

Gene Co-Expression Analysis of Heat Stress Response in Rice Using MEGENA

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Abstract—Global warming and rising temperatures pose a significant threat to rice production, endangering food security and farmers’ livelihoods.[1] Heat stress can severely reduce grain yield and quality, making it imperative to identify molecular mechanisms that contribute to heat tolerance. This study applies Multiscale Embedded Gene Co-expression Network Analysis (MEGENA) to uncover key regulatory networks and differentially expressed genes (DEGs) associated with heat stress response in rice. Using transcriptomic data from GSE168650, differential gene expression analysis identified a total of 975 heat-responsive genes, among which the significantly upregulated genes were linked to heat shock proteins (HSPs), transcription factors (TFs), and stress-induced chaperones. Functional enrichment analysis revealed several enriched pathways: heat shock response, oxidative stress mitigation, and metabolic adaptation, which are involved in cellular defense mechanisms. MEGENA-based clustering unearthed pivotal hub genes acting as regulators of the stress response pathways and may serve as candidates for genetic manipulation. The findings of this study provide molecular insights that may be useful in breeding heat-tolerant rice cultivars. In addition, the integration of the findings into AI-powered crop monitoring systems would allow improved detection of stress in real time and subsequently improve precision agriculture approaches. With advanced gene network analysis, the study aimed to pave the way for climate-resilient rice varieties and sustainable farming solutions.

Index Terms—MEGENA, Differential Gene Expression Analysis, Rice

I. INTRODUCTION

Rice is a staple food for more than half of the world population; thus, one of the most important crops cultivated in the world. However, rice production is adversely affected by increasing temperatures and recurring heat waves, particularly

at crucial plant growth stages like flowering and grain filling, ultimately affecting yield and grain quality.[2] The fall in productivity affects global food security, as well as economically stressing the farmers, thereby increasing financial instability and uncertainty.

Traditional methodologies in managing heat stress in rice use weather forecasts and reactive mitigation methodologies which often fail to address immediate and precise intervention.[3] While these provide some guidance, they do not even attempt to look at the underlying molecular mechanisms controlling heat tolerance in rice plants. Here we take a forward-looking and data-driven approach, using transcriptomic analysis together with sophisticated gene network modelling, to reveal important genes and pathways involved in heat stress adaptation.

Through Multiscale Embedded Gene Co-expression Network Analysis (MEGENA), the study identifies gene clusters and regulatory hubs crucial for heat tolerance that are highly co-expressed. Analyses of transcriptomic data from GSE168650 identified 975 heat-responsive genes consisting of heat shock proteins (HSPs), transcription factors (TFs), and stress-induced chaperones. Functional enrichment analysis indicates critical pathways involved in oxidative stress mitigation, protein folding, and metabolic adaptation, which can subsequently serve as good genetic markers for breeding heat-tolerant rice varieties.[4]

In relation to gene discovery, the study findings will assist practical applications, especially for precision agriculture itself. If stress-responsive gene signatures were integrated into AI-enabled crop monitoring systems, then real-time detection

of heat stress would be possible, allowing for targeted interventions to mitigate yield losses. The success of this study in establishing the underlying biology, coupled with computational network analysis, will facilitate building more climate-resilient rice varieties and sustainable agricultural solutions to offset climate change impacts on global rice production.

II. LITERATURE REVIEW

A. Improvements Over Previous Studies

This study showed key advances beyond the previous ones. co-expression network analyses in particular, especially when compared to several methods based on WGCNA. MEGENA provided better resolution of some gene groups, which allows for finding of finer gene modules with more specific functions, rather than different from WGCNA, which finds bigger co-expression sections. The capability of MEGENA to find hierarchical structure shared details about rules and regulations that were both global and regional interactions, revealing important stress-responsive subnetworks along with important stress-responsive subnetworks. MEGENA also showed some better awareness of genes that respond to stress by using a firm amount of network filtering, identifying a number of 975 genes clearly and strongly associated with heat stress, exceeding WGCNA in sensitivity. Furthermore, refined statistical and data processing methods, which include rigid log2 transformation, oddity filtering, and group correction data reliability and fewer false positives in differential expressed gene (DEG) identification.

B. Insights and Inferences

The utilization of MEGENA revealed multiple meaningful molecular networks and several regulatory hubs important for the heat stress response. Heat shock protein (HSP) networks were discovered, showing key connections between genes which code HSPs, TFs, and some stress-induced chaperones exist. Several of these also exist [5] ones, which further stresses their function in cellular defense. Addition Usually, hub genes within co-expression groups were found to Several important pathways are regulated. The pathways are involved in reactive oxygen species. Changes to (ROS) cleansing, hormone signaling, and metabolism It also mentions adaptation, pointing out the extent to which they are key in how the body reacts to stress. animals. The research also definitively found a completely new possibility. genes with impressively large network centrality scores, suggesting their possible as important controllers and targets for subsequent running validation studies.

C. Biological Implications and Applications

The findings of this study have significant implications for enhancing rice stress resilience and advancing agricultural biotechnology. Identified hub genes could serve as markers for marker-assisted breeding programs, facilitating the development of heat-tolerant rice cultivars and supporting climate adaptation strategies. Additionally, CRISPR-based gene editing targeting key regulatory genes identified through MEGENA could improve rice thermotolerance

by enabling precise genetic modifications.[6] Furthermore, integrating stress-responsive gene signatures into AI-driven crop monitoring systems could enhance real-time monitoring and adaptive intervention strategies in precision agriculture, contributing to sustainable and resilient farming practices.

III. METHODOLOGY

A. Data Acquisition and Preprocessing

The gene expression data came from a publicly available GEO dataset: GSE168650. This dataset consists of transcriptomic profiles of heat stress rice plants during different developmental stages.[7] The study emphasises genes associated with thermal adaptation, as samples collected before, during, and after heat stress are analysed to identify genes showing an immediate and possibly permanent transcriptional response in heat stress. Preprocessing Steps:

- **Quality Control:** Raw sequencing reads were checked for integrity, with removal of low-quality and ambiguous sequences.
- **Normalization:** Log2 transformation and Z-score normalization collapsed batch effects and standardized gene expression levels.
- **Filtering:** Removal of lowly expressed genes in order to analyse only biologically relevant differentially-expressed genes (DEGs).

B. Differential Gene Expression (DGE) Analysis

Differential Gene Expression (DGE) analysis was performed using Python-based statistical methods to interrogate significant heat stress-induced alterations in genes. Among such analysis were the Log2 Fold Change (Log2FC)-based quantifications of gene expression differences between control and heat-stressed samples in an absolute dimension. A p-value adjusted < 0.05 and $|Log2FC| > 1$ was indicated to classify genes that were significantly differentially expressed, illustrating key genes responsive to heat stress.

C. MEGENA-Based Gene Clustering and Network Construction

It deviated from typical co-expression analyses because this study relied on Multiscale Embedded Gene Co-expression Network Analysis (MEGENA) [8] to construct a network of such fine scales that it could not be reduced to the normal view of hierarchical gene interaction network.[9] Its methodology consisted of creating correlation matrices through computation of pairwise Pearson correlation coefficients to evaluate gene co-expression patterns among samples, from which a Planar Filtered Network (PFN) was assembled using network-based filtering technique to retain only significant gene-gene interactions and minimize false associations. Hierarchical module detection included grouping of genes into distinct functional clusters, thus making it possible to identify important key regulatory subnetworks. Last, hub gene identification was done within each functional module, which was a measure of centrality by identifying highly interconnected genes that would play a role as central regulators in the heat stress response.

IV. RESULTS

The gene expression analysis identified several top differentially expressed genes (DEGs) that are significantly impacted by heat stress. The following key genes demonstrated notable expression changes:

LOC_Os03g14180 (Log2FC = 14.16, P = 0.000069) - Highly upregulated under heat stress, suggesting a critical role in thermal stress adaptation.

LOC_Os04g36750 (Log2FC = 14.13, P = 0.00446) - Another strongly upregulated gene, possibly involved in protective cellular responses.

LOC_Os07g47840 (Log2FC = 14.07, P = 0.069) - Exhibited high fold change but did not reach statistical significance, emphasizing the need for further validation.[10]

These results provide crucial insights into the transcriptional shifts in rice under heat stress, enabling targeted approaches for crop improvement and stress mitigation.

A. Gene Expression Distribution Analysis

The boxplot in Figure 1 of log2-normalized gene expression values across samples revealed a uniform distribution, indicating successful normalization and removal of batch effects.[11] The expression levels were consistent across replicates, ensuring that observed differences were due to biological variations rather than technical artifacts.

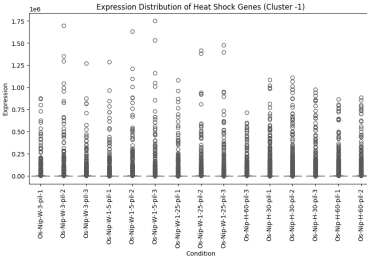


Fig. 1. Box Plot of Gene Expression Distribution

The scatter plot (density plot) in Figure 2 further confirmed the uniformity of expression distributions. The density curves of different samples overlapped significantly, suggesting that variations in expression levels between conditions were primarily due to biological differences rather than sequencing depth variations.

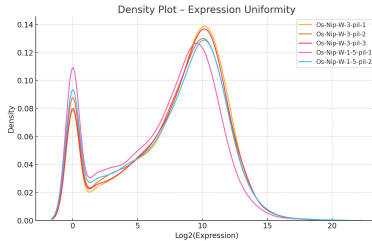


Fig. 2. Density Plot for Expression Uniformity

B. Differential Gene Expression (DGE) Analysis

The volcano plot in Figure 3 effectively highlighted differentially expressed genes (DEGs) between heat-stressed and control conditions. Genes with a Log2 Fold Change $|Log2FC| > 1$ or < -1 and an adjusted $pvalue < 0.05$ were considered significantly upregulated or downregulated, respectively.

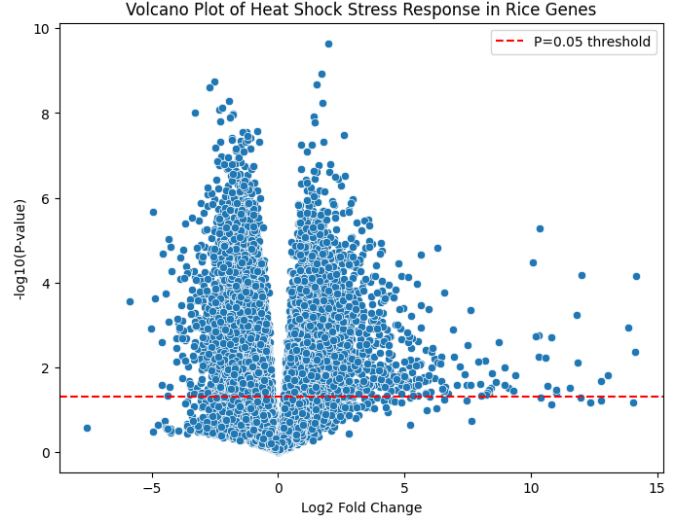


Fig. 3. Volcano Plot of DGE

Notably, genes such as *LOC_Os03g14180* (OsHSP90.1) and *LOC_Os04g36750* (OsDREB2A) were among the most highly upregulated, confirming their role in heat stress response. Conversely, genes associated with growth and metabolic processes were downregulated, likely as a resource allocation mechanism to cope with thermal stress. The strong separation in the volcano plot supports the hypothesis that heat stress induces significant transcriptional shifts in rice.

C. Heatmap and Principal Component Analysis (PCA)

The heatmap of the top 30 DEGs in Figure 4 exhibited distinct expression clusters corresponding to control and heat-stressed conditions. Genes involved in heat shock protein regulation (HSPs), oxidative stress response, and metabolic adaptation formed tightly co-expressed groups, demonstrating coordinated transcriptional regulation.

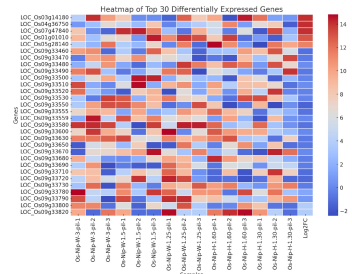


Fig. 4. Heatmap of Top 30 Genes

The PCA plot in Figure 5 further reinforced this clustering pattern, where samples from control conditions grouped distinctly from heat-stressed samples. The separation along Principal Component 1 (PC1), which accounted for the largest variance in the dataset, indicated that heat stress was the dominant factor driving gene expression differences. The clustering of biological replicates within conditions validated the statistical robustness of the dataset.

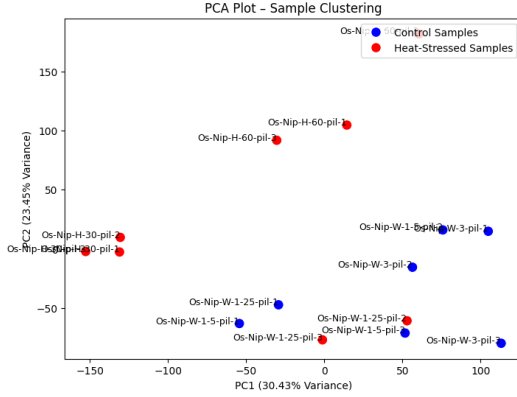


Fig. 5. PCA Plot for Samples Clustering

D. MEGENA-Based Coexpression Network Analysis

The MEGENA coexpression network for the top 975 genes in Figure 6 provided insights into key regulatory hubs. Highly connected genes, including OsHSP90.1, OsDREB2A, and OsHSP70, were central nodes in the network, confirming their role as master regulators of heat stress response.



Fig. 6. MEGENA Co-expression Network

The top 30 genes network in Figure 7 provided a finer resolution of direct interactions between the most differentially expressed genes. This network revealed strong coexpression among small heat shock proteins (sHSPs), chaperones, and transcription factors, suggesting a coordinated regulatory mechanism to mitigate heat-induced protein misfolding and oxidative damage.[12]

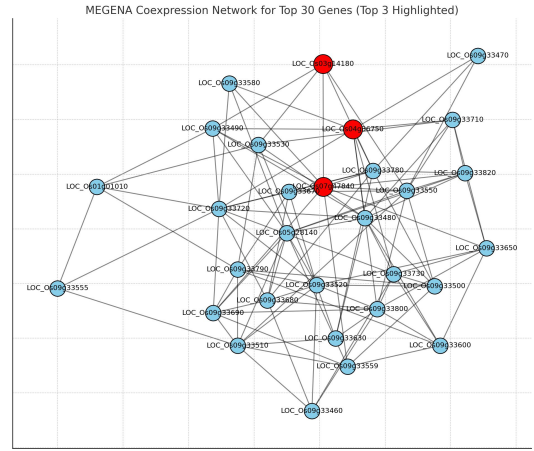


Fig. 7. MEGENA Co-expression Network for Top 30 Genes

E. Functional Insights and Biological Implications

The analysis of key genes mentioned in Table 1 highlighted their functional contributions:

- OsHSP90.1, OsHSP70, and OsHSP101: Molecular chaperones that prevent protein denaturation under stress.
- OsDREB2A and OsbZIP23: Transcription factors involved in activating stress-responsive pathways.
- OsAPX1 and OsCATB: Enzymes responsible for detoxifying reactive oxygen species (ROS), mitigating oxidative stress.
- OsPP2C68 and OsCIPK15: Signal transduction regulators that modulate stress response pathways.

The downregulation of metabolic genes such as OsSUT2 (sucrose transporter) and OsPOD1 (peroxidase) suggests that energy-intensive growth-related processes are suppressed under heat stress to conserve resources for cellular protection mechanisms.

V. CONCLUSION

This study successfully leveraged the MEGENA algorithm to identify a critical gene network involved in heat stress response in rice. The heatmap and volcano plot analyses revealed distinct patterns of upregulated and downregulated genes, highlighting their roles in stress adaptation and pinpointing potential targets for genetic modifications. Strip plots further confirmed significant shifts in gene expression under heat stress, reinforcing the validity of these candidate genes.

Compared to traditional methods such as WGCNA, MEGENA provided a more granular view of gene co-expression networks, allowing for the identification of 975 heat-shock-prone genes and key regulatory hubs. The hierarchical network structure captured by MEGENA highlighted both global and local regulatory interactions, offering deeper insights into the complexity of heat stress adaptation.

TABLE I
TOP 30 DIFFERENTIALLY EXPRESSED GENES WITH THEIR FUNCTIONAL ANNOTATIONS

| Gene ID | Log2FC | Gene Name | Functional Annotation |
|----------------|--------|---------------|---|
| LOC_Os03g14180 | 14.16 | OsHSP90.1 | Heat shock protein 90, involved in protein folding and stress response |
| LOC_Os04g36750 | 14.13 | OsDREB2A | Dehydration-responsive element-binding protein, regulates stress-responsive genes |
| LOC_Os07g47840 | 14.07 | OsHSP70 | Heat shock protein 70, functions as a molecular chaperone |
| LOC_Os01g01010 | 12.98 | OsAPX1 | Ascorbate peroxidase, involved in reactive oxygen species detoxification |
| LOC_Os05g28140 | 11.45 | OsSUT2 | Sucrose transporter, plays a role in phloem loading and sugar transport |
| LOC_Os09g33460 | -0.98 | OsWRKY45 | WRKY transcription factor, associated with disease resistance |
| LOC_Os09g33470 | -0.56 | OsNAC6 | NAC domain-containing protein, involved in stress responses |
| LOC_Os09g33480 | 0.25 | OsZIP23 | bZIP transcription factor, regulates stress-responsive genes |
| LOC_Os09g33490 | -0.64 | OsCPK4 | Calcium-dependent protein kinase, involved in signal transduction |
| LOC_Os09g33500 | -0.16 | OsRUB1 | Related to ubiquitin 1, involved in protein degradation pathways |
| LOC_Os09g33510 | 0.27 | OsPP2C68 | Protein phosphatase 2C, functions in ABA signaling and stress responses |
| LOC_Os09g33520 | -0.25 | OsMYB4 | MYB transcription factor, associated with cold tolerance |
| LOC_Os09g33530 | -0.17 | OsHSP24.1 | Small heat shock protein, functions in protein folding under stress |
| LOC_Os09g33550 | -1.42 | OsCATB | Catalase isozyme B, involved in hydrogen peroxide breakdown |
| LOC_Os09g33555 | -0.84 | OsP5CS1 | 1-Pyrroline-5-carboxylate synthetase, key enzyme in proline biosynthesis |
| LOC_Os09g33559 | -0.03 | OsLEA3 | Late embryogenesis abundant protein, associated with dehydration tolerance |
| LOC_Os09g33580 | -0.80 | OsGSTU4 | Glutathione S-transferase, involved in detoxification processes |
| LOC_Os09g33600 | 0.02 | OsDHAR1 | Dehydroascorbate reductase, plays a role in ascorbate recycling |
| LOC_Os09g33630 | -0.58 | OsPOD1 | Peroxidase, involved in lignin biosynthesis and defense |
| LOC_Os09g33650 | -0.61 | OsLOX1 | Lipoxygenase, associated with lipid metabolism and stress responses |
| LOC_Os09g33670 | 0.10 | OsRBOHB | Respiratory burst oxidase homolog, involved in reactive oxygen species production |
| LOC_Os09g33680 | -0.42 | OsCML31 | Calmodulin-like protein, functions in calcium signaling |
| LOC_Os09g33690 | -0.44 | OsCDPK7 | Calcium-dependent protein kinase, involved in cold and salt stress responses |
| LOC_Os09g33710 | -1.07 | OsHSP23.7 | Small heat shock protein, functions in protein protection under stress |
| LOC_Os09g33720 | -1.25 | OsAP2/ERF-108 | AP2/ERF domain-containing transcription factor, regulates stress-responsive genes |
| LOC_Os09g33730 | -0.52 | OsCIPK15 | CBL-interacting protein kinase, involved in abiotic stress signaling |
| LOC_Os09g33780 | 1.44 | OsHSP101 | ClpB/HSP100 family protein, functions in thermotolerance |
| LOC_Os09g33790 | 0.74 | OsHSP82 | Heat shock protein 82, acts as a molecular chaperone |
| LOC_Os09g33800 | 3.80 | OsHSP16.9 | Small heat shock protein, associated with heat stress tolerance |
| LOC_Os09g33820 | 3.85 | OsHSP18.0 | Small heat shock protein, involved in protection against heat stress |

VI. FUTURE RESEARCH DIRECTIONS

Functional validation can be conducted through experimental methods such as qPCR, CRISPR knockouts, or over-expression studies to confirm the roles of identified hub genes.[13] Additionally, pathway analysis is crucial for investigating metabolic and signaling pathways associated with stress-responsive genes, helping to uncover deeper biological mechanisms. These candidate genes can also be applied in marker-assisted breeding programs to develop heat-tolerant rice cultivars, ensuring improved resilience to environmental stress. Furthermore, integrating these findings with precision agriculture can enhance AI-driven predictive models for real-time monitoring and early detection of heat stress in crops, leading to more efficient and sustainable agricultural practices. These results demonstrate the effectiveness of MEGENA in capturing complex gene interactions and hierarchical relationships, making it a valuable tool for advancing agricultural

genomics and improving crop resilience in the face of climate change.

REFERENCES

- [1] T. Arivelarasan, V. S. Manivasagam, V. Geethalakshmi, K. Bhuvaneswari, K. Natarajan, M. Balasubramanian, R. Gowtham, and R. Muthurajan, "How far will climate change affect future food security? an inquiry into the irrigated rice system of peninsular india," *Agriculture*, vol. 13, no. 3, p. 551, Feb. 2023. [Online]. Available: <http://dx.doi.org/10.3390/agriculture13030551>
- [2] Y.-H. Xing, H. Lu, X. Zhu, Y. Deng, Y. Xie, Q. Luo, and J. Yu, "How rice responds to temperature changes and defeats heat stress," *Rice*, vol. 17, no. 1, Nov. 2024. [Online]. Available: <http://dx.doi.org/10.1186/s12284-024-00748-2>
- [3] M. K. Barati, B.-S. Soundharajan, and M. R. Nikoo, "Simulation of climate-adaptation responses

- to rainfall variability on rainfed yield anomalies,” *Environmental and Sustainability Indicators*, vol. 22, p. 100411, Jun. 2024. [Online]. Available: <http://dx.doi.org/10.1016/j.indic.2024.100411>
- [4] J. Xiong, H. Wang, Z. Zhong, S. Li, and P. Qin, “Emerging strategies to improve heat stress tolerance in crops,” *aBIOTECH*, Jan. 2025. [Online]. Available: <http://dx.doi.org/10.1007/s42994-024-00195-z>
 - [5] P. B. Kavi Kishor, P. Suravajhala, P. Rathnagiri, and N. Sreenivasulu, “Intriguing role of proline in redox potential conferring high temperature stress tolerance,” *Frontiers in Plant Science*, vol. 13, Jun. 2022. [Online]. Available: <http://dx.doi.org/10.3389/fpls.2022.867531>
 - [6] J. Li, C. Yang, J. Xu, H. Lu, and J. Liu, “The hot science in rice research: How rice plants cope with heat stress,” *Plant, Cell and Environment*, vol. 46, no. 4, p. 1087–1103, Dec. 2022. [Online]. Available: <http://dx.doi.org/10.1111/pce.14509>
 - [7] G. Cao, H. Huang, Y. Yang, B. Xie, and L. Tang, “Analysis of drought and heat stress response genes in rice using co-expression network and differentially expressed gene analyses,” *PeerJ*, vol. 12, p. e17255, Apr. 2024. [Online]. Available: <http://dx.doi.org/10.7717/peerj.17255>
 - [8] W.-M. Song and B. Zhang, “Multiscale embedded gene co-expression network analysis,” *PLOS Computational Biology*, vol. 11, no. 11, p. e1004574, Nov. 2015. [Online]. Available: <http://dx.doi.org/10.1371/journal.pcbi.1004574>
 - [9] H. Tao, S. Xu, H. Shen, J. Yang, Y. Xu, G. Huang, C. Feng, W. Wan, S. T. Woldegiorgis, W. Liu, and H. He, “Genome-wide characterization and functional analysis of heat shock transcription factors in wild and cultivated rice (*oryza sativa* L.),” *Plant Stress*, vol. 12, p. 100505, Jun. 2024. [Online]. Available: <http://dx.doi.org/10.1016/j.stress.2024.100505>
 - [10] H. Wu, Y. Ren, H. Dong, C. Xie, L. Zhao, X. Wang, F. Zhang, B. Zhang, X. Jiang, Y. Huang, R. Jing, J. Wang, R. Miao, X. Bao, M. Yu, T. Nguyen, C. Mou, Y. Wang, Y. Wang, C. Lei, Z. Cheng, L. Jiang, and J. Wan, “*scp1*floury endosperm24/*scp1*, a heat shock protein 101 (*scp1*hsp101/*scp1*), is required for starch biosynthesis and endosperm development in rice,” *New Phytologist*, vol. 242, no. 6, p. 2635–2651, Apr. 2024. [Online]. Available: <http://dx.doi.org/10.1111/nph.19761>
 - [11] S. Singh, A. Praveen, N. Dudha, and P. Bhadrecha, “Integrating physiological and multi-omics methods to elucidate heat stress tolerance for sustainable rice production,” *Physiology and Molecular Biology of Plants*, vol. 30, no. 7, p. 1185–1208, Jul. 2024. [Online]. Available: <http://dx.doi.org/10.1007/s12298-024-01480-3>
 - [12] H. Liu, Y. Wei, S. Xia, W. Xie, D. Ren, and Y. Rao, “Improvements in tolerance to heat stress in rice via molecular mechanisms and rice varieties,” *Agriculture*, vol. 15, no. 3, p. 318, Jan. 2025. [Online]. Available: <http://dx.doi.org/10.3390/agriculture15030318>
 - [13] P. Mthiyane, M. Aycan, and T. Mitsui, “Strategic advancements in rice cultivation: Combating heat stress through genetic innovation and sustainable practices—a review,” *Stresses*, vol. 4, no. 3, p. 452–480, Jul. 2024. [Online]. Available: <http://dx.doi.org/10.3390/stresses4030030>
 - [14] S. Anil Kumar, S. Kaniganti, P. Hima Kumari, P. Sudhakar Reddy, P. Suravajhala, S. P. and P. B. K. Kishor, “Functional and biotechnological cues of potassium homeostasis for stress tolerance and plant development,” *Biotechnology and Genetic Engineering Reviews*, vol. 40, no. 4, p. 3527–3570, Dec. 2022. [Online]. Available: <http://dx.doi.org/10.1080/02648725.2022.2143317>
 - [15] W. Tian, Q. Mu, Y. Gao, Y. Zhang, Y. Wang, S. Ding, K. D. Aloryi, N. E. Okpala, and X. Tian, “Micrometeorological monitoring reveals that canopy temperature is a reliable trait for the screening of heat tolerance in rice,” *Frontiers in Plant Science*, vol. 15, Feb. 2024. [Online]. Available: <http://dx.doi.org/10.3389/fpls.2024.1326606>
 - [16] S. Kundu, D. K. Saini, R. K. Meena, R. N. Bahuguna, and S. V. K. Jagadish, “High-throughput phenotyping and ai technologies for deciphering crop resilience to heat stress,” *Plant Physiology Reports*, vol. 29, no. 4, p. 699–715, Nov. 2024. [Online]. Available: <http://dx.doi.org/10.1007/s40502-024-00821-4>
 - [17] W. Taratima, C. Chuanchumkan, P. Maneerattanarungroj, A. Trunjaruen, P. Theerakulpisut, and A. Dongsansuk, “Effect of heat stress on some physiological and anatomical characteristics of rice (*oryza sativa* L.) cv. kdml105 callus and seedling,” *Biology*, vol. 11, no. 11, p. 1587, Oct. 2022. [Online]. Available: <http://dx.doi.org/10.3390/biology11111587>
 - [18] V. Ezin, W. W. Ahanchede, M. A. T. Ayenan, and A. Ahanchede, “Physiological and agronomical evaluation of elite rice varieties for adaptation to heat stress,” *BMC Plant Biology*, vol. 22, no. 1, May 2022. [Online]. Available: <http://dx.doi.org/10.1186/s12870-022-03604-x>
 - [19] G.-r. Dong, S.-m. Zhao, Y. Ding, Y.-q. Ma, X.-m. Ma, C.-l. Liu, and B.-k. Hou, “Rice glycosyltransferase *osdugt1* is involved in heat stress tolerance by glycosylating flavonoids and regulating flavonoid metabolism,” *Frontiers in Plant Science*, vol. 15, Jan. 2025. [Online]. Available: <http://dx.doi.org/10.3389/fpls.2024.1516990>
 - [20] M. M. Hossain, S. Ahmed, M. S. Alam, and A. Hossain, “Adverse effects of heat shock in rice (*oryza sativa* L.) and approaches to mitigate it for sustainable rice production under the changing climate: A comprehensive review,” *Heliyon*, vol. 10, no. 24, p. e41072, Dec. 2024. [Online]. Available: <http://dx.doi.org/10.1016/j.heliyon.2024.e41072>
 - [21] K. R. Mendes, A. Bonifacio, M. O. Martins, R. H. Sousa, M. V. Monteiro, and J. A. Silveira, “Heat shock combined with salinity impairs photosynthesis but stimulates antioxidant defense in

rice plants,” *Environmental and Experimental Botany*, vol. 225, p. 105851, Sep. 2024. [Online]. Available: <http://dx.doi.org/10.1016/j.envexpbot.2024.105851>

- [22] A. M. Distéfano, V. Bauer, M. Cascallares, G. A. López, D. F. Fiol, E. Zabaleta, and G. C. Pagnussat, “Heat stress in plants: sensing, signalling, and ferroptosis,” *Journal of Experimental Botany*, Jul. 2024. [Online]. Available: <http://dx.doi.org/10.1093/jxb/erae296>
- [23] I. Sadura and A. Janeczko, “Are heat shock proteins important in low-temperature-stressed plants? a minireview,” *Agronomy*, vol. 14, no. 6, p. 1296, Jun. 2024. [Online]. Available: <http://dx.doi.org/10.3390/agronomy14061296>