sanjib.panda@curaj.ac.in (S.K. Panda).

<https://doi.org/10.1016/j.stress.2026.101297>

Received 25 October 2025; Received in revised form 21 January 2026; Accepted 14 February 2026

Available online 15 February 2026

2667-064X/© 2026 The Authors. Published by Elsevier B.V. This is an open access article under the CC BY license (<http://creativecommons.org/licenses/by/4.0/>).

especially at the transcriptomic level. Most existing studies have treated these stresses in isolation, overlooking potential crosstalk (Bashir et al., 2014; Aung and Masuda, 2020; Regon et al., 2022; Kaur et al., 2023; Regon et al., 2024; Gupta et al., 2025).

In Keteki Joha, transcriptomic studies under drought and Fe stress (Regon et al., 2022, 2024; Gupta et al., 2025) have identified differentially expressed genes (DEGs) involved in stress mitigation, but they do not yet explain how plants integrate these signals during both types of stress exposure. Moreover, while many studies have identified components such as reactive oxygen species (ROS) scavenging enzymes, phytohormonal pathways, transcription factors (TFs) and miRNAs as key players in single-stress responses (Zhang et al., 2022; Bhoite et al., 2025; Das et al., 2025). For example, in rice, overexpression of the novel stress-related transcription factor *OsbZIP62* has been shown to enhance tolerance to both drought and oxidative stress (Yang et al., 2019). In a recent study, the ethylene signaling regulators *OsEIL1* and *OsEIL2* were shown to promote coleoptile elongation and seedling emergence in rice by enhancing the expression of ROS-scavenging genes (Qiao et al., 2024). Similarly, in rice, miRNAs such as *Osa-MIR169a*, *Osa-MIR171b/f*, *Osa-MIR397a*, and *Osa-miR530-3p* have been shown to modulate key target genes affecting spikelet fertility and grain quality, thereby playing a crucial role in shaping drought stress responses, particularly in sensitive varieties like Swarna (Kumar et al., 2024). In other study, in rice, miRNAs including *miR166*, *miR399*, *miR408*, and several novel candidates have been implicated in regulating iron uptake and transport, where reduced expression of specific novel miRNAs in *FER1*-overexpressing lines enhances *NRAMP4*-mediated iron loading into seeds (Paul et al., 2016). The common set for interplay of basic underlying stress conditions in drought and Fe excess remains poorly understood.

This raises several open questions: Are there similarities in how molecular signaling networks reorganize under drought and Fe stress? Are there shared regulatory nodes—such as specific TFs, miRNAs, or hormonal regulators—that could even mediate crosstalk between these stress pathways? And how do these networks change across developmental stages? Identifying such shared components could help pinpoint robust stress-response hubs for special attention in breeding or genome editing.

To answer these questions, we employed a metadata analysis of transcriptomic datasets from Keteki Joha plants that had been exposed in comparably similar experimental setups to drought and Fe stress at both seedling and mature stages (Regon et al., 2022; Regon et al., 2024). This enabled us to identify the interesting key genes, along with their pathways and regulatory networks, that coordinate the responses to both these stresses of drought and Fe excess, an outcome that we present here.

2. Methodology

2.1. Transcriptome data collection and metadata retrieval

Transcriptomic datasets from Keteki Joha rice exposed to drought and iron stress were obtained from previously published studies (Regon et al., 2022; Regon et al., 2024). These datasets included gene expression profiles from both seedling and mature plant stages under control and stress conditions. Metadata for each dataset, including developmental stage, stress type, and treatment conditions, was compiled prior to analysis.

2.2. Identification and filtering of differentially expressed genes (DEGs)

Differentially expressed genes (DEGs) were retrieved from each dataset as reported in the respective studies using their defined statistical thresholds. To identify shared and stress-specific transcriptional responses, DEGs were filtered based on their regulation patterns across conditions. Genes showing significant differential expression under both drought and iron stress were classified as commonly regulated, whereas

genes differentially expressed exclusively under either drought or iron stress were considered stress-specific. Filtering was performed jointly by considering DEGs from both seedling and mature developmental stages together, enabling the identification of conserved as well as stage-dependent stress responses. Hierarchical clustering of the filtered DEGs was performed using pheatmap v1.0.12 (Kolde, 2019) based on normalized expression values.

2.3. Regulatory gene prioritization and network-based filtering

Subsets of DEGs were narrowed down based on their functional roles. The prioritization focused on biologically relevant genes and criteria as indicated in the result section. Functional categories for reactive oxygen species (ROS) metabolism and antioxidant defense included enzymatic antioxidant production pathway such as superoxide dismutase (SOD), catalase (CAT), ascorbate peroxidase (APX), glutathione peroxidase (GPX), and glutathione reductase (GR), non-enzymatic antioxidant pathways, and ROS-producing pathways. A curated list of ROS- and antioxidant-associated genes in rice was compiled using Gene Ontology (GO) term searches in AmiGO 2 (<http://amigo.geneontology.org/>). Relevant GO terms included categories linked to ROS metabolism, hydrogen peroxide response, redox regulation, and cellular detoxification.

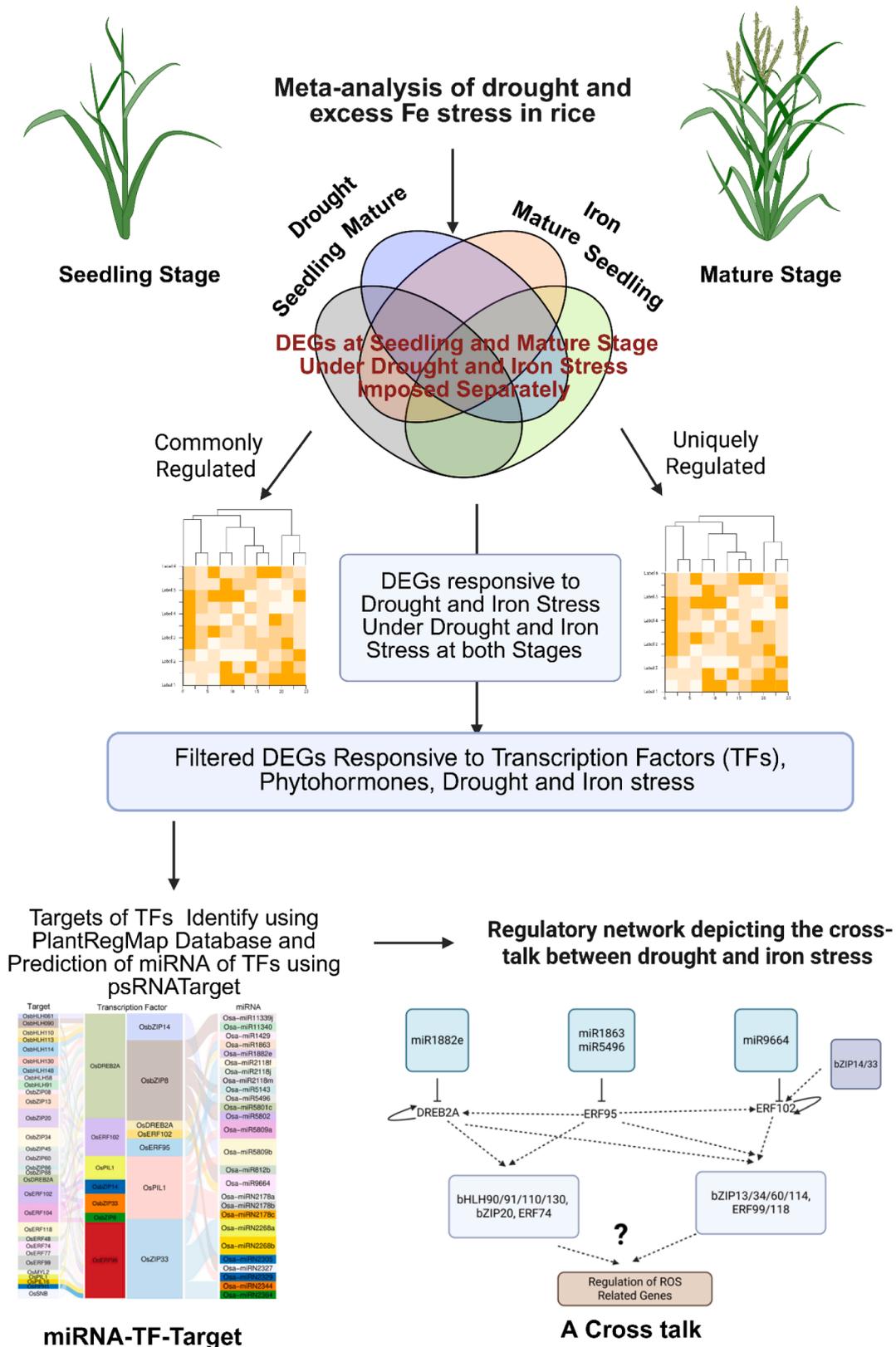
For transcription factor (TF) analysis, a genome-wide list of TFs and TF–target regulatory relationships for *Oryza sativa* were obtained from PlantRegMap (Tian et al., 2020). The DEG list was screened against this dataset to identify differentially expressed TFs and their experimentally supported or computationally predicted target genes. TF–target associations overlapping with the stress-responsive DEG pool were retained to construct a stress-relevant regulatory subnetwork. To focus on regulators with stronger biological impact, only TFs exhibiting substantial differential expression ($|\log_2 \text{fold change}| \geq 1.5$) were selected for network construction, while their downstream targets were retained regardless of fold-change magnitude, provided they were classified as DEGs. This step was intended to prioritize key regulatory drivers rather than to re-identify DEGs.

Curated gene sets were mapped to the DEG data to identify responsive regulatory modules at both developmental stages. Small RNA–TF gene target interactions were predicted as follows: Coding sequences (CDS) of TFs were retrieved from the PMI-ren rice sequence database (<https://www.pmiren.com>) and submitted to the psRNATarget web server (<https://www.zhaolab.org/psRNATarget>) to predict potential small RNA/miRNA binding partners (Dai et al., 2018; Guo et al., 2020). Predicted interactions were noted to identify TFs that may be regulated by small RNAs during stress. TF–target–miRNA interaction framework was visualized through a Sankey diagram generated using SRPlot (Tang et al., 2023). To further enhance the depth of analysis, a co-expression network was constructed using Cytoscape v3.10.3 (Kohl et al., 2010).

3. Results and discussion

3.1. Design of the meta-analysis approach to identify key regulator genes and networks for drought- and Fe excess stress in Keteki Joha rice

The advantage of using two Keteki Joha rice transcriptome datasets (Regon et al., 2022; Regon et al., 2024) is that they uniquely capture both similar developmental stage-specific and stress-specific gene expression under drought and Fe excess stress separately. These datasets were reduced to differentially expressed genes (DEGs) and then filtered for specific functional response terms and used in regulatory network analysis (general outline of the workflow in Fig. 1). By comparing DEGs across stages and stress conditions, we were able to uncover conserved regulatory mechanisms that might be missed in single-condition snapshots or by comparing outcomes of totally different experimental setups. This integrative approach identifies the responsive genes and provides insights into the underlying logic of regulatory hierarchies and stress



prioritization, as described in the subsequent paragraphs.

3.2. Developmental stages and different stress conditions: overview of DEGs

An overview of the available transcriptome data and their investigation in this study for identifying the overlapping and differing pathways for drought and Fe excess responses in Keteki Joha is provided (Fig. 2a). The seedling stage data and the mature stage data are from leaves only. The significantly regulated DEGs in both conditions were grouped into ten distinct clusters based on their expression patterns across different developmental stages and stress treatments (Table S1). In our analysis we describe as “commonly” regulated those genes that are similarly regulated in both stresses, and as “uniquely” regulated those genes that are either drought stress or Fe excess stress-regulated. Such genes are discriminated in either hierarchical clustering (Fig. 2a) or Venn diagram analysis (Fig. 2b). Interestingly, the extent of differential gene expression was greater at the mature stage compared to the seedling stage, suggesting a more robust transcriptional reprogramming in response to stress as plants advance in development. Additionally, a general trend of upregulation over downregulation was observed, indicating activation of stress-responsive pathways may outweigh repression of growth-related functions under combined abiotic stress.

3.2.1. Commonly regulated genes under drought and iron stress (Clusters 1 and 8)

Transcriptome profiling revealed Clusters 1 and 8 as the major groups of commonly regulated genes across both drought and iron stress and across seedling and mature stages. Cluster 1 genes were consistently upregulated (789 genes), indicating activation of stress perception pathways, hormone- and transcription-mediated signaling, osmotic adjustment, and redox regulation. This suggests a shared protective strategy involving resource allocation toward regulatory and defense processes. In contrast, Cluster 8 genes were downregulated (645 genes), predominantly representing photosynthesis-, secondary metabolism-, and growth-related transcripts. This repression likely conserves energy by limiting carbon assimilation and metabolic investment during stress. Together, these clusters reflect a coordinated trade-off where plants enhance defense and signaling (Cluster 1) while suppressing growth and photosynthetic output (Cluster 8) to maintain homeostasis under combined drought and iron stress.

3.2.2. Stage-specific regulation under combined drought and iron stress (Clusters 2, 5, and 7)

Stage-dependent regulation revealed that seedlings and mature plants adopt distinct strategies. Cluster 2 (seedling upregulated) showed activation of amino acid and small-molecule metabolism, catabolic and autophagy pathways, and transcriptional/RNA regulation, indicating rapid metabolic reprogramming for early stress adjustment. In mature plants, Cluster 5 displayed upregulation of carbohydrate and secondary

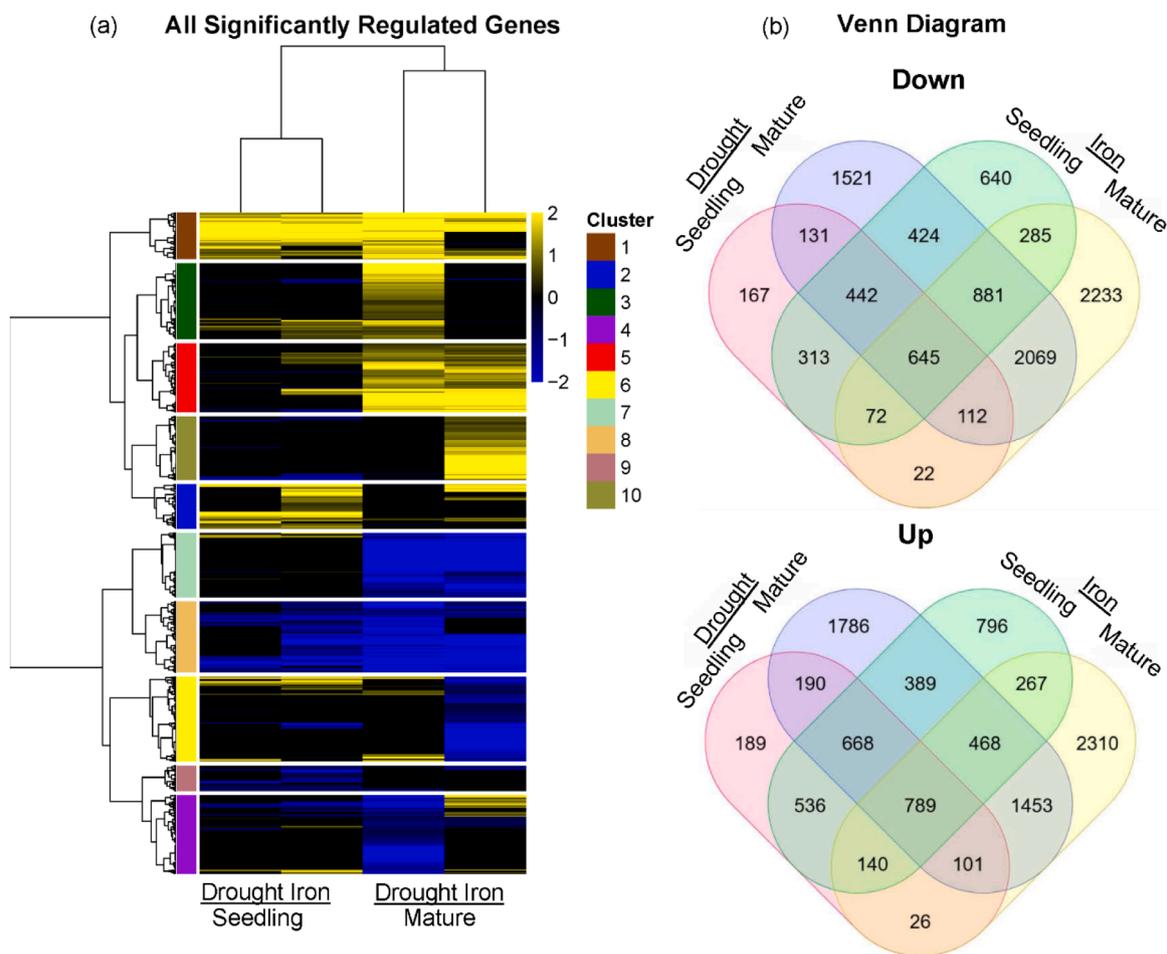


Fig. 2. (a) Clustering of differentially expressed genes (DEGs) under drought and iron stress at seedling and mature stages in Keteki Joha. The DEGs are grouped into eight distinct clusters based on their expression patterns across the different stress conditions and developmental stages. Here, blue to yellow color gradient is showing gradual fold changes from negative to positively regulated DEGs. (b) Venn diagrams illustrating the overlap and distribution of DEGs under drought and iron stress conditions.

metabolism, terpenoid pathways, ion transport, and proteostasis, reflecting a compensatory defense mode to stabilize metabolism and maintain Fe balance during reproductive growth. Conversely, Cluster 7 (mature downregulated) showed suppression of primary metabolism, cell wall formation, reproductive signaling, and hormone-mediated development, suggesting a shift away from growth investment toward survival. These patterns highlight a transition from metabolic flexibility in seedlings to defense prioritization in mature plants.

3.2.3. Iron stress-specific regulation (Clusters 6, 9, and 10)

Iron stress responses also varied by developmental stage. In seedlings, Cluster 9 exhibited strong downregulation of genes associated with ion transport, photosynthesis, and antioxidant defense, reflecting reduced nutrient homeostasis and metabolic vulnerability. In mature plants, Cluster 6 showed repression of secondary metabolism, phenylpropanoid/lignin biosynthesis, and ROS detoxification, indicating energy conservation at the expense of structural integrity and detoxification capacity. Conversely, Cluster 10 was upregulated and enriched in stress signaling, phosphorylation-based regulation, auxin-linked responses, and amino acid metabolism, suggesting that mature tissues compensate through signaling-mediated adaptation rather than structural reinforcement. These contrasting responses illustrate a developmental shift from impaired metabolic control in seedlings to signaling-dependent tolerance in mature plants.

3.2.4. Contrasting drought responses at the mature stage (Clusters 3 and 4)

Under drought at maturity, Cluster 3 was upregulated, with increased expression of ROS-detoxifying enzymes, ion transporters, protein-folding machinery, and carbohydrate metabolism genes, indicating enhanced redox stability, osmotic regulation, and metabolic flexibility. Conversely, Cluster 4 showed strong downregulation of photosynthesis, chloroplast maintenance, carbon fixation, ribosome biogenesis, and nutrient metabolism, reflecting a suppression of energy-intensive growth processes. This trade-off reinforces a drought adaptation mechanism where defense and cellular protection are prioritized (Cluster 3) while growth and biosynthetic activity are strategically limited (Cluster 4).

3.3. Unique and common drought- and iron-responsive genes across developmental stages in Keteki Joha

In the above paragraph, we outlined the genes regulated across different developmental stages under both stress conditions. To gain deeper insights, we further investigated the cross-talk between drought and iron stress by examining the regulation patterns of differentially expressed genes (DEGs) that are either commonly shared or uniquely responsive at both the seedling and mature developmental stages.

Uniquely drought- or iron-responsive DEGs were predominantly regulated at the mature stage (Fig. S1a, Table S2). Under drought stress, rice exhibits a set of genes uniquely regulated in a stage-specific manner. Among the drought-responsive genes, *OsDIRP1*, a drought-induced RING protein (E3 ubiquitin ligase), was consistently upregulated at both seedling and mature stages. Although previous studies describe it as a negative regulator of drought and salt stress but a positive regulator of cold stress (Cui et al., 2018), our results suggest a stage-specific activation under drought, indicating a context-dependent role. At the seedling stage, genes responsive to *OsDERF4* (ERF/DREB transcription factor) was specifically induced, whereas at the mature stage, *HIPP41* and *MYB76* were uniquely upregulated, reflecting their involvement in long-term drought adaptation. Conversely, *MIZ1*, *Ghd2* (BBX8), and *SDRLK-35* were downregulated, suggesting developmental fine-tuning of growth and stress-response pathways.

Similarly, among iron-responsive genes, *OsIAMT1* (Indole-3-acetic acid methyltransferase 1 / SABATH family protein) showed increased expression at the seedling stage, supporting early auxin-mediated stress adaptation. At the mature stage, *OsHIPP41* was again uniquely

upregulated, highlighting its dual role in drought and iron-related stress tolerance. In contrast, *OsABCG14*, *OsABCG40*, *OsABCG47*, *OsABCG29*, *OsABCA2*, and *OsISC42* (Rubredoxin-like protein) were strongly downregulated. Previous studies link *AtABCG14* to cytokinin transport (Zhang et al., 2014) and *ABCG40* to heavy metal detoxification (Dhara and Raichaudhuri, 2021), suggesting that drought may specifically affect iron-related detoxification and signaling pathways during later developmental stages. Collectively, seedlings appear to prioritize hormonal regulation and early stress signaling, whereas mature plants fine-tune iron homeostasis and stress-response networks, reflecting a developmental stage-specific regulation of both drought- and iron-responsive genes under drought stress.

Under iron excess conditions, uniquely expressed DEGs responsive to drought and iron stress were more prominent at the mature stage than at the seedling stage (Fig. S1b, Table S2). Drought-responsive genes under iron stress in rice show both stage-specific and common expression patterns. At the seedling stage, genes such as *SDRLK-17*, *OsNAC016*, and *OsCHR730/OsDNA2_11* are upregulated, reflecting early activation of signaling, transcriptional regulation, and genome maintenance. At the mature stage, upregulated genes include kinases (*OsSDK10*, *SDRLK-53*, *ECK1*), transcription factors (*OsDREB1G*, *OsERF096*, *OsAHL13*), antioxidant and metabolite-modifying enzymes (*OsGSTU37*, *UGT85E1*), and structural/signaling proteins (*OsRALF45*, *OsLTPd11*), while several genes such as *Os2R_MYB89*, *OsPIN10a*, *OsCUT1*, *OsGL1-3*, *OsGL1-2*, *SDRLK-22*, *OsFTIP6*, *OsSCE3* are downregulated, indicating reduced structural and hormonal responses. Importantly, some genes are consistently upregulated at both stages, including *OsGSTU30*, *OsCBL5*, *OsASLRK*, *OsUGT3*, and *OsNAC045*. Notably, *OsUGT3* (UDP-glycosyltransferase) and *OsNAC045* were consistently upregulated at both stages, aligning with previous studies showing that their overexpression confers enhanced tolerance to drought and salt stress in rice (Zhang et al., 2020; Wang et al., 2021). Overall, these patterns reveal a coordinated response, with seedlings emphasizing transcriptional and genome-level regulation, and mature plants balancing stress signaling, antioxidant defense, and structural adaptation.

Iron-responsive genes in rice exhibit stage-specific and shared regulation under iron stress. At the seedling stage, genes involved in iron uptake and homeostasis, such as *OsGFD1*, *OsTOM1*, *OsYSL15*, *OsOPT7*, *OsIRT2*, and transcription factors *OsbHLH156* and *OsbHLH133*, are downregulated, while genes associated with iron storage and compartmentalization, including *OsVIT2*, *OsPME2*, and *OsABCG48*, are upregulated, supporting redistribution and adaptation. At the mature stage, metal transport and detoxification genes, such as *OsABCG41*, *OsMATE12*, *Os10g0344900*, and *OsZIP9*, are upregulated, whereas *Os02g0599500*, *OsMATE33*, *Os09g0249000*, *OsPME17*, and *OsCRL4* are downregulated, indicating active nutrient mobilization alongside reduced stress signaling. Some genes, including *OsNAS1*, *OsNAS2*, *OsHRZ2*, and *OsIMA1*, are consistently downregulated at both stages, reflecting a core repression of iron uptake and regulatory pathways. Conversely, *IMA1* (ironman), a key regulator of iron uptake, was uniquely downregulated at both stages, supporting its negative regulation of iron homeostasis under excess conditions (Cao et al., 2024). Overall, seedlings focus on balancing uptake and compartmentalization, while mature plants emphasize transport, homeostasis, and metal redistribution under iron stress.

Further analysis of commonly regulated DEGs under drought and iron stress revealed eight expression clusters across developmental stages (Fig. S2). Among drought-responsive genes, Cluster 2 represented the commonly upregulated group at both stages, reflecting a shared adaptive mechanism. These genes were enriched for responses to salt stress, water deprivation, and chemical stimuli, indicating activation of broad abiotic stress pathways (Table S3, Fig. S3a). In contrast, Cluster 8, the commonly downregulated group, included genes linked to the MAPK signaling pathway, suggesting reduced energy-intensive signaling and a shift toward resource conservation during stress adaptation. For iron-responsive DEGs, Cluster 1 contained genes consistently upregulated

across stages, enriched for xenobiotic transport, detoxification, and iron-sulfur cluster assembly, highlighting roles in redox balance and iron metabolism. Meanwhile, Cluster 8 displayed consistent down-regulation and was associated with transition metal ion transport, indicating restricted metal mobilization to avoid toxicity (Table S3,

Fig. S3b).

Overall, the analysis of DEGs responsive to drought and iron stress across developmental stages reveals both unique and common regulatory patterns. Key genes involved in detoxification, metal transport, and stress signaling were differentially expressed, highlighting their

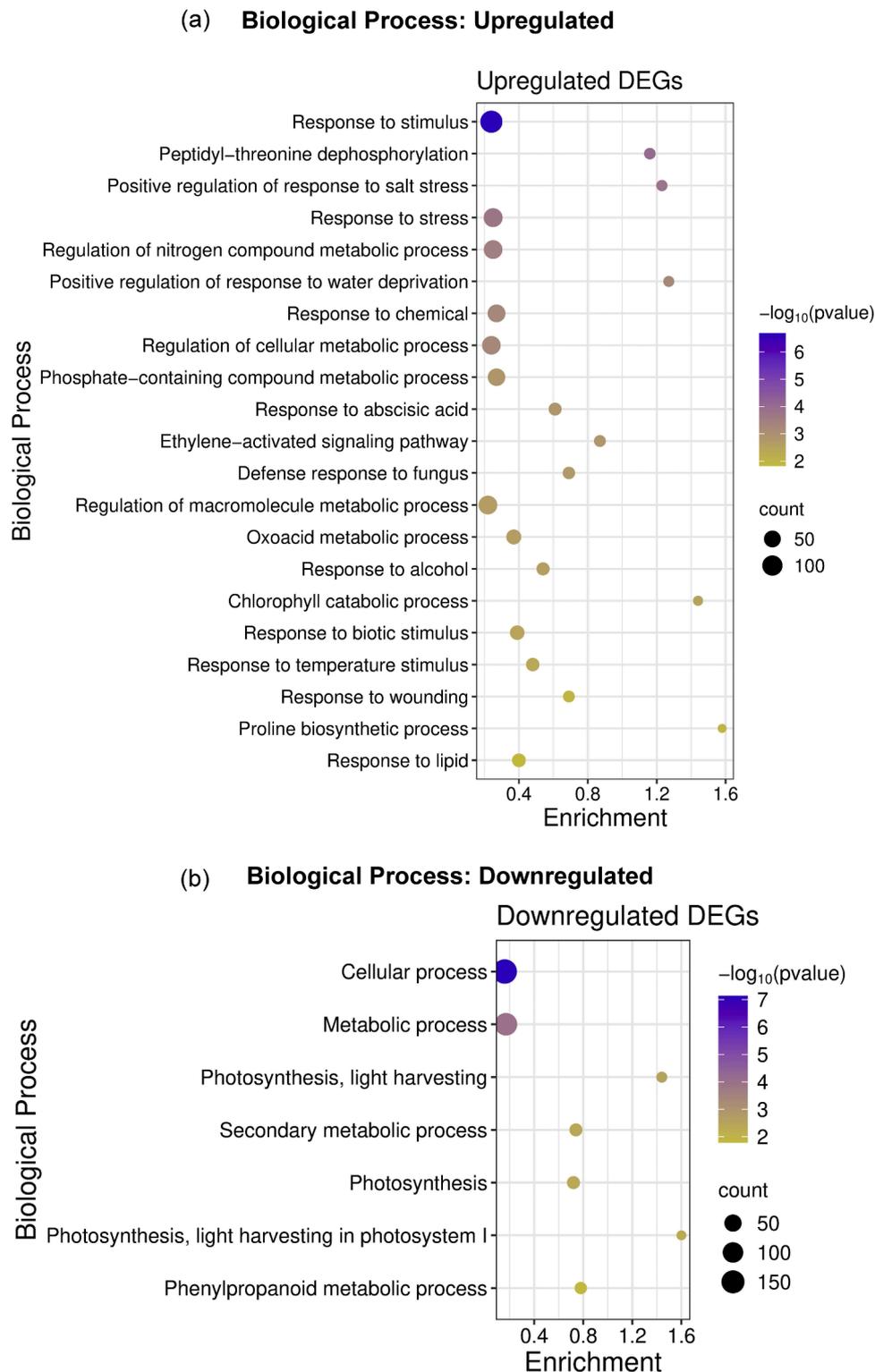


Fig. 3. Depiction of the involvement of commonly upregulated and downregulated differentially expressed genes (DEGs) in key biological processes in *Keteki Joha* under drought and iron stress at both seedling and mature stages. Gene ontology terms of related DEGs were identified using g:profiler (<https://biit.cs.ut.ee/gprofiler/gost>) and represented using SRplot (<https://www.bioinformatics.com.cn/en>). Here, blue to yellow color gradient shows gradual changes in p-value from higher to lower. Similarly size of the representing dots increases based on counts, that is number of genes linked with the biological process.

potential role in mediating cross-talk between drought and iron stress responses in Keteki Joha.

3.4. Peroxidase and peroxiredoxin: key reactive oxygen species regulators under different stress conditions

Peroxidases are a group of heme-containing oxidoreductase enzymes that catalyze the reduction of hydrogen peroxide using various electron donors, playing a crucial role in managing oxidative stress in plants (Kidwai et al., 2020). Among them, class III peroxidases—also referred to as secretory peroxidases—are predominantly localized in the vacuole or extracellular matrix and are considered key players in cell wall modification, lignification, and defense responses (Hiraga et al., 2001). In parallel, peroxiredoxins represent a distinct class of thiol-dependent peroxidases that serve as antioxidants by detoxifying reactive oxygen species (ROS), particularly peroxides, thereby preserving cellular redox homeostasis under stress conditions (Dietz, 2003). Their differential regulation under drought and excess Fe stress supports our hypothesis that diverse antioxidant systems contribute to genotype-specific tolerance. This addresses an open question raised in the introduction regarding the molecular mechanisms behind aromatic rice's variable stress response and emphasizes the value of transcriptomic comparisons for identifying key regulatory networks (Fig. 3).

In this meta-analysis, the roles of peroxidases and peroxiredoxins were examined under drought and iron (Fe) stress at different developmental stages. At the mature stage, peroxidases were more prominently regulated compared to the seedling stage. Notably, several peroxidases, including *PRX41*, *PRX71*, and *PRX11*, were commonly downregulated across both developmental stages under different stress conditions (Fig. 4a and b). A recent study by Ghosh et al. (2017) reported that *Os1-CysPRXB* is involved in root development and was upregulated at both stages. In contrast, *Os1-CysPRXA*, which is seed-specific and associated with storage tissue formation, was found to be upregulated at the seedling stage under both drought and Fe stress conditions (Fig. 4b). Class and predicted subcellular localization of reported peroxidases were listed in Table 1.

At the seedling stage, *PRX24* was found to be upregulated. This Class II peroxidase plays a key role in regulating ROS homeostasis in guard cells and is involved in stomatal movement. *PRX24* functions in coordination with *DCA1* (DST Co-Activator 1) and *DST* (Drought and Salt Tolerance) to enhance drought and salt stress tolerance (Cui et al., 2015). Additionally, *PRX24* has been shown to be essential for the formation of iron plaques on rice roots under alternate wetting and drying (AWD) conditions. These iron plaques serve as a physical barrier against toxic ions and enhance the availability and uptake of phosphorus (Yang et al., 2020).

At the mature stage, glutathione peroxidases (GPXs)—which are non-heme peroxidases—were upregulated under different stress conditions, functioning to prevent cellular damage through ROS scavenging (Fig. 4a). Supporting this, knockdown of *OsGPX1* led to reduced ROS-scavenging capacity under drought stress. The expression of *OsGPX1* is transcriptionally regulated by *OsADR3* (Abscisic Acid-Drought-ROS3), as demonstrated through yeast one-hybrid assays (Li et al., 2021). In another study, *OsGPX3* and *OsGPX5* were reported to be upregulated in root tissues after 12 hours of drought stress. However, *OsGPX5* showed a significant downregulation in shoot tissues under the same stress condition (Islam et al., 2014). Apart from peroxidases and peroxiredoxins, several other ROS-related genes also showed upregulation at the mature stage. One such group includes cytosolic Cu/Zn superoxide dismutases (*CSD1/2*), which are key antioxidant enzymes regulated by miR398. A recent study demonstrated that moderate suppression of *OsCSD1/2* via miR398 enhanced rice growth and yield. However, excessive downregulation impaired vein formation and significantly reduced biomass, highlighting the importance of dose-dependent regulation of ROS-scavenging genes (Lu et al., 2022). Another important ROS-responsive protein family is the lipocalins, known for their

conserved ability to bind and transport various lipids (Ji et al., 2023). In this meta-analysis, upregulation of *OsTIL1* was observed at the mature stage under drought and Fe stress (Fig. 4a). Functional studies using CRISPR/Cas9-mediated gene editing and overexpression of *OsTIL1* revealed its protective role in maintaining cell membrane integrity under oxidative stress. Overexpression of *OsTIL1* also led to increased expression of *OsFAD3-1/3-2/7* (fatty acid desaturases), particularly under cold stress (Ji et al., 2023). Supporting this, earlier studies reported that overexpression of *AtTIL* in *Arabidopsis* conferred enhanced tolerance to light stress, paraquat treatment, and freezing, while deletion of *AtTIL* increased sensitivity to heat stress (Chi et al., 2009; Tremblay et al., 2009). Plant sulfiredoxin (Srx) homologs are chloroplast-targeted enzymes that play a vital role in maintaining redox balance by reducing overoxidized 2-Cys peroxiredoxins, thus ensuring chloroplast redox homeostasis under oxidative stress conditions, upregulated at the mature stage (Liu et al., 2006).

Functional enrichment analysis revealed a conserved ROS-centered stress-response framework shared between seedling and mature stages under both drought and iron stress (Fig. 4c and d, Table S2). The consistent enrichment of oxidative stress-related processes indicates that maintenance of redox homeostasis and efficient detoxification of hydrogen peroxide constitute a core adaptive mechanism operating across developmental stages. This suggests that early and late growth phases rely on similar antioxidant strategies to protect cellular components from stress-induced oxidative damage.

In contrast, plants at the mature stage displayed an expansion of stress-responsive pathways, reflecting a transition toward more complex regulatory control (Fig. 4c, Table S2). The enrichment of processes associated with circadian rhythm regulation and broader cellular stress responses implies that, during the reproductive phase, stress adaptation is integrated with temporal regulation and enhanced signaling networks. Such coordination likely enables mature plants to fine-tune physiological and metabolic responses according to environmental cues and internal developmental timing, thereby ensuring stress resilience while safeguarding reproductive success.

3.5. Transcription factors to regulate drought and iron under different developmental states

To explore the transcriptional regulatory architecture underlying drought and iron stress responses across developmental stages, we integrated differential expression profiling with computational prediction of transcription factor- and miRNA-mediated regulatory interactions. This approach highlights the role of transcriptional integration as a potential mechanism underlying stress resilience. Differentially expressed genes (DEGs) identified under drought and iron (Fe) stress across developmental stages were filtered against a curated list of transcription factors (TFs), phytohormone-associated genes, and stress-responsive genes related to both drought and Fe conditions. These filtered genes were subsequently analyzed for predicted regulatory relationships, leading to the identification of seven key TFs and 30 putative target genes (Table S2, Fig. 5a). Collectively, this integrative analysis suggests a coordinated transcriptional regulatory framework involving TFs such as *DREB2A*, *ERF95*, and *ERF102* that may contribute to drought and Fe stress responses across different developmental stages in Keteki Joha.

Differentially expressed genes (DEGs) identified under drought and Fe stress across developmental stages were filtered against curated datasets of transcription factors, phytohormone-associated genes, and stress-responsive genes. The expression patterns of these TFs and their associated target genes were visualized using heatmap analysis (Fig. 5b), revealing coordinated expression trends suggestive of shared regulatory control. To further explore these relationships, a co-expression network was constructed. This network analysis identified *bZIP60* and *DREB2A* as highly connected hub nodes (Fig. 5c), implying their potential centrality in stress-responsive transcriptional programs.

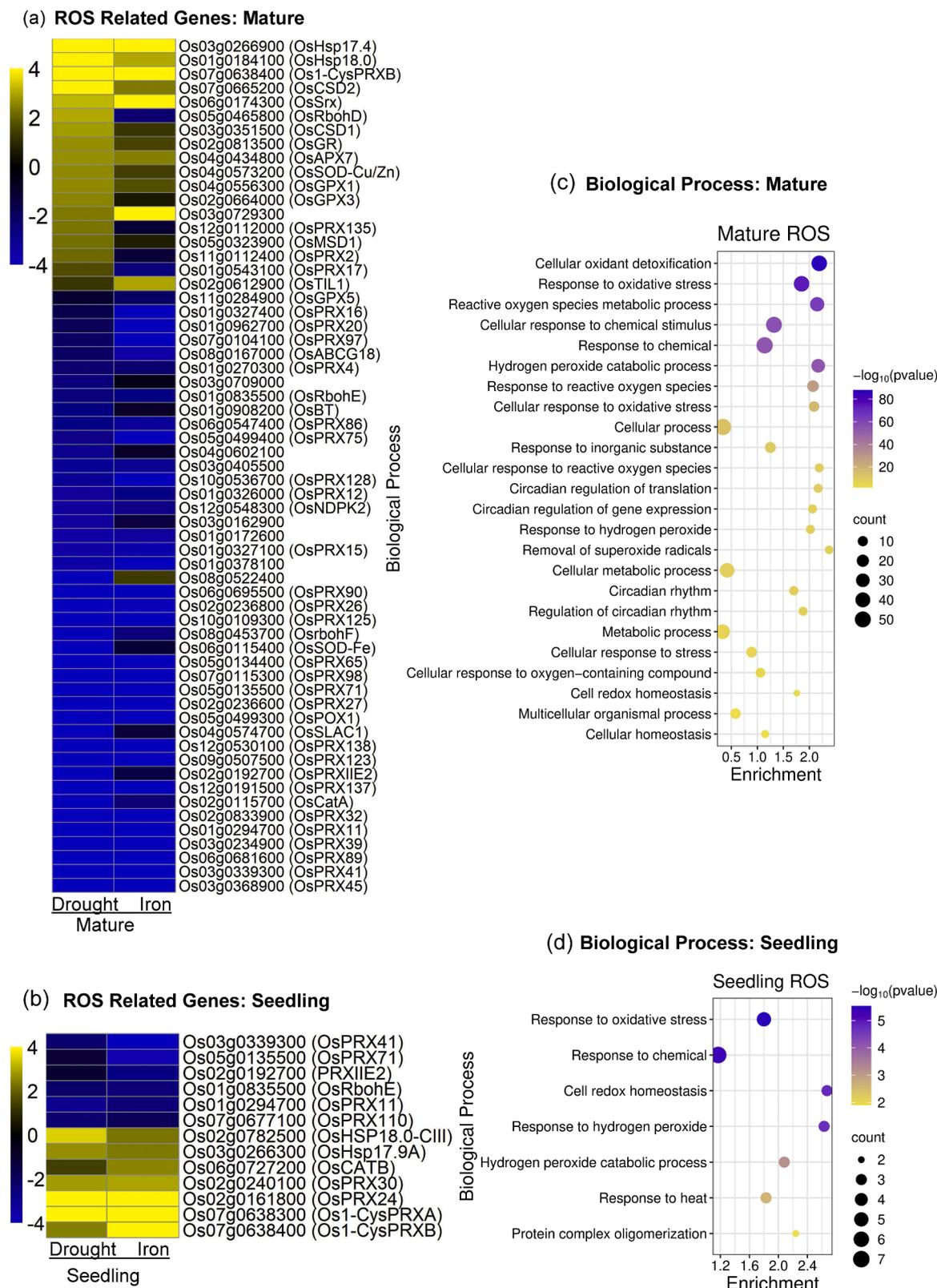


Fig. 4. (a) and (c) represent the regulation of differentially expressed genes (DEGs) associated with reactive oxygen species (ROS) under drought and iron stress at the mature and seedling stages, respectively. Here, blue to yellow color gradient is showing gradual fold changes from negative to positively regulated DEGs. (b) and (d) depict the involvement of biological processes linked to these ROS-related DEGs under drought and iron stress at the mature and seedling stages, respectively. Gene ontology terms of related DEGs were identified using g:profiler (<https://biit.cs.ut.ee/gprofiler/gost>) and represented using SRplot (<https://www.bioinformatics.com.cn/en>). Here, blue to yellow color gradient shows gradual changes in p-value from higher to lower. Similarly size of the representing dots increases based on counts, that is number of genes linked with the biological process.

Table 1

- List of differentially expressed peroxidase and peroxiredoxin genes under drought and iron stress across seedling and mature stages.

Gene_ID	Gene_Name	Stage	Class/Type	Localization (DeepLoc)
Os03g0339300	OsPRX41	Both	class III peroxidase	Extracellular
Os01g0294700	OsPRX11	Both	class III peroxidase	Extracellular
Os02g0192700	PRXIII2	Both	Type-II peroxidase	Vacuole Plastid
Os07g0638400	Os1-CysPRXB	Both	1 Cys-peroxiredoxin B	Cytoplasm
Os05g0135500	OsPRX71	Both	class III peroxidase	Extracellular
Os01g0326000	OsPRX12	Mature	class III peroxidase	Extracellular
Os10g0536700	OsPRX128	Mature	class III peroxidase	Extracellular
Os12g0112000	OsPRX135	Mature	class III peroxidase	Extracellular
Os12g0530100	OsPRX138	Mature	class III peroxidase	Extracellular
Os02g0236800	OsPRX26	Mature	class III peroxidase	Extracellular
Os06g0547400	OsPRX86	Mature	class III peroxidase	Extracellular
Os06g0695500	OsPRX90	Mature	class III peroxidase	Extracellular
Os07g0104100	OsPRX97	Mature	class III peroxidase	Extracellular
Os07g0115300	OsPRX98	Mature	class III peroxidase	Extracellular
Os05g0134400	OsPRX65	Mature	class III peroxidase	Extracellular
Os05g0499400	OsPRX75	Mature	class III peroxidase	Extracellular
Os05g0499300	OsPOX1	Mature	class III peroxidase	Vacuole Extracellular
Os01g0270300	OsPRX4	Mature	class III peroxidase	Extracellular
Os01g0327100	OsPRX15	Mature	class III peroxidase	Extracellular
Os11g0112400	OsPRX2	Mature	class III peroxidase	Extracellular
Os09g0507500	OsPRX123	Mature	class III peroxidase	Extracellular
Os10g0109300	OsPRX125	Mature	class III peroxidase	Extracellular
Os12g0191500	OsPRX137	Mature	class III peroxidase	Extracellular
Os01g0327400	OsPRX16	Mature	class III peroxidase	Extracellular
Os01g0543100	OsPRX17	Mature	class III peroxidase	Extracellular
Os02g0236600	OsPRX27	Mature	class III peroxidase	Extracellular
Os03g0234900	OsPRX39	Mature	class III peroxidase	Extracellular
Os03g0368900	OsPRX45	Mature	class III peroxidase	Extracellular
Os06g0681600	OsPRX89	Mature	class III peroxidase	Vacuole Extracellular
Os01g0962700	OsPRX20	Mature	class III peroxidase	Vacuole Extracellular
Os02g0833900	OsPRX32	Mature	class III peroxidase	Extracellular
Os02g0240100	OsPRX30	Seedling	class III peroxidase	Extracellular
Os07g0638300	Os1-CysPRXA	Seedling	1 Cys-peroxiredoxin	Cytoplasm
Os07g0677100	OsPRX110	Seedling	class III peroxidase	Extracellular
Os02g0161800	OsPRX24	Seedling	class III peroxidase	Vacuole Extracellular

Among the identified TFs, Dehydration Responsive Element Binding Protein 2A (*DREB2A*), a member of the AP2/ERF family, has been experimentally validated in multiple plant species as a regulator of heat, salt, and dehydration stress responses (Agarwal et al., 2017). Similarly, *ERF95* has been shown to regulate Fe homeostasis during seed maturation (Sun et al., 2020). The upregulation of *DREB2A* and *ERF95* observed in our dataset under drought and Fe stress conditions is therefore consistent with previously reported experimental findings, lending indirect support to their proposed involvement in stress regulation in Keteki Joha (Fig. 6).

In the inferred regulatory network, *DREB2A* and *ERF95* appear to be associated with members of the *bHLH*, *bZIP*, and *ERF* transcription factor families, forming a putative regulatory network that may coordinate plant responses to drought and Fe stress. Nevertheless, previous studies provide biological plausibility for these links. For instance, *ERF74* has been experimentally shown to regulate oxidative homeostasis via RbohD under stress conditions (Yao et al., 2017), and *bHLH130* has been reported to enhance resistance against *Phytophthora infestans* in tomato (Wang et al., 2025). Likewise, *bZIP20* has been shown to improve thermotolerance through ROS homeostasis and methyl jasmonate signaling in *Dimocarpus longan* (Zhai et al., 2025). These prior findings support the broader functional relevance of the TF families identified in our network, although the specific interactions proposed here remain to be experimentally validated.

ERF102 represents another notable regulatory node within the proposed miRNA-TF-target network (Fig. 6). Computational prediction suggests that *ERF102* is targeted by *miR9664*, a miRNA previously shown to regulate genes involved in plant immunity, including *RPM1* and *NPR1* (Hou et al., 2020; Li et al., 2021). Overexpression studies of *miR9664* have demonstrated compromised defense responses against *Magnaporthe oryzae* (Li et al., 2021), supporting a functional role for this miRNA-target module.

Experimental evidence from other plant systems indicates that *ERF102* is nuclear-localized and functions in cold acclimatization, often in coordination with *ERF103* (Illgen et al., 2020). In our network, *ERF102* is predicted to be regulated by upstream *bZIP14* and *bZIP33*, based on co-expression relationships. Both TFs have been implicated in drought stress tolerance and ROS regulation in *Vitis vinifera* and *Zea mays*, respectively (Yu et al., 2020; Cao et al., 2021), lending biological credibility to these inferred links.

Among the downstream targets or signaling components associated with *ERF102*, *GmbZIP114* in soybean has been reported to play a role in flower organ development (Yue et al., 2023). Similarly, *bZIP60*, an ER membrane-bound transcription factor, is activated through ER stress-induced cleavage and subsequent nuclear translocation. Its expression and activation in anthers even under non-stress conditions suggest an essential role in managing secretory demands during reproductive development (Iwata et al., 2008). Another key target, *AtbZIP34* in Arabidopsis, is expressed in both gametophytic and sporophytic floral tissues. Disruption of *AtbZIP34* results in defective pollen morphology, impaired germination, and abnormal exine formation, highlighting its importance in male reproductive development, lipid metabolism, and cellular transport (Gibalova et al., 2009).

Taken together, these findings suggest that *ERF102* may function as an integrative regulatory node linking environmental stress responses with developmental processes, particularly during reproductive stages. However, we emphasize that the proposed miRNA-TF-target regulatory framework is largely based on computational inference and comparative evidence from other plant species. Functional validation through approaches such as miRNA cleavage assays, ChIP-qPCR, and transgenic studies will be essential to confirm the direct regulatory roles proposed in this model.

4. Conclusion and future prospects

This study provides new insights into the regulatory mechanisms

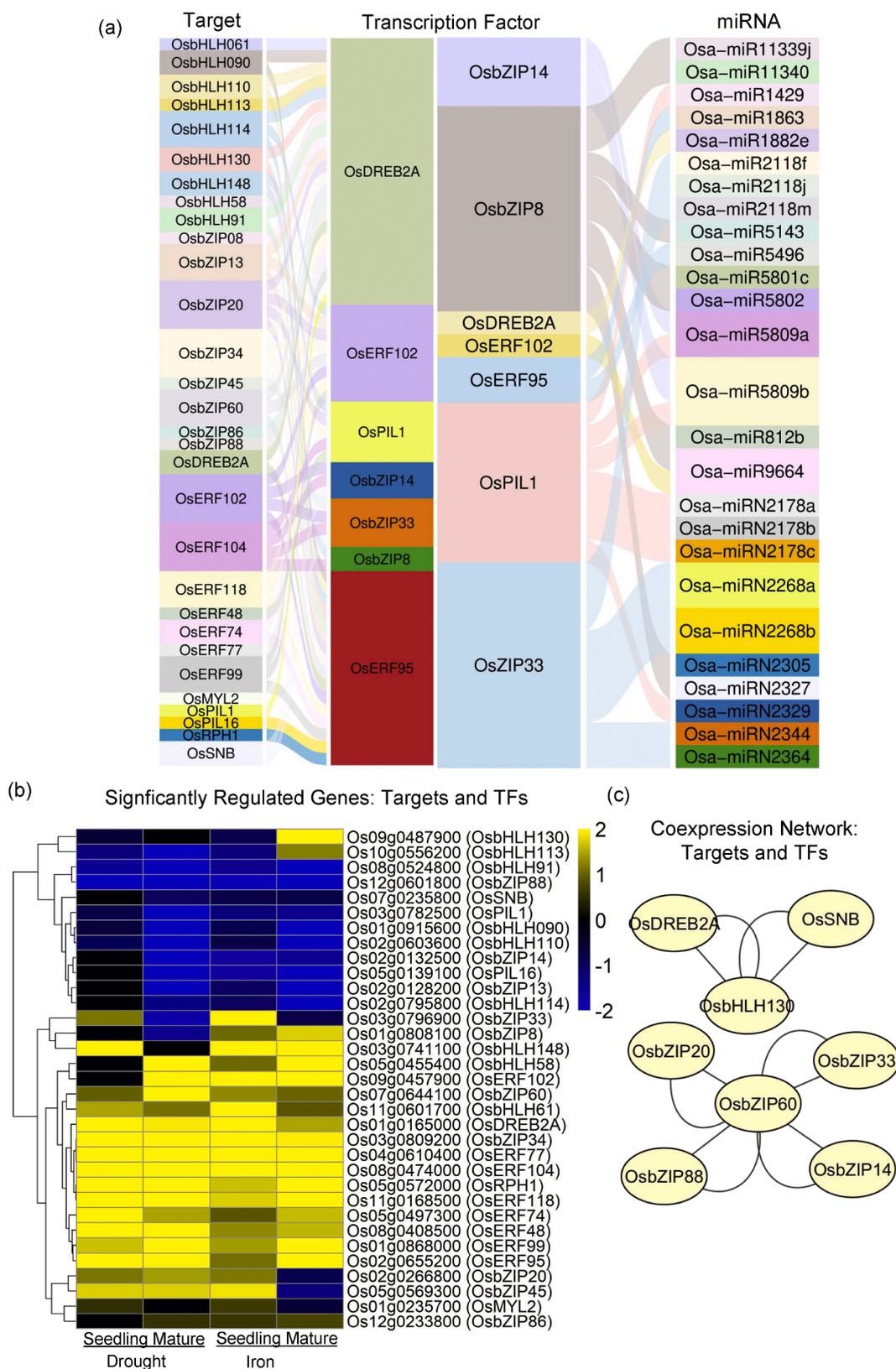


Fig. 5. (a) Interaction map showing the relationships between target genes, transcription factors (TFs), and associated miRNAs. Common regulators—including TFs, phytohormones, and differentially expressed genes (DEGs) responsive to drought and iron stress—at both seedling and mature stages are highlighted to depict their combined regulatory roles. This Sankey diagram was drawn using srplot. (b) Heatmap displaying the differential expression patterns of selected genes across various stress conditions and developmental stages. Here, blue to yellow color gradient is showing gradual fold changes from negative to positively regulated DEGs. (c) Co-expression network illustrating interactions between target genes and TFs, constructed based on combined scores obtained from STRING database analysis (<https://string-db.org/>). The network was resulted using string database and further visualized using Cytoscape 3.10.3.

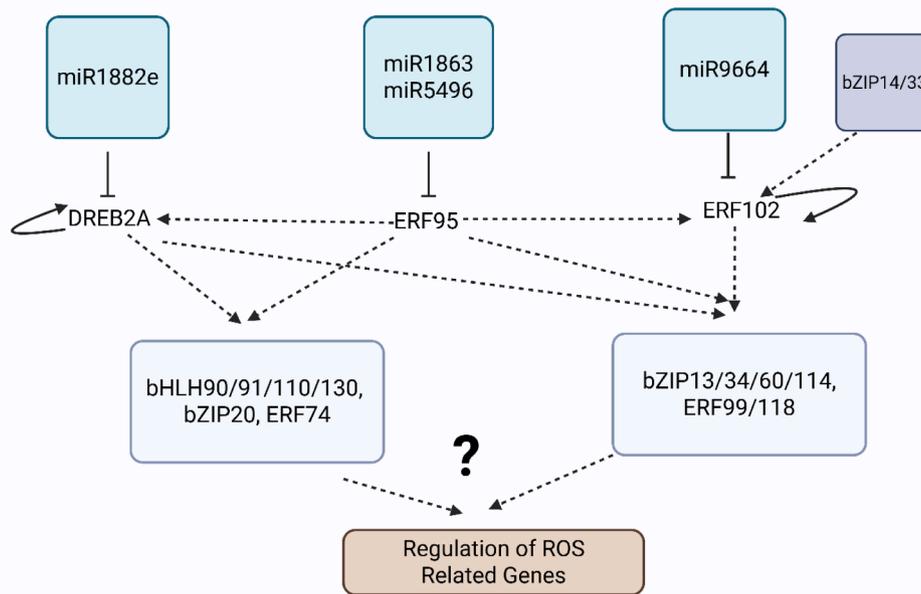


Fig. 6. Proposed regulatory network depicting the cross-talk between drought and iron stress via miRNA–TF–target interactions. Key miRNAs (miR1882e, miR1863, miR5496, miR9664) negatively regulate transcription factors (DREB2A, ERF95, ERF102), which in turn modulate downstream TFs (e.g., bHLH, bZIP, ERFs). These may ultimately regulate ROS-related genes to mitigate combined stress responses. Dotted lines indicate predicted regulatory links. Created by Biorender (<https://app.biorender.com>).

underlying drought and iron (Fe) stress tolerance in Keteki Joha rice (Table S3). By integrating transcriptomic data from seedling and mature stages, we identified common stress-response pathways involving ROS-related genes, transcription factors (TFs), and phytohormone signaling. A multilayered regulatory model was proposed, highlighting key TFs such as *DREB2A*, *ERF95*, and *ERF102* that coordinate stage-specific responses to combined stress. These findings emphasize the potential of targeting shared regulatory hubs for developing multi-stress-tolerant rice varieties. The study underscores the importance of integrating environmental signaling with developmental regulation. While transcriptome-based predictions are valuable, they are limited by the absence of post-transcriptional and proteomic data. Future work involving gene editing (e.g., CRISPR/Cas9) or overexpression studies is needed to validate these regulatory modules. In practical terms, genome editing strategies such as CRISPR/Cas9 or CRISPR/Cpf1 could be employed to validate and functionally characterize the identified regulatory hubs. For instance, targeted knockout or base-editing of negative regulators (e.g., IMA1 in iron homeostasis) could help enhance tolerance to Fe toxicity, while promoter engineering of key transcription factors (*DREB2A*, *ERF95*, *ERF102*) may allow fine-tuned expression under stress without penalizing growth. Similarly, multiplex genome editing could be used to simultaneously modulate TF–miRNA–target modules, creating rice lines with stacked tolerance to drought and Fe stress. Broadly, this research contributes to our understanding of stress cross-talk and lays a foundation for precision breeding. Expanding this approach across genotypes and incorporating proteomic or metabolomic data will help address the complex challenge of engineering crops resilient to multiple abiotic stresses.

Ethics approval and consent to participate

No ethical approval and consent is required.

Declaration of generative AI and AI-assisted technologies in the manuscript preparation process

During the preparation of this work, the author(s) used ChatGPT 4.0 for language and grammar improvement. After using this tool/service, the author(s) reviewed and edited the content as needed and take(s) full responsibility for the content of the published article.

CRediT authorship contribution statement

Divya Gupta: Writing – original draft, Validation, Software, Resources, Methodology, Investigation. **Hans-Jörg Mai:** Supervision, Software, Methodology, Investigation. **Petra Bauer:** Writing – review & editing, Investigation, Funding acquisition. **Sanjib Kumar Panda:** Writing – review & editing, Visualization, Supervision, Conceptualization.

Declaration of competing interest

The authors declare no competing interests.

Acknowledgements and funding

This work was supported by the Scheme for Promotion of Academic and Research Collaboration (SPARC), Ministry of Education, Government of India (Project No. SPARC/2024-2025/AGF/P3737). This work received funding by Deutsche Forschungsgemeinschaft (DFG, German Research Foundation) under Germany's Excellence Strategy – EXC-2048/1 – project ID 390686111. Funding through DAAD-DST (DST/INT/DAAD/P-14/2022(G) with India is greatly acknowledged.

Supplementary materials

Supplementary material associated with this article can be found, in the online version, at [doi:10.1016/j.stress.2026.101297](https://doi.org/10.1016/j.stress.2026.101297).

Figure S1- Heatmaps illustrating the expression profiles of uniquely regulated drought- and iron-responsive differentially expressed genes (DEGs) under drought and iron stress conditions in Keteki Joha. (a) Shows the expression of DEGs responsive to drought (left) and iron (right) under drought stress at seedling and mature stages. (b) Depicts the expression of DEGs responsive to drought (left) and iron (right) under iron stress at seedling and mature stages. Yellow represents upregulation, blue indicates downregulation, and black signifies no significant expression change (log₂ fold change scale from -4 to +4).

Figure S2- Transcriptomic analysis of commonly regulated drought- and iron-responsive DEGs in Keteki Joha under drought stress. Heatmaps showing hierarchical clustering of common DEGs responsive to (a) drought and (b) iron across seedling and mature stages under drought and iron treatments. Expression levels range from -2 to +2 (z-score), reflecting the intensity of differential expression across stress types and developmental stages. Here, yellow represents upregulation, blue indicates downregulation, and black signifies no significant expression change.

Figure S3- Heatmaps highlighting key commonly regulated DEGs selected based on biological relevance and magnitude of expression. (a) The left panel displays genes responsive to drought stress, and (b) the right panel shows genes responsive to iron stress under drought conditions. Expression values are scaled by log₂ fold change, ranging from -6 to +6 (drought) and -4 to +4 (iron). Here, D and I denote Drought and Iron, respectively. Here, yellow represents upregulation, blue indicates downregulation, and black signifies no significant expression change.

Table S1- Summary of Stage- and Stress-Specific Transcriptional Regulation in Response to Drought and Iron Stress in Keteki Joha.

Table S2- List of Differentially Expressed Genes (DEGs) Identified Under Drought and Iron Stress at Seedling and Mature Stages

Table S3- List of gene ontology and KEGG pathway of clusters commonly regulated under drought and iron stress at different developmental stages.

Data availability

Data will be made available on request.

References

Agarwal, P.K., Gupta, K., Lopato, S., Agarwal, P., 2017. Dehydration responsive element binding transcription factors and their applications for the engineering of stress tolerance. *J. Exp. Bot.* 68 (9), 2135–2148.

Aung, M.S., Masuda, H., 2020. How does rice defend against excess iron?: Physiological and molecular mechanisms. *Front. Plant Sci.* 11, 1102.

Bashir, K., Hanada, K., Shimizu, M., Seki, M., Nakanishi, H., Nishizawa, N.K., 2014. Transcriptomic analysis of rice in response to iron deficiency and excess. *Rice* 7 (1), 18.

Becker, M., Asch, F., 2005. Iron toxicity in rice—conditions and management concepts. *Plant Nutr. Soil Sci.* 168 (4), 558–573.

Bhoite, R., Onyemaobi, O., Halder, T., Shankar, M., Sharma, D., 2025. Transcription factors—Insights into abiotic and biotic stress resilience and crop improvement. *Curr. Plant Biol.* 41, 100434.

Bordoloi, D., Sarma, D., Sarma Barua, N., Das, R., Das, B.K., 2024. Morpho-molecular and nutritional profiling for yield improvement and value addition of indigenous aromatic Joha rice of Assam. *Sci. Rep.* 14 (1), 3509.

Cao, L., Lu, X., Wang, G., Zhang, Q., Zhang, X., Fan, Z., Cao, Y., Wei, L., Wang, T., Wang, Z., 2021. Maize ZmbZIP33 is involved in drought resistance and recovery ability through an abscisic acid-dependent signaling pathway. *Front. Plant Sci.* 12, 629903.

Cao, M., Platre, M.P., Tsai, H.H., Zhang, L., Nobori, T., Armengot, L., Chen, Y., He, W., Brent, L., Coll, N.S., Ecker, J.R., 2024. Spatial IMA1 regulation restricts root iron acquisition on MAMP perception. *Nature* 625 (7996), 750–759.

CHI, W.T., Fung, R.W., LIU, H.C., HSU, C.C., CHARNG, Y.Y., 2009. Temperature-induced lipocalin is required for basal and acquired thermotolerance in Arabidopsis. *Plant Cell Environ.* 32 (7), 917–927.

Cui, L.G., Shan, J.X., Shi, M., Gao, J.P., Lin, H.X., 2015. DCA1 acts as a transcriptional co-activator of DST and contributes to drought and salt tolerance in rice. *PLoS Genet.* 11 (10), e1005617.

Cui, L.H., Min, H.J., Byun, M.Y., Oh, H.G., Kim, W.T., 2018. OsDIRP1, a putative RING E3 ligase, plays an opposite role in drought and cold stress responses as a negative and positive factor, respectively, in rice (*Oryza sativa* L.). *Front. Plant Sci.* 9, 1797.

Dai, X., Zhuang, Z., Zhao, P.X., 2018. psRNATarget: a plant small RNA target analysis server (2017 release). *Nucleic Acids Res.* 46 (W1), W49–W54.

Das, A., Kesari, V., Rangan, L., 2010. Aromatic Joha rice of Assam—a review. *Agric. Revi.* (1), 31.

Das, S., Shil, S., Rime, J., Alice, A.K., Yumkhaibam, T., Mounika, V., Singh, A.P., Kundu, M., Lalhmangaihuali, H.P., Hazarika, T.K., Singh, A.K., 2025. Phytohormonal signaling in plant resilience: advances and strategies for enhancing abiotic stress tolerance. *Plant Growth Regul.* 105 (2), 329–360.

Dhara, A., Raichaudhuri, A., 2021. ABCG transporter proteins with beneficial activity on plants. *Phytochemistry* 184, 112663.

Dietz, K.J., 2003. Plant peroxiredoxins. *Annu Rev. Plant Biol.* 54 (1), 93–107.

Gho, Y.S., Park, S.A., Kim, S.R., Chandran, A.K.N., An, G., Jung, K.H., 2017. Comparative expression analysis of rice and Arabidopsis peroxiredoxin genes suggests conserved or diversified roles between the two species and leads to the identification of tandemly duplicated rice peroxiredoxin genes differentially expressed in seeds. *Rice* 10, 1–14.

Gibalová, A., Reňák, D., Matczuk, K., Dupl'áková, N., Cháb, D., Twell, D., Honys, D., 2009. AtbZIP34 is required for Arabidopsis pollen wall patterning and the control of several metabolic pathways in developing pollen. *Plant Mol. Biol.* 70, 581–601.

Guo, Z., Kuang, Z., Wang, Y., Zhao, Y., Tao, Y., Cheng, C., Yang, J., Lu, X., Hao, C., Wang, T., Cao, X., 2020. PmiREN: a comprehensive encyclopedia of plant miRNAs. *Nucleic Acids Res.* 48 (D1), D1114–D1121.

Gupta, D., Panda, S.K., Bauer, P., 2025. Meta-analysis of iron excess stress in rice: genes and mechanisms of tolerance to acidic soil. *Physiol. Plant* 177 (5), e70473.

Hiraga, S., Sasaki, K., Ito, H., Ohashi, Y., Matsui, H., 2001. A large family of class III plant peroxidases. *Plant Cell Physiol.* 42 (5), 462–468.

Hou, G., Du, C., Gao, H., Liu, S., Sun, W., Lu, H., Kang, J., Xie, Y., Ma, D., Wang, C., 2020. Identification of microRNAs in developing wheat grain that are potentially involved in regulating grain characteristics and the response to nitrogen levels. *BMC Plant Biol.* 20, 1–21. <https://worldpopulationreview.com>.

Illgen, S., Zintl, S., Zuther, E., Hincha, D.K., Schmittling, T., 2020. Characterisation of the ERF102 to ERF105 genes of Arabidopsis thaliana and their role in the response to cold stress. *Plant Mol. Biol.* 103, 303–320.

Iwata, Y., Fedoroff, N.V., Koizumi, N., 2008. Arabidopsis bZIP60 is a proteolysis-activated transcription factor involved in the endoplasmic reticulum stress response. *Plant Cell* 20 (11), 3107–3121.

Kar, S., Mai, H.J., Khalouf, H., Ben Abdallah, H., Flachbart, S., Fink-Straube, C., Bräutigam, A., Xiong, G., Shang, L., Panda, S.K., Bauer, P., 2021. Comparative transcriptomics of lowland rice varieties uncovers novel candidate genes for adaptive iron excess tolerance. *Plant Cell Physiol.* 62 (4), 624–640.

Kaur, S., Seem, K., Duhan, N., Kumar, S., Kaundal, R., Mohapatra, T., 2023. Transcriptome and physio-biochemical profiling reveals differential responses of rice cultivars at reproductive-stage drought stress. *Int. J. Mol. Sci.* 24 (2), 1002.

Kidwai, M., Ahmad, I.Z., Chakrabarty, D., 2020. Class III peroxidase: an indispensable enzyme for biotic/abiotic stress tolerance and a potent candidate for crop improvement. *Plant Cell Rep.* 39 (11), 1381–1393.

Kobayashi, T., Nishizawa, N.K., 2014. Iron sensors and signals in response to iron deficiency. *Plant Sci.* 224, 36–43.

Kohl, M., Wiese, S., Warscheid, B., 2010. Cytoscape: software for visualization and analysis of biological networks. *Data Mining in proteomics: from Standards to Applications.* Humana Press, Totowa, NJ, pp. 291–303.

Kolde, R., 2019. pheatmap: Pretty Heatmaps. R package version 1.0. 12 [online].

Kumar, D., Mulani, E., Singh, B.K., Dutta, B., Singh, A., Solanke, A.U., Sevanti, A.M., 2024. Understanding the role of miRNAs in governing the drought sensitive response of a rice mega variety, Swarna at reproductive stage. *Plant Stress* 11, 100302.

Li, J., Zhang, H., Yang, R., Zeng, Q., Han, G., Du, Y., Yang, J., Yang, G., Luo, Q., 2021a. Identification of miRNAs contributing to the broad-spectrum and durable blast resistance in the yunnan local rice germplasm. *Front. Plant Sci.* 12, 749919.

Li, J., Zhang, M., Yang, L., Mao, X., Li, J., Li, L., Wang, J., Liu, H., Zheng, H., Li, Z., Zhao, H., 2021b. OsADR3 increases drought stress tolerance by inducing antioxidant defense mechanisms and regulating OsGPX1 in rice (*Oryza sativa* L.). *Crop J.* 9 (5), 1003–1017.

Liu, X.P., Liu, X.Y., Zhang, J., Xia, Z.L., Liu, X., Qin, H.J., Wang, D.W., 2006. Molecular and functional characterization of sulfiredoxin homologs from higher plants. *Cell Res.* 16 (3), 287–296.

Lu, Y., Yao, K., Gong, Z., Zhang, Y., Meng, Y., Liu, Q., 2022. Molecular manipulations of miR398 increase rice grain yield under different conditions. *Front. Plant Sci.* 13, 1037604.

Oladosu, Y., Rafii, M.Y., Samuel, C., Fatai, A., Magaji, U., Kareem, I., Kamarudin, Z.S., Muhammad, I.I., Kolapo, K., 2019. Drought resistance in rice from conventional to molecular breeding: a review. *Int. J. Mol. Sci.* 20 (14), 3519.

Paul, S., Gayen, D., Datta, S.K., Datta, K., 2016. Analysis of high iron rice lines reveals new miRNAs that target iron transporters in roots. *J. Exp. Bot.* 67 (19), 5811–5824.

Qiao, J., Quan, R., Wang, J., Li, Y., Xiao, D., Zhao, Z., Huang, R., Qin, H., 2024. OsEIL1 and OsEIL2, two master regulators of rice ethylene signaling, promote the expression of ROS scavenging genes to facilitate coleoptile elongation and seedling emergence from soil. *Plant Commun.* 5 (3).

Regon, P., Dey, S., Rehman, M., Pradhan, A.K., Chowra, U., Tanti, B., Talukdar, A.D., Panda, S.K., 2022. Transcriptomic analysis revealed reactive oxygen species

- scavenging mechanisms associated with ferrous iron toxicity in aromatic Keteki Joha rice. *Front. Plant Sci.* 13, 798580.
- Regon, P., Saha, B., Jyoti, S.Y., Gupta, D., Kundu, B., Tanti, B., Panda, S.K., 2024. Transcriptional networks revealed late embryogenesis abundant genes regulating drought mitigation in aromatic Keteki Joha rice. *Physiol. Plant* 176 (3), e14348.
- Sahoo, S., Saha, B., Awasthi, J.P., Omissun, T., Borgohain, P., Hussain, S., Panigrahi, J., Panda, S.K., 2019. Physiological introspection into differential drought tolerance in rice cultivars of North East India. *Acta Physiol. Plant.* 41 (4), 53.
- Sun, Y., Li, J.Q., Yan, J.Y., Yuan, J.J., Li, G.X., Wu, Y.R., Xu, J.M., Huang, R.F., Harberd, N.P., Ding, Z.J., Zheng, S.J., 2020. Ethylene promotes seed iron storage during Arabidopsis seed maturation via ERF95 transcription factor. *J. Integr. Plant Biol.* 62 (8), 1193–1212.
- Tang, D., Chen, M., Huang, X., Zhang, G., Zeng, L., Zhang, G., Wu, S., Wang, Y., 2023. SRplot: A free online platform for data visualization and graphing. *PLoS. One* 18 (11), e0294236.
- Tian, F., Yang, D.C., Meng, Y.Q., Jin, J., Gao, G., 2020. PlantRegMap: charting functional regulatory maps in plants. *Nucleic Acids Res.* 48 (D1), D1104–D1113.
- Wang, R., Wang, Z., Wang, Z., Su, C., Zhu, J., Lv, R., Yang, R., Luan, Y., 2025. The basic helix-loop-helix (bHLH) transcription factor bHLH130 negatively regulates tomato resistance to phytophthora infestans. *Int. J. Biol. Macromol.*, 143908
- Wang, T., Ma, Y.Q., Huang, X.X., Mu, T.J., Li, Y.J., Li, X.K., Liu, X., Hou, B.K., 2021. Overexpression of OsUGT3 enhances drought and salt tolerance through modulating ABA synthesis and scavenging ROS in rice. *Environ. Exp. Bot.* 192, 104653.
- Yang, S., Xu, K., Chen, S., Li, T., Xia, H., Chen, L., Liu, H., Luo, L., 2019. A stress-responsive bZIP transcription factor OsbZIP62 improves drought and oxidative tolerance in rice. *BMC Plant Biol.* 19 (1), 260.
- Yang, X.J., Fu, Y.Q., Ma, S., Gan, H., Xu, W., Shen, H., 2020. The class III peroxidase gene OsPrx24 is important for root iron plaque formation and benefits phosphorus uptake in Rice plants under alternate wetting and drying irrigation. *Plant Soil.* 448, 621–646.
- Yao, Y., He, R.J., Xie, Q.L., Zhao, X.H., Deng, X.M., He, J.B., Song, L., He, J., Marchant, A., Chen, X.Y., Wu, A.M., 2017. ETHYLENE RESPONSE FACTOR 74 (ERF74) plays an essential role in controlling a respiratory burst oxidase homolog D (RbohD)-dependent mechanism in response to different stresses in Arabidopsis. *New Phytologist* 213 (4), 1667–1681.
- Yu, Y.H., Bian, L., Yu, K.K., Yang, S.D., Zhang, H.C., Wang, L.L., Zhang, G.H., Guo, D.L., 2020. Vitis vinifera bZIP14 functions as a transcriptional activator and enhances drought stress resistance via suppression of reactive oxygen species. *J. Berry. Res.* 10 (4), 547–558.
- Yue, L., Pei, X., Kong, F., Zhao, L., Lin, X., 2023. Divergence of functions and expression patterns of soybean bZIP transcription factors. *Front. Plant Sci.* 14, 1150363.
- Zhai, T., Guo, Y., Yang, M., Zhang, X., Lin, Y., Cai, D., Lan, S., Tang, M., Ma, W., Wang, S., Chen, Y., 2025. The bZIP20 transcription factor enhances thermotolerance in *Dimocarpus longan* by maintaining ROS homeostasis and involving the MeJA pathway. *Plant Physiol. Biochem.* 223, 109869.
- Zhai, Z., Gayomba, S.R., Jung, H.I., Vimalakumari, N.K., Piñeros, M., Craft, E., Rutzke, M.A., Danku, J., Lahner, B., Punshon, T., Guerinot, M.L., 2014. OPT3 is a phloem-specific iron transporter that is essential for systemic iron signaling and redistribution of iron and cadmium in Arabidopsis. *Plant Cell* 26 (5), 2249–2264.
- Zampieri, E., Pesenti, M., Nocito, F.F., Sacchi, G.A., Valè, G., 2023. Rice responses to water limiting conditions: improving stress management by exploiting genetics and physiological processes. *Agriculture* 13 (2), 464.
- Zhang, F., Yang, J., Zhang, N., Wu, J., Si, H., 2022. Roles of microRNAs in abiotic stress response and characteristics regulation of plant. *Front. Plant Sci.* 13, 919243.
- Zhang, K., Novak, O., Wei, Z., Gou, M., Zhang, X., Yu, Y., Yang, H., Cai, Y., Strnad, M., Liu, C.J., 2014. Arabidopsis ABCG14 protein controls the acropetal translocation of root-synthesized cytokinins. *Nat. Commun.* 5 (1), 3274.
- Zhang, X., Long, Y., Huang, J., Xia, J., 2020. OsNAC45 is involved in ABA response and salt tolerance in rice. *Rice* 13 (1), 79.