ARTICLE

Transcriptomic analysis of *Musa acuminata* cv. Mas reveals salinity stress-responsive small open reading frames

Wei Yang Kurk[1,2], Jennifer Ann Harikrishna[1], Kousuke Hanada[3] and Chee How Teo[1*]

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Abstract: *Soil salinity severely limits crop productivity, especially in fruit crops such as banana. While most studies focus on protein-coding genes, small open reading frames (sORFs) are emerging as potential regulators of salinity stress responses. This study aimed to investigate the transcriptional response of sORFs in M. acuminata cv. Mas under salinity stress using RNA sequencing and NanoString validation. Transcriptomic analysis was performed on banana plantlets treated with 0 mM and 300 mM NaCl to assess gene expression under control and high salinity conditions. A total of 136 differentially expressed sORFs were identified, including 131 annotated and 5 novel sORFs. Gene Ontology analysis showed their enrichment in oxidoreductase activity, ion transport, and photosynthesis, while KEGG analysis highlighted roles in tryptophan metabolism and MAPK signaling. These findings reveal the potential regulatory functions of sORFs in banana salinity stress responses and underscore their potential as targets for developing salinity-tolerant cultivars.*

Keywords: *Banana, differentially expressed sORFs, abiotic stress, RNA sequencing, salinity response*

INTRODUCTION

Abiotic stress is a major factor that greatly impacts global plant productivity and crop yield. Elevated soil salinity is one of the most significant abiotic stresses that affecting plant growth by disrupting plant cells' water and nutrient uptake (Hasanuzzaman and Nahar 2024). Recent studies have revealed the global distribution of salinity-affected areas, with Australia being the largest salinity-affected region, followed by North and Central Asia, South America, and South Asia (Shokat and Großkinsky 2019). Moreover, an annual global loss of approximately $27.3 billion in the agricultural sector has been estimated due to increased soil salinity (Qadir et al. 2014). Understanding the molecular mechanisms of salinity stress tolerance in crops is crucial for improving agricultural productivity and global food security.

Bananas are climacteric fruits with high nutritional value that belong to the monocotyledonous herbaceous plant group. According to FAOSTAT (2020), the annual global banana production has reached nearly 120 million tonnes, cultivated across 5.2 million hectares of agricultural land. However, banana research has progressed more slowly than other major food crops. Bananas are mainly cultivated as a staple food in the least developed countries, particularly in

***Corresponding author:**
E-mail: cheehow.teo@um.edu.my

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[1] Universiti Malaya, Centre for Research in Biotechnology for Agriculture, 50603, Kuala Lumpur, Malaysia
[2] Universiti Malaya, Institute for Advanced Studies, 50603, Kuala Lumpur, Malaysia
[3] Kyushu Institute of Technology, Department of Bioscience and Bioinformatics, 680-4 Kawazu, 820-8502, Iizuka-shi - Fukuoka, Japan

Africa (Sreedharan et al. 2013). Recent advances in high-throughput sequencing technologies, such as RNA sequencing, have accelerated the discovery of the molecular mechanisms underlying plant abiotic stress tolerance, including pathways related to MAPK signaling, secondary metabolite biosynthesis, and plant hormone signal transduction (Alamholo and Alireza 2023). Small open reading frames (sORFs) have emerged as a new frontier in functional genomics, encoding short peptides (<100 amino acids) that participate in various physiological and stress responses (Hanada et al. 2013). A previous transcriptomic study examined banana responses to salinity stress (Hu et al. 2017), but the transcriptional landscape of sORFs in *M. acuminata* cv. Mas remains unexplored. Therefore, this study provides the first sORF transcriptional landscape in cv. Mas using RNA sequencing, providing new insights into their potential roles and associated biological pathways in salinity stress adaptation.

MATERIAL AND METHODS

Plant material and growth conditions

In this study, cv. Mas was chosen because of the lack of prior research on its salinity response and its importance as a major commercial cultivar in Malaysia (DOA 2009). Tissue culture of plantlets of cv. Mas were purchased from Horus Green Nursery Banana Tissue Culture. Banana plantlets at the five-leaf stage with approximately equal height (8 cm) were selected for the salinity stress treatment. Morphologically similar banana seedlings were acclimatized in black polybags with drainage holes (12 cm × 8 cm × 9.5 cm) containing organic black soil under a controlled environment for 7 days (16 h light/8 h dark cycle; 60% relative humidity; 28 °C).

Treatment with salinity stress

After 7 days of environmental adaptation, the bananas were subjected to 0 mM (0 dS m^{-1}), 100 mM (10.7 dS m^{-1}), 200 mM (19.8 dS m^{-1}), and 300 mM (28.1 dS m^{-1}) of NaCl (R&M Chemical, Biolution). For the salinity stress treatment, each banana plantlet received 50 mL of saline water twice weekly for 14 days. Control banana plantlets were irrigated with an equal volume of distilled water. Each treatment was conducted in triplicate.

Total RNA extraction

After 7 days of treatment, only the second youngest leaf from the plantlets treated with 300 mM and 0 mM NaCl was extracted for RNA-Seq. The 300 mM NaCl treatment was chosen because it produced clear salinity stress symptoms, indicating a sufficient stress level for transcriptomic analysis. The time point for RNA sequencing was selected based on preliminary observations (Supplementary Figure 1) and a previous study (Hu et al. 2017). Each treatment included three biological replicates, resulting in a total of 6 RNA samples for sequencing. A Nanophotometer (Implen GmbH, Germany) was used to measure RNA concentration, while agarose gel electrophoresis was used to assess RNA integrity.

Identifying sORFs by transcriptomic sequencing and bioinformatics analysis

The RNA samples were sent to the Beijing Genomics Institute (BGI) in China for RNA sequencing. Biological replicates from the 0 mM NaCl treatment were designated as MR1-3, while those from the 300 mM NaCl treatment were labeled as MR 4–6. Trimmomatic was used to preprocess the raw RNA-Seq data to remove adapters and low-quality bases. The cleaned reads were then aligned using the HISAT2 aligner to the Musa_acuminata_pahang_v4 banana reference genome (https://banana-genome-hub.southgreen.fr/filebrowser/download/1440408). StringTie (Pertea et al. 2015) was used to assemble and merge the RNA-Seq alignments into a core transcript set. Cuffcompare, a tool within Cufflinks, was used to identify novel transcripts by focusing on those transcripts classified under the “u,” “i,” “o,” and “j” class codes. The coding potential of these novel transcripts was then evaluated using the Coding Potential Calculator (CPC). Novel genes were identified from the set of predicted coding transcripts by excluding those with exact matches or overlaps with previously annotated genes. These novel transcripts and genes were then integrated with reference transcripts to establish a comprehensive dataset for downstream analysis. Gene expression levels were determined using RNA-Seq by Expectation-Maximization (RSEM) (Li and Dewey 2011), with normalization based on Fragments per Kilobase per Million mapped fragments (FPKM). Differentially expressed genes (DEGs) were identified using DESeq2 (Love et al. 2014), applying a minimum fold change (FC) of >1 or < −1, and an adjusted p-value (Padj) ≤ 0.05.

To identify differentially expressed sORFs (DE sORFs), both annotated and novel sORFs with coding sequences (CDSs) shorter than 360 base pairs (bp), a minimum FC > 1 or < −1, and a Padj ≤ 0.05 were selected. The identified DE sORFs were further categorized into two groups: those predicted to contain signal peptides (SignalP_sORF) and those that shared sequence homology to small peptides in the SWISS-PROT database (SWP_sORF). Signal peptide prediction was performed using SignalP 6.0 (https://services.healthtech.dtu.dk/services/SignalP-6.0/) with "Eukarya" and "Short output" as the parameters. The sORF sequences were also subjected to a local BLASTP search against the SWISS-PROT small peptide dataset (https://www.uniprot.org/help/downloads) to identify homology with known peptides using the following parameters: -evalue 1e-05 -max_target_seqs 1 -outfmt 6.

Functional categories of DEGs and DE sORFs

Gene Ontology (GO) classification and KEGG functional enrichment analyses were performed to determine the functions of DEGs and DE sORFs. The identified DEGs and DE sORFs were annotated using the GO database via AmiGo 2 (https://amigo.geneontology.org/amigo/landing). The GO classification results were then organized into three main ontologies: biological process (BP), molecular function (MF), and cellular component (CC). Additionally, KEGG Orthology (KO) annotation and KEGG pathway mapping for DEGs and DE sORFs were conducted using BlastKOALA (https://www.kegg.jp/blastkoala/). To further investigate their function, GO and KEGG analyses were performed using the phyper function in R. The p-values for the hypergeometric test were calculated using the following formula:

$$P = 1 - \sum_{i=0}^{m-1} \frac{\binom{M}{i}\binom{N-M}{n-i}}{\binom{N}{n}}$$

Only GO and KEGG terms with adjusted p-values ≤ 0.05 were considered significantly enriched. SRPlot, an open-access data visualization and graphing platform (https://www.bioinformatics.com.cn/en), was used to visualize the final results.

Validation of RNA-Seq data via NanoString analysis

To confirm the expression levels of the selected sORFs identified in RNA-Seq under salinity stress, NanoString analysis was conducted following the standard protocol provided by NanoString Technologies (https://nanostring.com/). For the NanoString analysis, a 1 µg aliquot of total RNA was used for each sample. Seven CodeSets were utilized, with two serving as housekeeping genes, namely eEF-1-alpha (*eEF-1-alpha*) and glyceraldehyde 3-phosphate dehydrogenase (*GAPDH*). The remaining five CodeSets were designed for specific sORFs of interest. Five sORFs were selected based on their adjusted p-value and log2FoldChange. The generated data were analyzed using the nSolver 4.0 Analysis Software (https://nanostring.com/wp-content/uploads/nSolver_setup_windows_x64_4.0.70.zip). Finally, the correlation analysis between the NanoString and RNA-Seq results was performed using the Pearson correlation coefficient in SRPlot.

RESULTS AND DISCUSSION

A comprehensive transcriptome analysis was performed on the young leaves of cv. Mas after 7 days of exposure to salinity stress. Although the transcriptomes of other banana cultivars under salinity conditions have been previously reported (Hu et al. 2017), the present study offers novel insights into the expression patterns of sORFs in bananas in high salinity environments, which have not yet been thoroughly examined.

The Cuffcompare analysis revealed an average of 674 novel genes and 27,287 known genes per sample, resulting in a total of 27,961 genes identified across all samples (Table 1). The prediction of novel genes indicates the existence of previously unannotated transcripts that can enhance banana salinity stress tolerance by encoding stress-responsive peptides. Meanwhile, the identified genes provide a comprehensive view of the core functional elements in bananas grown in saline conditions. Several salinity stress-induced sORFs unique to bananas were identified among these known and novel genes. These sORFs require further analysis to elucidate their expression patterns and functional roles in the response to salinity stress.

Transcriptome data analysis showed that approximately 77% (25,341 genes) of the genes in cv. Mas showed no significant difference in expression between the control and treatments (Figure 1A). Of the 5,156 DEGs identified, 2,663 genes showed higher expression and 2,493 showed lower expression in the salinity-treated samples (Figure 1A). Approximately 3% of DEGs were homologous to genes previously well-characterized as abiotic stress-responsive,

Table 1. Summary of the number of known and novel genes discovered in the control (MR1-3) and salinity-stressed banana samples (MR4-6)

Sample	Known gene	Novel gene	Total gene number
MR1	27,486	675	28,161
MR2	27,001	650	27,651
MR3	27,067	644	27,711
MR4	27,431	693	28,124
MR5	27,113	689	27,802
MR6	27,626	691	28,317

including those encoding late embryogenesis abundant (*LEA*) proteins, calmodulin-binding proteins (*CaMBP*), and plasma membrane intrinsic proteins (*PIPs*) (Trono and Pecchioni 2022). These findings confirm that the salinity stress treatment effectively triggered an expected physiological stress response in cv. Mas. The DEG profile of cv. Mas was predominantly characterized by upregulation, in contrast to the downregulation trend observed in *M. acuminata* cv. BD (Wei et al. 2022). This divergence suggests that cv. Mas may activate a distinct set of transcriptional responses, potentially prioritizing gene induction over suppression under salinity stress.

Despite the identification of over 5,156 DEGs, a relatively smaller proportion of sORFs (2.6%) were differentially expressed under saline stress. In total, 136 DE sORFs were identified in cv. Mas, comprising 131 annotated sORFs and 5 novel sORFs (Table 2). Of these, 86 were downregulated and 50 were upregulated (Figure 1B). These sORFs responded to high salinity either directly or indirectly, although their specific functions remain uncharacterized. Out of the 136 DE sORFs, 18 were predicted to encode peptides with the characteristics of signal peptides (Table 2). These included 11 upregulated and 7 downregulated DE sORFs, suggesting that their encoded peptides may be transmembrane and have a potential role in protein secretion and targeting processes in banana plants under salinity stress (SignalP_sORF, Figure 1C).

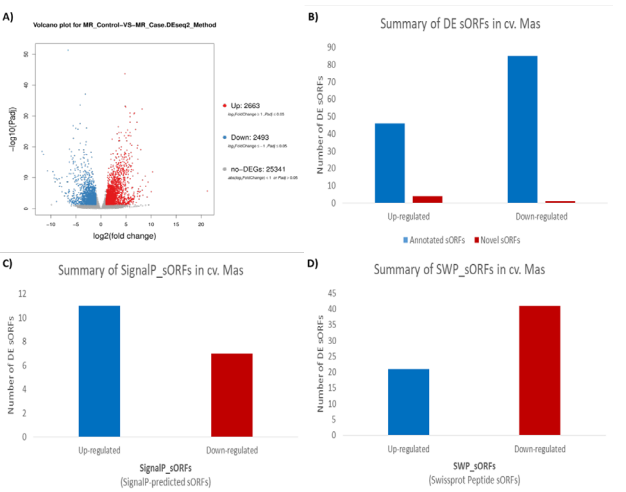

Figure 1. Overview of the DEGs and DE sORFs identified in cv. Mas under salinity stress. A) Volcano plot of the DEGs. B) Summary of the identified DE sORFs. The X-axis represents the up- or down-regulation of sORFs. The Y-axis represents the number of sORFs. C) Summary of the identified SignalP_sORFs (sORFs that contain the predicted signal peptide-like sequences). The X-axis represents the up- or downregulation of sORFs. The Y-axis represents the number of sORFs. D) Summary of identified SWP_sORFs (sORFs that shared sequence homology with small peptides in the SWISS-PROT database). The X-axis represents the up- or downregulation of sORFs. The Y-axis represents the number of sORFs.

A total of 62 of the 136 DE sORFs, 62 shared homology with small peptide sequences documented in the SWISS-PROT database (Table 2). Among these sORFs, 21 were upregulated and 41 were downregulated under salinity stress conditions (SWP_sORF, Figure 1D). Their change in expression under the stress condition suggests that their encoded peptides could improve plant salinity tolerance. Increasing evidence supports that sORFs function as regulators of

Table 2. Summary of small open reading frames in the transcriptome of bananas

Description of the sORF	Number of sORF
Total number of DE sORFs in the banana transcriptome	136
DE annotated sORFs in the banana transcriptome	131
Novel DE sORFs in the banana transcriptome	5
DE sORFs with signal peptides (SignalP_sORF)	18
DE sORFs with a homolog in SWISS-PROT (SWP_sORF)	62

various developmental processes (Xiao et al. 2025) and mediate responses to environmental stress (Zhou et al. 2022). These findings support the importance of the DE sORFs identified in this study, particularly those homologous to small peptides previously reported to be involved in abiotic stress mitigation. The discovery of 62 DE sORFs with homology to known small peptides suggests that they encode functional peptides rather than transcriptional noise. This study also highlights the differential expression of some sORFs that contain predicted signal peptide-like sequences, with most of these sORFs (11/18) showing higher expression levels under high salinity conditions. Signal peptides are short

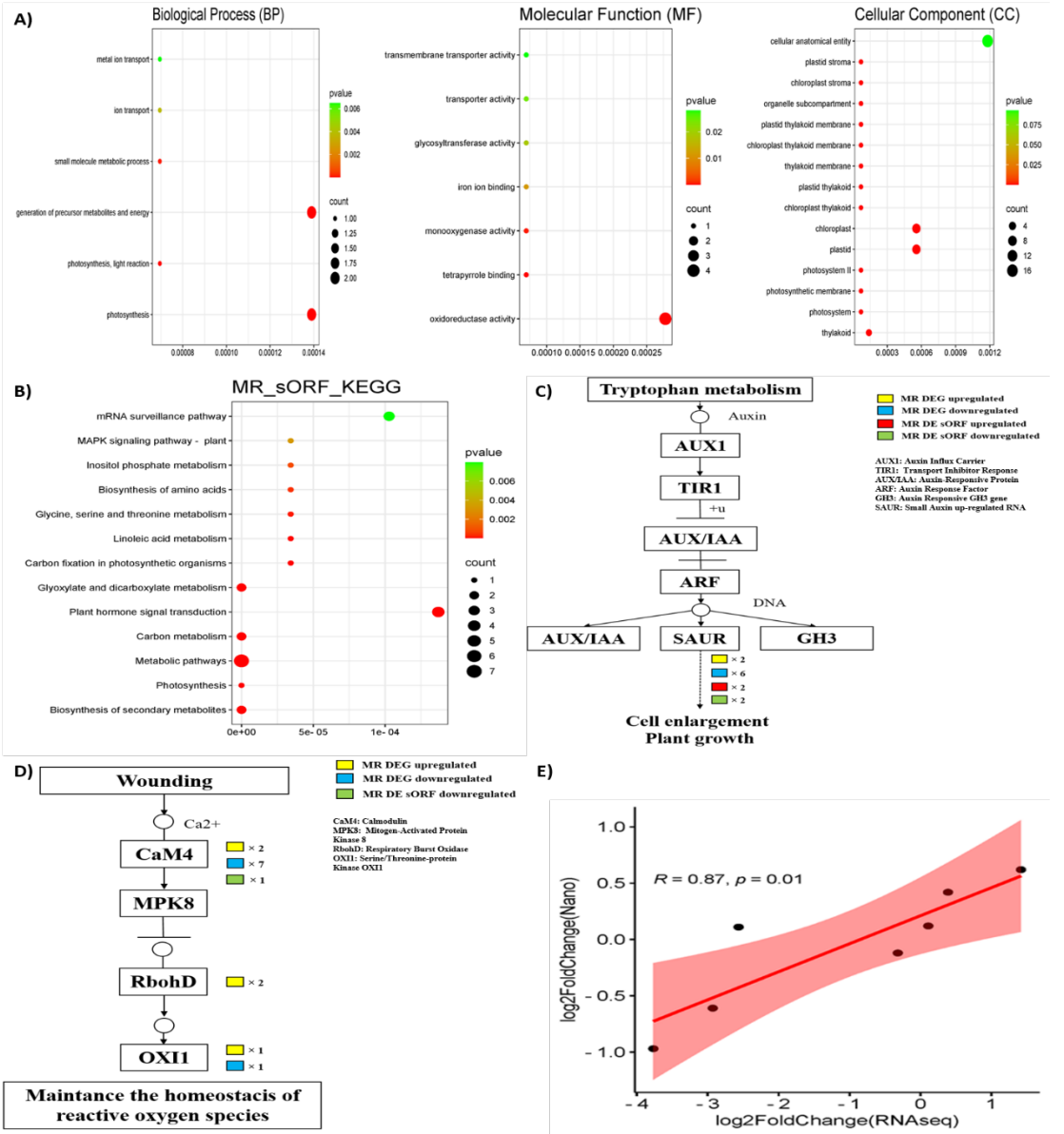

Figure 2. Functional enrichment and validation of DE sORFs in cv. Mas under salinity stress. (A) GO enrichment of DE sORFs. The x-axis represents the enrichment factor, and the y-axis represents the GO term name. B) KEGG functional enrichment of the DE sORFs. The x-axis represents the enrichment factor, while the y-axis represents the pathway name. C) Tryptophan metabolism of the plant hormone signal transduction pathway, in which two DE sORFs were downregulated and two DE sORFs were upregulated. D) The wounding - MAPK signal pathway, in which one DE sORF was downregulated in the *CaM4*. E) Correlation plot of the expression profile between RNA sequencing and NanoString, with a correlation coefficient of 0.87.

sequences found at the N-terminus of proteins that direct their secretion by providing targeting information (Owji et al. 2018). Interestingly, 2 DE sORFs shared sequence homology with phytosulfokines (*PSK*s) and were predicted to have the characteristics of signal peptides using SignalP 6.0. *PSK*s are well-known peptides involved in plant signaling and ROS homeostasis maintenance by modulating peroxidase activity (Kim et al. 2021). Both sORFs were significantly upregulated under salinity stress, suggesting the involvement of small signaling peptides in the regulation of oxidative stress responses. Overall, these DE sORFs provide a promising foundation for future functional characterization and serve as good candidates for enhancing banana salinity tolerance.

DE sORFs in cv. Mas could be categorized into various groups, with "photosynthesis" (GO:0015979), "photosynthesis, light reaction" (GO:0019684), and "generation of precursor metabolites and energy" (GO:0006091) being the most enriched GO terms in the BP category (Figure 2A). For the CC ontology, the most enriched terms were "thylakoid" (GO:0009579), "photosystem" (GO:0009521), and "photosynthetic membrane" (GO:0034357). The most enriched MF terms were "oxidoreductase activity" (GO:0016491), "tetrapyrrole binding" (GO:0046906), and "monooxygenase activity" (GO:0004497). The "biosynthesis of secondary metabolites" pathway was the most enriched KEGG pathway, followed by "photosynthesis," "metabolic pathways," "carbon metabolism," and "plant hormone signal transduction" (Figure 2B). Notably, several DE sORFs were annotated to plant hormone signaling pathways, particularly tryptophan metabolism. Within this pathway, four DE sORFs were differentially expressed in the small auxin upregulated RNA (SAUR) protein, with two being upregulated and two downregulated (Figure 2C). For the wounding signaling that was involved in the MAPK signaling pathway, a DE sORF associated with calcium-binding proteins such as calmodulins (*CaMs*) (K14492) was found to be downregulated under high salinity conditions (Figure 2D).

The enrichment of terms such as "thylakoid," "photosynthetic membrane," and "photosystem" in the CC category indicates that these sORFs may function within chloroplast-related compartments, which are responsible for photosynthesis. In the BP category, key enriched terms such as "photosynthesis," "photosynthesis, light reaction," and "generation of precursor metabolites and energy" further support their involvement in photosynthesis, consistent with Song et al. (2020)'s findings. Thus, the enrichment of these terms suggests that even under salinity stress conditions, bananas rely heavily on photosynthesis as a fundamental process for energy production and growth. Additionally, the enrichment of the terms "oxidoreductase activity" and "monooxygenase activity" in the MF category suggests that sORFs have potential enzymatic roles in redox regulation. Ion homeostasis imbalance caused by salinity stress can lead to oxidative stress and ROS generation (Yang and Guo 2018). Enzymes with oxidoreductase activities facilitate electron transfer to ROS and induce ROS scavenging (Martemucci et al. 2022). The enrichment of the terms "ion transport" and "transporter activity" suggests that these DE sORFs may play a role in maintaining ion homeostasis under salinity stress. Plants can counteract the impaired cellular homeostasis by activating ion transport mechanisms that regulate the uptake of ions (Balasubramaniam et al. 2023). Together, these findings underscore the potential role of sORFs in photosynthesis, ion regulation, and oxidative stress responses, although they only represent a small fraction of the banana transcriptome.

Among the enriched pathways of DE sORFs, the "biosynthesis of secondary metabolites" pathway was the most enriched, underscoring its importance in the salinity stress response. To put that into perspective, the enhanced accumulation of flavonoids in rice has been shown to improve tolerance to combined salinity and heat stress by influencing physiological, biochemical, and molecular responses (Jan et al. 2021). The involvement of sORFs in plant hormone signal transduction pathways has also been increasingly documented, underscoring their potential roles as hormone-mediated response regulators (Ong et al. 2023, Ng et al. 2025). During tryptophan metabolism, most DEGs related to the SAUR protein were downregulated. A similar pattern of *SAUR* gene downregulation under abiotic stress was reported by Teoh et al. (2022). This pattern also extended to the DE sORFs, with two upregulated and two downregulated in response to salinity stress. SAUR proteins modulate adaptive growth and stress responses (Stortenbeker and Bemer 2019). For instance, *TaSAUR78* overexpression in *Arabidopsis* enhanced salinity tolerance by reducing ROS accumulation (Yuan et al. 2019). In addition to auxin, the interaction among other phytohormones, such as strigolactones, abscisic acid, ethylene, and gibberellin, plays a crucial role in salinity adaptation. The interplay between abscisic acid and strigolactones contributes to drought tolerance in both mycorrhizal and non-mycorrhizal plants (Khan et al. 2024). These findings suggest that the regulation of *SAUR*s by both DEGs and sORFs may indirectly influence hormone-mediated stress adaptation in bananas under salinity stress. Moreover, most DEGs and DE sORFs associated with *CaM4* were downregulated in the MAPK signaling pathway. CaM4 acts as a negative regulator of ROS production in *Arabidopsis* by suppressing the expression of respiratory

burst oxidase homologs (*RBOHs*) (Takahashi et al. 2011). Elevated ROS levels activate OXI1 kinase, which in turn triggers MAPK cascade activation (Rentel et al. 2004). MAPK signaling is crucial for maintaining ROS homeostasis and enhancing plant tolerance to abiotic stress (Cristina et al. 2010). These findings suggest that sORFs may function downstream of ROS signaling or contribute to redox homeostasis, aligning with their GO enrichment in oxidoreductase activity. From a practical perspective, these identified sORFs could serve as potential gene targets for functional validation and genetic improvement programs aimed at enhancing salinity stress tolerance in cv. Mas.

DE sORFs associated with salinity stress were analyzed using the NanoString technology to validate the RNA-Seq findings. The results demonstrated a strong positive correlation between the two datasets, with a correlation coefficient (R) of 0.87 (Figure 2E). This finding underscores the high reliability of our RNA-Seq data, which is consistent with the findings of previous studies that validated RNA-Seq using NanoString (Ong et al. 2023, Ng et al. 2025). This agreement further confirms that these DE sORFs play an important role in the responses of bananas to salinity stress, especially in the pathways related to hormone signaling and redox regulation. Although the NanoString results provide strong validation of the transcriptional profiles, further studies integrating proteomic and functional analyses are needed to further clarify their biological roles.

CONCLUSION

This study provides the first comprehensive transcriptomic analysis and annotation of sORFs in cv. Mas under high salinity stress, highlighting their potential involvement in stress adaptation. Although sORFs represented a relatively small proportion of the differentially expressed transcripts, they were significantly enriched in functional categories and pathways associated with photosynthesis, ion transport, redox homeostasis, secondary metabolite biosynthesis, and plant hormone signaling. In particular, several DE sORFs shared homology with known small peptides, such as phytosulfokines, previously reported to function in abiotic stress mitigation. The differential regulation of *SAUR* and *CaM4*-associated sORFs further supports their involvement in plant hormone signal transduction and MAPK signaling pathways, respectively. These findings contribute to a better understanding of sORF-related tolerance mechanisms in bananas and support the development of salinity-tolerant cultivars. Future studies should analyze and compare banana transcriptomes under different abiotic stress conditions to identify shared stress-responsive sORFs.

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DATA AVAILABILITY

The datasets generated and/or analyzed during the current research are accessible in the NCBI BioProject repository, available at https://www.ncbi.nlm.nih.gov/bioproject/PRJNA1299623.

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