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Revisiting the functions of ethylene response factors (ERFs) in tomato

Shizhe Yu[1], Han Wang[1], Pedro Garcia-Caparros[2] and Mingchun Liu[1]*

[1] *Key Laboratory of Bio-resource and Eco-environment of Ministry of Education, College of Life Sciences, Sichuan University, Chengdu 610065, Sichuan, China*
[2] *Department of Agronomy, University of Almeria, 04120 Almeria, Spain*
* Corresponding author, E-mail: mcliu@scu.edu.cn

Abstract

Ethylene is a pivotal phytohormone that regulates a wide array of biological processes in plants, including growth, development, fruit ripening, and responses to environmental stresses. Ethylene-response factors (ERFs), members of the (*APETALA2/ERF*) superfamily, act as key downstream regulators in the ethylene signaling pathway, through modulating the expression of ethylene-responsive genes. Extensive studies have demonstrated that ERFs are involved in multiple aspects of plant development such as seed germination, plant growth, flowering, fruit development, and ripening, as well as responses to both biotic and abiotic stresses. This review systematically examines the roles and molecular mechanisms of ERFs in various developmental processes in tomato (*Solanum lycopersicum* L.). Furthermore, we discuss the potential future research directions and the possible applications by manipulation of ERFs based on their important roles in plant growth, fruit ripening, and stress response.

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Introduction

Solanum lycopersicum L., commonly known as the tomato, is an herbaceous plant of the Solanaceae family and a modern, widely cultivated vegetable recognized for its red, sweet, and sour edible fruit[1]. Tomato fruits are low in calories and rich in the antioxidant lycopene, along with essential vitamins, and many minerals, providing humans with a rich source of nutrients that are of great nutritional value[2]. Due to its relatively simple growth and development process, short cycle, and fully sequenced genome, tomato is often used as a model system for studying the regulatory mechanisms of fruit development, ripening, and quality formation[3]. Tomato fruit is classified as climacteric, similar to apple, banana, peach, and kiwifruit. Climacteric fruits exhibit a marked increase in respiration rate and ethylene production during the ripening process[4−6]. These characteristics of climacteric fruits are frequently utilized in agricultural practices to regulate the post-ripening process and optimize storage conditions of fruits for various crops[7,8]. Ethylene is a fundamental phytohormone and it was identified as a key factor in the regulation of the ripening process of climacteric fruits by promoting color change, softening, and flavor development, thereby enhancing both edibility and economic value[6,9]. In addition to its role in climacteric fruit ripening, ethylene also plays a pivotal role in various plant growth and developmental processes[9]. ERFs are known to act at the downstream of the ethylene signal pathway and mediate the diverse functions of ethylene by directly regulating the expression of ethylene-responsive genes.

ERFs belong to the AP2/ERF (APETALA2/Ethylene Response Factor) family which is a crucial gene family in plants, playing an important role in the response to biotic and abiotic stresses, as well as in various aspects of plant growth and development. AP2/ERF transcription factors are characterized by the presence of one or two highly conserved AP2/ERF domains, which enable them to bind to specific DNA sequences. This binding influences the expression of downstream target genes, leading to various responses in the plant. AP2/ERF domains typically comprise about 60 to 70 highly conserved amino acid residues, which are crucial for binding to DNA cis-acting elements. Based on the number and similarity of AP2 domains, the AP2/ERF family can be divided into three subfamilies: AP2, ERF, and RAV (Related to ABI3/VP). The AP2 subfamily contains two duplicated AP2/ERF domains, whereas the ERF subfamily contains only a single AP2/ERF domain[10]. The ERF subfamily is further categorized into ERF and dehydration-responsive element binding (DREB) subgroups based on conserved amino acid residues within the AP2/ERF domain[11,12]. The differences in these amino acid residues lead to variations in promoter affinity and recognition specificity between ERF and DREB[13]. The RAV subfamily has a highly conserved AP2 domain, similar to the ERF subfamily, but also contains an additional B3 domain, contributing to its unique regulatory functions[14,15]. In different species, more detailed classifications of the ERF family have been established[11−17]. For instance, in rice and *Arabidopsis thaliana*, a distinct soloist subfamily has been identified[14]. This subfamily comprises ERF transcription factors with significant structural differences from other subfamilies while maintaining highly conserved nucleotide sequences across different species. Nevertheless, the functions and molecular mechanisms of the soloist subfamily remain largely unclear at present[18]. The ERF family is involved in the regulation of various physiological processes such as seed germination, leaf growth, root development, flowering, fruit development, and ripening[18−22]. Moreover, the ERF family also plays important roles in plant responses to both biotic and abiotic stresses, encompassing drought, high salinity, low temperature, pathogens, and other stress-related stimuli[18,23−26]. Several ERF genes have been identified as potential regulators of primary or secondary metabolic processes[27]. Members from the ERF family typically regulate physiological processes in plants by binding to specific cis-acting elements located within the promoter of genes associated with stress responses (DRE/C-repeat (CRT) *cis*-elements), or developmental pathways (GCC-box)[10]. Protein interaction analyses suggests that AP2/ERF proteins can interact with other regulatory proteins to coordinately regulate plant growth and development[28]. Overall, the ERF family plays an important role in plant development and stress response, and further elucidation of their functions and mechanisms is crucial for systematically understanding their contributions to plant physiology.

In tomato, 77 ERF family genes have been identified and divided into nine subfamilies (ERF.A-ERF.J)[29,30]. So far, various tomato ERF family genes have been reported to play important roles in various developmental processes and responses to biotic and abiotic stress (Fig. 1). In this review, we summarized the role and mode of action of the ERF family in tomato and discussed the potential use of these genes by molecular breeding in crop improvement.

Functions of ERF family genes in tomato vegetative growth and reproductive development

The functions of ERF family members during the vegetative growth stage of tomato mainly include the regulation of hypocotyl elongation, root development, and overall plant growth. For instance, ERF transcription factor *SlERF.J2* has been reported to act as a negative regulator of hypocotyl elongation and plant stature in tomato[31]. *SlERF.J2* exerts its regulatory role by binding to the promoter region of Indole Acetic Acid protein *IAA23*, thereby suppressing its expression and subsequently influencing plant stature and hypocotyl elongation in tomato plants[31]. Similarly, the ERF.B subfamily gene *SlERF.B3*, has been reported to regulate root development and plant growth by integrating ethylene and auxin signaling pathways via modulating the expression of an auxin response factor *SlIAA27*[19]. Further study showed that *SlERF.B3* promotes the expression of *SlIAA27* by directly binding to specific sequences within the promoter region of *SlIAA27*, thereby initiating its expression and affecting plant sensitivity to auxin[19]. In addition, *SlERF36* was identified as a regulator controlling the growth cycle of tomato plants[32]. Subsequent investigations revealed a correlation between these physiological changes and alterations in gibberellic acid (GA) levels[32]. More recently, it was reported that overexpression of *SlERF.H5* or *SlERF.H7* resulted in strong growth inhibition phenotypes[33]. It has been shown that *SlERF.H5* and *SlERF.H7* inhibit the expression of *GA20ox1*, a key gene involved in gibberellin synthesis, thereby affecting plant growth[33]. These findings illustrate the key role of ERFs in mediating plant development through interactions with other hormones such as auxin and gibberellins.

During the reproductive developmental process in tomato, ERF family members have been shown to play an important role in regulating flowering time and flower abscission Specifically, *SlERF52* functions as a positive regulator of flower abscission in tomato[34]. *SlERF52* is specifically expressed in the pedicel abscission zone (AZ), where it up-regulates the expression of genes associated with flower abscission and cell wall hydrolysis, such as cell-wall hydrolytic enzymes Cel and PG (*Cel5*, *TAPG1*, *TAPG2,* and *TAPG4*). This regulatory activity promotes the progression of flower abscission in tomato plants[34]. The EAR motif containing transcription factor *SlERF36* was also reported to modulate the onset of flowering in tomato[32,35]. In addition, it was shown that overexpression of *SlERF5* in tomato resulted in earlier flowering, an increase in the number of petals and the diameter of the flowers[36]. However, these alterations in reproductive growth did not influence changes in fruit ripening quality[36]. Despite these findings, there is limited research focusing on the regulation of ERF transcription factors during the reproductive growth stage, and detailed molecular mechanisms are not yet well elucidated. Addressing this knowledge gap represents a significant direction for future research on ERF transcription factors and their role in reproductive development.

Role of the ERF family in tomato fruit ripening and quality regulation

ERF family members have been shown to play important roles in regulating fruit ripening and quality in tomato. Fruit ripening signifies a pivotal transition in the life cycle of plants, particularly in species with fleshy fruits such as tomatoes, garnering considerable attention and study from researchers[21,28]. Although the ripening process of fruits exhibits distinct characteristics and unique pathways across different plant species, common features include changes in fruit color, texture, aroma, sugar content, acidity, and other biochemical substances. During the ripening process, many ERF genes exhibit differential expression patterns, suggesting their involvement in the ripening process[31]. Among these, *LeERF1* has been reported to positively mediate the ethylene response and

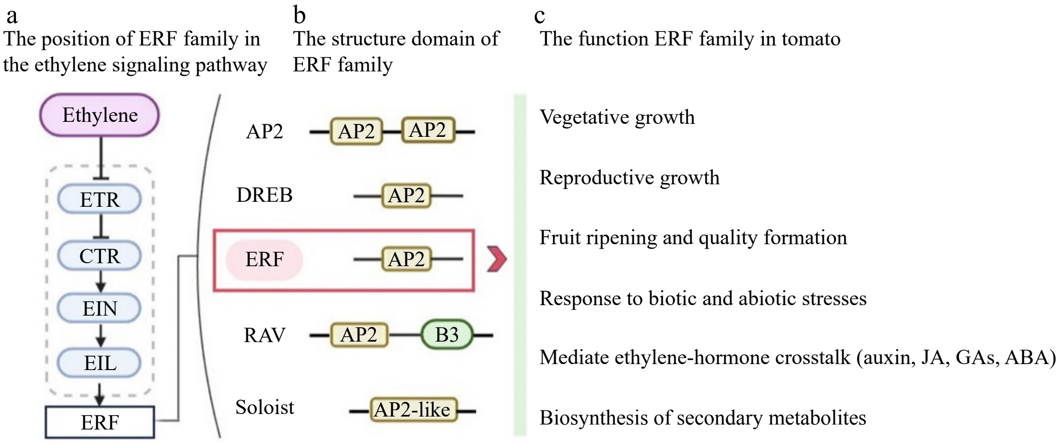

Fig. 1 The location of ERF in ethylene signal pathway and the roles of ERFs in various developmental process and response to biotic and abiotic stress. (a) Hierarchical positioning of ERF transcription factors within the ethylene signaling cascade. Simplified schematic illustrates the sequential activation of core pathway components (abbreviations defined below) culminating in ERF-mediated transcriptional regulation. (b) Phylogenetic classification and domain architecture of the AP2/ERF superfamily. Conserved AP2/DNA-binding domains are highlighted across subfamilies (DREB, ERF, RAV, Soloist), with structural variations denoted by color-coded motifs. (c) Multifunctional roles of ERFs in plant development and stress adaptation. Network analysis reveals ERF involvement in: Developmental transitions (vegetative/reproductive growth); Fruit ripening and quality trait modulation; Cross-talk with hormonal pathways (jasmonic acid, auxin, gibberellins, abscisic acid); Biotic/abiotic stress response coordination; Secondary metabolite biosynthesis. Abbreviations: AP2/ERF – APETALA2/Ethylene Response Factor; DREB – Dehydration-Responsive Element Binding; RAV – Related to ABI3/VP1; ETR – Ethylene Receptor; CTR – Constitutive Triple Response; EIN – Ethylene Insensitive 3; EIL – EIN3-Like; ERF – Ethylene Receptor Factor; JA – Jasmonic Acid; GA – Gibberellin; ABA – Abscisic Acid.

regulate the fruit ripening process in tomato[28]. The expression of the *PG* gene, which is highly correlated with fruit softening was upregulated in *LeERF1* overexpression (*LeERF1*-sn) lines[28]. Conversely, *SlERF.F12* was reported to act as a repressor in fruit ripening by interacting with the corepressor *TPL2*, facilitating the recruitment of HDA1 and HDA3 to form a co-repressor protein complex[21]. This complex binds to the promoters of ripening-related genes, such as 1-aminocyclopropane-1-carboxylate (ACC) synthase (ACS) *ACS2, ACS4, PG2a,* and Pectate Lyase (*PL*), thereby inhibiting their expression and delaying the ripening process[21]. In a study conducted in 2022, it was demonstrated that *SlERF.D6* plays a significant role in tomato fruit ripening and steroidal glycoalkaloid metabolism[20]. More recently, *SlERF.D6* was reported to act as a key ripening regulator by the formation of a transcriptional cascade with *SlDEAR2* and *SlTCP12*[37]. Additionally, *SlERF.E4* has been identified to bind to the promoter region of the *β-D-N-acetylhexosaminidase (β-Hex)* gene, where it acts as a positive transcriptional regulator. Molecular mechanisms revealed that *SlERF.E4* promotes the expression of *β-Hex* during tomato fruit ripening, thereby facilitating fruit softening through conjunction with Ripening Inhibitor (*RIN*) and Abscisic Acid Stress Ripening (*SlASR1*)[22]. Using dominant repression technology (SRDX), *S1ERF.B3* was shown to exert a significant effect on tomato fruit ripening[38]. Inhibition of *SlERF.B3* activity by the SRDX fusion protein led to the downregulation of Phytoene Synthase *PSY1* and Phytoene Desaturase *PDS* expression, while upregulated Lycopene Cyclase *b-LCY1* and genes associated with ethylene production and ripening[38]. Similarly, the downregulation of *SlERF6* expression resulted in elevated ethylene production, accompanied by increased expression of *ACS2* and ACC oxidase (ACO) *ACO1*, suggesting that *SlERF6* acts as a negative regulator in fruit ripening[39]. Furthermore, this study demonstrated that *SlERF6* controls carotenoid biosynthesis by negatively regulating the expression of Heat Shock Protein 21 *HSP21* and 1-Deoxy-D-xylulose-5-phosphate synthase *DXS*[39]. Three ethylene response factors *Pti4*, *Pti5*, and *Pti6* also have been shown to function in fruit ripening[40]. Overexpression of these genes resulted in a shorter fruit ripening time by upregulation of ripening-related genes such as *ACS2* and *ACS4*[40]. In contrast, the expression of *LeERF3b* was downregulated during fruit ripening but significantly increased in the Never-ripe (*Nr*) mutant[24]. These findings suggest that *LeERF3b* may act as a negative regulator in fruit ripening[24]. A recent study revealed that *SlERF.H5* and *SlERF.H7* genes play vital roles in tomato fruit softening[33]. These ERFs can bind to the DRE cis-acting element in the promoter region of the Cellulose Synthase gene *SlCESA3*, thereby increasing the expression of *SlCESA3* and leading to enhanced synthesis of cellulose in the fruits[33]. In addition, *SlERF.G3-Like* has recently been proven to be related to fruit ripening in tomato, with its expression directly regulated by the well-known fruit ripening regulator RIN[41]. Moreover, *SlERF.G3-Like* exerts a regulatory effect on several downstream genes involved in tomato fruit ripening and quality, including *SlACS2, SlACO1, SlPL, PG2a,* Chalcone synthase *CHS1,* Flavonol synthase *FLS*, and Flavonoid 3'-hydroxylase *F3H*[41]. Collectively, the functions of the ERF family in fruit ripening have been extensively investigated compared to their roles in vegetative and reproductive growth. Studies have demonstrated that the regulatory pathways governed by ERF family genes in fruit ripening are diverse, contributing to complex regulatory networks. The effects of ERF family genes on fruit ripening encompass various traits such as fruit color, texture, flavor substances, and secondary metabolites. However, fully comprehending the specific pathways through which ERF family genes regulate these tomato traits, as well as their intricate relationship with ethylene signaling remains a challenging endeavor. Future research endeavors are anticipated to make significant breakthroughs in elucidating these pathways addressing these fundamental questions and contributing to advancements in tomato breeding and fruit quality improvement.

Functions of the ERF family in response to biotic and abiotic stresses

The ERF family, known for its responsiveness to ethylene signaling, is also recognized for its crucial role in mediating plant responses to both biotic and abiotic stresses[42]. ERF family members are involved in the regulation of disease and insect resistance in tomato when confronted under biotic stress conditions[43]. Studies have shown that the expression of some ERF transcription factors is induced by pathogens and insect infestations, thereby initiating defense responses in tomato[44]. It was shown that the expression of *ERF2* gene in tomato plants was upregulated in response to *Stemphylium lycopersici* infection[45]. Silencing *ERF2* led to a susceptible phenotype, reduced hypersensitivity response, and alterations in physiological activities such as reactive oxygen species (ROS) production[45]. Furthermore, *ERF2* confers resistance to the invasion by *S. lycopersici* by playing a key role in multiple SA, JA, and ROS signaling pathways[45]. Several members of the ERF family, particularly the B3 subfamily, including *SlERF.A1*, *SlERF.B4*, *SlERF.C3*, and *SlERF.A3*, play a critical role in conferring resistance to *Botrytis cinerea* in tomato[46]. Silencing these genes has been shown to increase susceptibility to pathogens and diminish pathogen-induced jasmonic acid/ethylene-mediated signaling responses[46]. This downregulation consequently affected the expression of defense genes involved in the immune responses of plants[46]. In another study, overexpression of *ERF68* induced spontaneous cell death and activated multiple defense pathways, including salicylic acid (SA), ethylene (ET), jasmonic acid (JA), and hypersensitive response in tomato[44]. In addition, *Pti4*, *Pti5*, and *Pti6* genes, previously identified as key players in plant defense responses, share a conserved DNA binding domain characteristic of Ethylene-responsive element binding proteins (EREBPs)[47,48]. This domain facilitates interactions with Pto kinases, thereby regulating the expression of downstream pathogenesis-related (PR) genes[48]. In the absence of this binding domain, Pti4, Pti5, and Pti6 are unable to interact with Pto kinases, rendering tomato plants more susceptible to disease[47,48]. The expression of Tomato Stress Responsive Factor *TSRF1* was upregulated in response to ethylene, salicylic acid, or tomato *Ralstonia solanacearum* infection[49]. Overexpression of *TSRF1* constitutively activates the expression of PR genes in tomato, thereby enhancing tomato resistance to *Ralstonia solanacearum* infection[49]. Furthermore, recent studies have highlighted the significant role of the *SlERF.C1* in *Botrytis cinerea* response[50]. *SlERF.C1* interacts with the mitogen - activated protein kinase SlMPK8, thereby enhancing the regulation of *SlERF.C1* to the downstream PR genes by phosphorylating SlERF.C1[50].

In response to abiotic stresses such as drought and salt stress, ERF family members are involved in regulating adaptative responses and stress tolerance mechanisms in tomato[51]. It has been shown that the expression of various ERF transcription factors can be induced by abiotic stresses such as high salinity, drought, and low temperature[51]. ERF transcription factors play crucial roles in modulating growth and developmental processes in tomato, ultimately enhancing the plant´s ability to tolerate and adapt to adverse environmental conditions[52]. Notably, *SlERF5* exhibited significant upregulation in response to various abiotic stresses such as high salt, drought, flooding, and low temperature, suggesting that *SlERF5* plays a pivotal role in the response to abiotic stresses in tomato[52]. Overexpression of the *SlERF5* resulted in increased resistance to abiotic stresses such as drought and salt stress in transgenic plants[52]. Similarly, the ethylene response factor *ERF.C1* also named *TERF1* or *JERF2* gene, which responds to ethylene signaling, exhibits increased tolerance to salt stress when overexpressed during seed germination and vegetative growth stages[25]. These findings suggest that *TERF1* acts as a positive regulator in the plant's response to salt stress[25]. Overexpression of *JERF3* in transgenic plants enhances plant tolerance to salt stress, demonstrating *JERF3's* role as a key regulator in mediating salt stress responses[53]. In addition, the *JERF1* gene demonstrates versatility in binding not only to the GCC-box motif but also to the DRE-box[54]. This gene responds not only to ethylene signaling but also to stressors such as salt stress, abscisic acid, and methyl jasmonate[54]. Through these interactions, *JERF1* activates the expression of PR genes containing the GCC-box, thereby enhancing tomato plant tolerance to salt stress[54]. These findings provide further evidence supporting the pivotal role of ERF family genes in diverse stress response.

The function of ERFs in ethylene-hormone crosstalk

Functioning as the principal ethylene-responsive transcription factors, ERFs likely play a pivotal role as signaling hubs that facilitate the integration of ethylene pathways with other phytohormone signaling networks. Interactions between ethylene and auxin have long been reported at both the physiological and molecular levels, and in recent years more evidence supports the cross-talk between the two hormones[26,55]. Ethylene-responsive gene *SlERF.B3* has been shown to integrate ethylene and auxin signaling via regulation of the expression of the auxin signaling component *SlIAA27*, suggesting that *SlERF.B3* may act as a key mediator linking ethylene and auxin signaling in tomato[19]. Similarly, *SlERF.D7* amalgamates auxin and ethylene signaling pathways via regulating the transcript accumulation of *SlARF2* paralogs in tomato, thereby orchestrating tomato fruit ripening processes[56]. It was shown that *SlERF.J2* suppresses IAA23 expression and modulates auxin and GA homeostasis, thereby regulating hypocotyl elongation and plant height in tomato[31]. Furthermore, in addition to auxin, ethylene signaling also interacts with other plant hormone pathways, such as those regulated by Jasmonic acid (JA), abscisic acid (ABA), and gibberellins (GAs). Jasmonate-inducible ERF transcription factors have been shown to act as key regulators that integrate JA signaling to activate steroidal glycoalkaloid biosynthesis in tomato, potentially mediating crosstalk between ethylene and JA pathways in plant defense responses[57]. Ethylene-induced *ERF15* and *ERF16* act as master transcriptional activators of JA biosynthetic genes, orchestrating the rapid jasmonate burst in tomato during herbivory, with *ERF16* further amplified by a JA-*MYC2* feedback loop[58]. Moreover, *SlERF.B8* plays a positive role in tomato cold tolerance by triggering jasmonate biosynthesis and acts as a crucial node integrating ethylene and JA signaling pathways[59]. Additionally, recent studies have demonstrated that ERFs can mediate the crosstalk between ethylene and other plant hormones such as GAs and ABA to affect plant growth and development[60−62]. *SlERF.H6* mediates the interplay between ethylene and gibberellin signaling to regulate the SGA biosynthesis in tomato[63]. *SlERF36* accelerates growth transitions and reduces the plant life cycle by regulating GA levels and responses[32]. Ethylene response factor *Pti4* is involved in the regulation of fruit ripening, seed germination, and responses to drought and *Botrytis cinerea* infection through adjustments to ABA metabolism and signaling[64]. Tomato *ERF84* can be markedly induced by ABA, and its overexpressing plants confer hypersensitivity to ABA at the germination stage[65]. Similarly, *ERF15* positively regulates ABA-mediated cold tolerance in tomato plants by activating *CBF1* and *WRKY6* expression[66]. These studies supported the important role of ERFs in mediating the crosstalk between different plant hormones. Despite the growing number of studies showing the phytohormone crosstalk mediated by ERFs, the underlying mechanisms still require further investigation.

Functions of the ERF family in the regulation of secondary metabolites biosynthesis

As a key transcription factor family, ERFs also play a vital role in regulating secondary metabolite biosynthesis in tomato. In addition to the well-known functions in controlling the biosynthesis of carotenoids[67], ERFs have been shown to act as key regulators in the modulation of the biosynthesis of flavonoids in tomato. For example, ethylene response factor *SlERF.G3-Like* was reported to positively promote the accumulation of flavonoids in tomato fruits by directly regulating the expression of key structure genes involved in flavonoid biosynthesis[41]. Except for the important roles in the biosynthesis of carotenoids and flavonoids, ERFs are involved in steroidal glycoalkaloids (SGAs) metabolism. *GAME9*, an ERF family member, was reported to modulate SGA metabolism by regulating the expression of *GAME17*[68]. More recently, a distal enhancer GAME Enhancer 1 (GE1) was shown to recruit GAME9-MYC2 complex to form a chromatin loop, thereby regulating the metabolism of steroidal glycoalkaloids (SGAs) in tomato[69]. In addition, metabolome-wide association analysis identified *SlERF.H6* as a critical regulator in controlling SGA metabolism in tomato. *SlERF.H6* binds to the GCC-box present in the promoter regions of multiple GAME genes, negatively regulating their expression, and thus SGA biosynthesis[63]. Similarly, *SlERF.D6* has been identified as a dual regulator, influencing both fruit ripening and SGA metabolism. *SlERF.D6* suppresses the transcription of *GAME12*, thereby negatively regulating tomatidine synthesis[20]. ERFs are also shown to be involved in the regulation of phenolic biosynthesis in tomato. Ethylene response factor *SlERF7* was reported to promote UV-C-induced phenolic biosynthesis in postharvest tomato fruit by binding to the promoter of *SlPAL5*[70]. Moreover, two ERF genes *ERF1* and *ERF4* were found to be differentially expressed in high-phenolic tomato introgression line IL7-3[71]. Further studies demonstrated that *ERF1* acts as a key regulator of phenolic transport into the vacuole, while *ERF4* acts as an auxiliary transcription factor in modulating phenolic metabolism[71]. These findings collectively highlight the multifaceted roles of ERF transcription factors in orchestrating secondary metabolite biosynthesis in tomato, with implications for fruit development, coloration, and nutritional quality.

Conclusions

The ERF family of transcription factors has emerged as a pivotal player in tomato breeding, offering immense potential for improving agronomic traits, fruit quality, and stress resilience. Their multifaceted roles in regulating vegetative growth, reproductive development, fruit ripening, and stress responses underscore their significance as candidates for crop enhancement (Table 1). These studies offer significant insights into the regulatory mechanisms that govern tomato growth and development offering valuable references for improving both tomato yield and quality. However, despite these successes, several limitations persist. The functional redundancy and pleiotropic effects of ERF genes often complicate their precise manipulation, as altering one ERF member may inadvertently affect multiple physiological processes. Additionally, the intricate crosstalk between ERFs and other hormonal pathways, such as auxin, gibberellins, and jasmonates, remains poorly understood, limiting our ability to predict outcomes of genetic modifications. Current research also lacks comprehensive field studies to validate the performance of ERF-engineered tomatoes under real-world conditions, leaving gaps between laboratory findings and practical applications. Looking ahead, future research should prioritize unraveling the complex regulatory networks governed by ERFs, particularly their interactions with other signaling pathways, to enable more precise and predictable genetic interventions. Advances in CRISPR-based genome editing and systems biology approaches could facilitate the targeted modulation of ERF genes while minimizing unintended effects. Moreover, integrating ERF manipulation with traditional breeding techniques may accelerate the development of novel tomato cultivars with optimized traits. Another promising direction is the exploration of ERF homologs across diverse tomato wild relatives, which could uncover untapped genetic variation for stress adaptation and fruit quality, thereby further developing new tomato varieties with optimized plant structure, high quality, and enhanced resistance.

Table 1. Summary of the role of ethylene response factors (ERFs) in tomato.

Gene identifiers	Names	New names	Function	Ref.
Solyc02g090790	ERF.J2	SlERF.J2	Plant growth	[31]
Solyc05g052030	ERF.B3	SlERF.B3	Root development	[19]
Solyc10g006130	SlERF36	SlERF.F1	Plant growth	[32]
Solyc03g117130	SlERF52		Flower abscission	[34]
Solyc10g006130	SlERF36	SlERF.F1	Flowering time	[35]
Solyc03g093560	SlERF5	SlERF.B2	Flowering time	[36]
Solyc05g050830	SlERF.H5	SlERF.H5	Plant growth	[33]
Solyc06g066540	SlERF.H7	SlERF.H7	Plant growth	[33]
Solyc06g065820	LeERF1	SlERF.H1	Fruit ripening	[28]
Solyc02g077840	SLERF.F12		Fruit ripening	[21]
Solyc04g071770	ERF.D6	SlERF.D6	Fruit ripening	[20]
Solyc01g065980	ERF.E4	SlERF.E4	Fruit ripening	[22]
Solyc05g052030	ERF.B3	SlERF.B3	fruit ripening and ethylene response	[38]
Solyc10g065980	ERF6	SlERF.E4	Fruit ripening and carotenoid synthesis	[39]
Solyc05g052050	Pit4	SlERF.A3	Fruit ripening	[40]
Solyc02g077370	Pit5	SlERF.C6	Fruit ripening	[40]
Solyc06g082590	Pit6	SlERF.G2	Fruit ripening	[40]
Solyc10g009110	LeERF3b	SlERF.F5	Fruit ripening	[24]
Solyc05g050830	SlERF.H5	SlERF.H5	Fruit firmness	[33]
Solyc06g066540	SlERF.H7	SlERF.H7	Fruit firmness	[33]
Solyc02g077790	SlERF.G3-like		Fruit ripening	[41]
Solyc02g077370	ERF2	SlERF.C6	Disease resistance	[45]
Solyc08g078180	SlERF.A1	SlERF.A1	Disease resistance	[46]
Solyc03g093540	SlERF.B4	SlERF.B4	Disease resistance	[46]
Solyc09g066360	SlERF.C3	SlERF.C3	Disease resistance	[46]
Solyc05g052050	SlERF.A3	SlERF.A3	Disease resistance	[46]
Solyc08g078180	ERF68	SlERF.A1	Disease resistance	[44]
Solyc05g052050	Pit4	SlERF.A3	Disease resistance	[47,48]
Solyc02g077370	Pit5	SlERF.C6	Disease resistance	[47,48]
Solyc06g082590	Pit6	SlERF.G2	Disease response	[47,48]
Solyc09g089930	TSRF1	SlERF.C4	Disease resistance	[49]
Solyc05g051200	SlERF.C1	SlERF.C1	Disease resistance	[50]
Solyc03g093560	SlERF5	SlERF.B2	Drought and salt tolerance	[52]
Solyc05g051200	TERF1/JERF2	SlERF.C1	Salt tolerance	[25]
Solyc03g123500	JERF3	SlERF.E3	Salt tolerance	[53]
Solyc06g063070	JERF1	SlERF.E2	Salt tolerance	[54]
Solyc05g052030	ERF.B3	SlERF.B3	Ethylene-Auxin crosstalk	[38]
Solyc03g118190	SlERF.D7	SlERF.D7	Ethylene-Auxin crosstalk	[56]
Solyc02g090790	SlERF.J2	SlERF.J2	Ethylene-Auxin crosstalk	[31]
Solyc06g054630	ERF15		Ethylene-ABA crosstalk	[66]
Solyc01g090320	SlERF.B8	SlERF.B8	Ethylene-ABA crosstalk	[59]
Solyc03g120840	SlERF.H6	SlERF.H16	Ethylene-ABA crosstalk	[63]
Solyc10g006130	SlERF36	SlERF.F1	Ethylene-ABA crosstalk	[32]
Solyc05g052050	Pit4	SlERF.A3	Ethylene-ABA crosstalk	[64]
Solyc04g071770	SlERF84	Sl-ERF.D6	Ethylene-ABA crosstalk	[65]
Solyc02g077790	SlERF.G3-like		Flavonoid synthesis	[41]
Solyc01g090340	GAME9	SlERF.B9	SGA synthesis	[68]
Solyc03g120840	SlERF.H6	SlERF.H6	SGA synthesis	[63]
Solyc04g071770	SlERF.D6	SlERF.D6	SGA synthesis	[20]
Solyc03g123500	SlERF7	SlERF.E3	Phenolic compounds synthesis	[70]
Solyc05g051200	SlERF1	SlERF.C1	Phenolic compounds synthesis	[71]
Solyc07g053740	SlERF4	SlERF.F4	Phenolic compounds synthesis	[71]

The gene identifiers can be found at https://solgenomics.net/, the Name of ERF genes are derived from the cited literature, the new names refer to the nomenclature in the study by Chen et al.[31].

Author contributions

The authors confirm contribution to the paper as follows: study conception and design: Liu M; draft manuscript preparation: Yu S, Wang H, Garcia-Caparros P, Liu M. All authors reviewed the results and approved the final version of the manuscript.

Data availability

Data sharing not applicable to this article as no datasets were generated or analyzed during the current study.

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Conflict of interest

The authors declare that they have no conflict of interest.

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