AP2/ERF transcription factors in crop plants disease resistance response

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, the APETALA2/ethylene response factor (AP2/ERF) family members have emerged as pivotal regulators of plant growth, development, and responses to environmental stresses. AP2/ERF transcription factors are key regulators of plant disease resistance, integrating pathogen signals to mediate salicylic acid (SA), jasmonic acid (JA), and ethylene (ET) pathways, activate defense genes, enhance ROS production, and modulate cell wall defenses for effective immune responses. They influence immune responses by modulating hypersensitive reactions, and by serving as virulence targets for pathogen effectors. By enhancing defense responses, AP2/ERF TFs contribute to developing genetically improved crops with increased resistance to biotrophic and necrotrophic pathogens, thereby reducing crop losses and improving yield stability under disease pressure. 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 to enhance 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 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 regulating 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].

Transcription factors (TFs) are regulatory proteins that specifically bind to cis-regulatory elements located within the promoter regions of genes, thereby modulating gene expression through activation or repression [5]. Structurally, TFs typically consist of a DNA-binding domain (DBD) and either an activation domain (AD) or a repressor domain (RD), which mediate their regulatory activity [6]. The DBD confers sequence specificity, enabling TFs to recognize and bind to conserved DNA motifs in the promoter regions of target genes [7]. The AD or RD further dictates the functional role of the TF by facilitating transcriptional activation or repression, classifying TFs as transactivators or transrepressors, respectively.

TFs function as molecular regulators of gene expression, effectively acting as on/off switches for transcriptional processes. Their biosynthesis involves distinct cellular compartments: transcription of TF-encoding genes occurs in the nucleus, while translation of the corresponding mRNA takes place in the cytoplasm. Post-translationally, TFs are imported into the nucleus via the nucleoporin complex, where they scan genomic DNA for their specific binding sites. This ability to translocate between compartments and regulate gene expression at specific loci supports their classification as diffusible regulatory molecules (DRMs) [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]. In addition to reactive oxygen species (ROS) production and the hypersensitive response (HR), plant immune responses activated during pattern-triggered immunity (PTI) and effector-triggered immunity (ETI) encompass mitogen-activated protein kinase (MAPK) cascades, activation of membrane-localized ion channels, elevated cytoplasmic calcium ion (Ca^{2+}) concentrations, phytohormone biosynthesis, and extensive transcriptional reprogramming of defense-related genes. The orchestration of these defense responses necessitates precise regulation and coordination between the two interconnected branches of plant immunity, PTI and ETI [11].

Pathogen recognition by cell membrane-anchored pattern recognition receptors (PRRs) initiates a complex cascade of intracellular signaling events. These events involve key signaling molecules and ions, including calcium ions (Ca^{2+}), nitric oxide (NO), and ROS. Although ROS are widely recognized for their cytotoxic potential due to their capacity to damage proteins, nucleic acids, and lipids, they also serve as pivotal signaling molecules. ROS regulates diverse physiological processes and mediates plant responses to biotic stress, including pathogen invasion [12]. The regulatory function of transcription factors (TFs) within these signaling networks underscores their critical role as molecular mediators in plant immunity. Consequently, TFs represent promising targets for engineering disease-resistant plant varieties.

3. AP2/ERF TFs, FEATURE AND THEIR CLASSIFICATION

“The AP2/ERF transcription factor family represents a large, plant-specific group of transcriptional regulators that play critical roles in modulating plant growth, development, and responses to biotic and abiotic stresses. Members of this family are defined by the presence of a conserved AP2/ERF domain, a 60–70 amino acid (aa) motif responsible for the recognition and binding of cis-regulatory elements in target gene promoters” [13,14]. “Within the AP2/ERF domain, arginine and tryptophan residues located in the β-sheet are essential for DNA binding, while alanine and aspartic acid residues further influence DNA-binding specificity and affinity, differentiating the ERF subfamilies” (Fig. 1) [15].

“The first AP2/ERF domain-containing protein was identified in *Arabidopsis thaliana*, a model plant species [16]. Based on the number of AP2/ERF domains and distinct biological functions, the AP2/ERF superfamily is traditionally divided into four primary subfamilies: AP2, ERF, RAV (RELATED TO ABSCISIC ACID INSENSITIVE 3/VIVIPAROUS 1), and Soloist” [17]. Members of the ERF and RAV subfamilies typically harbor a single AP2/ERF domain, whereas AP2 family members generally contain two AP2/ERF domains (Fig. 2). Unique to the RAV subfamily is the presence of an additional DNA-binding motif, the B3 domain, enhances their regulatory specificity (Fig. 2). Within the ERF subfamily, further classification divides members into the ERF and CBF/DREB (C-repeat-binding factor/dehydration-responsive element-binding protein) groups, based on conserved amino acid residues in their DNA-binding domains (Fig. 2) [18]. This structural and functional diversity underscores the central role of the AP2/ERF family in fine-tuning gene expression in response to developmental cues and environmental signals.

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" [20]. 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, 21]. "Upon activation, MAPKs phosphorylate various downstream targets, including protein kinases, transcription factors (TFs), structural proteins, and enzymes, to initiate cellular responses" [22].

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 [23]. Although SA and JA/ET typically have antagonistic effects, they can also synergize in response to rice viral infections [24].

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 [25]. 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 [26]. 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* [27]. 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* [28].

A class II ERF transcription factor, *SlERF3*, was identified in tomatoes and characterized for its role in resistance to *Ralstonia solanacearum*. Overexpression of *SlERF3* significantly impacted tomato plant growth. To investigate its function in biotic stress resistance, the ERF-associated amphiphilic repression (EAR) domain of *SlERF3* was deleted, and the truncated protein (*SlERF3ΔRD*) 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 [29]. 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) [30].

Dong et al. highlighted the pivotal role of the soybean transcription factor GmERF5 in conferring resistance to root and stem rot diseases caused by *Phytophthora sojae*. Overexpression of GmERF5 in transgenic soybean lines led to heightened resistance against the pathogen, which was accompanied by increased expression of defense-related genes, including *PR10*, *PR1-1*, and *PR10-1*. Notably, GmERF5 was identified as the first soybean ERF transcription factor containing an EAR motif, underscoring its significance in the response to pathogen infection [31].

In another study, the ERF gene *GmERF113* was found to exhibit increased expression during *P. sojae* infection in the resistant soybean cultivar 'Suinong 10'. Overexpressing *GmERF113* in the susceptible cultivar 'Dongnong 50' markedly enhanced pathogen resistance in transgenic plants. This resistance was associated with the upregulation of defense-related genes such as *PR1* and *PR10-1*, suggesting that *GmERF113* plays a key role in soybean responses to biotic stress [32].

Additionally, research by Tian et al. identified the negative regulatory role of the potato transcription factor *StERF3*, which contains an EAR domain at its C-terminus, in defense against *Phytophthora infestans*. Subcellular localization studies revealed that *StERF3* predominantly resides in the nucleus, but bimolecular fluorescence complementation (BiFC) assays demonstrated its interaction with specific cytoplasmic proteins, resulting in dual localization in the cytoplasm and nucleus. Silencing *StERF3* in potato plants significantly enhanced resistance to *P. infestans* and led to increased expression of defense genes such as *PR1*, *NPR1*, and *WRKY1*. Conversely, overexpression of *StERF3* compromised resistance to the pathogen [33].

"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 gene expression in plant resistance to TMV infection and viral propagation" [34].

"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" [35]. 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. Advances in structural biology have enabled the resolution of crystallographic structures for numerous proteins. Future research on AP2/ERF transcription factors is expected to harness these technologies to explore and characterize the specific three-dimensional structural features associated with disease resistance, focusing on the crystallographic properties of AP2/ERF proteins that regulate this process. 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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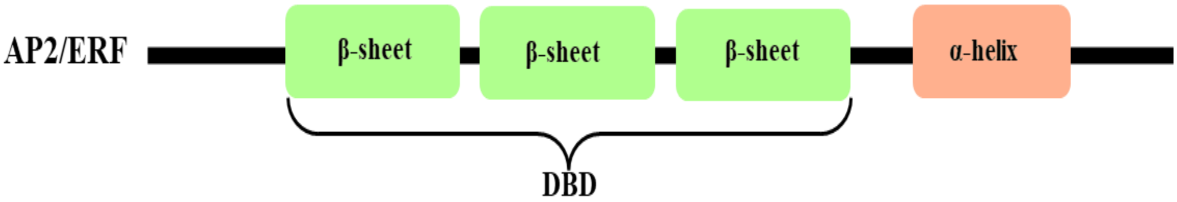

Fig. 1. Schematic representation of various transcription factors. DBD, DNA binding domain; AP2, apetala 2 domain.

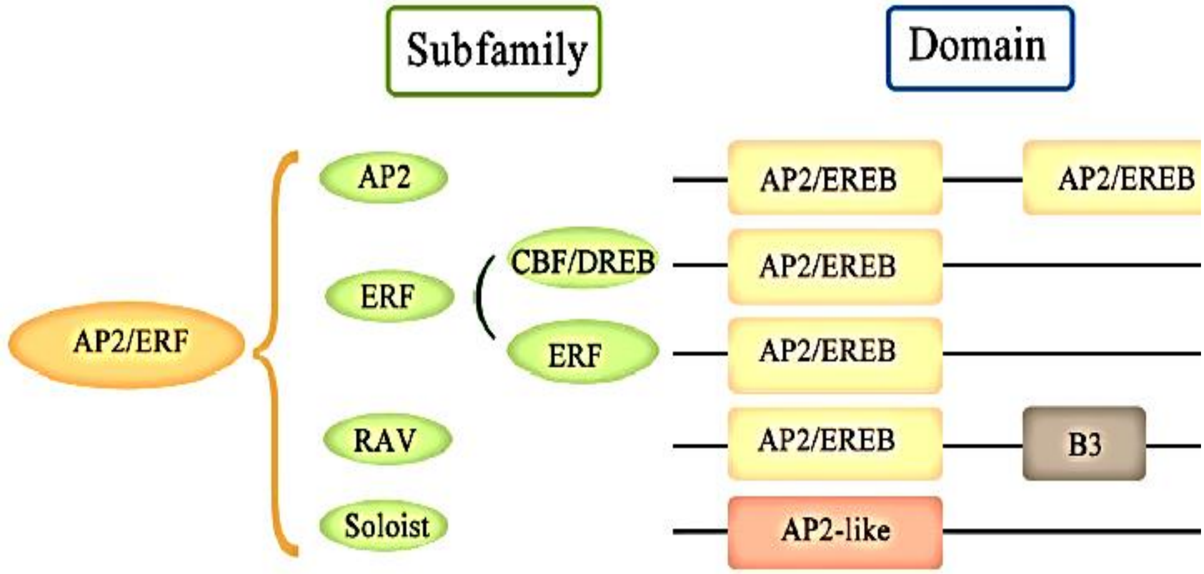

Fig. 2. Schematic illustration of domain architectures in different members of the AP2/ERF transcription factor family. The figure depicts the distribution and number of domains characteristic of different AP2/ERF subfamilies. Abbreviations: AP2, APETALA2; ERF, ethylene response factor; RAV, RELATED 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 (*Xanthomonas oryzae*)	*OsEREBP1*	MAPK	26
	Insect	Striped stem borer (*Chilo suppressalis*	*OsERF3*	SA/JA/ET	27
Wheat	Fungal	Stripe/Yellow rust (*Puccinia striiformis* f. sp. *tritici*)	*TaAP2-15*	SA/JA	28
		Common root rot (*Bipolaris sorokiniana*)	*TaPIEP1*	JA/ROS	36
Tomato	Bacterial	Bacterial wilt (*Ralstonia solanacearum*)	*SlERF3*, *SlERF5*	SA/JA	29, 37
	Fungal	Rhizopus soft rot (*Rhizopus nigricans*)	*SlERF1*	JA/SA	38
		Gray leaf spot (*Stemphylium lycopersici*)	*SlERF1*	JA/SA	39
		Septoria leaf spot (*Septoria lycopersici*)	*SlERF2*	SA/JA/ROS	40
Soybean	Bacterial	Bacterial wilt (*Ralstonia solanacearum*)	*GmERF3*	JA/ROS	30
	Fungal	Root rot (*Phytophthora sojae*)	*GmERF5*, *GmERF113*	MAPK	31,32
Potato	Fungal	Late blight (*Phytophthora infestans*)	*StERF3*	SA/JA/ROS	33
Tobacco	Viral	Tobacco mosaic virus (TMV)	*NtERF5*	SA/JA	34
Pepper	Bacterial	Bacterial spot of pepper **(***Xanthomonas campestris* pv. *vesicatoria***)**	*RAV1*	SA	41

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