

# Ethylene Response Factors: A Key Regulatory Hub in Hormone and Stress Signaling<sup>1</sup>

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Ethylene is essential for many developmental processes and a key mediator of biotic and abiotic stress responses in plants. The ethylene signaling and response pathway includes Ethylene Response Factors (ERFs), which belong to the transcription factor family APETALA2/ERF. It is well known that ERFs regulate molecular response to pathogen attack by binding to sequences containing AGCCGCC motifs (the GCC box), a cis-acting element. However, recent studies suggest that several ERFs also bind to dehydration-responsive elements and act as a key regulatory hub in plant responses to abiotic stresses. Here, we review some of the recent advances in our understanding of the ethylene signaling and response pathway, with emphasis on ERFs and their role in hormone cross talk and redox signaling under abiotic stresses. We conclude that ERFs act as a key regulatory hub, integrating ethylene, abscisic acid, jasmonate, and redox signaling in the plant response to a number of abiotic stresses.

Environmental stresses, including drought, salinity, high light, and extreme temperatures, influence plant growth and productivity. These abiotic stresses result in reductions in growth, stomatal and nonstomatal limitations on photosynthesis, and alterations in both hormonal balance and reduction/oxidation (redox) processes, potentially leading to enhanced lipid peroxidation, protein oxidation, and DNA damage (Munns and Tester, 2008; Mittler et al., 2011; Munné-Bosch et al., 2013). Plant responses and adaptation to abiotic stresses are controlled by molecular signal transduction cascades. In these cascades, plant hormones as a part of the signal network function as central integrators that link and reprogram the complex stress-adaptive signaling cascades (Ma et al., 2006; Golldack et al., 2014).

Several plant hormones, such as ethylene (Zhao and Schaller, 2004; Cheng et al., 2013), abscisic acid (ABA; Wu et al., 2007), jasmonates (Cela et al., 2011; Cheng et al., 2013), salicylic acid (Jayakannan et al., 2015), GAs (Magome et al., 2008), cytokinins (Wu et al., 2014b), auxin (He et al., 2005), and brassinosteroids (Divi et al., 2010), have been reported to be involved in stress signaling. Despite its simple two-carbon structure, the plant hormone ethylene serves as a key mediator of biotic and abiotic stress factors. Transcription factors (TFs) control the majority of stress response genes, and of more than 1,800 TFs identified in *Arabidopsis* (*Arabidopsis thaliana*; Arabidopsis Genome Initiative, 2000; Riechmann et al., 2000; Gong et al., 2004), the APETALA2 (AP2)/Ethylene Response Factor (ERF) superfamily plays a pivotal role in adaptation to biotic

and abiotic stresses, such as those caused by pathogens, wounding, cold and heat stress, UV light, drought, and salinity (Mizoi et al., 2012). A genome-wide analysis of plant species has identified, for instance, the following numbers of members of the AP2/ERF superfamily: *Arabidopsis*, 147 (Nakano et al., 2006); *Populus* spp., 200 (Zhuang et al., 2008); *Brassica* spp., 291 (Song et al., 2013); *Citrus* spp., 108 (Ito et al., 2014); *Vitis* spp., 149 (Licausi et al., 2010); *Solanum* spp., 155 (Charfeddine et al., 2015); and *Oryza* spp., 180 (Nakano et al., 2006; Sharoni et al., 2011).

Sakuma et al. (2002) classified AP2/ERF TFs into five subfamilies: AP2, related to ABSCISIC ACID INSENSITIVE3 (ABI3)/VIVIPAROUS1 (VP1), dehydration-responsive element (DRE) binding protein, ERF, and others according to the number and similarity of the DNA binding domains. ERFs have been extensively reported to be involved in the response to pathogen attack by binding to sequences containing AGCCGCC motifs (the GCC box), a cis-acting ethylene response element (Solano et al., 1998; Berrocal-Lobo et al., 2002; Lorenzo et al., 2002). However, recent research has shown that several ERFs also bind to DREs and play a regulatory role in plant responses to abiotic stresses (Cheng et al., 2013). Although the role of AP2/ERF TFs as mediators of stress responses and development programs has been reviewed recently (Xu et al., 2011; Mizoi et al., 2012; Licausi et al., 2013), little emphasis has been put on the role of ERFs in abiotic stress tolerance. Here, we focus on the role of ERFs in plant tolerance to abiotic stresses, with an emphasis on hormone cross talk, redox regulation, and abiotic stress signaling.

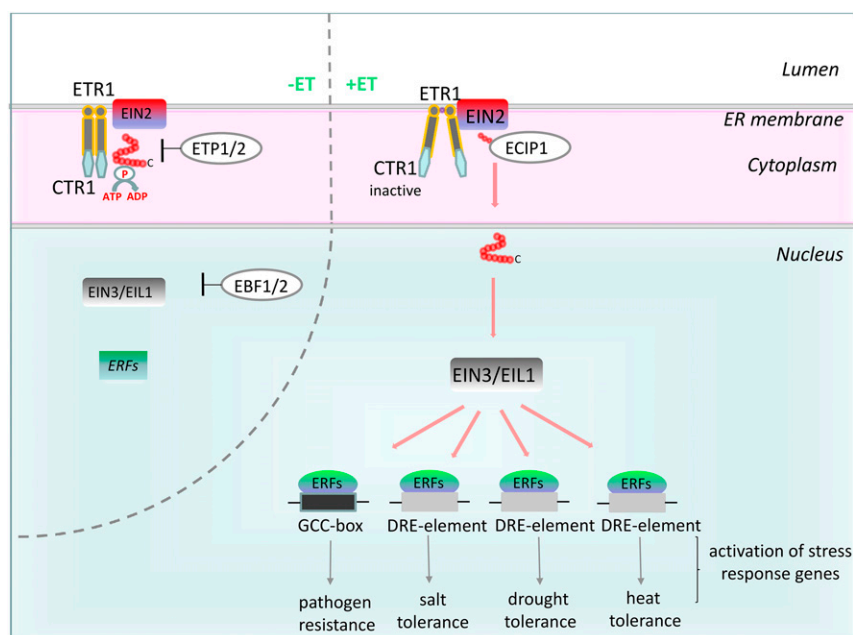
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## ERFs IN ETHYLENE RESPONSE

The ethylene signaling and response pathway to the cell nucleus, where the transcription of hundreds of



**Figure 1.** Model of the ethylene (ET) signaling pathway to ERFs. In the absence of ethylene (left), the ethylene receptors promote CTR1 kinase activity, resulting in the phosphorylation of the C-terminal domain of EIN2. Because of the protein turnover involving the F-box proteins ETP1/2 and EBF1/2, the protein levels of both EIN2 and EIN3/EIL1 are extremely low. In the presence of ethylene (right), the inactivation of the ethylene receptors and CTR1 results in the dephosphorylation and cleavage of the EIN2 C terminus and translocation to the nucleus, where they regulate EIN3/EIL1 activation directly or indirectly. The direct targets of EIN3 are the TF genes *ERFs*, such as *ERF1*, which activates, depending on the stress conditions (either biotic [pathogen infection] or abiotic [e.g. dehydration, salinity, or heat shock] stress), a specific set of stress response genes by binding to the specific cis-acting GCC box and DRE elements. ER, Endoplasmic reticulum; EIP1, EIN2 C-TERMINUS INTERACTING PROTEIN1.

genes is altered, was revealed as a result of the analysis of the model system *Arabidopsis* (Fig. 1). Ethylene is sensed by five receptors localized at the endoplasmic reticulum membrane that are divided into subfamily I (Ethylene Response1 [ETR1] and Ethylene Response Sensor1 [ERS1]) and subfamily II (ETR2, ERS2, and Ethylene Insensitive4 [EIN4]; Chen et al., 2005; Lacey and Binder, 2014). The ethylene signaling and response pathway also includes the downstream components Constitutive Triple Response1 (CTR1), EIN2, EIN3/Ethylene Insensitive-Like Protein1 (EIL1), and ERFs (Kendrick and Chang, 2008; Stepanova and Alonso, 2009). CTR1 is a negative regulator of ethylene signaling. In the absence of ethylene, the receptors promote CTR1 kinase activity, which phosphorylates the C-terminal domain of EIN2 and thereby, prevents its nucleus localization. However, in the presence of ethylene, the receptors and CTR1 are inactive (Kieber et al., 1993; Gao et al., 2003; Huang et al., 2003; Ju et al., 2012). In contrast, EIN2, which is localized at the ER membrane along with the ethylene receptors and CTR1, positively regulates ethylene signaling (Bisson et al., 2009; Bisson and Groth, 2010). In the absence of ethylene, EIN2 protein levels are reduced because of the interaction with two F-box proteins: Ethylene Insensitive2-Targeting Protein1 (ETP1) and ETP2 (Qiao et al., 2009). In the presence of ethylene, the inactivation of the receptors and CTR1 results in the dephosphorylation and cleavage of the EIN2 C terminus and translocation to the nucleus, where it directly or indirectly regulates EIN3/EIL1 activation (Ju et al., 2012). An MA3 domain-containing protein (EIP1) interacts with the EIN2 C terminus, leading to enhanced ethylene response (Lei et al., 2011). In the absence of ethylene, the EIN3/EIL1 protein levels are extremely low because of the protein turnover involving the F-box proteins Ethylene Insensitive3-Binding F-Box Protein1 (EBF1) and EBF2.

The presence of ethylene down-regulates EBF1 and EBF2 and leads to the accumulation of EIN3/EIL1 proteins, which initiates a transcriptional cascade that results in the activation and repression of hundreds of genes (An et al., 2010). In *Arabidopsis*, one of the direct targets of EIN3 is the *ERF* genes (Solano et al., 1998). *AtERF* and *ERF* will be used in this review interchangeably.

Recent studies revealed that ERFs are key regulators in abiotic stress tolerance in several species. Enhanced *ERF* expression has been reported after drought, salinity, light stress, and cold and heat treatments among other abiotic stresses (Table I). Several *ERF* genes have been reported to be induced by salt stress (38 study cases), drought (27 study cases), low temperature (18 study cases), heat stress (3 study cases), and changes in light availability (14 study cases). It should be noted that *ERF* gene expression is common to various abiotic stresses, including salt, drought, and cold stress treatment (12 study cases), salt and drought (8 study cases), and others. The effects of overexpressing *ERF* genes in plant response to abiotic stress have been studied in various plant systems (Table II).

Several TFs from *Arabidopsis* and other plant species that belong to the ERF subfamily have been reported to be capable of binding to both GCC box and DRE elements (Table I). For instance, *AtERF1* binds specifically to GCC boxes in the promoter regions of the *ethylene- and jasmonate-responsive plant defensin (PDF1.2)* and *basic-chitinase (b-CHI)* genes (Solano et al., 1998) and DRE elements in the promoters of the  $\Delta^1$ -*Pyrraline-5-Carboxylate Synthetase1 (P5CS1)*, *Germin-Like Protein9 (GLP9)*, *osmotin34 (OSM34)*, *similar to RCD one5 (SRO5)*, *responsive to desiccation29B (RD29B)*, *Early Response to Dehydration7 (ERD7)*, and *RD20* genes, thus conferring not only resistance to pathogen attack but also, tolerance to several abiotic stresses, including drought, salt,

**Table 1.** Expression of genes from the ERF subfamily under abiotic stress

—, Not studied; *JERF1*, Jasmonate and Ethylene Response Factor1; *OPBP1*, Osmotin Promoter Binding Protein1; *BIERF3*, BTH-Induced ERF Transcriptional Factor3; *TSRF1*, Tomato Stress-Responsive Factor1; *TERF*, Tomato Ethylene Response Factor; *SIERF*, Tomato Ethylene Response Factor; *SHN1*, ethylene-responsive transcription factor WIN1.

Species	ERFs	Up-Regulation under Stress					References
		Salt	Drought	Cold	Heat	Light	
Arabidopsis	<i>AtERF1</i> <sup>a</sup>	Yes	Yes	—	Yes	—	Cheng et al., 2013
Arabidopsis	<i>AtERF4</i>	Yes	—	—	—	—	Seo et al., 2010
Arabidopsis	<i>AtERF5</i>	No	Yes	—	—	—	Dubois et al. (2013)
Arabidopsis	<i>AtERF6</i>	Yes	Yes	Yes	No	Yes	Dubois et al. (2013); Sewelam et al. (2013); Wang et al. (2013a); Vogel et al. (2014)
Arabidopsis	<i>AtERF98</i>	Yes	—	—	—	—	Zhang et al. (2012)
Arabidopsis	<i>AtERF104</i>	—	—	—	—	Yes	Vogel et al. (2014)
Arabidopsis	<i>AtERF105</i>	—	—	—	—	Yes	Vogel et al. (2014)
<i>Brassica rapa</i>	<i>BrERF4</i>	No	—	—	—	—	Seo et al. (2010)
Pepper ( <i>Capsicum annuum</i> )	<i>CaERFLP1</i> <sup>a</sup>	Yes	No	No	—	—	Lee et al. (2004)
Pepper	<i>CaPF1</i> <sup>a</sup>	Yes	Yes	Yes	—	—	Yi et al. (2004)
Chickpea ( <i>Cicer arietinum</i> )	<i>CarERF116</i>	Yes	Yes	Yes	Yes	—	Deokar et al. (2015)
<i>Chrysanthemum nankingense</i>	<i>CnERF1</i>	No	—	Yes	—	—	Gao et al. (2015)
<i>Camellia reticulata</i>	<i>CitERF</i>	Yes	Yes	Yes	—	—	Yang et al. (2011)
<i>Citrus sinensis</i>	<i>CsERF</i>	Yes	Yes	Yes	—	—	Ma et al. (2014)
<i>Gossypium hirsutum</i>	<i>GhERF1</i>	Yes	Yes	Yes	—	—	Qiao et al. (2008)
<i>G. hirsutum</i>	<i>GhERF2</i>	Yes	Yes	Yes	—	—	Jin et al. (2010)
<i>G. hirsutum</i>	<i>GhERF3</i>	Yes	Yes	Yes	—	—	Jin et al. (2009)
<i>G. hirsutum</i>	<i>GhERF5</i>	Yes	Yes	Yes	—	—	Jin et al. (2010)
<i>G. hirsutum</i>	<i>GhERF6</i>	Yes	Yes	Yes	—	—	Jin et al. (2010)
Soybean ( <i>Glycine max</i> )	<i>GmERF3</i> <sup>a</sup>	Yes	Yes	No	—	—	Zhang et al. (2009)
<i>Jatropha curcas</i>	<i>JcERF1</i>	Yes	Yes	—	—	—	Yang et al. (2014)
Chinese boxthorn ( <i>Lycium chinense</i> )	<i>LchERF</i>	Yes	Yes	—	—	—	Wu et al. (2014a, 2014b)
Common bird's-foot trefoil <i>Lotus corniculatus</i>	<i>LcERF054</i>	Yes	No	—	—	—	Sun et al. (2014a)
<i>L. corniculatus</i>	<i>LcERF080</i>	Yes	—	—	—	—	Sun et al. (2014b)
Alfalfa ( <i>Medicago sativa</i> )	<i>MsERF8</i>	Yes	Yes	—	—	—	Chen et al. (2012)
Tobacco ( <i>Nicotiana tabacum</i> )	<i>JERF1</i> <sup>a</sup>	Yes	Yes	Yes	—	—	Wu et al. (2007)
Tobacco	<i>JERF3</i> <sup>a</sup>	Yes	Yes	Yes	—	—	Wang et al. (2004)
Tobacco	<i>OPBP1</i>	Yes	—	—	—	—	Guo et al. (2004)
Tobacco	<i>OsBIERF3</i>	Yes	—	—	—	—	Cao et al. (2006)
Tobacco	<i>Tsi1</i> <sup>a</sup>	Yes	—	—	—	—	Park et al. (2001)
Tomato ( <i>Lycopersicon esculentum</i> )	<i>LeERF3b</i>	Yes	Yes	Yes	No	Yes	Chen et al. (2008); Severo et al. (2015)
Tomato	<i>TSRF1</i> <sup>a</sup>	Yes	Yes	—	—	—	Zhang et al. (2007)
Tomato	<i>TERF1</i> <sup>a</sup>	Yes	Yes	—	—	—	Gao et al. (2008)
Tomato	<i>LeERF1</i>	Yes	—	—	—	—	Hu et al. (2014)
Tomato	<i>LeERF2</i>	Yes	—	—	—	Yes	Hu et al. (2014); Severo et al. (2015)
Tomato	<i>SIERF5</i>	Yes	Yes	Yes	Yes	—	Pan et al. (2012)
Tomato	<i>ERF A.1</i>	—	—	—	—	Yes	Severo et al. (2015)
Tomato	<i>ERF A.3 (Pti4)</i>	—	—	—	—	Yes	Severo et al. (2015)
Tomato	<i>ERF B.1</i>	—	—	—	—	Yes	Severo et al. (2015)
Tomato	<i>ERF B.2</i>	—	—	—	—	Yes	Severo et al. (2015)
Tomato	<i>ERF B.3 (LeERF4)</i>	—	—	—	—	Yes	Severo et al. (2015)
Tomato	<i>ERF C.6 (ERF5)</i>	—	—	—	—	Yes	Severo et al. (2015)
Tomato	<i>ERF D.1</i>	—	—	—	—	Yes	Severo et al. (2015)
Tomato	<i>ERF D.3</i>	—	—	—	—	Yes	Severo et al. (2015)
Tomato	<i>ERF G.2 (Pti6)</i>	—	—	—	—	Yes	Severo et al. (201)
Tomato	<i>TERF2/LeERF2</i>	—	No	Yes	—	—	Zhang and Huang (2010)
Sugarcane ( <i>Saccharum officinarum</i> )	<i>SodERF3</i>	Yes	—	—	—	—	Trujillo et al. (2008)
Wheat ( <i>Triticum aestivum</i> )	<i>TaERF1</i> <sup>a</sup>	Yes	Yes	Yes	—	—	Xu et al. (2007)
<i>T. aestivum</i>	<i>TaERF3</i>	Yes	Yes	—	—	—	Rong et al. (2014)
<i>Tamarix hispida</i>	<i>ThERF1</i> <sup>a</sup>	Yes	Yes	—	—	—	Wang et al. (2014); Liu et al. (2014)
<i>T. hispida</i>	<i>ThERF5</i>	Yes	Yes	—	—	—	Liu et al. (2014)
<i>T. hispida</i>	<i>ThERF12</i>	Yes	No	—	—	—	Liu et al. (2014)
<i>Triticum turgidum</i>	<i>TdSHN1</i> <sup>a</sup>	Yes	Yes	Yes	—	—	Djermal and Khoudi (2015)

<sup>a</sup>ERFs described as capable of binding to GCC box and DRE elements.

**Table II.** Abiotic stress response studied in transgenic plants overexpressing ERFs

BIERF3, BTH-induced ERF transcriptional Factor3; TERF, Tomato Ethylene Response Factor; SIERF, Tomato Ethylene Response Factor.

Gene	Transgenic Plants	Effect	References
<i>AtERF1</i>	Arabidopsis	Salt, drought, and heat stress tolerance	Cheng et al. (2013)
<i>AtERF4</i>	Arabidopsis	Hypersensitive to salt stress	Yang et al. (2005)
<i>AtERF5</i>	Arabidopsis	Hypersensitive to osmotic stress	Dubois et al. (2013)
<i>AtERF6</i>	Arabidopsis	Hypersensitive to osmotic stress	Dubois et al. (2013)
<i>AtERF98</i>	Arabidopsis	Salt tolerance	Zhang et al. (2012)
<i>BrERF4</i>	Arabidopsis	Salt and drought tolerance	Seo et al. (2010)
<i>CarERF116</i>	Arabidopsis	Osmotic and freezing tolerance	Deokar et al. (2015)
<i>LcERF054</i>	Arabidopsis	Salt tolerance	Sun et al. (2014a)
<i>CaPF1</i>	Arabidopsis	Freezing tolerance	Yi et al. (2004)
<i>CaPF1</i>	Virginia pine ( <i>Pinus virginiana</i> )	Heat and heavy metal tolerance	Tang et al. (2005)
<i>CaPF1</i>	Potato ( <i>Solanum tuberosum</i> )	Drought, freezing, heat, and heavy metal tolerance	Youm et al. (2008)
<i>CaERFLP1</i>	Tobacco	Salt tolerance	Lee et al. (2004)
<i>CsERF</i>	Tobacco	Cold tolerance	Ma et al. (2014)
<i>JERF1</i>	Rice ( <i>Oryza sativa</i> )	Drought tolerance	Zhang et al. (2010)
<i>JERF3</i>	Tobacco	Salt, drought, and freezing tolerance	Wang et al. (2004); Wu et al. (2008)
<i>Tsi1</i>	Tobacco	Salt tolerance	Park et al. (2001)
<i>OPBP1</i>	Tobacco	Salt tolerance	Guo et al. (2004)
<i>TaERF1</i>	Arabidopsis	Salt, drought, and freezing tolerance	Xu et al. (2007)
<i>OsBIERF3</i>	Tobacco	Salt tolerance	Cao et al. (2006)
<i>SodERF3</i>	Tobacco	Salt and drought tolerance	Trujillo et al. (2008)
<i>TERF1</i>	Rice	Salt and drought tolerance	Gao et al. (2008)
<i>TERF1</i>	Tobacco	Salt tolerance	Huang et al. (2004)
<i>MsERF8</i>	Tobacco	Salt tolerance	Chen et al. (2012)
<i>GmERF8</i>	Tobacco	Salt and drought tolerance	Zhang et al. (2009)
<i>JcERF1</i>	Tobacco	Salt tolerance	Yang et al. (2014)
<i>LchERF</i>	Tobacco	Salt tolerance	Wu et al. (2014a)
<i>TSRF1</i>	Tobacco	Negative regulator of salt stress	Zhang et al. (2007)
<i>TSRF1</i>	<i>Zea mays</i>	Salt tolerance	Wang et al. (2013a, 2013b)
<i>TSRF1</i>	Rice	Drought tolerance	Quan et al. (2010)
<i>LeERF1</i>	Tomato	Salt tolerance	Hu et al. (2014)
<i>LeERF2</i>	Tomato	Salt tolerance	Hu et al. (2014)
<i>SIERF5</i>	Tomato	Salt and drought tolerance	Pan et al. (2012)
<i>ThERF1</i>	Arabidopsis	Negative regulator of salt and drought stress	Wang et al. (2014)
<i>TERF2/LeERF2</i>	Tobacco	Freezing tolerance	Zhang and Huang (2010)

and heat stress (Cheng et al., 2013). Interestingly, the affinity of ERF1 for the DRE elements in the promoter of the *P5CS1* was much higher than it was for the GCC box in the promoters of *b-CHI* and *PDF1.2* (Cheng et al., 2013). Other ERFs also specifically bind to both GCC box and DRE elements (Table I). The pepper *ethylene-responsive factor-like protein1* (*ERFLP1*) gene was identified from *Xanthomonas* spp.-infected plants and encodes the *CaERFLP1* protein. *CaERFLP1* showed enhanced expression under salt stress but not cold or drought stress. Overexpression of *CaERFLP1* led to increased salt stress tolerance in tobacco plants (Lee et al., 2004; Table II). Expression of *pathogen and freezing tolerance-related protein1* (*CaPF1*) was induced in plant response to various abiotic stresses, including cold, salt, and drought stress in Arabidopsis. Overexpression of *CaPF1* resulted in enhanced resistance to freezing in Arabidopsis (Yi et al., 2004), and in potato, it resulted in enhanced resistance to freezing, heat, heavy metal, and oxidative stress (Youm et al., 2008). Other examples of ERFs binding to both GCC box and DRE elements include ERF3 from soybean (Zhang et al., 2009); JERF1, JERF3, and tobacco stress-induced protein1 (*Tsi1*) from tobacco

plants (Park et al., 2001; Wang et al., 2004; Wu et al., 2007); *TSRF1* from tomato plants (Zhang et al., 2007); and *SHN1* from wheat (*Triticum durum*; Djemal and Khoudi, 2015), which are all induced by drought, salt, and/or cold stress. A complete list of the TF genes that encode proteins from the ERF subfamily, including those that bind to both GCC box and DRE elements, and are involved in abiotic stress tolerance is given in Table I.

#### ERFs AND HORMONE CROSS TALK

Plant response and adaptation to environmental stresses require the coordinated interaction of hormone signaling pathways to regulate the expression of TF genes that allows the plant to fine tune specific stress responses. Expression of ERFs as downstream components of the ethylene signaling and response pathway can be induced by ethylene as well as biotic and abiotic stresses. Jasmonic acid and ABA have also been reported to be involved in the regulation of ERFs under abiotic stresses. Moreover, ethylene signaling interacts with other plant hormone pathways, such as those regulated by salicylic acid,

**Table III.** Hormonal effects on the transcription of *ERF* genesBRs, Brassinosteroids; GAs, gibberellins; —, not studied; *TERF*, Tomato Ethylene Response Factor; *SlERF*, Tomato Ethylene Response Factor.

Gene	Induced Expression							References
	Ethylene	ABA	Jasmonates	Salicylic Acid	GAs	Auxin	BRs	
<i>AtERF1</i> <sup>a</sup>	Yes	Yes	Yes	—	—	—	—	Cheng et al. (2013)
<i>AtERF4</i>	Yes	Yes	Yes	—	—	—	—	Yang et al. (2005)
<i>BrERF4</i>	Yes	No	Yes	—	—	—	—	Seo et al. (2010)
<i>CaPF1</i> <sup>a</sup>	Yes	Yes	Yes	—	—	—	—	Yi et al. (2004)
<i>CarERF116</i>	Yes	Yes	—	Yes	Yes	—	—	Deokar et al. (2015)
<i>CsERF</i>	Yes	Yes	Yes	Yes	No	No	No	Ma et al. (2014)
<i>GhERF1</i>	Yes	Yes	—	—	—	—	—	Qiao et al. (2008)
<i>GhERF2</i>	Yes	Yes	—	—	—	—	—	Jin et al. (2010)
<i>GhERF3</i>	Yes	Yes	—	—	—	—	—	Jin et al. (2009)
<i>GhERF5</i>	Yes	Yes	—	—	—	—	—	Jin et al. (2010)
<i>GhERF6</i>	Yes	Yes	—	—	—	—	—	Jin et al. (2010)
<i>GmERF3</i> <sup>a</sup>	Yes	Yes	Yes	Yes	—	—	—	Zhang et al. (2009)
<i>JcERF1</i>	Yes	Yes	—	—	—	—	—	Yang et al. (2014)
<i>LchERF</i>	Yes	—	—	—	—	—	—	Wu et al. (2014a)
<i>LcERF054</i>	Yes	Yes	Yes	No	—	—	—	Sun et al. (2014a)
<i>TSRF1</i>	Yes	—	—	Yes	—	—	—	Zhang et al. (2007)
<i>MsERF8</i>	Yes	Yes	Yes	Yes	Yes	Yes	—	Chen et al. (2012)
<i>JERF1</i> <sup>a</sup>	Yes	Yes	Yes	—	—	—	—	Wu et al. (2007)
<i>JERF3</i> <sup>a</sup>	Yes	Yes	Yes	—	—	—	—	Wang et al. (2004)
<i>OPBP1</i>	Yes	—	Yes	No	—	—	—	Guo et al. (2004)
<i>Tsi1</i> <sup>a</sup>	Yes	No	Yes	Yes	—	—	—	Park et al. (2001)
<i>TERF1</i> <sup>a</sup>	Yes	—	—	—	—	—	—	Gao et al. (2008)
<i>SlERF5</i>	Yes	Yes	No	No	—	—	—	Pan et al. (2012)
<i>SodERF3</i>	Yes	Yes	Yes	No	—	—	—	Trujillo et al. (2008)
<i>TaERF1</i> <sup>a</sup>	Yes	Yes	—	Yes	—	—	—	Xu et al. (2007)

<sup>a</sup>ERFs described as capable of binding to GCC box and DRE elements.

gibberellins, and brassinosteroids, during plant adaptation to abiotic stresses. Indeed, exogenous application of these phytohormones has led to induced expression of a number of *ERF* genes (Table III). However, the molecular transduction mechanisms underlying pathway cross talk are still only partly understood.

### Jasmonates

Lorenzo et al. (2002) have reported that *ERF1* is a downstream component of not only the ethylene but also, the jasmonate signaling pathway in Arabidopsis. Lorenzo et al. (2002) observed that *ERF1* expression can be induced rapidly by ethylene and jasmonic acid as well as synergistically by both hormones, and they suggested that *ERF1* acts as a key element in the regulation of ethylene/jasmonic acid-dependent defense response genes (Lorenzo et al., 2002). Recent studies using the jasmonic acid-insensitive mutant *jasmonic acid amido-synthetase1-1* exposed to drought, salt, and heat stress revealed blocked *ERF1* expression, indicating that *ERF1* induction requires jasmonic acid as well as ethylene signaling under a number of abiotic stresses (Cheng et al., 2013). Ethylene/jasmonic acid signaling is also required in the induction of other *ERFs* to a number of abiotic stresses; examples of these *ERFs* include *ERF6* (Sewelam et al., 2013), *JERF1* (Wu et al., 2007, 2008), *JERF3* (Wang et al., 2004), *Tsi1* (Park et al., 2001), *OPBP1* (Guo et al., 2004) and *GmERF3* (Zhang et al., 2009).

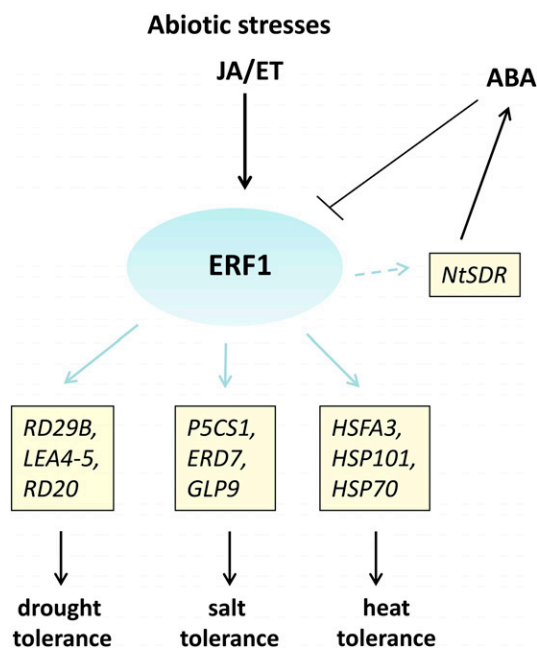
### ABA

ABA plays an important role in the response of plants to abiotic stresses, such as drought, salinity, and extreme temperatures. *ERF1* overexpression has been observed to enhance drought, salt, and heat stress resistance in Arabidopsis plants accompanied with increased levels of ABA and Pro (Cheng et al., 2013). As an osmolite, Pro contributes to stress tolerance because its accumulation may prevent water loss. ABA has been reported to partially modulate Pro accumulation (Sharma et al., 2011). However, ABA negatively regulates *ERF1* induction as shown in the ABA-hypersensitive *abi1* and *abi2* knockout mutants. Nevertheless, in the constitutive ethylene signaling mutant *ctr1*, *ERF1* expression was even higher than in wild-type plants after ABA treatment. This indicates that ethylene/jasmonic acid signaling could not be blocked by the negative effect of ABA (Cheng et al., 2013). ABA treatment also repressed the expression of *ERF6* in Arabidopsis (Sewelam et al., 2013).

In contrast to *ERF1* and *ERF6*, other *ERF* genes have been reported to be induced by ABA, including *CsERF* (Ma et al., 2014), *GmERF3* (Zhang et al., 2009), *LchERF* (Wu et al., 2014a), *JERF3* (Wu et al., 2008), *TSRF1* (Quan et al., 2010), *TaERF1* (Xu et al., 2007), and *JERF1* (Wu et al., 2007). In addition, plants overexpressing *TaERF1* were found to be highly sensitive to exogenous ABA treatment, resulting in rapid stomatal closure (Xu et al.,

2007). Interestingly, *JERF1* overexpression also increased leaf and root growth of tobacco significantly under salinity and low temperature accompanied by increased ABA levels (Wu et al., 2007). *JERF1* was found to interact with multiple cis-acting elements and may activate both stress-responsive and ABA biosynthesis-related genes (such as *tobacco short-chain dehydrogenase/reductase [NtSDR]*), resulting in enhanced tolerance to salinity and cold stress in tobacco (Wu et al., 2007). Also, *TSRF1* overexpression in tobacco enhanced expression of the ABA biosynthesis-related gene *NtSDR*, resulting in increased ABA contents. Moreover, overexpression of *TSRF1* in tobacco plants resulted in enhanced drought tolerance and increased Pro contents (Quan et al., 2010; Cheng et al., 2013). Complex interaction signaling between ABA, ethylene, and ERF proteins, such as ERF1, *JERF1*, and *TSRF1*, seems to regulate ABA biosynthesis; however, ABA also acts as a negative regulator of *ERF1* gene induction (Cheng et al., 2013). Interestingly, all three ERF proteins can bind to both GCC box and DRE elements and induce salt, heat, drought, and cold tolerance (Table I). A model for ethylene, jasmonic acid, and ABA cross talk through ERF1 under abiotic stress is shown in Figure 2.

Some proteins from the ERF subfamily can also act as negative regulators, such as *AtERF4* and *AtERF7*,



**Figure 2.** Proposed model for ethylene (ET), jasmonic acid (JA), and ABA cross talk through ERFs under abiotic stress. ERF1 induces expression of genes involved in abiotic stress tolerance. It has been postulated that, through the activation of *JERF1* and *TSRF1* (ERFs from the same ERF subfamily), ERF1 activates expression of *NtSDR*, an ABA biosynthesis-related gene. In turn, ABA might down-regulate *ERF1* expression under abiotic stress. However, the negative effect of ABA does not seem to block ET/JA signaling. *LEA4-5*, *Late-Embryogenesis Abundant Protein4-5*; *HSFA3*, *Heat-Shock Transcription Factor A3*; *HSP101*, *Heat-Shock Protein101*.

which are localized in the nuclear bodies and modulate ABA responses. Induced *AtERF4* expression has been reported to make plants less sensitive to ABA, inhibit the expression of genes that are responsive to ABA, and confer hypersensitivity to salt stress in Arabidopsis (Yang et al., 2005). It has been suggested that *AtERF7* activation inhibits the expression of genes induced by ABA, thereby decreasing tolerance to drought stress (Song et al., 2005).

### Other Hormones

Salicylic acid has long been known to play a role in the induction of defense mechanisms in plants; however, recent studies revealed that it participates in abiotic stress signaling (Stevens et al., 2006; Horváth et al., 2007). It has been revealed that salicylic acid signaling enhances salt and oxidative stress tolerance in Arabidopsis by the induction of the *NONEXPRESSER OF PATHOGENESIS RELATED1 (NPR1)* gene (Jayakannan et al., 2015). Upon pathogen infection, ethylene is known to enhance salicylic acid/NPR1-dependent defenses through the ethylene signaling and response pathway (Leon-Reyes et al., 2009). Salicylic acid treatment induced expression of the ethylene TF genes *AtERF6* (Sewelam et al., 2013), *TaERF1* (Xu et al., 2007), *TSRF1* (Huang et al., 2004), *MsERF8* (Chen et al., 2012), *GmERF3* (Zhang et al., 2009), and *CarERF116* (Deokar et al., 2015), whereas expression of *SodERF3* (Trujillo et al., 2008) and *CsERF* (Ma et al., 2014) was reduced by salicylic acid.

Recently, *ERF6* has been reported to be involved in cross talk between the ethylene and gibberellin/DELLA pathway. *ERF6* expression inhibits leaf growth by activating the transcription of the *GIBBERELIN2-OXIDASE6* gene, resulting in inactivation of gibberellins by DELLA stabilization under osmotic stress conditions in Arabidopsis (Dubois et al., 2013). However, the rapid *ERF6* activation was found to be independent of EIN3/EIL1. It has been shown that *ERF6* is activated by a mitogen-activated protein kinase cascade, including MITOGEN-ACTIVATED PROTEIN KINASE3 (MPK3)/MPK6. Phosphorylation of *ERF6* by MPK3/MPK6 in gain-of-function transgenic plants increases *ERF6* protein stability in vivo (Dubois et al., 2013; Meng et al., 2013).

Brassinosteroids have been found to mediate thermotolerance and salt tolerance and induce expression of several hormone-responsive genes, such as *PDF1.2*, suggesting cross talk between brassinosteroids and the ethylene, jasmonic acid, ABA, and salicylic acid signaling pathways (Divi et al., 2010). In *Citrus* spp. plants, expression of the *CsERF* gene was neither induced nor reduced after treatment with brassinosteroids, auxin, and gibberellin 3 (Ma et al., 2014). In contrast, gibberellin 3 treatment induced expression of both the *CaERF116* and *MsERF8* genes (Chen et al., 2012; Deokar et al., 2015).

### ERFs AND REDOX SIGNALING

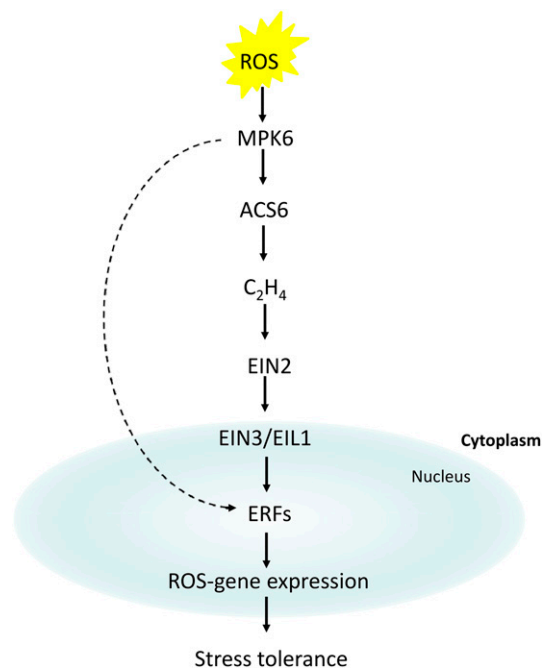
The reactive oxygen species (ROS) signaling network controls a broad range of biological processes,

including biotic and abiotic stress responses, by activating defense genes (Mittler et al., 2011). ROS, such as  $^1\text{O}_2$ , hydrogen peroxide,  $\text{O}_2^-$ , and  $\bullet\text{HO}$ , are molecules that are considered to be both signaling and potentially damaging molecules (Iqbal et al., 2014). Salinity, drought, and cold stresses enhance ROS production, which results in an imbalance between ROS production and ROS scavenging (Miller et al., 2010). Antioxidants, such as ascorbic acid, glutathione, carotenoids, and tocopherols, as well as enzymes, such as superoxide dismutase, ascorbate peroxidase, catalase, and glutathione peroxidase, play an essential role in ROS scavenging mechanisms (Apel and Hirt, 2004; Munné-Bosch et al., 2013). Moreover, Pro plays a potential role in ROS detoxification because it is typically accumulated in response to osmotic stress (Sharma et al., 2011). Extracellular ROS, which are produced by peroxidases and NADPH oxidases, can transmit intracellular signals rapidly to the nucleus and/or amplify signals passing from the chloroplast to the cell nucleus through the action of secondary messengers, such as mitogen-activated protein kinases and plant hormones. Therefore, the TFs activated by ROS result in the transcription of a large number of genes (Miller et al., 2010; Munné-Bosch et al., 2013).

Oxidative stress treatment induced *ERF1* expression (Sewelam et al., 2013), and overexpression of *ERF1* leads to Pro accumulation and induces expression of *P5CS1* (Cheng et al., 2013). This, in turn, catalyzes the first step of Pro synthesis, resulting in enhanced drought tolerance in *Arabidopsis* (Cheng et al., 2013). This result suggests, on the one hand, that *ERF1* might regulate ROS signaling and on the other hand, that Pro accumulation seems to be a common response of ERFs to stress. This is, indeed, documented for the majority of TFs from the ERF subfamily that enhance abiotic stress tolerance, such as *JERF1* (Zhang et al., 2010), *TSRF1* (Quan et al., 2010), *GmERF3* (Zhang et al., 2009), *Tomato Ethylene-Response Factor5* (Pan et al., 2012), *CsERF* (Ma et al., 2014), *JcERF1* (Yang et al., 2014), *LeERF1*, *LeERF2* (Hu et al., 2014), *MsERF8* (Chen et al., 2012), *LcERF054*, *LcERF080* (Sun et al., 2014a, 2014b), *LchERF* (Wu et al., 2014a), and *TaERF3* (Rong et al., 2014). Overexpression of *LeERF1*, *LeERF2*, and *MsERF8* has been reported to elevate Pro accumulation and reduce malondialdehyde levels, an indicator of lipid peroxidation, in tomato and tobacco plants under salt stress (Cheng et al., 2013; Hu et al., 2014). Tang et al. (2005) have reported that overexpression of *CaPF1* enhances biotic and abiotic stress tolerance in transgenic Virginia pine by regulating antioxidant enzyme activities. This result coincides with that for transgenic potato plants that overexpress *CaPF1* and were more tolerant after oxidative stress treatment than control plants (Youm et al., 2008). *AtERF98* has been reported to enhance salt tolerance by regulating the expression of ascorbate biosynthesis genes, resulting in reduced ROS levels in *Arabidopsis* (Zhang et al., 2012). *JERF3* regulates the expression of ROS-related genes, such as *SUPEROXIDE DISMUTASE*, *ASCORBATE PEROXIDASE1* (*APX1*), *NtAPX2*, and *GLUTATHIONE PEROXIDASE* in tobacco plants, resulting in

decreased accumulation of ROS and enhancing tolerance to drought, salt, and freezing (Wu et al., 2008). *ERF6* shows highly induced expression under oxidative stress treatment, such as hydrogen peroxide, and high light stress. Up-regulation of ROS-responsive gene expression analyzed in *erf6* mutants revealed that *ERF6* seems to be a negative regulator of ROS-responsive gene expression. In contrast, several antioxidant enzymes, such as *MONO-DEHYDROASCORBATE REDUCTASE3*, *CATALASE3*, and *VITAMIN C DEFECTIVE2*, showed down-regulation in *erf6* mutants, indicating that *ERF6* is a positive antioxidant regulator under biotic and abiotic stresses (Sewelam et al., 2013). Wang et al. (2013a) reported that *ERF6* can bind specifically to the ROS-responsive cis-acting element7 (*ROSE7*)/GCC box, and enhances high light tolerance given that *ROSE7*-type genes showed no activation in *erf6-1* mutants under high light stress.

So far, little is known about the involvement of ROS signaling in the activation of ERFs. The MAPK cascade is well known to play an important role in ROS signaling. Ethylene synthesis is known to be positively regulated by the MPK6-mediated phosphorylation of *ACC SYNTHASE2* (*ACS2*) and *ACS6* (Liu and Zhang, 2004). Recently, several studies revealed that *ERF6* is activated independently of *EIN3/EIL1* by *MPK6* phosphorylation, resulting in ROS-responsive gene expression in *Arabidopsis* (Dubois et al., 2013; Meng et al., 2013; Sewelam et al., 2013; Wang et al., 2013b). It is



**Figure 3.** Proposed model for ROS signaling to ERFs. Biotic and abiotic stresses enhance ROS production, resulting in the activation of *MPK6*, which activates ethylene biosynthesis by phosphorylation of *ACS6*. Then, *EIN2*, *EIN3/EIL1*, and finally, *ERF1* are activated, which could result in the activation of ROS gene expression that enhances stress tolerance. Recently, it has been suggested that *ERF6* is activated by *MPK6* phosphorylation independently of *EIN3/EIL1* under oxidative stress.

hypothesized that inactive ERF6 is kept at a basal level and can be rapidly phosphorylated, thereby reducing the time lag in transcriptional activation (Dubois et al., 2013; Fig. 3).

ERFs may also play a role in linking redox and hormonal regulation in plant responses to abiotic stresses. Tocopherols, which belong to the vitamin E group of compounds, are lipid-soluble antioxidants found in the chloroplasts. Photosynthetic tissues accumulate  $\alpha$ -tocopherol in chloroplasts and to a lesser extent, its immediate precursor  $\gamma$ -tocopherol. *ERF1* expression in the  $\gamma$ -tocopherol methyltransferase (*vte4*) mutant, which is deficient in  $\alpha$ -tocopherol but accumulates  $\gamma$ -tocopherol, was reduced in parallel with lower jasmonic acid levels in the *vte4* mutant compared with the wild type (Cela et al., 2011). These results indicate that  $\gamma$ -tocopherol represses jasmonic acid and ethylene signaling and response pathways in salt-stressed *vte4* plants, thus suggesting a link between redox and hormonal signaling in the regulation of *ERF1* expression in Arabidopsis. In another example of retrograde signaling from the chloroplast to the nucleus, Vogel et al. (2014) found that *ERF6*, *ERF104*, and *ERF105* expression was rapidly (within 1 min) up-regulated upon exposure to high light in Arabidopsis. This response was deregulated in triose phosphate translocator (*tpt*) mutants. Similarly, activation of MPK6 was up-regulated after 1 min in the wild type but not in the *tpt* mutant (Vogel et al., 2014). Vogel et al. (2014) propose that metabolite export through the *tpt* in the chloroplast leads to subsequent MPK6 activation and *ERF* gene expression in the nucleus, therefore representing an additional mechanism of chloroplast to nucleus retrograde signaling.

## CONCLUSION AND PROSPECTS

Molecular genetic studies have been pivotal in dissecting the ethylene signaling and response pathway. New insights from recent years have revealed that ERFs regulate not only biotic but also, abiotic stress responses. Thus, overexpression of a number of *ERFs* enhances salt, drought, light stress, and cold and heat tolerance as well as pathogen resistance in Arabidopsis plants. Ethylene, jasmonic acid, and ABA have been reported to be involved in the regulation of *ERFs* under abiotic stresses. For instance, *ERF1* is involved in both ethylene and jasmonic acid signaling pathways. Moreover, plants that overexpress *ERF1* enhance ABA levels under drought stress, indicating that *ERF1* may regulate ABA biosynthesis. However, ABA negatively regulates *ERF1* induction. Furthermore, induced *ERF* expression under oxidative stress suggests that ERFs might regulate ROS-responsive gene expression, thereby conferring stress tolerance. Because of the fact that many stresses act hand in hand with each other and not in isolation, it is clear that there is cross talk between biotic and abiotic stress responses. The specific binding activity of several ERFs to both GCC box and DRE elements depending on the stress conditions supports this hypothesis. There are still, however, many gaps in

our knowledge on ERFs and hormonal cross talk, and the answers to remaining questions are important to increase our understanding of stress adaptation. Alongside the cross talk with jasmonic acid and ABA, the cross talk between ERFs and auxin, cytokinin, gibberellin, salicylic acid, and brassinosteroid responses should be studied in more detail. ERFs seem to regulate ROS-responsive gene expression, but more evidence of synergistic ERFs- and ROS-responsive genes is needed.

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