

## Transcriptional profiling of ERF027 in *Gossypium hirsutum* L. under salt stress and calcium treatment

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Received: April 23, 2025; Reviewed: May 26, 2025; Accepted: June 16, 2025

Salinity is one of the major abiotic stresses limiting cotton productivity worldwide, particularly in irrigated arid and semi-arid regions. Calcium ions ( $\text{Ca}^{2+}$ ) function as key secondary messengers in the salt stress signaling network, potentially modulating the expression of stress-responsive transcription factors. This study investigated the expression dynamics of the ethylene response factor ERF027 in upland cotton cultivar Garabagh-11 under sodium chloride (NaCl), calcium chloride ( $\text{CaCl}_2$ ), and combined NaCl+ $\text{CaCl}_2$  treatments. Using quantitative real-time PCR, we show that ERF027 is significantly upregulated in response to NaCl, suggesting its involvement in salt-induced transcriptional reprogramming. In contrast,  $\text{CaCl}_2$  alone induced only a modest increase in ERF027 expression, while combined NaCl+ $\text{CaCl}_2$  treatment reduced ERF027 expression by ~20% compared to NaCl alone, indicating that calcium may attenuate salt-triggered gene activation. These findings imply a buffering effect of  $\text{Ca}^{2+}$  signaling, possibly via improved ion homeostasis and modulation of ethylene-associated stress pathways. ERF027, a member of the AP2/ERF transcription factor family, appears to be a salt-inducible regulator that is sensitive to ionic interactions and calcium-mediated suppression. The study highlights a potential regulatory interface between salt and calcium signaling in cotton, offering insights into the transcriptional control of stress responses. These results lay the foundation for future efforts to manipulate calcium signaling pathways or ERF gene networks to enhance salt tolerance in cotton breeding programs.

**Keywords:** Upland cotton, ethylene response factor, salinity, calcium signaling, gene expression

### INTRODUCTION

Upland cotton (*Gossypium hirsutum* L.), also known as common cotton, represents a strategically important crop from both economic and agroecological perspectives (Li et al., 2025). Among the four cultivated species within the genus *Gossypium*, *G. hirsutum* holds the leading position in global cotton fiber production due to its high yield potential, broad adaptability to diverse soil and climatic conditions, and moderate tolerance to abiotic stresses (Ashraf et al., 2023). Genetically, *G. hirsutum* is an allotetraploid species with the genomic constitution AtDt ( $2n=4x=52$ ), originating from an ancient interspecific hybridization between diploid progenitors of the A- and D-genome lineages (*Garboreum* and *G. raimondii*, respectively), followed by whole-genome duplication (Li et al., 2015). The *G. hirsutum*

genome exhibits a complex evolutionary architecture shaped by both ancient (paleopolyploidy) and more recent polyploidization events, resulting in a wide repertoire of functional and structural genes. The assembled genome spans approximately 2.17 Gb and contains over 76,000 protein-coding genes as well as a broad array of non-coding RNAs. High proportions of retrotransposons, which are dominant in both At and Dt subgenomes, along with frequent homoeologous exchanges (HEs), have contributed to the formation of a dynamic regulatory network and the diversification of adaptive traits, including stress tolerance (Jian et al., 2023).

One of the most significant limiting factors for cotton cultivation, particularly in arid and semi-arid regions, is soil salinization (Zhang et al., 2025). This problem is especially acute in countries with extensive irrigated agriculture, such as Azerbaijan,

where approximately 40-44% of irrigated lands are affected by varying degrees of salinity. The Kura-Araz lowland is most severely impacted due to its flat topography, high evapotranspiration, and shallow groundwater table, all of which promote salt accumulation in the upper soil layers. In addition to natural factors, anthropogenic influences such as inefficient water management, inadequate drainage infrastructure, and climate change exacerbate the problem. Cotton exhibits moderate salt sensitivity, and both yield and fiber quality can decline significantly under saline conditions. Therefore, improving salt tolerance in cotton is a critical objective for sustainable agriculture, particularly under the increasing challenges posed by climate change and land degradation (Zhang et al., 2022).

In response to salt stress, plants initiate a cascade of molecular, cellular, and physiological adaptations aimed at maintaining ionic and osmotic homeostasis, preventing oxidative damage, and sustaining metabolic activity (Zhao et al., 2025). The initial response involves sodium ion perception by root cells, where key roles are played by non-selective cation channels, lipid-based sensors (such as GIPCs), and calcium-dependent signaling pathways (Dey et al., 2023; Jiang et al., 2022). Among the early signaling components that mediate salt perception and the downstream regulatory processes, calcium ions ( $\text{Ca}^{2+}$ ) are especially pivotal as ubiquitous secondary messengers. Salt-induced cytosolic  $\text{Ca}^{2+}$  transients activate a broad range of calcium-binding proteins and signaling cascades, including the Salt Overly Sensitive (SOS) pathway, ultimately modulating the expression of stress-responsive genes and restoring ion homeostasis (Zhu, 2022).

Transcription factors play a central role in reprogramming gene expression under stress conditions. In this context, members of the AP2/ERF, MYB, and NAC transcription factor families have emerged as key regulators of abiotic stress responses, including salinity (Basu and Kumar, 2023). The APETALA2/ETHYLENE RESPONSE FACTOR (AP2/ERF) family, one of the largest TF families in plants, plays a pivotal role in abiotic stress resistance (Cheng et al., 2020). Many ERF genes are salt-inducible and confer increased stress tolerance when overexpressed. For example, overexpression of *GhERF13.12* in cotton enhanced salt tolerance in transgenic plants (Lu et al., 2021). However, the regulatory networks controlling ERF transcriptional activity in response to combined stress conditions remain poorly understood in cotton.

The present study aims to analyze the expression dynamics of the *ERF027* transcription

factor under NaCl,  $\text{CaCl}_2$ , and combined NaCl +  $\text{CaCl}_2$  treatments. By examining transcriptional changes in response to these conditions, this work seeks to elucidate the potential involvement of calcium ions in the regulation of salt-inducible transcription factors. A deeper understanding of these interactions will provide new insights into the molecular mechanisms of salt tolerance and contribute to the development of salt-tolerant cotton genotypes through molecular breeding and genetic engineering approaches.

## MATERIALS AND METHODS

**Plant material and treatments.** Seeds of upland cotton Garabagh-11 (*Gossypium hirsutum* cv.) were provided by Gene Pool of the Institute of Genetic Resources of the Ministry of Science and Education of the Republic of Azerbaijan. Seeds were surface-sterilized and germinated at room temperature for 4 days until the coleoptile emerged. Germinated seedlings were transplanted to multi-cell seed trays (96 cell pots, with 5 cm<sup>3</sup> volume for a single cell) containing soil-sand mixture (3:1 ratio) and transferred in a growth chamber at 16:8 h light/dark period 27°C and 22°C respectively, relative humidity 50-60%. Four-day-old seedlings were divided into four groups and treated as follows: (A) distilled water (control), (B) 10 mM  $\text{CaCl}_2$ , (C) 150 mM NaCl, or (D) combined 150 mM NaCl+10 mM  $\text{CaCl}_2$ . Treatments were applied for 10 days. After treatment, leaf tissues were harvested, flash-frozen in liquid nitrogen, and stored at -80°C until RNA extraction.

**RNA extraction and cDNA synthesis.** Total RNA was isolated from leaf tissues using the Monarch Total RNA Miniprep Kit (New England Biolabs, Inc.) as per the manufacturer's guidelines. Genomic DNA was eliminated by treating the RNA with RNase-free DNase I. The integrity and purity of the extracted RNA were evaluated via agarose gel electrophoresis. RNA concentrations were determined using a NanoDrop Thermo Scientific-2000C spectrophotometer (USA). Complementary DNA (cDNA) synthesis was carried out from the isolated RNA using the LunaScript RT SuperMix Kit (New England Biolabs, Inc.), following the instructions provided by the manufacturer, in a final reaction volume of 20 µl.

**Quantitative Real-Time PCR.** qRT-PCR analysis was conducted using the Mic Real-Time PCR cycler (Bio Molecular Systems), employing a total reaction volume of 20 µl per well. The PCR mixture for each sample consisted of 10 µl of Luna® Universal qPCR Master Mix (New England Biolabs), 1 µl of cDNA template diluted at a 1:5

ratio, 0.5 µl of each primer (forward and reverse; final concentration 10 µM), and 7 µl of nuclease-free water to complete the final volume. Amplification conditions were as follows: initial enzyme activation and DNA denaturation step at 94 °C for 1 minute, followed by 45 amplification cycles comprising denaturation at 95 °C for 15 seconds and primer annealing/extension at 60 °C for 30 seconds. Reactions were run in technical triplicates for each of the three biological replicates. Negative controls lacking template (NTCs) were included for every primer pair to monitor for contamination or non-specific amplification. The internal control used for the normalization of expression levels was elongation factor 1- $\alpha$  (Elf1- $\alpha$ ), selected for its stable expression across the tested conditions. The primer sequences used for each gene target are provided in Table 1. Prior to relative quantification, primer efficiency for each pair was empirically determined by generating a standard curve with a serial dilution series of pooled cDNA. Efficiency was calculated using the formula:  $\text{Efficiency}(\%) = (10^{(-1/\text{slope})} - 1) \times 100$ , and was considered acceptable within the range of 90–110%. Melting curve analysis was carried out immediately after amplification to verify the specificity of each PCR product. The relative gene expression levels in treated samples compared to the control were computed using the  $2^{-\Delta\Delta C_t}$  comparative method, as described by Livak and Schmittgen (2001).

**Table 1.** Sequences of primers used for qRT-PCR

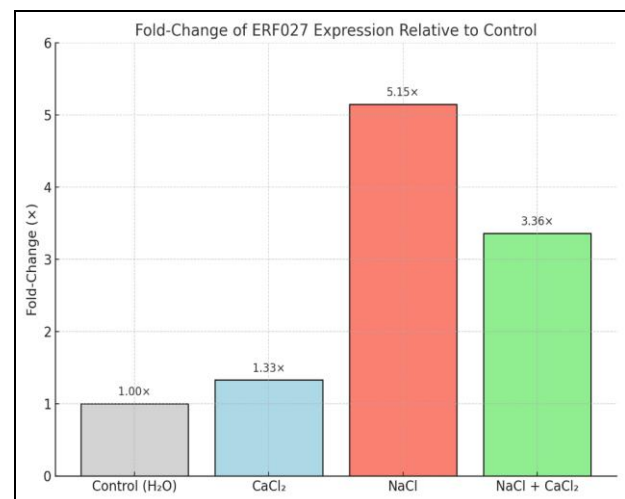
Gene	Gene ID	Direction	Sequences
ERF027	GH_D03G1741	F	CGACACCGGAAATGGCTGCT
		R	CGGCTGACGACGTAGAACCC
Elf1- $\alpha$	Elf1- $\alpha$	F	CAGATTGGCAACGGCTACG
		R	CGGACAGCAAAACGACCAAG

**Statistical analysis:** The statistical analysis was carried out using SAS software ver9.2 (SAS Institute, 2008). Standard deviation (SD) values are from at least three biological replicates.

## RESULTS AND DISCUSSION

Quantitative real-time PCR analysis revealed distinct expression patterns of the ERF027 transcription factor in cotton under various stress and supplementation conditions. The fold change in ERF027 expression relative to the control (distilled water treatment) was assessed across three experimental treatments: CaCl<sub>2</sub>, NaCl, and NaCl +

CaCl<sub>2</sub>. In control plants (H<sub>2</sub>O), the baseline expression level of ERF027 was normalized to 1.00-fold. Treatment with calcium chloride (CaCl<sub>2</sub>) alone resulted in a modest upregulation of ERF027, reaching 1.33-fold relative to the control, indicating that calcium ions alone have a limited stimulatory effect on ERF027 expression in non-saline conditions. In contrast, exposure to sodium chloride (NaCl) induced a dramatic increase in ERF027 expression, reaching 5.15-fold relative to control levels. This sharp elevation suggests strong responsiveness of the ERF027 transcription factor to salt stress, implicating its potential role in the salinity stress signaling cascade in cotton. Interestingly, combined treatment with NaCl and CaCl<sub>2</sub> resulted in a reduced, though still elevated, expression level of ERF027 at 3.36-fold compared to control. This value, while significantly higher than control and CaCl<sub>2</sub> alone, was notably lower than the expression level observed under NaCl treatment alone. These findings suggest that exogenous calcium may modulate or partially suppress the salt-induced upregulation of ERF027.



**Fig. 1.** Transcript level of ERF027 transcription factor gene in leaves of upland cotton Garabagh-11 under control (H<sub>2</sub>O) and 10 mM CaCl<sub>2</sub>, 150 mM NaCl, and combined 150 mM NaCl + 10 mM CaCl<sub>2</sub> conditions. The fold change in expression was calculated using the  $2^{-\Delta\Delta C_t}$  method.

These data indicate that ERF027 is a salt-inducible transcription factor in cotton, with expression levels strongly enhanced under saline conditions. The partial mitigation of ERF027 induction by supplemental calcium may be attributed to calcium's role in stabilizing cellular ion homeostasis (Luan et al., 2023). Importantly, exogenous CaCl<sub>2</sub> itself did not induce ERF027 (fold-change ~1.1), but its addition to the salt treatment decreased ERF027 levels by ~20% compared to salt alone. This suggests that Ca<sup>2+</sup>

signaling dampens the stress signal that activates ERF027. One possible mechanism is that supplemental  $\text{Ca}^{2+}$  ameliorates the ionic imbalance caused by NaCl, thereby lowering the stress stimulus. For instance, Rahman et al. (2016) showed that adding  $\text{Ca}^{2+}$  to salt-stressed rice seedlings inhibited  $\text{Na}^+$  influx and  $\text{K}^+$  leakage, improving ion homeostasis and reducing damage. By stabilizing the cell membrane and activating the Salt Overly Sensitive (SOS) pathway,  $\text{Ca}^{2+}$  can limit  $\text{Na}^+$  entry into cells (Zhu, 2022). This would result in less activation of downstream stress signals (e.g. ethylene) that drive ERF transcription. Thus, the partial suppression of ERF027 induction may reflect a buffering effect of  $\text{Ca}^{2+}$  on salt stress.

The upregulation of ERF027 under sodium chloride stress and its partial attenuation by calcium supplementation highlight the dynamic regulation of stress-related transcriptional networks in cotton. ERF027 belongs to the AP2/ERF transcription factor family, which is widely recognized for orchestrating abiotic stress responses through the regulation of downstream genes and hormonal signaling pathways (Xie et al., 2021). Similar ERF genes have been identified as salt-responsive in several plant species, including tomato, sorghum, and Arabidopsis, where they play key roles in coordinating transcriptional responses to osmotic and ionic stress (Li et al., 2023; Xie et al., 2021).

Previous studies have shown that ERF1 in Arabidopsis enhances salt tolerance via crosstalk with ethylene, jasmonic acid (JA), and abscisic acid (ABA) signaling (Cheng et al., 2020). In sorghum, SbERF027 contributes to cold and drought stress resilience (Fan et al., 2023). Transcriptomic analyses in halophytes and glycophytes further support the involvement of ERF027-like genes in salt stress signaling, underscoring the conserved nature of this regulatory mechanism.

The decrease in ERF027 expression observed in the NaCl +  $\text{CaCl}_2$  treatment compared to NaCl alone (~20% reduction) suggests a buffering effect of calcium on salt stress perception and signaling. Calcium ions ( $\text{Ca}^{2+}$ ) function as pivotal secondary messengers during early responses to salt stress. Salt-induced  $\text{Ca}^{2+}$  influxes activate calcium sensors, such as calmodulins (CaMs), calcineurin B-like proteins (CBLs), and calcium-dependent protein kinases (CDPKs), which in turn trigger signal transduction pathways including the Salt Overly Sensitive (SOS) cascade (Ma et al., 2020; Zhang et al., 2021). This pathway mediates  $\text{Na}^+$  efflux through the plasma membrane  $\text{Na}^+/\text{H}^+$  antiporter SOS1, thereby restoring ion homeostasis and attenuating stress signaling.

Such calcium-mediated stress alleviation has also been reported in rice, where exogenous  $\text{Ca}^{2+}$

reduces  $\text{Na}^+$  uptake and  $\text{K}^+$  leakage, thereby maintaining membrane stability and minimizing damage (Rahman et al., 2016). The partial suppression of ERF027 expression in the presence of calcium could therefore reflect a decrease in the severity of cellular stress due to improved ion balance, thus reducing the need for activation of downstream transcriptional responses.

Moreover, calcium signaling interacts with ethylene biosynthesis. CDPKs can phosphorylate and stabilize 1-aminocyclopropane-1-carboxylic acid synthase (ACS), a key enzyme in ethylene production (Li et al., 2022). This interplay suggests that  $\text{Ca}^{2+}$  may both promote and fine-tune ethylene signaling, which in turn regulates ERF gene expression. However, in the present study, the net outcome of calcium application was a reduction in ERF027 transcript levels under combined salt and calcium stress. This suggests that the ameliorative effects of calcium on ion toxicity may override any potential stimulatory impact on ethylene-driven transcription.

The mechanistic basis of calcium's modulation of ERF027 remains to be fully elucidated. It is plausible that calcium not only affects upstream signaling components but also influences chromatin accessibility, transcriptional repressors, or epigenetic regulators that modulate ERF027 expression (Zhang et al., 2021). Additionally, recent discoveries of candidate sodium sensors such as MOCA1 (MONOCATION-INDUCED [ $\text{Ca}^{2+}$ ] INCREASES 1) and associated glycosyl inositol phosphoryl ceramide (GIPC) lipids in the plasma membrane offer new insight into how plants may rapidly detect extracellular sodium and trigger calcium influx (Singh and Choudhary, 2024). The resulting calcium waves are sodium-specific, propagating through root and shoot tissues within seconds, and are known to activate transcription factors including members of the AP2/ERF family (Vincent et al., 2021; Xie et al., 2021).

Importantly, these early  $\text{Ca}^{2+}$  signatures are decoded by CBL–CDPK complexes, which not only activate SOS1 but may also affect nuclear gene expression through yet unidentified targets (Bihani and Srivastava, 2025). The specificity and speed of these signals point to a highly coordinated system in which ERF027 may function as a key node downstream of ion detection, calcium signaling, and hormonal integration (Luan et al., 2023).

Taken together, the current findings support a model in which ERF027 serves as an important regulator of the cotton salt stress response. Its expression is rapidly induced by NaCl, and this induction is modulated by calcium availability. This modulation likely reflects calcium's dual role as a stabilizer of ion homeostasis and a regulator of

signal transduction. The observed “fine-tuning” of ERF027 expression has potential agronomic implications: enhancing calcium nutrition or selecting genotypes with efficient calcium uptake and signaling may provide a strategy to reduce salt stress damage in cotton and other crops.

Future research should aim to identify the upstream regulatory elements controlling ERF027 expression, its direct downstream gene targets, and whether it operates within specific transcriptional modules involving other factors such as DREB2A, ZFP179, or MAPK5.

## CONCLUSION

This study demonstrates that the ERF027 transcription factor in *Gossypium hirsutum* is strongly induced by salt stress and that this induction is partially repressed by calcium. These results suggest that calcium signaling buffers the salt stress signal, likely by improving ionic balance, thereby attenuating ERF027 activation. Understanding this regulatory interplay between calcium and ethylene response factors enriches our knowledge of salt stress adaptation in cotton. In practical terms, manipulating calcium availability could modulate stress-regulatory networks and contribute to the development of more salt-resilient cotton cultivars.

## FUNDING

This work was supported by the Ministry of Science and Education of the Republic of Azerbaijan under the project titled "Creation of infrastructure for the development of new directions of genetic engineering in Azerbaijan, application of genome editing methods in biomedical research and genome selection" (2024-2025)

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#### Duz stresi və kalsiumla işlənmə şəraitində *Gossypium hirsutum* L. bitkisində ERF027 geninin transkripsiya profili

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Torpağın şorlaşması dünyada, xüsusilə quraq və yarımquraq ərazilərdə pambığın məhsuldarlığını məhdudlaşdıran əsas abiotik stress amillərindən biridir. Kalsium ionları duz stresinə cavab verən siqnal ötürmə şəbəkələrində əsas ikincili messenger funksiyasını yerinə yetirərək stresə cavabdeh transkripsiya faktorlarının ekspressiyasını modulyasiya edə bilər. Bu tədqiqatda Qarabağ-11 pambıq sortunda etilenə cavabdeh ERF027 transkripsiya faktoru geninin natrium xlorid (NaCl), kalsium xlorid (CaCl<sub>2</sub>) və onların birgə tətbiqi (NaCl + CaCl<sub>2</sub>) şəraitində ekspressiya dinamikası araşdırılmışdır. qPZR analiz göstərmişdir ki, NaCl-un təsirindən ERF027 geninin ekspressiyası əhəmiyyətli dərəcədə artmışdır ki, bu da onun duzla induksiya olunan transkripsiya proqramlaşdırılmasında iştirak etdiyini göstərir. Əksinə, yalnız CaCl<sub>2</sub> tətbiqi ERF027 geninin ekspressiyasında cüzi artıma səbəb olduğu halda, NaCl + CaCl<sub>2</sub> birgə təsiri zamanı ERF027 geninin ekspressiyası NaCl-un təsiri ilə müqayisədə təxminən 20% azalmışdır ki, bu da kalsiumun duzla induksiya olunan genlərin aktivliyini zəiflətdiyini göstərir. Bu nəticələr Ca<sup>2+</sup>-un ion homeostazını yaxşılaşdırması və etilenlə əlaqəli stress yollarının modulyasiyası hesabına siqnalların ötürülməsində bufer təsiri həyata keçirə biləcəyini göstərir. AP2/ERF transkripsiya faktorları ailəsinə mənsub olan ERF027 zülalının duzla induksiya olunan və kalsium vasitəsilə tənzimlənməyə həssas olan tənzimləyici funksiya daşdığı ehtimal olunur. Tədqiqat pambıq bitkisində duz və kalsium siqnal sistemləri arasında mümkün tənzimləyici əlaqəni vurğulayır və stress reaksiyalarının transkripsiya səviyyəsində tənzimlənməsi haqqında maraqlı məlumatlar təqdim edir. Bu nəticələr gələcəkdə pambığın seleksiyası proqramlarında duza davamlılığı artırmaq məqsədilə kalsium siqnal yollarının və ERF gen şəbəkələrinin hədəflənməsi üçün əsas yaradır.

**Açar sözlər:** Pambıq, etilenə cavabdeh faktor, şoranlaşma, kalsium siqnallarının ötürülməsi, gen ekspressiyası

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