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In Silico Genome-wide Identification and Characterization of *ERF1* Transcription Factors in Citrus Sinensis and *Citrus clementina* for Potential CTV Resistance

Ngangbam Sana Singh, Wricha Tyagi and Ng. Tombisana Meetei

School of Crop Improvement, College of Post Graduate Studies in Agricultural Sciences, CAU (Imphal), Umiam, Meghalaya (793 103), India

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Corresponding ntmeetei@gmail.com

0000-0002-3729-6445

ABSTRACT

A study was conducted *in silico* during October to December, 2025, at College of Post Graduate Studies in Agricultural Sciences, CAU (Imphal), Umiam, Meghalaya (793 103) India, to understand the role of ERF1 genes in conferring resistance to *Citrus tristeza virus* (CTV) in citrus species, primarily focusing on genome-wide identification of ERF1 genes in *Citrus sinensis* and *Citrus clementina*, their domains and gene structure. CTV infection in citrus species cause symptoms like stem pitting and decreased yield, and posed a serious threat to the world's citrus production. The AP2/ERF superfamily's ethylene response factor (ERF) transcription factors are essential for plant stress responses, including pathogen resistance through GCC box binding and hormone signaling pathways. ERF1 orthologs in *Citrus sinensis* and *Citrus clementina* were yet to be characterized. With this idea, an *in-silico* genome-wide identification of putative ERF1 orthologs was performed using *Arabidopsis thaliana AtERF1* (NP_567530.4) as a query *via* Phytozome BLAST. The top hits were chosen as putative orthologs based on e-value, % identity, and alignment length. Five orthologs were identified each in *C. sinensis* and *C. clementina*. Gene structures suggested 1–3 exons with varying GC content; proteins ranged from 167 to 400 aa (MW 18–44 KDa, pI 5.46–10.03). All orthologs identified contained conserved AP2/ERF domain (IPR001471), with some having zinc fingers. Gene ontology predicted DNA binding, transcription factor activity, nucleus localization, and many roles in biological processes, including chitin response, vascular development, and defensive signaling. These results clarified the structural diversity and functional annotations of ERF1 in citrus, paving the way for future functional studies and crop enhancement techniques that targeted ERF1 genes.

KEYWORDS: Citrus, CTV, ERF1, gene structure, resistance

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1. INTRODUCTION

Citrus is one of the major fruit tree crops throughout the world, belonging to the Rutaceae family. Citrus fruits include a variety of nutrients, including citric acid, flavonoids, phenolics, pectins, limonoids, and ascorbic acids, making them beneficial for health and beauty (Kumar et al., 2010). Furthermore, their nutritional, therapeutic, and cosmetic qualities have been demonstrated (Ali Esmail and Al-Snafi, 2016). *Citrus tristeza virus* (CTV) is one of the most important factors that causes great economic losses in the citrus industry. Over the past century, CTV has caused a rapid loss of about 100 million citrus trees growing on sour orange rootstock globally (Catara et al., 2021). CTV belongs to the genus *Closterovirus* of the Closteroviridae family (Agranovsky, 2016; Aknadibossian et al., 2025). Citrus plants infected with CTV display developmental retardation, seedling yellowing, wilting, stem pitting, and smaller fruit, affecting citrus quality and productivity (Dawson et al., 2015; Aknadibossian et al., 2025). The ethylene response factor (ERF) subfamily, a branch of the Apetala2/Ethylene Responsive Factor (AP2/ERF) superfamily, is one of the most common transcription factor families in plants, which has emerged as an important regulatory element in response to a variety of s stresses, including metabolite regulation, hormone regulation, plant morphogenesis, and stress response (Xu et al., 2020; Yu et al., 2021). Typically, members of the AP2/ERF family possess a minimum of one copy of a DNA-binding domain known as the AP2 domain, which comprises around 60 to 70 amino acids (Xie et al., 2019; Zhang et al., 2020). The first ERF was identified from tobacco (*Nicotiana tabacum* L.) as an ethylene response element binding protein (Ohme-Takagi and Shinshi, 1995). Since their discovery in tobacco and increasingly complete genome sequences, *ERF*s have been identified and characterized in a variety of plants, including *Zea mays* (Zhang et al., 2022) and *Glycine max* (Jiang et al., 2020). Studies suggest that *ERF* transcription factors interact with cis-acting elements, including the GCC element (AGCCGCC) and activate or inhibit the expression of target genes involved in pathogen invasion and disease resistance in plants (Fujimoto et al., 2000; Liang et al., 2008). AtERF14 in *Arabidopsis thaliana* plays a crucial role in plant resistance mechanisms against the necrotrophic fungal disease *Fusarium oxysporum* (Oñate-Sánchez et al., 2007). Transient heterologous expression of PmERF49 and PmERF52 in *Nicotiana benthamiana* considerably increased resistance against the fungal disease *Botrytis cinerea* (Xu et al., 2025). However, the role of *ERF* genes in response to pathogens varies depending on the specific gene, pathogen, and host plant involved. Moreover, *ERF* transcription factors serve as a crucial regulatory component in the plant hormone defense signaling pathway, engaging in the salicylic acid (SA), jasmonic acid (JA), and other hormonal defense signaling pathways. Through the SA and JA defense pathways, SlERF01 has been demonstrated to increase tomato disease resistance. Exogenous SA and JA treatment triggers SlERF01 of the tomato ERF family, which increases resistance to *Stemphylum lycopersici* by activating PR1 gene expression (Yang et al., 2020). Recently, Citrus roots, stems, and leaves were found to have different CsERF1 gene expression patterns, with roots and leaves having higher levels of this gene's expression than stems after CTV infection. Expression analysis of genes related to SA and JA defense signaling pathways in transgenic plants suggested that CsERF1 is involved in SA and JA-mediated defense pathways, regulating the expression of key genes, such as PR, to stimulate the citrus immune response to CTV infection. (Chen et al., 2025). The ERF1 orthologs in *Citrus sinensis* and *Citrus clementina* remain uncharacterized to date. Therefore, a study was conducted during October to December, 2025, to identify ERF1 genes in *Citrus sinensis* and *Citrus clementina* and analyze their domains and gene structure to understand their roles in CTV resistance.

2. MATERIALS AND METHODS

2.1. Identification of putative ERF1 in Citrus sinensis and Citrus clementina

The study was conducted *in silico* during October to December, 2025, at College of Post Graduate Studies in Agricultural Sciences, CAU (Imphal), Umiam, Meghalaya, India. The amino acid sequences of *Arabidopsis thaliana* AtERF1 (NP567530.4), was downloaded from the NCBI database (https://www.ncbi.nlm.nih.gov). Using the downloaded sequence as a query sequence, a protein blast was conducted in the Phytozome database (https://phytozome-next.jgi.doe.gov/blast-search) against *Citrus sinensis* and *Citrus clementina* genomes. Orthologs having maximum alignment length, minimum e-value, and maximum % identity were taken as putative orthologs of *Citrus sinensis* and *Citrus clementina*. The size of the genes, CDS, and protein sequences was retrieved from the Phytozome database (https://phytozome-next.jgi.doe.gov) (Goodstein et al., 2012). The orthologs of *Citrus sinensis* and *Citrus clementina* were then BLAST against *Arabidopsis thaliana* in the Phytozome database (https://phytozome-next.jgi.doe.gov/blast-search). The best hits in *Arabidopsis thaliana,* e-values, and their molecular functions were retrieved. Further, the gene ontology of the putative orthologs of *Citrus sinensis* and *Citrus clementina* was conducted.

2.2. Gene ontology

To further investigate the potential function of the proposed *ERF1* genes, the gene ontology (GO) annotations of the

Citrus sinensis and *Citrus clementina* family members were conducted. The GO annotation for all genes was predicted by InterProScan 5 (Jones et al., 2014) according to the GO annotation guidance 'GO_REF:0000002'. GO term, GO category, and GO description or molecular function was retreived.

2.3. Gene structure

To determine *ERF1* gene structures, the *ERF1* gene size, the number of introns and exons, as well as the GC content, the CDS, cDNA, and gene sequences were retrieved from the Phytozome database (https://phytozome-next.jgi.doe.gov) (Goodstein et al., 2012). These sequences were subsequently analyzed, and the gene structures were predicted through GSDS (Gene Structure Display Server 2.0 software) (https://gsds.gao-lab.org) (Hu et al., 2015).

2.4. Domain analysis of ERF1

To analyze domains of the putative *ERF1* genes of *Citrus sinensis* and *Citrus clementina*, all the coding sequences (CDS) of the *ERF1* Genes were downloaded from the Phytozome database (https://phytozome-next.jgi.doe.gov) (Goodstein et al., 2012). The CDS sequences were then used to predict protein domains using the InterPro database (https://www.ebi.ac.uk/interpro/search/sequence/) (Blum et al., 2025). Length of the amino acids, molecular weight of the protein, and their isoelectric point (PI) were retrieved.

3. RESULTS AND DISCUSSION

3.1. Identification of putative ERF1 in Citrus sinensis and Citrus clementina

A protein BLASTp in the phytozome database using *A. thaliana* AtERF1 (NP_567530.4) resulted in 100 hits in both the species (*Citrus sinensis* and *Citrus clementina* genomes). However, only the first 5 hits were taken as orthologs of *ERF1* in *Citrus sinensis* and *Citrus clementina* based on the e-value, % identity, and alignment length. In *Citrus sinensis,* the % identity ranged from 40 to 54%. However, orange1.1g044938m, 54% identity with a lowest e-value of 3.38e-69 and longest alignment of 271, emerged as the closest ortholog of *Citrus sinensis*, while in *Citrus clementina,* the % identity ranged from 40 (Ciclev10022025m) to 55% identity (Ciclev10021652m). With 55% identity and an e-value of 4.27e-73, Ciclev10021652m was found to be the closest ortholog for *Citrus clementina* (Table 1). A flowchart was given in Figure 1. Reciprocal BLAST validation against *A. thaliana* confirms functional orthology with *Arabidopsis* ERF1 (AT4G17500.1) as a top matching hit. Orange1.1g044938m in *Citrus sinensis* and Ciclev10021652m in *Citrus clementina* both align to AT4G17500.1 (ERF1) with highly significant e-values (2.00e-65, 5.00e-67), indicating direct functional conservation (Table 2).

3.2. Gene ontology

Further analysis of the GO annotations in the *ERF1* orthologs of *Citrus sinensis* and *Citrus clementina* predicted via InterProScan revealed conserved transcription factor functionality across orthologs. All orthologs were localized in the nucleus (GO:0005634) with DNA-binding (GO:0003677), sequence-specific transcription factor activity (GO:0003700), and biological processes such as regulation of transcription, DNA-templated (GO:0006355). Interestingly, *orange1.1g044938m* of *Citrus sinensis* and Ciclev10021652m of *Citrus clementina* show chitin response, vasculature development, and cell division roles. Surprisingly, Ciclev10005820m of *Citrus clementina* uniquely links to the defense response and ethylene signaling (Table 3 and Table 4). The subcellular location of ERF1 was consistent with that of other plant transcription factors, with the majority localized in the nucleus. Similarly, the pineapple AcoERFs genes reported the presence of (GO: 0006355) and (GO: 0003700), suggesting that the genes were involved in DNA-binding, regulation of transcription, and DNA-templated (Huang et al., 2020).

Table 1: Details of putative orthologs of ERF1

Species	ID	% identity	e-value	Align len.	Bit score
Citrus sinensis	orange1.1g044938m	54	3.38e-69	271	215.312
	orange1.1g028566m	48	4.30e-45	205	151.369
	orange1.1g015846m	47	1.63e-35	209	131.339
	orange1.1g031071m	47	1.37e-28	146	107.457
	orange1.1g047100m	40	6.79e-26	220	102.064
Citrus clementina	Ciclev10021652m	55	4.27e-73	271	224.942
	Ciclev10005891m	48	8.86e-46	205	152.91
	Ciclev10016995m	47	1.49e-28	146	107.071
	Ciclev10022025m	40	4.99e-26	220	102.064
	Ciclev10005820m	50	1.91e-23	138	95.1301

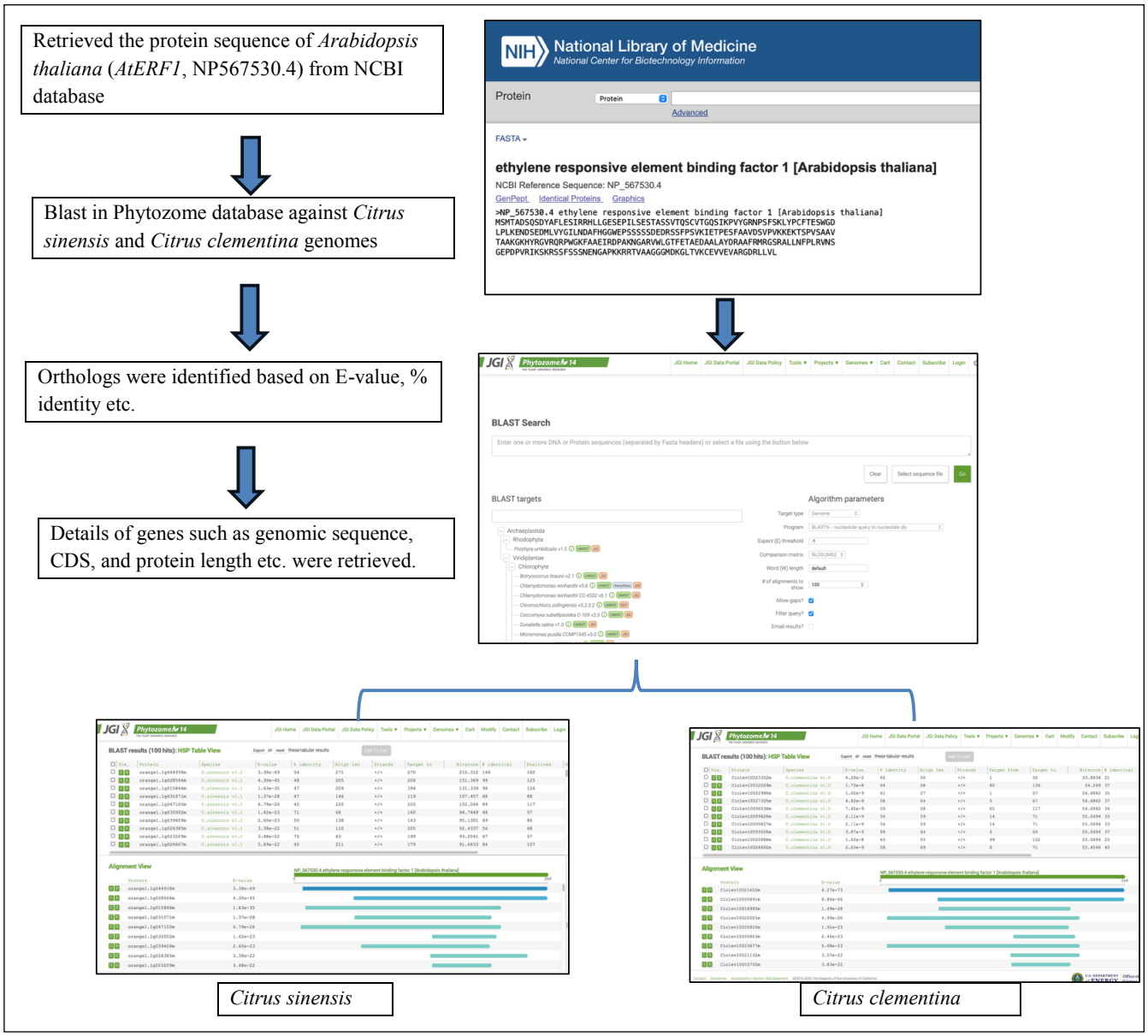

Figure 1: Flowchart of finding putative orthologs of ERF1

3.3. Gene structure

To further understand the structural diversity of *Citrus sinensis* and *Citrus clementina* ERF1, the exon-intron organization of ERF1 genes was analyzed. Our findings revealed variations in exon number, position, and length among the orthologs. Interestingly, the number of exons ranged from 1 to 3, and introns ranged from 0 to 2. Unlike other orthologs, *Citrus sinensis* ortholog (orange1.1g 015846 m) was found to have 3 exons and two introns. All the remaining orthologs have only one exon without any introns (Figure 2 and Figure 3). The results were aligned with the findings of NnERF in *Nelumbo nucifera,* where they possessed in the range of 0 to 3, and 73.83% of the genes were intronless (Xu et al., 2024), 66.22% in pineapple (Huang et al., 2020). The presence of lengthy, numerous intros could delay transcriptional output, potentially suppressing gene expression in extreme situations. Genes with fewer or smaller introns, on the other hand, might have more efficient expression in response to stress situations (Heyn et al., 2015).

3.4. Domain analysis of ERF1

To gain further insight into the protein, we investigated the domain of *Citrus sinensis* and *Citrus clementina ERF1* and showed that the proteins of *Citrus sinensis* and *Citrus clementina* E*RF1* genes varied in size, molecular weight, and isoelectric point (pI). The genomic length varied from 702 nt (orange1.1g047100m) to 3023 nt (orange1.1g015846m),

Table 2: Details of hits in *Arabidopsis thaliana*

Species	ID	Arabidopsis thaliana ID	e-value	Molecular function in Arabidopsis thaliana
Citrus clementina	Ciclev10021652m	AT4G17500.1	5.00e-67	ethylene responsive element binding factor 1
	Ciclev10005891m	AT4G17500.1	2.00e-44	ethylene responsive element binding factor 1
	Ciclev10016995m	AT3G23240.1	4.00e-31	ethylene response factor 1
	Ciclev10022025m	AT2G44840.1	8.00e-43	ethylene-responsive element binding factor 13
	Ciclev10005820m	AT3G23240.1	2.00e-65	ethylene response factor 1
Citrus sinensis	orange1.1g044938m	AT4G17500.1	2.00e-65	ethylene responsive element binding factor 1
	orange1.1g028566m	AT4G17500.1	6.00e-44	ethylene responsive element binding factor 1
	orange1.1g015846m	AT2G44840.1	3.00e-21	ethylene-responsive element binding factor 13
	orange1.1g031071m	AT3G23240.1	1.00e-31	ethylene response factor 1
	orange1.1g047100m	AT2G44840.1	8.00e-43	ethylene-responsive element binding factor 13

Table 3: Gene ontology of *Citrus sinensis* ERF1

Citrus sinensis ID	GO Term	GO category	GO Description
orange1.1g044938m	GO:0001944	Biological process	vasculature development
	GO:0010200	Biological process	response to chitin
	GO:0045893	Biological process	positive regulation of transcription, DNA-templated
	GO:0051301	Biological process	cell division
	GO:0005634	Cellular component	nucleus
	GO:0003677	Molecular function	DNA binding
	GO:0003700	Molecular function	transcription factor activity, sequence-specific DNA binding
orange1.1g028566m	GO:0006355	Biological process	regulation of transcription, DNA-templated
	GO:0005634	Cellular component	nucleus
	GO:0003677	Molecular function	DNA binding
	GO:0003700	Molecular function	transcription factor activity, sequence-specific DNA binding
orange1.1g015846m	GO:0006355	Biological process	regulation of transcription, DNA-templated
	GO:0005634	Cellular component	nucleus
	GO:0003677	Molecular function	DNA binding
	GO:0003700	Molecular function	transcription factor activity, sequence-specific DNA binding
orange1.1g031071m	GO:0006355	Biological process	regulation of transcription, DNA-templated
	GO:0005634	Cellular component	nucleus
	GO:0003677	Molecular Function	DNA binding
	GO:0003700	Molecular Function	transcription factor activity, sequence-specific DNA binding
orange1.1g047100m	GO:0006355	Biological Process	regulation of transcription, DNA-templated

Table 3: Continue...

Citrus sinensis ID	GO term	GO category	GO description
	GO:0005634	Cellular Component	nucleus
	GO:0003677	Molecular Function	DNA binding
	GO:0003700	Molecular Function	transcription factor activity, sequence-specific DNA binding

Table 4: Gene ontology of *Citrus clementina* ERF1

Citrus clementina ID	GO term	GO category	GO description
Ciclev10021652m	GO:0001944	Biological Process	vasculature development
	GO:0010200	Biological Process	response to chitin
	GO:0045893	Biological Process	positive regulation of transcription, DNA templated
	GO:0051301	Biological Process	cell division
	GO:0005634	Cellular Component	nucleus
	GO:0003677	Molecular Function	DNA binding
	GO:0003700	Molecular Function	transcription factor activity, sequence specific DNA binding
Ciclev10005891m	GO:0006355	Biological Process	regulation of transcription, DNA-templated
	GO:0005634	Cellular Component	Nucleus
	GO:0003677	Molecular Function	DNA binding
	GO:0003700	Molecular Function	transcription factor activity, sequence specific DNA binding
Ciclev10016995m	GO:0006355	Biological Process	regulation of transcription, DNA-templated
	GO:0005634	Cellular Component	Nucleus
	GO:0003677	Molecular Function	DNA binding
	GO:0003700	Molecular Function	transcription factor activity, sequence specific DNA binding
Ciclev10022025m	GO:0006355	Biological Process	regulation of transcription, DNA-templated
	GO:0005634	Cellular Component	Nucleus
	GO:0003677	Molecular Function	DNA binding
	GO:0003700	Molecular Function	transcription factor activity, sequence specific DNA binding
Ciclev10005820m	GO:0006355	Biological Process	regulation of transcription, DNA-templated
	GO:0006952	Biological Process	defense response
	GO:0009873	Biological Process	ethylene-activated signaling pathway
	GO:0005634	Cellular Component	Nucleus

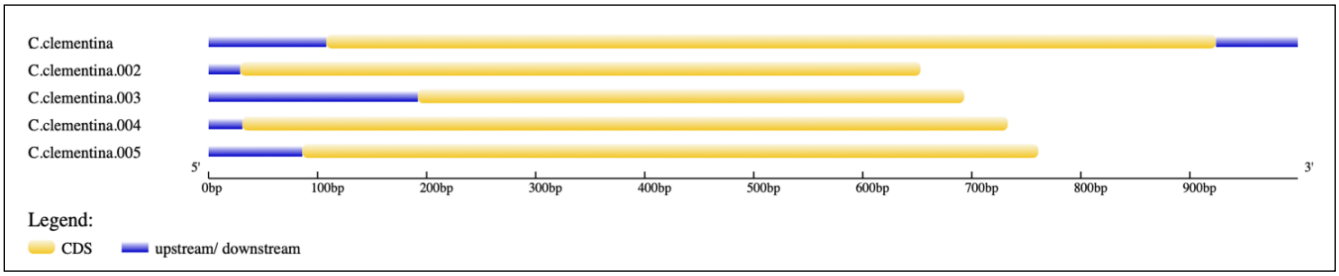

Figure 2: Gene structure of *Citrus clementina*

whereas the CDS ranged from 501 nt (orange1.1g031071m) to 1200 nt (orange1.1g015846m). The size of the protein ranged from 167aa (orange1.1g031071m) to 400aa (orange1.1g015846m), with a molecular weight of 18451.7 Da to 44600.5 Da, respectively (Table 5). While isoelectric point varied from 5.46 (Ciclev10005820m*)* to 10.03 (orange1.1g015846m). However, all 10 orthologs of *Citrus sinensis* and *Citrus clementina* E*RF1* genes contain the

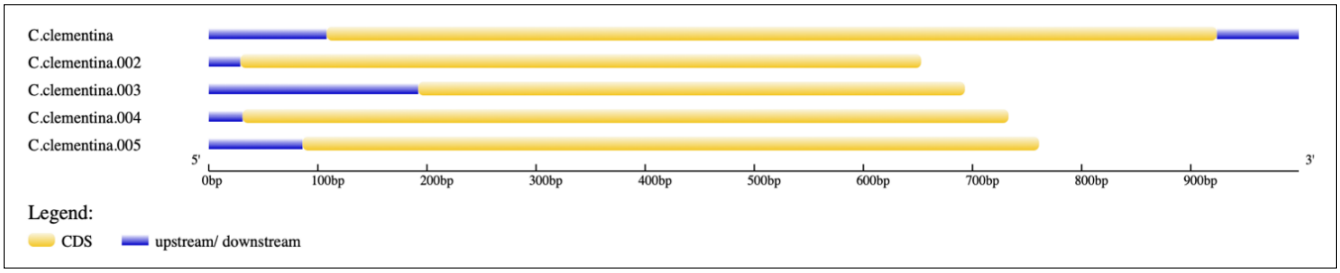

Figure 3: Gene structure of *Citrus sinensis*

Table 5: Properties of ERF1 protein

Species	ID	Genomic length	CDS length	Protein length	Molecular weight (Da)	pI
Citrus sinensis	orange1.1g044938m	816nt	816nt	272aa	29367.9 Da	9.1617
	orange1.1g028566m	860nt	624nt	208aa	22954.5 Da	9.0362
	orange1.1g015846m	3023nt	1200nt	400aa	44600.5 Da	10.0257
	orange1.1g031071m	894nt	501nt	167aa	18451.7 Da	8.4849
	orange1.1g047100m	702nt	702nt	234aa	25618.4 Da	7.094
Citrus clementina	Ciclev10021652m	1193nt	816nt	272aa	29340 Da	9.8527
	Ciclev10005891m	950nt	624nt	208aa	22928.5 Da	9.0658
	Ciclev10016995m	980nt	501nt	167aa	18454.6 Da	7.611
	Ciclev10022025m	848nt	702nt	234aa	25618.4 Da	7.094
	Ciclev10005820m	999nt	675nt	225aa	25310.2 Da	5.4614

Table 6: Domain of ERF1

Species	ID	Interpro ID	Description	Interval
Citrus sinensis	orange1.1g044938m	IPR036955	AP2/ERF domain superfamily	137–199
		IPR001471	AP2/ERF domain	138–202
		IPR016177	DNA-binding domain	138–198
	orange1.1g028566m	IPR016177	DNA-binding domain	96–156
		IPR001471	AP2/ERF domain	96–160
		IPR036955	AP2/ERF domain superfamily	95–156
	orange1.1g015846m	IPR016177	DNA-binding domain	321–381
		IPR036236	Zinc finger C2H2 superfamily	16–66, 134–183
		IPR003656	Zinc finger, BED-type	13–60, 131–187
		IPR001471	AP2/ERF domain	321–386
		IPR036955	AP2/ERF domain superfamily	320–381
	orange1.1g031071m	IPR016177	DNA-binding domain	58–118
		IPR001471	AP2/ERF domain	58–122
		IPR036955	AP2/ERF domain superfamily	57–118
	orange1.1g047100m	IPR001471	AP2/ERF domain	134–198
		IPR036955	AP2/ERF domain superfamily	133–193
		IPR016177	DNA-binding domain	134–193
Citrus clementina	Ciclev10021652m	IPR036955	AP2/ERF domain superfamily	137–199

Species	ID	Interpro ID	Description	Interval
		IPR016177	DNA-binding domain	138–198
		IPR001471	AP2/ERF domain	138–202
	Ciclev10005891m	IPR036955	AP2/ERF domain superfamily	95–156
		IPR001471	AP2/ERF domain	96–160
		IPR016177	DNA-binding domain	96–156
	Ciclev10016995m	IPR001471	AP2/ERF domain	58–122
		IPR016177	DNA-binding domain	58–118
		IPR036955	AP2/ERF domain superfamily	57–118
	Ciclev10022025m	IPR036955	AP2/ERF domain superfamily	83–144
		IPR001471	AP2/ERF domain	84–148
		IPR016177	DNA-binding domain	84–144
	Ciclev10005820m	IPR036955	AP2/ERF domain superfamily	83–144
		IPR001471	AP2/ERF domain	84–148
		IPR016177	DNA-binding domain	84–144

signature AP2/ERF domain (IPR001471), DNA-binding domain (IPR016177), and superfamily (IPR036955). Uniquely, orange1.1g15846m ortholog of *Citrus sinensis* was found to possess zinc finger domains (C2H2/BED-type) (Table 6). Similar functional domain analysis in soybean revealed that GmERF205 has three conserved domains: one AP2 domain and two LCR domains. GmERF205 was largely found in the nucleus, with the AP2/ERF domain serving as its structural component (Wu et al., 2025).

4. CONCLUSION

A total of 10 ERF1 genes was found in *Citrus sinensis* and *Citrus clementina* (5 in each). Presence of domains such as AP2/ERF domain (IPR001471) and DNA-binding domain (IPR016177) emphasized their significance in ethylene defense signaling. GO annotations confirmed nuclear transcription factor, sequence-specific transcription factor activity (GO:0003700), GCC box-mediated defense, chitin response (GO:0010200), and vascular development (GO:0001944), which regulated PR genes for antiviral immunity, particularly against CTV. These results suggested ERF1 as a candidate gene imparting CTV resistance in Citrus species.

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6. REFERENCES

Agranovsky, A.A., 2016. Closteroviruses: molecular biology, evolution and interactions with cells. In: Plant viruses: evolution and management. Singapore: Springer Singapore, 231–252. DOI: 10.1007/978-981-10-1406-2_14.

Aknadibossian, V., Bar-Joseph, M., Catara, A.F., Cook, G., Donovan, N., Hajeri, S., Folimonova, S.Y., 2025. Citrus tristeza virus: From devastating epidemics to effective management in citrus-producing regions around the world. Plant Disease (ja). https://doi.org/10.1094/PDIS-08-25-1639-FE.

Al-Snafi, A.E., 2016. Nutritional value and pharmacological importance of citrus species grown in Iraq. IOSR Journal of Pharmacy 6(8), 76–108. Available from: https://www.iosrphr.org/papers/v6i8V1/H0680176108.pdf.

Blum, M., Andreeva, A., Florentino, L.C., Chuguransky, S.R., Grego, T., Hobbs, E., Bateman, A., 2025. InterPro: the protein sequence classification resource in 2025<? mode longmeta?>. Nucleic Acids Research 53(D1), D444–D456. https://doi.org/10.1093/nar/gkae1082.

Catara, A.F., Bar-Joseph, M., Licciardello, G., 2021. Exotic and emergent citrus viruses relevant to the mediterranean region. Agriculture 11(9), 839. https://doi.org/10.3390/agriculture11090839.

Chen, Q., Yan, F., Liu, J., Xie, Z., Jiang, J., Liang, J., Liu, J., 2025. Citrus transcription factor *CsERF1* is involved in the response to *citrus tristeza disease*. Frontiers in Plant Science 15, 1528348. https://doi.org/10.3389/fpls.2024.1528348.

Dawson, W.O., Bar-Joseph, M., Garnsey, S.M., Moreno, P., 2015. Citrus tristeza virus: making an ally from an enemy. Annual Review of Phytopathology 53(1), 137–155. DOI: 10.1146/annurev-phyto-080614-120012.

Fujimoto, S.Y., Ohta, M., Usui, A., Shinshi, H., Ohme-

Takagi, M., 2000. Arabidopsis ethylene-responsive element binding factors act as transcriptional activators or repressors of GCC box–mediated gene expression. The Plant Cell 12(3), 393–404. DOI: 10.1105/tpc.12.3.393.

Goodstein, D.M., Shu, S., Howson, R., Neupane, R., Hayes, R.D., Fazo, J., Rokhsar, D.S., 2012. Phytozome: a comparative platform for green plant genomics. Nucleic Acids Research 40(D1), D1178–D1186. https://doi.org/10.1093/nar/gkr944.

Heyn, P., Kalinka, A.T., Tomancak, P., Neugebauer, K.M., 2015. Introns and gene expression: cellular constraints, transcriptional regulation, and evolutionary consequences. Bioessays 37(2), 148–154. https://doi.org/10.1002/bies.201400138.

Huang, Y., Liu, Y., Zhang, M., Chai, M., He, Q., Jakada, B.H., Qin, Y., 2020. Genome-wide identification and expression analysis of the *ERF* transcription factor family in pineapple (*Ananas comosus* (L.) Merr.). PeerJ 8, e10014. Available from: https://peerj.com/articles/10014/.

Hu, B., Jin, J., Guo, A.Y., Zhang, H., Luo, J., Gao, G., 2015. GSDS 2.0: an upgraded gene feature visualization server. Bioinformatics 31(8), 1296–1297. https://doi.org/10.1093/bioinformatics/btu817.

Jiang, W., Zhang, X., Song, X., Yang, J., Pang, Y., 2020. Genome-wide identification and characterization of APETALA2/ethylene-responsive element binding factor superfamily genes in soybean seed development. Frontiers in Plant Science 11, 566647. https://doi.org/10.3389/fpls.2020.566647.

Jones, P., Binns, D., Chang, H.Y., Fraser, M., Li, W., McAnulla, C., Hunter, S., 2014. InterProScan 5: genome-scale protein function classification. Bioinformatics 30(9), 1236–1240. https://doi.org/10.1093/bioinformatics/btu031.

Kumar, S., Jena, S.N., Nair, N.K., 2010. ISSR polymorphism in Indian wild orange (*Citrus indica Tanaka*, Rutaceae) and related wild species in North-east India. Scientia Horticulturae 123(3), 350–359. DOI: 10.1016/j.scienta.2009.10.008.

Liang, H., Lu, Y., Liu, H., Wang, F., Xin, Z., Zhang, Z., 2008. A novel activator-type *ERF* of *Thinopyrum intermedium*, *TiERF1*, positively regulates defence responses. Journal of Experimental Botany 59(11), 3111–3120. DOI: 10.1093/jxb/ern165.

Ohme-Takagi, M., Shinshi, H., 1995. Ethylene-inducible DNA binding proteins that interact with an ethylene-responsive element. The Plant Cell 7(2), 173. DOI: 10.1105/tpc.7.2.173.

Onate-Sanchez, L., Anderson, J.P., Young, J., Singh, K.B., 2007. *AtERF14*, a member of the ERF family of transcription factors, plays a nonredundant role in plant defense. Plant Physiology 143(1), 400–409. https://doi.org/10.1104/pp.106.086637.

Wu, N., Feng, Y., Jiang, T., Li, Z., Liu, Y., Yuan, M., 2025. Genome-wide study and expression analysis of soybean *ERF* transcription factors and overexpression of *GmERF205* enhances drought resistance in soybean. BMC Genomics 26(1), 726. Available from: https://link.springer.com/article/10.1186/s12864-025-11829-x.

Xie, Z., Nolan, T., Jiang, H., Tang, B., Zhang, M., Li, Z., Yin, Y., 2019. The AP2/ERF transcription factor TINY modulates brassinosteroid-regulated plant growth and drought responses in Arabidopsis. The Plant Cell 31(8), 1788–1806. https://doi.org/10.1105/tpc.18.00918.

Xu, S., Yao, S., Huang, R., Tan, Y., Huang, D., 2020. Transcriptome-wide analysis of the *AP2/ERF* transcription factor gene family involved in the regulation of gypenoside biosynthesis in *Gynostemma pentaphyllum*. Plant Physiology and Biochemistry 154, 238–247. DOI: 10.1016/j.plaphy.2020.05.040.

Xu, Y., Jiang, J., Zeng, L., Liu, H., Jin, Q., Zhou, P., Wang, Y., 2024. Genome-wide identification and analysis of *ERF* transcription factors related to abiotic stress responses in *Nelumbo nucifera*. BMC Plant Biology 24(1), 1057. Available from: https://link.springer.com/article/10.1186/s12870-024-05772-4.

Xu, M., Yu, M., Li, M., Cheng, G., Chen, K., Song, Y., Chen, F., 2025. Identification and functional analysis of ERF family genes in *Pinus massoniana* during infection of *Bursaphelenchus xylophilus*. Pest Management Science. https://doi.org/10.1002/ps.70401.

Yang, H., Shen, F., Wang, H., Zhao, T., Zhang, H., Jiang, J., Li, J., 2020. Functional analysis of the *SlERF01* gene in disease resistance to *S. lycopersici*. BMC Plant Biology 20(1), 376. Available from: https://link.springer.com/article/10.1186/s12870-020-02588-w.

Yu, W., Yu, Y., Wang, C., Zhang, Z., Xue, Z., 2021. Mechanism by which salt stress induces physiological responses and regulates tanshinone synthesis. Plant Physiology and Biochemistry 164, 10–20. https://doi.org/10.1016/j.plaphy.2021.04.011.

Zhang, H., Zhao, Y., Zhu, J.K., 2020. Thriving under stress: how plants balance growth and the stress response. Developmental Cell 55(5), 529–543. https://doi.org/10.1016/j.devcel.2020.10.012.

Zhang, J., Liao, J., Ling, Q., Xi, Y., Qian, Y., 2022. Genome-wide identification and expression profiling analysis of maize AP2/ERF superfamily genes reveal essential roles in abiotic stress tolerance. BMC Genomics 23(1), 125. https://link.springer.com/article/10.1186/s12864-022-08345-7.