



RNA-seq unveils pathways for drought and salinity resilience in Egyptian rice Sakha 102

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Abstract

Refining stress-specific and communal adaptive mechanisms for drought and salinity is fundamental for developing resilient rice lines efficiently adapting arid or semi-arid agroecosystems. RNAseq profiling of Egyptian rice cultivar Sakha 102 seedlings subjected to osmo-equivalent doses of mannitol and NaCl showed a 24.7% overlap in differentially expressed genes (DEGs) between osmotic and salinity stresses, with 47% of DEGs unique to osmotic stress and 3.6% specific to salinity. Drought specifically upregulates genes like hexokinase I (involved in sugar sensing) and leaf trichome cell wall strengthening, whereas salinity stress activates signaling genes, including Cysteine-Rich Receptor-Like Protein Kinases and the cytoplasmic kinase *RLCK223*. Additionally, both stresses induce common genes such as chlorine channel I and inorganic phosphate transporter 1–5. Importantly, the downregulated genes network seemed to offer valuable complementary strategies focusing on the prioritizing of certain adaptive energy-trade off mechanism over growth. We proposed a model illustrating some distinct and overlapping molecular adaptive responses in the rice cultivar Sakha 102. We propose considering suggested results to improve stress-specific breeding and precision genome editing programs (ex: CRISPR-base genome editing) for developing efficient stress-resilient rice varieties.

Keywords Rice · Drought · Salinity · RNA-seq

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Introduction

Asian rice (*Oryza sativa* L.) is the model plant for monocots and the second most important staple food, after wheat, for more than half of mankind (Edwards et al. 2024), nevertheless, it is extremely susceptible to edaphic environmental stresses including drought and/or salinity (Lv et al. 2022; Hazman et al. 2023). Climate change intensifies these challenges, threatening rice production and the livelihoods of millions of small farmers (Kongpraphrut et al. 2025; Hazman et al. 2025a, b). Egypt ranks as the top rice producer in North Africa and the Middle East, and the second largest in Africa, following Nigeria (FAO 2022). However, drought or soil salinity poses major challenges to agriculture in the Nile Delta and the newly reclaimed low-fertility sandy soil areas, leading to crop yield losses of 25% (Shin et al. 2022). Egyptian agroecosystem is an arid or semi-arid with a minimal rainfall of an averaging less than 20 mm annually in most areas (Nada et al. 2014); and with over 80% of Nile River water used for agriculture (Abdelhafez et al. 2020). Hydrological drought problem in Egypt is intensified due to the rapidly growing population (expected to exceed 160 million by 2050) thus heightening competition between water resources (mainly River Nile) across agriculture, domestic, and industrial sectors, straining the Nile's limited supply and necessitating urgent water management reforms to balance these needs (Shin et al. 2022). Additionally, about 37% of Egypt's cultivated soils are affected by salinity that driven by seawater intrusion in the Nile Delta's coastal areas, high water tables, poor irrigation practices and inadequate drainage system (Mohamed 2016; Arafa et al. 2024).

In spite of the high similarity between drought and salinity effects, rice can specifically sense drought or salinity then tailor stress-specific adaptive responses for each stress type (Hazman et al. 2016). Both of these edaphic stress types—drought and salinity—challenged rice plants by a certain level of physiological drought. On one hand, drought decreases rhizosphere water potential and intensifies nutrient deficiency by reducing soil water needed for nutrients dissolution and transport into roots. Salinity, on the other hand, triggers a similar effect through Na^+ that hold water molecules in soil and compete primarily with K^+ leading to physiological drought and nutrient deficiency, respectively. Importantly, salt stress triggers specific ions toxicity, primarily sodium, which if highly accumulated in the cytoplasm can eventually denature and inhibit vital metabolic enzymes and devastate sensitive cellular and physiological functions (Hazman et al. 2022; Mal and Panchal 2024). As indirect yet extremely serious consequence, drought and/or salinity can trigger the overproduction of reactive oxygen

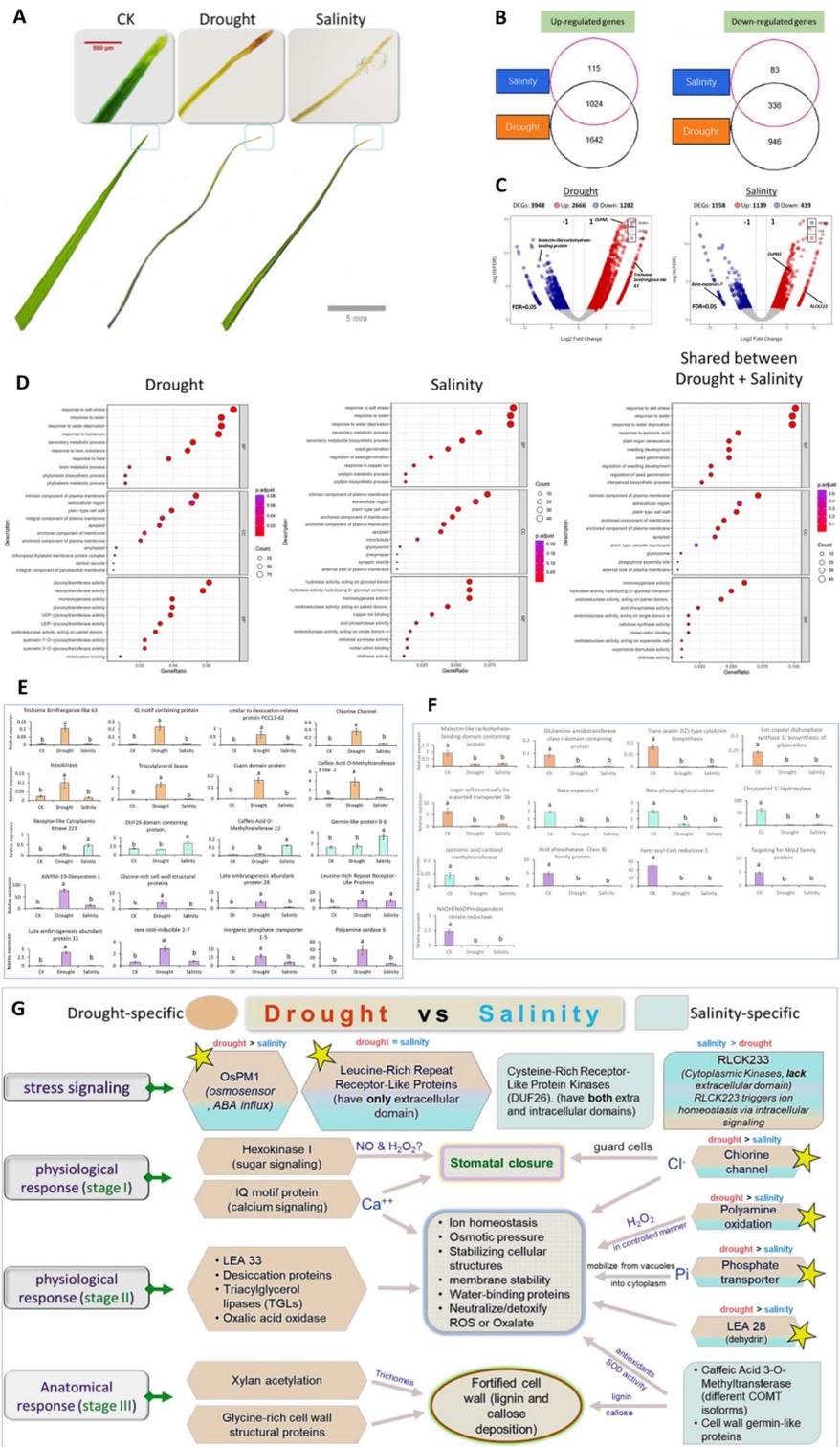
species (ROS) such as superoxide radicals (O_2^-), hydrogen peroxide (H_2O_2), and hydroxyl radical ($\text{OH}\cdot$). Excessive ROS production could result from disrupted electron transport and energy sinking in photosynthesis. This disruption occurs due to extended unbalanced CO_2/O_2 exchange caused by stomatal adaptive closure. Moreover, ROS could be enzymatically generated by ROS-producing enzymes such as membrane NADPH oxidase and cell-wall oxalic acid oxidase (Hazman et al. 2025a, b).

Developing new rice genotypes (inbreds and hybrids) with effective resilience under drought and/or salinity stress requires sufficient understanding of *unique* versus *communal* molecular adaptive mechanisms (Bashir et al. 2019). The shared and unique core molecular mechanisms triggered by rice in response to drought and/or salt stress could be efficiently revealed using the application of high-throughput technologies such as RNA sequencing or RNA-seq (Ren et al. 2023). The RNA-seq is very beneficial in deepening our knowledge to decipher complex physiological and biochemical adaptive networks by identifying wide range of co-working up and down-regulated key stress-responsive genes (Aslam et al. 2024). This knowledge is thought to be beneficial for precision breeding/genome engineering strategies (ex: CRISPR) of new rice cultivars with enhanced resilience under arid and semi-arid agroecosystems (Ganie et al. 2021). This study tests the hypothesis that drought and salinity stress in Sakha 102 (Japonica) trigger both overlapping and unique gene regulation networks, shaping well-suited adaptive responses at the molecular level. In this work, we have subjected the Egyptian rice Sakha 102 seedlings (Japonica, sensitive to drought and salinity) to osmotically equivalent doses of mannitol and NaCl to mimic drought and salinity stresses, respectively. We conducted a RNA sequencing analysis to generate differentially expressed genes (DEGs), along with gene ontology (GO) and Kyoto Encyclopedia of Genes and Genomes (KEGG) data, aiming to uncover some of stress-specific key molecular mechanisms underlying both individual and common stress tolerance responses to drought and/or salinity in rice (for experimental design and methodology see Supplementary file 1).

Can we phenotypically distinguish between drought and salinity stress

To effectively address the impact of environmental stressors on rice resilience in arid and semi-arid regions, it is essential to differentiate between drought and salinity symptoms using a precise physiological approach (Hazman and Brown 2018). In the salt-sensitive rice Sakha 102 (Mekawy et al. 2015), phenotypic responses varied under osmo-equivalent

Fig. 1 Phenotypical and gene expression analysis in rice variety Sakha 102 exposed or not to osmo-equivalent doses of drought (mannitol) and salinity (NaCl) stress. **A** phenotypic response of Egyptian rice cultivar Sakha 102 under control (CK), drought (≈ 205 mM mannitol) and salinity (≈ 102 mM NaCl). **B** Venn diagram showing the upregulated and downregulated of differentially expressed genes (DEGs) between drought and salt stress treatments. **C** Volcano plots of DEGs detected in Sakha 102 under drought and salinity versus control. Significantly up- and down-regulated genes were represented by red and blue dots, respectively. \log_2 fold change (\log_2FC) of 1 and a false discovery rate (FDR) of 0.05. **D** Significantly rich GO terms in Sakha 102 under drought, salinity, and both drought/salinity in relative to control conditions. Relative expression of upregulated (**E**) and downregulated (**F**) genes uniquely involved in the adaptive response to osmotic stress (brown columns), salinity (blue columns), and shared in both drought and salinity (purple columns) in Sakha 102 rice seedlings. *OsActin* was used as the internal control. Error bars indicate mean \pm SD ($n=3$). **G** a graphical model representing suggested specific molecular adaptive responses to drought and salinity, and shared in both stress types in rice cultivar Sakha 102



drought and salinity treatments (Fig. 1A). Drought stress (mimicked by mannitol) resulted in symptoms like whole leaf rolling, wilting, and desiccation, whereas salinity stress

caused related but distinct symptoms, including leaf tip burning, yellowing (chlorosis), reduced leaf tip growth, and salt crystal accumulation (Hazman et al. 2016).

Communal and stress-specific adaptive transcriptomics under drought versus salinity

To our knowledge, this is the first report that utilized RNA-seq approach for scanning and comparing gene regulation networks between rice plants of the same genotype subjected to osmo-equivalent doses of osmosis and salinity. RNA-seq is a powerful technique used to deeply explore rice transcriptome under drought or salt stress (Ren et al. 2023). RNA-seq analysis of Egyptian rice Sakha 102 revealed a 24.7% overlap in differentially expressed genes (DEGs) between osmotic and salinity stresses, with 47% of exclusive DEGs to osmotic stress and 3.6% uniquely to salinity under osmo-equivalent conditions (Tables S1 and S2). Specifically, 1642 DEGs were uniquely upregulated under drought stress, compared to 115 uniquely upregulated DEGs in salt stress, with 1024 DEGs commonly upregulated in both stress conditions (Fig. 1B, Table S1). Conversely, the pattern of downregulated genes revealed 946 DEGs specific to drought stress and 83 DEGs specific to salt stress, alongside 336 DEGs that were commonly downregulated in both drought and salinity stress in Sakha 102 third leaves (Fig. 1B, Table S2). Volcano plots presented the number of upregulated and downregulated genes under drought and salinity (see and Fig. 1C, Tables S3 and S4).

The Gene Ontology (GO) classification of differentially expressed genes (DEGs) highlighted clear functional differences across the transcriptional comparisons. In drought-stressed Sakha 102 leaves compared to control conditions, 4673 differentially DEGs were significantly assigned to 112, 7, and 20 Gene Ontology (GO) terms in the categories of biological process (BP), cellular components (CC), and molecular function (MF), respectively (Table S5). For salt-stressed Sakha 102 leaves compared to controls, 1241 DEGs were significantly enriched in the BP (60 terms), CC (7 terms), and MF (15 terms) categories (Table S6). Of these, 875 DEGs were common to both drought and salinity stress, and they were classified into 40 GO terms in BP, 5 terms in CC, and 13 terms in MF (Table S7). We chose the top 10 GO terms with the lowest false discovery rate (FDR) from each category based on the enrichment analysis results and visualized these enriched terms, as depicted in Fig. 1D. The top 10 GO terms with the lowest false discovery rate (FDR) were selected from the enrichment analysis results and plotted in Fig. 1D. We have noted that the GO terms “response to salt stress”, “response to water”, and “response to water deprivation” were enriched in both stress types with the category BP. The GO terms “intrinsic component of plasma membrane”, “extracellular region”, and “plant-type cell wall” were enriched in CC. Additionally, the GO terms that were found to be enriched in MF category are

“monooxygenase activity”, “hydrolase activity, hydrolyzing O-glycosyl compound”, and “oxidoreductase activity, acting on single donors” (Fig. 1D, Table S8). On the other hand, “glycosyltransferase activity” and “hexosyltransferase activity” were the highest value GO terms (MF category) specifically enriched under drought stress (Fig. 1D, Table S9). Equally important, the GO terms “hydrolase activity, acting on glycosyl bonds” and “hydrolase activity hydrolyzing O-glycosyl compound” were uniquely enriched in case of salinity stress (Fig. 1D, Table S10). In the same context, the shared 10 top upregulated and downregulated GO terms in response to both drought and salinity were achieved (Supplementary Fig. S1, Tables S11 and S12). Kyoto Encyclopedia of Genes and Genomes (KEGG) revealed that 8 pathways were significantly enriched uniquely under drought, salinity, and both stress (Supplementary Fig. S2, Tables S13-15). The common upregulated and downregulated adaptive pathways in response to drought and salinity under applied experimental conditions were presented in Supplementary Fig. S3, Table S16 and Table S17.

Refining gene regulation networks of drought versus salinity adaptive response

For validating genes uniquely identified by RNA-seq in response to drought and salinity, and the shared between them, we selected several key upregulated (Fig. 1E, Table S18, and supplementary figure S4) and downregulated (Fig. 1F, Table S19, and supplementary figure S5) with the highest expression ratio \log_2 fold change (\log_2 FC) to be validated using qRT-PCR Gel Express method (Hazman 2022). FPKM (Fragments Per Kilobase of transcript per Million mapped reads) gene expression values were presented as \log_2 Fold Change (\log_2 FC) in supplementary figures S4 and S5 for upregulated and downregulated gene respectively, that were selected and validated by qRT-PCR. Several reports compared fine adaptive molecular responses in rice under drought and salinity stress (Tang et al. 2019; Hao et al. 2022). In the presented work, it is proposed that rice has the ability to sense and react to drought and salinity stresses through a combination of stress-specific pathways and overlapped adaptive mechanisms (Li et al. 2024). By integrating RNA-seq data with qRT-PCR analysis, a potential model was proposed to depict stress-specific pathways and shared overlapping adaptive strategies in rice under drought and salinity stress (see Fig. 1G). Based on the revealed upregulated gene expression profile (Fig. 1E), it is suggested that specialized membrane-bound osmo-sensors AWPM-19-like protein 1 contributed into osmotic stress sensing (triggered by drought and salinity) through its extracellular domain, while its intracellular domain may facilitate ABA transport

and signaling within the cell (Yao et al. 2018). In the same context, salinity stress may be specifically sensed intracellularly by a Receptor-like Cytoplasmic Kinase 223 that lacks an extracellular domain (Sade et al. 2020). Rapid stomatal closure, an adaptive response to drought and salinity, could be facilitated by sugar signaling (Wu et al. 2023), calcium-sensing IQ-Motif Containing protein 3 (Zhou et al. 2012), and chloride channels 1 which all induce stomatal closure and adjusting ion homeostasis (Liu et al. 2023). Several key physiological components are shared between drought and salinity responses, including dehydrins LEA proteins for osmotic adjustment and stabilizing cellular structures (Sun et al. 2021). Also, inorganic phosphate transporters which is believed to promote the mobilization of inorganic phosphorous from vacuoles to cytoplasm under drought or stress (Wang et al. 2018), and polyamine oxidase (Sagor et al. 2021); all combined can contribute to maintaining ions balance, stabilizing cell structures, and neutralizing reactive oxygen species (ROS). At the anatomical level, adaptive responses might include secondary cell wall strengthening through lignin and callose deposition (Hazman and Brown 2018). Driven by xylan residue acetylation, especially in trichomes, cell wall enforcement under drought conditions could be improved (Bischoff et al. 2010; Zhang et al. 2021), while caffeic acid O-methyltransferase may play a similar role under salinity stress (Wu et al. 2013).

Plant adaptive responses under drought and salinity constitute a finetuned energy trade-off network between upregulated and downregulated genes. This could facilitate achieving well-balanced and efficient survival mechanisms. Indeed, the downregulation of several stress-related genes were recorded in this study in response to drought and salinity (Fig. 1F). During osmotic or salt stress, plants redirect energy consumption and resources utilization from growth to stress management. The molecular mechanisms coordinating the balance between growth and stress are still not well understood. Under stress, plants prioritize adaptive or resistance strategies over normal growth and development (Zhu et al. 2023). During drought and other forms of abiotic stress, soluble sugar metabolism could be a dynamic process that includes both degradation and synthesis processes (Yu et al. 2025). The expression profile of downregulated genes indicated that under drought or salinity, Sakha 102 plants reduce glycolysis (beta-phosphoglucomutase) and sugar membrane transporter activity (OsSWEET3b) to conserve energy during stress. This reduction limits carbon allocation to other tissues, such as roots, enabling sugar to be re-metabolized in critical survival-related processes. Alternatively, the reduction in glycolysis and sugar transport might be a mere damage response due to the reduction in the level of photosynthesis (Gautam et al. 2022). Importantly, cell growth reduction is a well-known adaptive response

under stress. Cell-division related genes *Beta-expansin-7* (involved in loosening cell wall) and *Targeting for Xklp2 family protein* (related to cell division and microtubules organization) were significantly downregulated under either stress type. In the same context, the downregulation of cell division related hormones including trans-zeatin and gibberellins might be promoted to encourage minimizing growth rate under stress conditions (Liao et al. 2023). Nitrogen (N) is a fundamental macronutrient essential for optimal plant growth and development; it is a primary component of amino acids, chlorophyll, adenosine triphosphate (ATP), and nucleic acids (DNA and RNA) (Hazman et al. 2025a, b). Nevertheless, the impact of salinity on nitrogen metabolism is multifaced and can differ significantly based on plant and soil characteristics (Ashraf et al. 2018). We propose that applied drought and salt stress at the time of measurements showed a severe reduction in the nitrogen assimilation (*NADH/NADPH-dependent Nitrate reductase*) and nitrogen reallocation (*glutamine amidotransferase class I containing protein*) compared to control plants due to minimized N uptake efficiency (Tian et al. 2021). The downregulation of *Malectin-like carbohydrate-binding domain containing protein* might lead to reducing ROS generated by membrane NADPH oxidase, the process which is needed to trigger antioxidative response, in particular under drought (Jing et al. 2021). Interestingly, it was noted that phosphorous (P) metabolism under drought and salinity stress might be varied based on the type of source compound. While inorganic phosphate mobilization from vacuoles to the cytoplasm was upregulated (*inorganic phosphate transporter 1–5*, see Fig. 1E) in response to drought and salinity (Wang et al. 2018), the mobilization of phosphorous from organic compounds is believed to be downregulated (*Acid Phosphatase class B*) to balance phosphorus mobilization (an ATP needed process) thus equilibrium stability between resources and energy demands (Zhang et al. 2018). Likewise, wax formation seemed to be a non-prioritized adaptive water saving strategy under drought or salt stress in cereals due to its excessive high energy cost, thus its modulation (down regulated *Fatty acyl CoA reductase* gene) is thought to be an adaptive strategy to allow better energy usage towards other complementary traits like root architecture or stomatal regulation (Xue et al. 2017). In the same context, *Chrysoeriol 5'-hydroxylase* was down regulated under either stress type to reserve limited energy available under stress episode for other adaptive efficient mechanism such as stomatal closure or synthesizing protective proteins, ex: dehydrins (Lam et al. 2015). Finally, the balance between jasmonates (jasmonic acid metabolites) Methyl-JA and JA-Ile under stress conditions is speculated to be modulated. Both stress types trigger JA biosynthesis, but the metabolic flux often favors JA-Ile over MeJA (downregulated *Jasmonic acid carboxylase*)

because JA-Ile directly mediates stress responses, such as stomatal closure, antioxidant defense, and osmotic adjustment (Riemann et al. 2015).

Conclusion

It is recently reported that plants can individually sense and respond to drought and salinity, despite of the great similarity between them in terms of damage symptoms and adaptive response mechanisms. We propose that decoding stress-specific and communal adaptive molecular mechanisms in rice is beneficial in enhancing the efficiency of molecular breeding programs aiming to develop rice lines with enhanced resilience under arid and semi-arid agroecosystems. It was possible to decipher the fine differences between stress-specific pathways for either osmotic or salt stress, additionally, it was possible to highlight some common adaptive mechanisms between drought and salinity. Importantly, based on the downregulated gene regulation networks, it is proposed that rice (here Sakha 102) under drought and/or salinity might give precedence to availing adaptive mechanism such as stomatal closure and synthesizing dehydrins proteins over other energy-consuming mechanisms as wax synthesis or specific secondary metabolites as tricin. Finally, we highly emphasize that further studies are needed to decipher more fine details considering examining different rice cultivars representing japonica and indica subspecies under different stress time points.

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Author contributions LG, PN, MR, MH designed the experiments and supervised the research, MH, SF, GA, AE, MR, HT performed the measurements, analyzed the data and wrote the manuscript.

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Data availability No datasets were generated or analysed during the current study.

Declarations

Competing interests The authors declare no competing interests.

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