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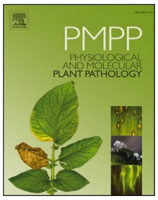

Regulation of *Capsicum* immunity against microbial pathogens: Transcription factors in focus

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ABSTRACT

Induction of stress-related genes is primarily reckoned as a major step in plant responses to any stress. The plant genomes possess multiple types of transcription factors (TFs) belonging to diverse families and many of them are unique to plants. The TFs are regulators of transcriptional reprogramming linked with stress responses in plants. TF gene(s) frequently retorts to numerous stresses and then their respective polypeptides may contribute in the positive or negative regulation of apparently dissimilar processes. Many plant TFs are induced by biotrophic as well as necrotrophic pathogens. Functional characterization of TFs provides solid evidence of their role in the regulation of plant defense responses. This advocates the fact that TF does not work alone, but the immune response to pathogens mediated by it, is strongly linked to enhancing the effect of TF on the transcription of defense associated genes. The plant-plant difference in transcriptional responses of TF and Defense associated genes highlights that a TF may regulate defense positively or negatively. This diversity in responses is proof of functional diversity among TFs. Their functions in plant immunity and abiotic stress tolerance in plants have been characterized but still need investigations in *Capsicum annuum*. This article focuses upon recent progress in our understanding of the role of the TFs involved in *Capsicum* defense against Microbial pathogenesis especially against bacterial pathogens. We have dissected collateral interactions between TFs, proteins and nuclear receptors working for *Capsicum* defense. Besides, we have also reviewed and discussed the topical concepts of transcriptional intervention for controlling the activity of TFs.

1. Introduction

Plant stress-tolerance to abiotic and biotic stresses is controlled by multifarious signaling cascades [1]. Significant overlaps among gene expression patterns during different stress conditions reveal the induction of genes individually as well as collectively. This coordinated induction of genes and regulation of plant responses unveil complex regulatory mechanisms, necessary for survival in changing environment [2,3]. Induction of stress-related genes primarily takes place at the transcriptional level and is reckoned as a major step in plant responses to any stress [4]. Therefore, plant genomes are blessed with multiple types of transcription factors (TFs), belonging to diverse gene families and many of them are unique to plants [5]. The *TFs* regulate transcriptional reprogramming, linked with stress responses in plants [6]. Any

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alteration in expression patterns of these genes or function helps us to elucidate a diverse range of signaling cascades and regulatory networks. For example, a single *WRKY/Zinc finger protein/bZIP*/MYB TF gene frequently retorts to numerous stresses, and then, their respective polypeptides may contribute in the positive or negative regulation of dissimilar processes [7–11]. TF proteins may function through protein-protein interactions as well as auto- or cross-regulation. These particular attributes help in understanding the TF-regulated multifaceted mechanisms of signaling and transcriptional reprogramming. For instance, overexpressing *ORCA3* increased the relative expression level of many metabolite biosynthetic genes and enhanced accrual of alkaloids [12].

In the case of plant-pathogen interaction, pathogen-associated molecular patterns (PAMPs) are perceived by plant receptors and trigger PAMP-triggered immunity (PTI). Contrarily, some bacterial pathogens deliver effector proteins into plant cells which interfere PTI [13]. Consequently, the residual defense becomes inadequate to tackle pathogens. These effectors can be precisely recognized by plant resistance (R) proteins and result in effector-triggered immunity (ETI) [14,15]. This ETI comprises of multifaceted defense program inclusive of reactive oxygen species (ROS) production, hypersensitive responses (HR) and induction of defense genes [16,17]. Many plant TFs are induced by bio- and necro-trophic pathogens as well. Functional characterization of many TFs provides solid evidence of their participation in the regulation of plant defense responses. For example, *AtERF1* augmented the resistance to necro-trophic fungi [18]. *AtMYB30* activates HR like cell death against pathogen attack. *AtMYB44* and *CabZIP63* positively regulate plant resistance to aphids [19] and *Ralstonia solanacearum* [20], respectively. Likewise, many WRKY-TFs also contribute positively or negatively in plant defense [8,9,21–23].

Capsicum annuum is an important horticultural crop [24] that is vulnerable to different pathogens, especially bacterial and fungal pathogens, and disease aggravates under high temperature and humidity. Different TFs has been characterized for their role in pepper immunity to pathogens [25–29], but many of them are still not characterized. Most of the differences in expression, molecular cloning and functional characterization of TFs have confirmed their involvement in plant defense against diseases. Hence, the cellular mechanisms for tackling infection, transcriptional reprogramming, gene expression and biosynthesis of metabolic mediators are of substantial concern. Interactive partners of TFs and transcriptional machinery is of immense significance in the *trans*-activation and regulation of transcription for appropriate immune responses. Molecular observation of function(s) and regulation of TFs is central in the understanding of plant defense regulation and can offer novel therapeutic approaches for different plant diseases. This review focuses on recent progress in our understanding of the role of the TFs, involved in plant defense against microbial pathogenesis. We have discussed collateral interactions between TFs, proteins and nuclear receptors working for plant defense, we have also reviewed the topical concepts of transcriptional intervention for controlling the activity of

Table 1

Different Capsicum transcription factors take part in imparting resistance to bacterial pathogens. These TFs are induced by different molecules and are localized to various locations inside plant cell.

TF Family	TF Type	Role in defense	Induced by	Subcellular localization	Reference
bZIP	*CabZIP1*	Regulate enhanced disease resistance e.g. *Pseudomonas* and environmental stress tolerance	ET, SA, MeJA, Pathogen Infection, Abiotic elicitors and Environmental stresses	Nucleus	[58,153]
	CabZIP2	*Overexpression enhanced resistance to Pseudomonas syringaea cv. tomato*	SA, MeJA, ET	Cytoplasm	[58,154]
	PPI1	PPI1 regulate expression of plant defense-related genes against attack of *Pseudomonas syringae* pv. syringae 61, and *Xanthomonas campestris* pv. vesicatoria	pathogen attack	Nucleus	[155]
	bZIP2	It is positive regulator of immunity against *Xanthomonas campestris* pv. vesicatoria	pathogen attack, salicylic acid, methyl jasmonate, and ethylene	Nucleus, Cytoplasm	[58,154]
	bZIP63	Its silencing impaired pepper resistance to bacterial pathogen.	Ralstonia attack	Nucleus	[20,58]
ERF	pCaERFLP1	OE of pCaERFLP1 in tobacco rendered plants more resistant to *Pseudomonas syringae* and higher tolerance to high salinity	Pathogen attack, Ethylene,		[29]
	ERFLP1	Positive regulator of genes in salt tolerance and defence against pathogens. In transgenic tobacco plants, ectopic expression of gene resulted in enhanced tolerance against *Pseudomonas syringae*	ethylene, mechanical wounding and high salinity.	Nucleus	[29]
	PTI1	Its expression improved pepper defense against *P. capsici* by enhancing expression of defense linked genes.	SA, MeJA, ETH	Not determined	[27]
WRKY	WRKY1	VIGS-induced silencing of *CaWRKY1* in pepper reduced growth of *Xanthomonas axonopodis* pv *vesicatoria* race 1. OE of CaWRKY1 in tobacco accelerated HR cell death in response to *TMV* and *Pseudomonas syringae* pv. tabaci, and resulted also in higher bacterial growth.	Salicylic acid	Nucleus	[156]
	WRKY27	OE of *CaWRKY27* in tobacco showed enhanced resistance to *Ralstonia solanacearum.*	SA, MeJA, ETH	Nucleus	[157]
	WRKY40	OE of *CaWRKY40* in tobacco enhanced resistance to *Ralstonia solanacearum*. Silencing of Ca*WRKY40* in pepper enhanced susceptibility to *R. solanacearum*.	SA, JA, ET, Ralstonia	Nucleus	[158]
	CaWRKY58	OE of *CaWRKY58* in tobacco enhanced susceptibility to *Ralstonia solanacearum*. Silencing of *CaWRKY58* in pepper by VIGs enhanced resistance to the highly virulent *R. solanacearum* strain FJC100301.	Suppressed by JA	Nucleus	[159]
	CaWRKYd	TRV-based VIGS revealed that silencing of CaWRKYd reduced HR cell death upon infection with TMV-Po and resulted in enhanced accumulation of TMV-Po coat protein locally and systemically.	SA, MeJA	Nucleus	[160]
ZNF	*CaPIF1*	Overexpression *CaPF1 improve* resistance towards *Pst* infection and stronger tolerance towards freezing temperature	ethephon, SA	Nucleus	[161, 162]
	CaRFP1	Its expression mainly support plant defense against *X. campestris* pv. Vesicatoria and *Pseudomonas syringae*	SA, MeJA	Not determined	[163]
	Rma1H1	It is important in pepper responses to abiotic stresses.	Abiotic stresses	Endoplasmic reticulum and plasma membrane	[164]
	CaZNF830	Its silencing impaired pepper defense and tolerance to thermal stress.	SA	Nucleus	[11]
	C3H14	Virus induce gene silencing reduced pepper resistance to *Ralstonia incoculation*	SA	Nucleus	[165]

TFs (Table 1).

1.1. WRKY-TFs

WRKY proteins in higher plants are the TFs, containing a characteristic zinc-finger possessing one or two amino acid containing WRKY domains. For example, the WRKY gene family comprises of 72 and 109 members in Arabidopsis and Rice, respectively. Based on their primary structure, we can divide WRKY-TFs into three main groups (I, II and III) as well as some subgroups, e.g. IIa, IIb [8,23,30–32]. Commonly, WRKY-TFs perform their function as transcriptional regulators by binding the W-box in the promoter region, associated with defense actions [33,34]. Nevertheless, many other evidences propose targeting of other promoter elements, i.e. WK-box, sugar responsive *cis*-element by WRKY-TFs [35]. WRKY-TFs participate in endorsing resistance to biotic as well as abiotic stresses (Fig. 1, Table 1) [23,36–41]. Other than involvement in stress responses, many WRKY-TFs coordinate different biological processes [42]. For instance, *GhWRKY15* is strongly involved in growth and development [43], *AtWRKY34* and *ATWRKY2* are needed for male gametogenesis [44], *GmWRKY58* is crucially involved in flowering [45] while *AtWRKY70* regulates immune responses and enhance senescence [46]. Such multidimensional functions of WRKY-TFs propose them as a central point in the crosstalk between diverse physiological processes. But, the roles of the many WRKY-TF family members in signaling crosstalk and physiological activities demand extensive research, particularly in non-model plants.

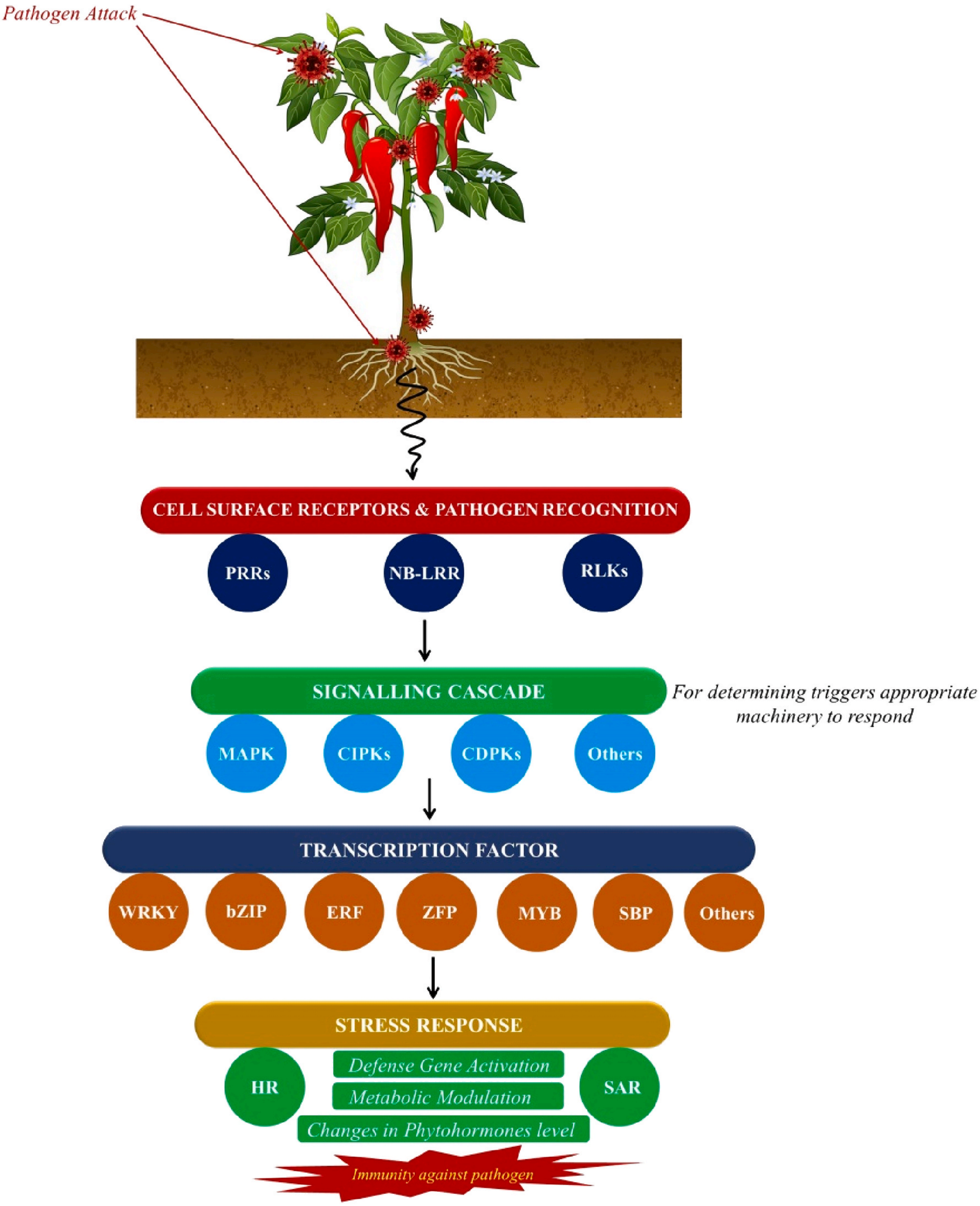

Fig. 1. Pathogen attack and cellular response with the help of TFs.

Several reports have confirmed the involvement of WRKY-TFs in defense responses to multi types of stresses [8,23,40,46,47]. Induction of expression of many WRKY genes by microbial pathogenesis [48] and insect herbivory [49] reveals their significance in plant defense actions. For instance, *CaWRKY40* is induced by *R. solanacearum* and its silencing compromises pepper immunity. Its overexpression in transgenic *Nicotiana benthamiana* suggests positive regulation of resistance against *R. solanacearum* attack [50]. During defense responses, many PR- and HR-related genes perform the function of defense marker for the ongoing biological condition of the plant. Actions of these defense-associated genes are triggered by plant pathogens [51]. It has been observed that relative expression levels of HR- and PR-associated genes, e.g. *HSR201, PR1a* and *CHN50* is directly linked with overexpression and loss of *CaWRKY40* [50]. This advocates the fact that *CaWRKY40* does not work alone but the immune response to *Ralstonia* mediated by it, strongly linked to enhancing effect of TF on the transcription of defense genes. This plant-plant difference in responses of TFs and defense-associated genes highlights that a TF may not precisely mimic the defense-linked function of an endogenous ortholog of such TF, e.g. positive and negative regulation of defense. The reduction in transcript levels of negative growth regulators by TF(s) avoids unnecessary defense expenditures. Taking aid from existing reports, it is apparent that *AtWRKY25* and *AtWRKY33* perform role against stresses negatively and positively to *P. syringae* attack and salinity, respectively [21,42,46,47]. An ortholog of *WRKY40* in Capsicum, *WRKY40b* is a negative regulator of defense response against *Ralstonia*. This negative regulation of pepper defense was supported by downregulation of many plant defense positive regulator genes such as *RLK1*, *EIN3*, *FLS2*, *CNGIC8*, and *CDPK13* [9]. It simply means that *CaWRKY40b* works as repressor rather than as activator. This advocates the assumption that WRKY-TFs work in the form of a network. The function of *CaWRKY40b* significantly resembles to *AtWRKY33* [22]. Besides, the enrichment of *CaWRKY40b* promoter with just like the promoters of *CaWRKY6* and *CaWRKY40* indicates the involvement of these TFs in a WRKY-web for regulating *Capsicum annum* immunity against *R. solanacearum*.

Likewise, several reports have proven that a sole TF may retort to unlike stresses and play a role in numerous contrasting signaling pathways. The role of *CaWRKY40* in *Capsicum* response to high-temperature stress and *Ralstonia* attack [50] is the best example. This advocates extensive crosstalk between immunity and thermo-tolerance signaling pathways [7,50,52]. Several other genes and TFs in different plant species also contribute to such signaling crosstalks [7,53–55]. Pathogen invasion also induces endogenous production of phytohormones such as Salicylic Acid (SA), Jasmonic Acid (JA) and Ethylene (ET). The defense responses are strictly dependent upon the production of phytohormones and type of recognized pathogen [56]. The qRT-PCR analysis revealed up-regulation of *CaWRKY30* after the attack of various pathogens, including *Meloidogyne incognita*, Tobacco mosaic virus (TMV), *R. solanacerum*, and *P. capsici*. The rapid accumulation of *CaWRKY30* transcripts after exogenous application of SA shows a significant contribution of phytohormones in the regulation of plant defense [57]. The downregulation of expression of *CaWRKY30* with methyl jasmonic acid (MeJA) [57] further substantiates the finding that SA is particularly important for regulating defense against bio-trophic pathogens. Therefore, it can be inferred that *CaWRKY30* might take part in plant defense responses to diverse pathogens infection. The induction of WRKY-TFs by phytohormones and related defense responses highlights crucial collaboration for plant survival.

1.2. Basic leucine zipper domain (bZIP)

The TFs having one basic leucine zipper domain (*bZIP*) are recognized as universal plant TF family [58]. The *bZIP*-TFs possess a *bZIP* domain consisting of 40–80 amino acid residues with two motifs. The basic region is required for binding of TF to its target DNA whilst the leucine zipper is essential for TF dimerization [59,60]. The *bZIP*-TFs are very significant contributors in the plant life cycle by controlling different processes such as seed development, tissue differentiation, cell elongation, floral maturity, energy metabolism and signaling, and immunity responses [10,60–65]. Among different plant species, *bZIP*-TFs, e.g. *bZIP2, bZIP*23, *CabZIP*63 have been recognized for their role in modulation of biotic and abiotic stress responses (Table 1; Fig. 1) [66,67]. *bZIP*-TFs execute substantial roles in controlling the plant defense actions in the form of a cohort network. Nonetheless, the precise roles of many pathogen-responsive *bZIPs* along their coordination with *bZIP* and other TFs taking part in plant defense regulation need to be focused particularly in non-model plants.

CabZIP53 is a *bZIP*-TFs family member in pepper and transcriptionally up-regulated by *Ralstonia* attack or heat stress. This is evidence that *CabZIP53* is a positive regulator of pepper defense against biotic and abiotic stress. Generally, it is on record that up-regulation of genes in plant-one stress interaction might play a role even in case of plant interaction with other stresses simultaneously of non-simultaneously [10,68]. The virus-induced gene silencing (VIGS) of *CabZIP53* enhanced the susceptibility of *Capsicum* plants to *Ralstonia* and reduced thermo-tolerance by down-regulating the defense and thermo-tolerance linked marker genes, like *NPR1*, *DEF1*, *HSP24*, *ABR1* [20,25,69]. Likewise, the transiently over-expressing *CabZIP53* triggered HR along with the incremented expression of defense marker genes [10]. Correspondingly, *CabZIP25* highly expressed in vegetative tissues after phytohormones treatment. Transgenic *Arabidopsis thaliana* plants overexpressing *CabZIP25* displayed comparative increase in germination, biomass and chlorophyll contents as compared to wild type and *CabZIP25*-silenced plants under salt stress [26]. The observed increase in chlorophyll content under salinity due to *OE-CabZIP25* plants provides the tolerance reason. For supporting our stance about multi-functionality of pepper *bZIPs*, we argue that not only biotic stresses but *bZIPs* also regulate pepper responses to abiotic stresses, e.g. *CabZIP*, *CaBZ1*, *CaAIBZ1* [26,70,71]. Our opinion is that *bZIPs* and other TFs employ different regulatory approaches, and therefore, present a different manner of regulation.

Shen et al. [20] reported *CabZIP63* as a positive regulator of pepper immunity against bacterial pathogen and thermo-tolerance. The evidence suggests a partly redundant role for *CabZIP53* and *CabZIP63* because of loss of function for both exhibit obvious phenotypic impacts on defense or thermo-tolerance in pepper. Hetero- or homo-dimerization is necessary for DNA-binding and transcriptional regulation by *bZIP* [72,73]. This protein-protein interaction for *bZIP* can be the best support by its interaction with *NPR1* and *TGA* factors mediating the expression of PR1 [74]. *bZIPs* can also make feedback loops with other TFs to mediate defense response, i.e. *CabZIP53-CaWRKY40*. Similarly, *CaWRKY40* is transcriptionally regulated by *CaWRKY6* and *CabZIP63* but also modulated indirectly by *CaCDPK15* genes and confirming feedback loops positively in pepper genome [10,20,25]. We argue that the presence of many regulators in the transcriptional webs supports transcriptional reprogramming of genes and also trigger quick defense responses. The corroboration of data from earlier reports [75] advocates our stance that positive feedback relations are natural and help plants in signaling and responses.

1.3. Zinc Finger Proteins transcription factors (ZNF)

Zinc Finger Proteins are ranked among the most crucial TF family performing diverse functions for plants. Their functions in plant immunity and abiotic stress tolerance in plants have been characterized but still need investigations in pepper [76–79]. A pepper ZNF-TF, i.e. *ZNF830* positively regulates pepper responses pathogen attack and heat stress. This nucleus localized TF shows homology with ZNF-TFs in different plants based on the presence of C_2H_2 type conserved amino acid sequence. The promoter of this TF possesses heat shock element (HSE), G-boxes and W-box that helps in inferring its possible transcriptional actions against microbial attack and high-temperature stress.

The silencing of *CaZNF830* constantly enhances pepper vulnerability to bacterial pathogenesis and heat stress. Parallel with this, increments in pathogen growth and disease index were observed as compared to non-silenced pepper plants. Contrastingly, transiently over-expressing *ZNF830* significantly activated HR like cell death along with high Ion leakage and H_2O_2 accumulation. These physical phenotypes in non-silenced plants were supported by up-regulated defense marker genes such as *HIR1 PR1*, *NPR1 ABR1* and *HSP24* and vice versa [11]. This provides an insight into crosstalk showing regulatory potential for coordination of the plant responses to multiple stresses and prioritizing immunity reactions over other metabolic events, Besides many other ZNFs in different plant species like *ZFP1* in *C. annuum* [80], and tandem zinc finger protein in *A. thaliana* [81], are strongly involved in defense actions. While *VOZ2* [82], *ZAT6* [83] and *ZAT12* [84–86] significantly perform functions against stress. *CaC3H14* is a positive regulator of pepper immunity to *Ralstonia* and its regulation requires *CaWRKY40* [77]. Its transient overexpression increased HR like cell death and conferred resistance to the pathogen. The up-regulation defense marker genes in transiently overexpressing *CaC3H14* and vice versa in VIGS plants confirmed the role of this TF in pepper defense (Table 1). The up-regulation of *CaC3H14* revealed the modulation of the interaction between SA and JA/ET signaling in antagonistic fashion [77]. An interesting feature exhibited by *CaZFP1* is its constitutive expression in pepper stem, roots and flowers while no transcript level in leaves and fruit. It helps us to build opinion that *CaZFP1* would be involved in early defense responses. Later studies involving the localization of these TF-transcripts in phloem cells against *Colletotrichum* infection prove its role in biotic stress resistance [87]. Likewise, *CaPF1* overexpressing transgenic pine plants not only protect plant cells from oxidative damage but also improve the cell size and number [88]. *LOL1* in *Capsicum chinensis* influences fruit color development and chlorophyll variations. Transcripts of *CaRZFP1* are responsive to high-temperature stress that shows its role as TF in red pepper [89].

The crosstalk and defense priority functions of TFs are supported by earlier discussed data in case of WRKY- and *bZIP*-TFs., e.g. *WRKY25* [82, 83] and *WRKY33* [82,84–86] that positively regulates plant immunity and thermos-tolerance. The available information about positive regulation of plant resistance to biotic and abiotic stresses display plant capacity to handle frequent interactions with stress conditions. The same fact supports pepper tolerance to these stresses because pepper evolution took place under the combined pressure of pathogens and high temperature and humidity. Moreover, induction of *TFs by* stresses and their corresponding functions represent triggering of at least some dissimilar signaling pathways for dealing with stresses. During this response, growth may be affected just to save metabolic expenditures and to provide more metabolic resources to machinery combating stress.

1.4. Ethylene-responsive factors (ERF)

Ethylene-responsive factors (ERF) perform multifarious functions in plant resistance to abiotic as well as biotic stresses. For the very first time, ERFs in tobacco were observed regulating the PR genes expression after their binding to the GCC-box in the promoter [27,29,90]. ERF-TFs family is divided into subfamily ERF and DREB based on the difference of amino acids at position 14 and 19 in the AP2/ERF domain. Besides, many ERFs containing Ala and Asp at 14th and 19th position in AP2/ERF domains may bind DRE as well as GCC boxes [91–93]. So far, many ERFs have been identified and characterized in different plants for their role in abiotic and biotic stress tolerance, e.g. *TaERF1, CaPF1, CaPTI1, CaERFLP1, CaAIEF1* [29,94–96]. Recently, it has been confirmed that ERFs may have tissue-dependent expression against plant pathogens. Jin et al. [27] observed differential expression of *PTI1* in *C. annuum* resulted in immunity to *P. capsici* and tolerance to cold and drought. Parallel with these findings, *CaPTI1*was induced by signaling molecules like SA, JA and ET. The loss of function studies in pepper proved the hampered defense and resistance to abiotic stress through low expression levels of defense and stress-related genes, i.e. *PR1, DEF1, SAR82*. Therefore, we postulate that ERFs can be induced by different signaling molecules, and through these signaling pathways help in immune responses for plant protection against phytopathogens. The similar JA-dependent immune response has been regulated by *AtERF2* [97]. *SlPTI-4,-5,-6* interact with other TFs and regulate SA response indirectly for triggering PR genes expression as well as aphids [25,98, 99]. This endorses our stance about phytohormone dependent regulation of plant immunity against microbial ingressions and TF-web taking part in the defense. Often, ERFs are reckoned as activators of immunity responses in plants. Some ERFs such as ERF3 in tobacco, potato and *Arabidopsis* possess ERF-associated amphiphilic repression (EAR) motif in C-terminal which act as a repressor [100,101]. But an exception has been noted in case of *GmERF5* having EAR motif but induced by pathogen and SA [102]. This diversity in responses is proof of functional diversity among ERFs. To further strengthen opinion about ERF functions, we present a distinct role of *CaERFLP1* in activating transcription. Lee et al. [29] clarified that induction of *CaERFLP1*mRNA by an infection in hot peppers is proof of transactivation of GCC- and DRE/CRT-genes for activating stress response. The same function of ERF was recommended in case of *TaERF1* in *N. tabacum* leaves [96]. We have much evidence which proves strong involvement of ERFs in immunity regulation. For instance, constitutive expression of nucleus localized *CaERF5* in tobacco enhanced immunity to *Ralstonia* by up-regulation of defense marker genes [93,103]. Unlike growth arrest seen in case of WRKY, ZNF-TFs, the level of constitutive defense activation in oe-CaERF5 plants (*C. annuum)* was little to activate any contrary effect on plant development. Therefore, we can infer that overexpression of CaERF5 can be an appropriate strategy for plant protection, growth and productivity. Contrastingly, some ERF such as *ERF922* in rice decrease plant immunity against *M. oryzae* by reducing expression of defense marker genes like *OsPAL, OsPR* [104]. Similarly, ERFs can work in network and phosphorylated by *MPK3/MPK6* against bacterial infection after activation of *PLANT DEFENSIN 1.1* and *1.2.* On the other hand, these TFs also work by managing the production of antimicrobial secondary metabolites to control pathogenic destruction. For instance, artemisinin levels are increased in addition to defense gene expression by overexpression of *Artemisia annua* ORA [105]. The present facts reveal collective damage control functioning in most of the ERF-TFs. These not only manage at the molecular level but also at biochemical level to protect plants in case of microbial pathogenesis. The demonstrated data strongly proposes manipulation of these TF in improving plant traits. Besides, unraveling correlated function and phylogenetic relationship among ERF and other TFs would elucidate their significance in plant immune response (Table 1).

1.5. DNA-binding with one zinc finger proteins (Dofs)

The Dofs are reckoned as a significant group of plant TFs that take part in various biological processes such as seed dormancy, flowering, guard cell-specific gene expression and stress response [106–110]. The *Dof* domain, possessing a C2C2-type zinc finger motif, performs dual activities, i.e. DNA binding and protein-protein interactions [106,107, 111,112]. *Dofs* have been identified in different algae, mosses, and model as well as non-model plants [113,114]. Mostly *Dofs* have been reported for their involvement in diverse physiological functions via interactions with different regulatory proteins and gene promoters [115]. *Dofs* have also been recorded playing a role in plant biotic stress tolerance [116]. However, the role of most of the biotic stress associated *Dofs* is largely unknown. It has been observed that *Dof*-TFs in *C. annuum* exhibited dissimilar expression levels against biotic stress. These variations in expression were observed to be pathogen-specific [107,112]. The expression levels of three *CaDofs*, i.e. *Dof*-4, -5, -32 were altered during resistance responses to TMV-P0 and/or PepMoV and *P. capsici.* On the other hand, *CaDof*-10 and -11 were up-regulated against both of the viral pathogens. This up-regulation proposes involvement in pepper defense against viral attack. Besides, resembling expression patterns as well as temporal alterations in some pepper *Dofs*, i.e. *Dof*-09 and -17, to diverse pathogens point out a common role against biotic stresses. Consequently, the differentially controlled *CaDofs* might strengthen immunity against biotic stresses. These observations offer deep insight into the evaluation of *Dofs* in understanding biological processes in pepper and other plants.

1.6. SQUAMOSA promoter binding protein (SBP)-box gene

SQUAMOSA promoter binding protein (SBP)-box plant-specific TFs take part in multiple physio-biochemical processes like organogenesis, induction of flowering, leaf initiation and signal transduction [117–119]. *SBPs* are significant contributors to the regulatory web of the floral formation and development and biotic stress tolerance in different plant species [120–122]. For example, *SPL14* in *Arabidopsis* determine sensitivity to fumonisin B1 that induce PCD [123]. *SBP5* seemingly activate SAR against *Erysiphe necator* by SA pathway [124]. However, little is currently known about the SBP-box genes in pepper, especially regarding resistance to *Phytophthora* blight. But in pepper, not so many SBP-TFs have been observed for their diverse functions. Zhang et al. [120] had identified and cloned a set of *CaSBP* genes in pepper. It was observed that *CaSBP* genes relate more closely to genes in *L. esculentum* or *A. thaliana* than to *OsSBPs*. This exhibits descendants of a common ancestor. An interesting fact revealed by Zhang et al. [120] was a different expression level in different tissues. For instance, in flowers and fruits, relative expression levels were comparatively low in comparison with root, stem and leaves, i.e. *CaSBP*-3, -6, -5. This reflects that *CaSBP* genes may have some role in the transition to reproductive growth from vegetative phase [120]. Similarly, up-regulation of many pepper SBP-TFs was observed in roots against *P. capsici* inoculation, i.e. *CaSBP*-2, -5, -6, -11. The expression patterns of *CaSBPs* resemble somewhat with an expression of defense marker genes in roots such as *CABPR*1, *CAPO*1*, CABGLU* during compatible and incompatible interactions with pathogens [28,125,126]. Immune response to *P. capsici* is negatively regulated by *CaSBP12*. The overexpression of *CaSBP12* in *N. benthamiana* plants increased the susceptibility of these plants to *P. capsici* infection with high ion leakage lipid peroxidation than wild-type. Correspondingly, relative expression levels of defense maker gene sin tobacco displayed modulation in the presence of overexpressing and silenced *CaSBP12* [127]. An interesting fact revealed unlike some previous studies was no role of *CaSBP12* in pepper growth and development. The non-silenced *CaBSP12* plants exhibited tolerance to salinity. *CaBSP12* silenced plant tackled hazardous effects of biotic stress by the low accumulation of H_2O_2 and O_2^- that facilitate us in making opinion that ROS produced were scavenged by antioxidants enzymes and positively affected defense. Such a role has already been reported for some other TFs like *CaHSP25, VpBSp16* against different stresses [128–130]. Based on the discussed facts, we propose that more and more SBPs in pepper must be identified and validated for their role in immunity against diseases. Their interactive partners and network member TFs must also be verified by employing different techniques.

1.7. NAC TFs and pepper immunity

In land plants, NAC domain proteins play diverse role in different biological processes and are found as a great multigene family [131–134]. The plant NAC domain proteins in are characterized by presence of a well conserved N-terminal region inclusive of *NAM (NO APICAL MERISTEM)*, *ATAF1, 2* and *CUC2 (CUP-SHAPED COTYLEDON)* [132,135,136]. The typical NAC protein possess at its N-terminal, a NAC domain while C-terminal is characterized by a divergent transcription regulatory region (TRR). The distinctive structure of NAC proteins TFs also reflects differences in DNA binding sites for recognizing the target genes [136,137]. Around 160 amino acid residues in the NAC domain confer DNA binding sites with/without ability for the protein binding and dimerization [133,138,139]. The TRR domain play role of activator/repressor and may perform protein-binding activity occasionally [140]. Many of the NAC TFs perform roles in the plant biological and physiological processes such as leaf senescence, shoot apical meristem formation, embryo development, regulatory role in synthesis of secondary cell wall, signal transduction, mineral transport, hormonal regulation [133,141–145]. Besides, multiple NAC TFs are significantly involved in regulation of plant resistance against biotic and abiotic stresses.

The reports regarding role of NAC TFs in plant defense against biotic stress exhibit their preferential functions during host as well as non-host incompatible interactions with pathogens. For instance, a nuclear protein in pepper, *NAC1* can activate transcription in yeast that recommends its function as TF and ability to take part in defense against microbial infection [139]. The up-regulation of *CaNAC1* after SA, ET, and JA treatments advocates its induced expression kinetics and signaling cascade during pathogen attack. This also gives rise to a cross talk in JA-/SA mediated signaling events. This cross talk also gives rise to stance that in parallel with synergistic or antagonistic behavior of TF for phytohormones, TF may individually respond to any stress. We advocate our opinion on the basis of Arabidopsis *ATAF1* That work in negative fashion during response to fungal and bacterial pathogen attack. The expression of this TF was down-regulated after treatment with SA and JA as well as *Botrytis cinerea* or *Pseudomonas syringae pv. Tomato* [146]. *ATAF1* overexpressing plants not only showed insignificant resistance to pathogens but also presented suppressed expression of pathogenesis related genes. Interestingly, the expression of NAC TFs may be tissue specific can also be induced by environmental stimuli. Such tissue specific expression is actually demonstrator of transcriptional role in plant growth and development [147]. It has been observed that *TaNAC4* expressed strongly in wheat seedling roots as compared to leaves and stem against stripe rust infection. Expression of *TaNAC4* was directly proportional to exogenous application of ET and MeJA while showed inverse relationship with SA in terms of induction [148]. The similar response has been recorded in expression of *OsNAC19* after application of MeJA and ABA [149]. This is adequate proof of involvement of NAC TFs in phyto-hormonal cross talk and relevant responses. Different NAC TFs may show homology in function for response to one stress condition but heterologous responses by same NAC TF to different stresses are also evident. In tomato, *SlSRN1* well positively regulated defense against *Botrytis* infection and exhibited manifold increase in expression after application of JA. But this TF negatively regulated response of tomato plants to drought [150]. Similarly, *SmNAC* is induced by *R. solanacearum* and MeJA. Interesting is the fact that induction of *SmNAC* decreased SA accumulation and effected *S. melongena* growth. Some *NAC* transcription faction such as *StNTP1* and *StNTP2* negatively regulates plant immunity. Similarly, expression of NAC TFs can be suppressed by bacterial toxins that compromise host innate immunity [134,151,152]. Therefore, the direct evidence in form of reduce disease severity by action of NAC TFs such as *SlSRN1, NAC1* would be supportive to dissect plant innate immunity and role of different TFs as universal regulator of immune responses against microbial pathogens.

2. Concluding remarks

Microbial infection in plants is one of the most serious pathogenic attacks, which causes a million dollars losses worldwide. Consequently, it is immensely needed to develop pathogen-resistant crops, i.e. Capsicum. We discussed different TF families indicating the critical roles in resistance to biotic stress and their application contributing a great enhancement in crop breeding. The role of TFs potentially suggests new ways in biotechnology to develop novel crop varieties with enhanced resistance against biotic stresses. Though, many reports focused on the development of pathogen-resistant phenotypes by overexpressing TF under controlled conditions, but field testing trials and performance evaluation as well as validation of engineered varieties under natural conditions still require extensive efforts. Ultimately, this approach hampers variety development and its commercial marketing. We recommend working out the mechanisms regulated by diverse pathways confirming the responses of engineered crop varieties under normal or stressed conditions. In future, regulatory networks and TFs must be understood and elucidated to produce biotic stress-resistant varieties. Moreover, TF must be identified and characterized by the involvement in responses to multiple stresses. The problems like growth retardation, developmental defects, decreased yields must be overcome through tissue-specific promoters. Ultimately, functional validity, crosstalk, and interactions of TFs while countering pathogen attack needs extensive elaboration and understanding. TFs and their downstream target genes should also be focused to elucidate regulatory mechanisms contributing to plant stress tolerance progress.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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