

AP2/ERF transcription factor gene families in crop plant disease responses

ABSTRACT

Biotic stresses include the infestation of crops by an array of pathogenic microbes like bacteria, viruses, fungi, nematodes, and insect pests. Pathogenic microbes have always threatened crop plants and their produce. With the growing global population and changing environmental conditions, there is a need for crops that can tolerate stress. Over the years, significant progress has been made in elucidating the functional role of the major transcription factors (TFs) families in plant disease resistance. Among the TFs, members of the APETALA2/ethylene response factor (AP2/ERF) family have emerged as pivotal regulators of plant growth, development, and responses to environmental stresses. Recent research has highlighted the crucial roles of AP2/ERFs in plant immunity, demonstrating their involvement in various mechanisms of disease resistance. They influence immune responses by modulating hypersensitive responses, and stomatal immunity, and by serving as virulence targets for pathogen effectors. This review offers a comprehensive overview of the current understanding of AP2/ERF transcription factors in defense responses to microbial pathogens to plant disease resistance by acting downstream of mitogen-activated protein kinase (MAPK) cascades. It also emphasizes recent developments and outlines future research directions aimed at enhancing disease resistance.

Keywords: AP2/ERFs, transcription factors, biotic stress, disease resistance, secondary metabolites, transactivation, ROS, HR, PR protein

1. INTRODUCTION

Biotic stress encompasses the negative impacts of pathogens, pests, and weeds on plant growth, development, and overall productivity. Pathogens, such as bacteria, fungi, viruses, and nematodes, lead to plant diseases that decrease both yield and quality. Additionally, pests like insects, mites, and mammals damage plants by feeding on their tissues and facilitating the spread of infections [1]. Collectively, they account for about 20–30% of the annual loss in agriculture [2]. In response to biotic stress, plants have evolved defense mechanisms that trigger a range of signal perception and transduction pathways. These pathways involve the activation of protein kinases or phosphatases, stimulation of downstream target proteins, and the production of phytohormones. The interaction between these signaling networks tightly

regulates the expression of stress-responsive genes, protecting various biotic challenges [3]. The ongoing evolutionary pressure and the constant threat of pathogenic microbes have driven crops to develop various morphological, physiological, and molecular defenses, to counteract microbial attacks. One such mechanism involves the regulation of pathogenesis-related (PR) genes, which are upregulated or downregulated in response to pathogen attack, influencing downstream processes to reduce crop damage. In general, plant immunity and defense genes can be categorized into three main groups: metabolomics, protein kinases, and transcription factors (TFs) [4].

TFs are regulatory proteins that bind specifically to *cis*-regulatory elements in the promoter regions of genes, resulting in activation or suppression of gene expression [5]. Generally, these TFs have DNA binding domains (DBD) and activation domains (AD) or repressor domains (RD) in their sequences [6]. TFs show sequence specificity and bind to conserved DNA elements (or motifs) present in the promoter sequence of the concerned gene [7]. On the other hand, the AD or RD of TF mediates positive or negative modulation of genes, and hence the TFs are classified as transactivators or transrepressors. In other words, TFs also act as the on/off switch of gene expression, thereby regulating their function. The transcription and translation of genes encoding transcription factors (TFs) occur in distinct cellular locations, with transcription taking place in the nucleus and translation in the cytoplasm. After translation, TFs are transported back into the nucleus through the membrane-bound nucleoporin complex, where they search for their target sequences in the genomic DNA. As a result, they are often referred to as diffusible regulatory molecules (DRM) [8].

2. MOLECULAR MECHANISMS OF PLANT-PATHOGEN INTERACTIONS

The interaction mechanism between plants and pathogens is crucial for understanding how plant immune systems operate, which is essential for advancing disease-resistance breeding. Research has shown that plants have developed sophisticated immune systems in their ongoing battle with pathogens. Plant immunity can be categorized into two primary layers. The first layer involves the immune response triggered by pathogen-associated molecular patterns (PAMPs), known as PAMP-triggered immunity (PTI). This layer consists of immune responses initiated by pattern recognition receptors (PRRs) on the surface of plant cells, which detect PAMPs. In turn, pathogens employ various tactics to evade PTI, such as

secreting toxic effectors. In response, plants have developed nucleotide-binding leucine-rich repeat (NLR) proteins that monitor and inhibit the activity of these effectors, thereby strengthening their resistance. This layer of immunity is referred to as effector-triggered immunity (ETI) [9]. The ETI activates multiple stress responses, including the hypersensitive response (HR). HR involves the localized death of host cells at the infection site, serving to limit the spread of the pathogen. This response is marked by rapid and localized cell death, which not only disrupts metabolic processes in surrounding cells but also initiates systemic acquired resistance (SAR). SAR is a broad, non-specific defense mechanism that enhances the plant's ability to resist a range of pathogens [10]. Besides ROS and HR, other immune responses triggered in PTI and ETI include mitogen-activated protein kinase (MAPK)-cascades, activation of membrane-localized ion channels, increased cytoplasmic calcium ions (Ca^{2+}), phytohormone production, and transcriptional reprogramming of defense genes. The mounting of defense response requires tight regulation and co-ordination between the two interconnected branches of host immunity, i.e., PTI and ETI [11]. The recognition of pathogens by cell membrane-anchored pattern recognition receptors (PRRs) triggers a cascade of intracellular signaling events, involving molecules and ions such as calcium ions (Ca^{2+}), nitric oxide (NO), and reactive oxygen species (ROS). While ROS are recognized for their ability to damage biomolecules, including proteins, DNA, and lipids, they also play a critical role as signaling molecules, regulating various physiological processes and mediating plant responses to pathogen attacks [12]. Thus, the regulatory nature of the TFs makes them key targets in developing disease-free plants.

3. AP2/ERF TFs, FEATURE AND THEIR CLASSIFICATION

The AP2/ERF transcription factor family is a large, plant-specific group of transcription factors that play key roles in regulating plant growth, development, and responses to biotic and abiotic stress. Individual members of this group are characterized by the presence of a conserved 60-70 amino acid (aa) long AP2/ERF domain that is responsible for recognizing and binding to *cis*-regulatory elements in target genes [13,14]. More specifically, arginine and tryptophan residues within the β -sheet of the AP2/ERF domain are pivotal for DNA binding [15]. Alanine and aspartic in the DNA binding domain of ERF proteins are located on the β -sheet in the DNA binding domain, which determines the DNA binding affinity and

specificity of the two subfamilies (Fig. 1). In plants, the first AP2/EREB domain-containing protein was identified in the model plant *Arabidopsis thaliana* [16]. The AP2/ERF superfamily is traditionally classified into four main subfamilies: AP2, ERF, RAV (RELATED TO ABSCISIC ACID INSENSITIVE 3/VIVIPAROUS 1), and Soloist, based on the number of AP2/EREB domains and their respective biological functions [17]. Members of the RAV and ERF subfamilies typically possess a single AP2/EREB domain, whereas AP2 family members generally contain two (Fig. 2). RAV family members are characterized by the presence of both a single AP2/EREB domain and an additional DNA-binding domain, the B3 domain (Fig. 2). Additionally, within the ERF subfamily, members are further subdivided into two groups, ERF and CBF/DREB (C-repeat-binding factor/dehydration-responsive element-binding protein), based on conserved amino acid residues within their DNA-binding domains (Fig. 2) [18]. These transcription factors (TFs) play a crucial role in the regulation of plant responses to biotic stress, as well as in mediating phytohormone signaling and their associated crosstalk. Generally, AP2/ERF TFs function as either transactivators or repressors, modulating the transcription of target genes through sequence-specific binding to their promoter regions. The DREB subgroup within the AP2/ERF family recognizes the conserved core sequence A/GCCGAC in the promoters of stress-responsive genes, thereby regulating their expression. In contrast, TFs from the ERF subgroup bind to the GCC-box (AGCCGCC), a core sequence involved in the modulation of genes that govern biotic stress responses [19].

4. AP2/ ERF TFs PATHWAY IN REGULATING PLANT DISEASE RESISTANCE

AP2/ERF TFs are key regulators of plant disease resistance, mediating responses to both biotic and abiotic stresses. These TFs, particularly from the ERF and DREB subfamilies, function by binding to specific DNA sequences in the promoters of defense-related genes, modulating their expression. ERF TFs, activated by ethylene (ET), jasmonic acid (JA), and salicylic acid (SA) signaling, regulate genes involved in resistance to biotrophic pathogens through the GCC-box. DREB TFs, on the other hand, are involved in responses to necrotrophic pathogens. Crosstalk between these phytohormones and AP2/ERF TFs enhances plant immune responses, including pattern-triggered immunity (PTI) and effector-triggered immunity (ETI), by promoting the expression of defense-related proteins and antimicrobial compounds. Thus, AP2/ERF TFs play a central role in orchestrating plant resistance to pathogens.

4.1 AP2/ERFs in MAPK Cascades-Mediated Plant Disease Resistance

Mitogen-activated protein kinase (MAPK)-mediated signaling pathways are highly conserved across eukaryotes. In plants, MAPKs typically function downstream of sensors or receptors that detect either endogenous signals (e.g., peptide ligands) or exogenous stimuli (e.g., PAMPs and environmental factors), thereby regulating plant growth, development, and immune responses [14, 20]. Upon activation, MAPKs phosphorylate various downstream targets, including protein kinases, transcription factors (TFs), structural proteins, and enzymes, to initiate cellular responses [21].

4.2 Integration of AP2/ERF with Hormone Responses

Salicylic acid (SA), jasmonic acid (JA), and ethylene (ET) are key phytohormones involved in plant defense, with SA primarily defending against biotrophic pathogens and JA/ET regulating immunity against necrotrophic pathogens and herbivores [22]. Although SA and JA/ET typically have antagonistic effects, they can also synergize in responses to viral infections in rice [23].

5. APPLICATION OF AP2/ERF TFs IN CROP PLANT DISEASE RESPONSES

The AP2/ERF family consists of approximately 163 members in rice and 62 in wheat, playing crucial roles in regulating responses to both biotic and abiotic stresses [24]. One key member, OsEREBP1, functions downstream in a signaling pathway activated upon rice interaction with the bacterial blight pathogen *Xanthomonas oryzae*. Overexpression of *OsEREBP1* induces the expression of genes involved in lipid metabolism, including lipase and chloroplastic lipoxygenase, as well as genes associated with jasmonate and ABA biosynthesis. Additionally, GFP-tagged OsEREBP1 has been shown to localize to plastid nucleoids [25]. While the involvement of AP2/ERF proteins in herbivore-induced defense responses remains poorly understood, the striped stem borer (*Chilo suppressalis*), a major herbivore pest of rice, could provide insights into this aspect of plant defense. A study by Lu et al. suggests that the expression of *OsERF3* in rice is rapidly upregulated in response to feeding by the striped stem borer (*Chilo suppressalis*) and that *OsERF3* plays a role in mediating resistance to *C. suppressalis* [26]. However, the role of the AP2 transcription factor in biotic stress remains unclear. In wheat, *TaAP2-15*, an AP2 transcription factor, is localized to the nucleus of both *Nicotiana benthamiana* and wheat cells. Virus-induced gene silencing (VIGS) of *TaAP2-15* using barley stripe mosaic virus (BSMV) increased wheat susceptibility to *Pseudomonas syringae* (Pst). Expression analysis of pathogenesis-related genes, *TaPR1* and *TaPR2*, revealed downregulation, while genes involved in reactive oxygen

species (ROS) scavenging, such as *TaCAT3* and *TaFSOD3D*, were upregulated. These findings collectively confirm the involvement of *TaAP2-15* in wheat resistance to *Pst* [27].

A class II ERF transcription factor, *SIERF3*, was identified in tomatoes and characterized for its role in resistance to *Ralstonia solanacearum*. Overexpression of *SIERF3* significantly impacted tomato plant growth. To investigate its function in biotic stress resistance, the ERF-associated amphiphilic repression (EAR) domain of *SIERF3* was deleted, and the truncated protein (*SIERF3ARD*) was overexpressed in transgenic tomato plants. These plants exhibited elevated expression of *PR1*, *PR2*, and *PR5* genes and demonstrated enhanced resistance to *R. solanacearum* compared to control plants [28]. Additionally, a novel transcription factor, *GmERF3*, belonging to the AP2/ERF family, was isolated from soybean (*Glycine max*). This transcription factor contains a 58-amino-acid AP2/ERF domain and two nuclear localization signal motifs. A GAL4-based assay in yeast confirmed *GmERF3* as a transactivator, and localization studies showed its presence in the nucleus of onion epidermal cells. Furthermore, ectopic expression of *GmERF3* in tobacco plants induced the expression of pathogenesis-related (*PR*) genes, enhancing resistance against *R. solanacearum*, *Alternaria alternata*, and tomato mosaic virus (TMV) [29].

Dong et al. reported the positive role of soybean *GmERF5* in response to root and stem rot diseases caused by *Phytophthora sojae*. Transgenic soybean plants overexpressing *GmERF5* demonstrated enhanced resistance to the pathogen, accompanied by induced expression of *PR10*, *PR1-1*, and *PR10-1*. *GmERF5* is the first identified ERF transcription factor (TF) from soybean containing an EAR motif, highlighting its crucial role in pathogen infection response [30]. Similarly, an ERF gene, *GmERF113*, was identified for its induced expression during *P. sojae* infection in the resistant soybean cultivar ‘Suinong 10’. When *GmERF113* was overexpressed in the susceptible cultivar ‘Dongnong 50’, the transgenic plants exhibited significantly improved resistance to the pathogen. The overexpression lines also showed upregulated expression of *PR1* and *PR10-1*, suggesting the involvement of *GmERF113* in biotic stress responses [31]. In another study, Tian et al. demonstrated that potato *StERF3*, which contains an EAR domain at its C-terminus, negatively regulates potato resistance to *Phytophthora infestans*. Localization studies revealed that *StERF3* is predominantly localized in the nucleus. Additionally, bimolecular fluorescence complementation (BiFC) assays showed that physical interactions between *StERF3* and certain cytoplasmic proteins can redirect its localization to both the cytoplasm and nucleus. Silencing *StERF3* in potato plants significantly enhanced resistance to *P. infestans*, while

overexpression lines exhibited compromised resistance. Silenced plants also showed elevated expression of defense-related genes, including *PR1*, *NPR1*, and *WRKY1* [32]

A yeast one-hybrid approach was employed to isolate *NtERF5*, a transcription factor (TF) from the AP2/ERF family in *Nicotiana tabacum*. In this assay, *NtERF5* exhibited weak binding to the GCC-box present in the promoters of various pathogenesis-related genes. The expression of *NtERF5* was found to be induced in response to infections with *Pseudomonas syringae* and tobacco mosaic virus (TMV). Interestingly, while overexpression of *NtERF5* did not enhance plant resistance to *P. syringae*, it significantly restricted the spread and size of local hypersensitive response lesions caused by TMV infection. In the *NtERF5*-overexpressing lines, only 10–30% of viral mRNA accumulation was observed compared to wild-type plants. These findings suggest that *NtERF5* regulates the expression of genes involved in plant resistance to TMV infection and viral propagation [33].

Citrus canker, a devastating disease of sweet orange caused by the bacterial pathogen *Xanthomonas citri* subsp. *citri* (Xcc), leads to significant global crop losses. The citrus AP2/ERF family TF *CsAP2-09* localizes to the nucleus, and its expression is upregulated in wild-type citrus plants infected with Xcc. In *CsAP2-09*-overexpressing lines, a substantial reduction in disease lesions and disease index was observed. Conversely, RNAi-mediated silencing of *CsAP2-09* resulted in a marked increase in these parameters, suggesting an active role of *CsAP2-09* in the plant's defense response to Xcc infection [34]. Additional details on AP2/ERF family transcription factors involved in crop plant immunity are summarized in Table 1.

6. CONCLUSION

Pathogenic microorganisms represent a persistent threat to crop plants, contributing to significant reductions in yield that necessitate effective management strategies. The use of cultivars with host resistance is the most effective and cost-efficient strategy to minimize these losses. Transcription factors (TFs), as key regulators of defense-related genes, are promising candidates for crop improvement. Several TF families, including AP2/ERF, have been extensively studied for their roles in plant defense. These TFs are being incorporated into various plant species and economically important crops via genetic engineering to

improve resistance to biotic stresses. Based on the above, we anticipate the following future research directions for AP2/ERF transcription factors: With the advancements in structural biology, the crystallographic structures of many proteins have been resolved. Future studies on AP2/ERF transcription factors will likely leverage these technologies to identify and summarize the specific three-dimensional structural features associated with disease resistance by analyzing the crystallographic characteristics of AP2/ERF proteins involved in regulating disease resistance. Despite progress, several challenges remain in fully understanding the role of AP2/ERF genes in disease resistance responses, necessitating a multidisciplinary research approach. This overview highlights AP2/ERF TFs, with the potential, to enhance biotic stress tolerance, offering valuable insights for plant biotechnology. These findings could lead to novel, strategies for sustainable agriculture and food security, ultimately improving crop productivity amid evolving environmental challenges.

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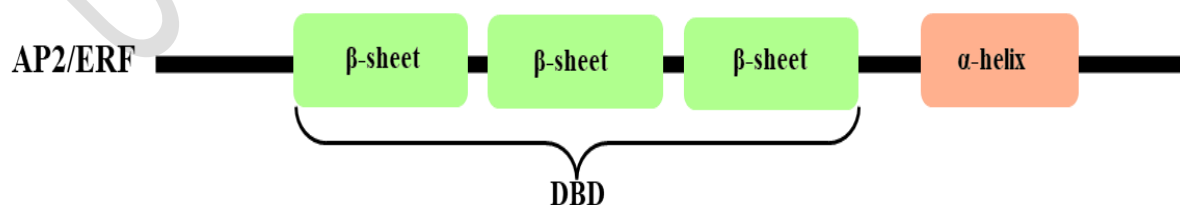


Fig. 1. Schematic representation of various transcription factors. DBD, DNA binding domain; AP2, apetala 2 domain.

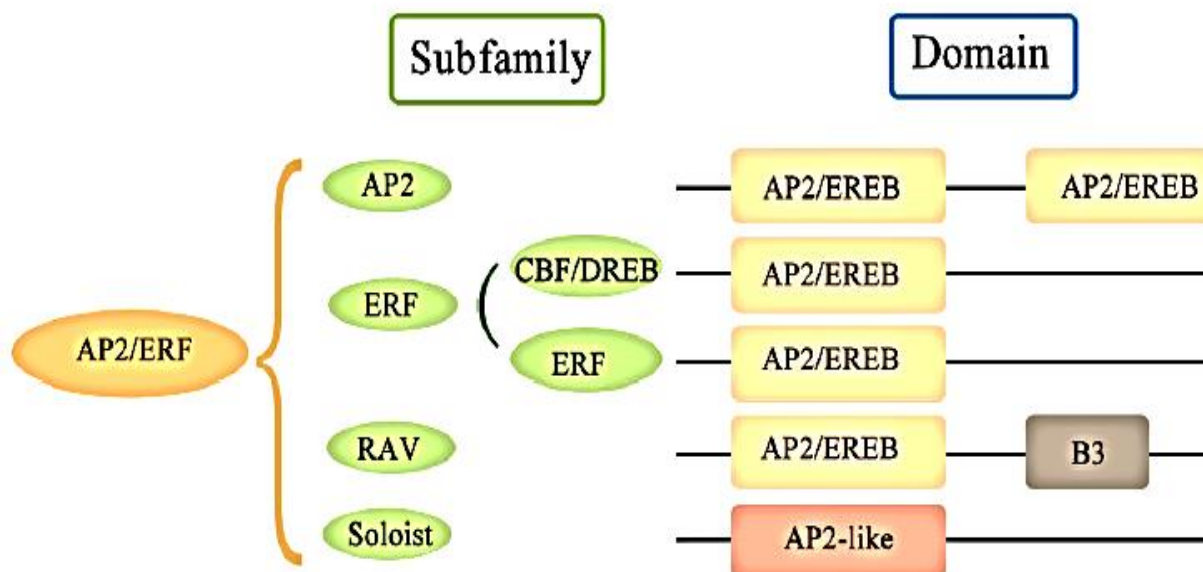


Fig. 2. Schematic representation of the domain structures in different AP2/ERF family members. The positions and quantities of domains across various AP2/ERF types are illustrated. AP2, APETALA2; ERF, ethylene response factors; RAV, RELATED to ABSCISIC ACID INSENSITIVE 3/VIVIPAROUS 1; DREB, dehydration-responsive element-binding protein [14].

Table 1: List of AP2/ERF transcription factors gene families in crop plant disease response.

Crop	Pathogen	Disease	Gene	Defense responses	Reference
Rice	Bacterial	Bacterial blight (<i>Xanthomonas oryzae</i>)	<i>OsEREBP1</i>	MAPK	25
	Insect	Striped stem borer (<i>Chilo suppressalis</i>)	<i>OsERF3</i>	SA/JA/ET	26
Wheat	Fungal	Stripe/Yellow rust (<i>Puccinia striiformis</i> f. sp. <i>tritici</i>)	<i>TaAP2-15</i>	SA/JA	27

		Common root rot (<i>Bipolaris sorokiniana</i>)	<i>TaPIEP1</i>	JA/ROS	35
Tomato	Bacterial	Bacterial wilt (<i>Ralstonia solanacearum</i>)	<i>SlERF3, SlERF5</i>	SA/JA	28, 36
	Fungal	Rhizopus soft rot (<i>Rhizopus nigricans</i>)	<i>SlERF1</i>	JA/SA	37
		Gray leaf spot (<i>Stemphylium lycopersici</i>)	<i>SlERF1</i>	JA/SA	38
		Septoria leaf spot (<i>Septoria lycopersici</i>)	<i>SlERF2</i>	SA/JA/ROS	39
Soybean	Bacterial	Bacterial wilt (<i>Ralstonia solanacearum</i>)	<i>GmERF3</i>	JA/ROS	29
	Fungal	Root rot (<i>Phytophthora sojae</i>)	<i>GmERF5, GmERF113</i>	MAPK	30,31
Potato	Fungal	Late blight (<i>Phytophthora infestans</i>)	<i>StERF3</i>	SA/JA/ROS	32
Tobacco	Viral	Tobacco mosaic virus (TMV)	<i>NtERF5</i>	SA/JA	33
Pepper	Bacterial	bacterial spot of pepper (<i>Xanthomonas campestris</i> pv. <i>vesicatoria</i>)	<i>RAV1</i>	SA	40