REVIEW ARTICLE

Dissecting the Role of Promoters of Pathogen-sensitive Genes in Plant Defense

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Abstract: Plants inherently show resistance to pathogen attack but are susceptible to multiple bacteria, viruses, fungi, and phytoplasmas. Diseases as a result of such infection leads to the deterioration of crop yield. Several pathogen-sensitive gene activities, promoters of such genes, associated transcription factors, and promoter elements responsible for crosstalk between the defense signaling pathways are involved in plant resistance towards a pathogen. Still, only a handful of genes and their promoters related to plant resistance have been identified to date. Such pathogen-sensitive promoters are accountable for elevating the transcriptional activity of certain genes in response to infection. Also, a suitable promoter is a key to devising successful crop improvement strategies as it ensures the optimum expression of the required transgene. The study of the promoters also helps in mining more details about the transcription factors controlling their activities and helps to unveil the involvement of new genes in the pathogen response. Therefore, the only way out to formulate new solutions is by analyzing the molecular aspects of these promoters in detail. In this review, we provided an overview of the promoter motifs and cis-regulatory elements having specific roles in pathogen attack response. To elaborate on the importance and get a vivid picture of the pathogen-sensitive promoter sequences, the key motifs and promoter elements were analyzed with the help of PlantCare and interpreted with available literature. This review intends to provide useful information for reconstructing the gene networks underlying the resistance of plants against pathogens.

1. INTRODUCTION

Plants are sessile entities and are prone to constant biotic and abiotic stress. The response of a plant to a particular pathogen is a process of a well-knitted underlying molecular network that occurs due to multiple factors. Plants activate various pathways and gene functions upon infection by a pathogenic agent. Decoding the process of resistance in response to a pathogen attack is a complex and intertwined network of multiple aspects. One such aspect is the activation of certain gene expressions which has a key role in plant defense mechanisms. In this aspect, promoter sequences are the key elements. The role of a promoter in gene expression and regulation is well known. Inducible plant defense is a result of the concomitance of inducible promoters, various related cis-regulatory elements, signal transduction pathways, and pathogen-specific responses [1]. The promoters of the genes which are induced by pathogenic elicitors or upon pathogen attack are here mentioned as 'pathogen-sensitive promoters' or 'pathogen-induced promoters' [2]. The regulatory mechanism of such promoters also varies concerning pathogen and the presence of particular regulatory elements. Here, in this systematic review, we have summarized some of these promoters and tried to provide a better understanding of the elements responsible for the trigger of such promoters during a pathogen attack. We have taken the reference of the TGP: Database on PlantPromoters for Transgenesis (TGP; http://wwwmgs.bionet.nsc.ru/mgs/dbases/tgp/home.html) [3]. This database contains information on experimentally verified plant promoters providing data on the size of the promoters, nucleotide sequences, different transcription patterns along with specific stimuli and substances prompting the promoter activity. TGP was constructed on the SRS platform and it is user-friendly as it simplifies the selection of promoters with required

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characteristics [2]. In response to the constant threat posed by the pathogens, the plants have evolved their response as well as sensitive detection systems to counter it and evoke adequate defense mechanisms. In most of the cases, the pathogen injects a vast range of effector molecules to inhabit the host. The pathways leading to resistance against a particular pathogen are mainly intertwined signaling pathways among which small signaling molecules namely salicylate, jasmonate, and ethylene play the key roles which enable the plant to fine-tune the defense responses in both local and systemic tissues [4]. In the next section, we have tried to shed light on some of the key factors which together play an important role in aiding the pathogen-induced promoters and help in the expression of the defense-related genes.

Word cloud is a simple yet impactful way of data visualization where the font size of the particular word or phrase represents the frequency of its appearance. It means that the more a specific word appears the more is its importance in a study. We have analyzed the titles and abstracts of the research articles related to the pathogen-induced promoter and represented the data as below (Fig. **1**). The PubMed IDs were collected from the database and texts were mined from the title and abstract sections using R scripts. A preprocessing step was carried out to get rid of all stop words and noises as much as possible. Using the package "wordcloud", a wordcloud was constructed (Fig. **1**). Upon observation, word counts of the words such as 'promoter', 'gene', 'expression', 'stress', 'wounding', 'fungal', 'induced' and 'pathogen' appear to be more based on the font size of the word cloud. It can be seen from the word cloud that the ongoing work in the field of pathogen inducible promoters mainly encompasses gene expression patterns using different promoters of interest under reporter genes, which is mainly Gus, and whether it could be induced by pathogens of interest or not.

2. SOME OF THE KEY FACTORS INVOLVED IN PLANT DEFENSE RESPONSE

2.1. Phytohormones

Plant hormones are well known for performing the role of regulators in abiotic and biotic stresses [4]. Plant hormones such as Salicylic Acid (SA), Jasmonic Acid (JA) and Ethylene (ET) are considered as integral parts of the plant immune system [5].

There are several genes and their promoters which play vital roles in JA mediated defense signaling pathway against pathogen attack. Histone acetylation has a major role in the regulation of the pathogen inducible genes. Histone acetylase and deacetylase control the function of histone acetylation. Zhou *et al.* (2005) [6] showed that *HDA19* might have a role in the regulation of gene expression involved in JA and ET signaling of pathogen response in *Arabidopsis thaliana*. In rice, commonly bacterial blight is observed which is caused by the infection of *Xanthomonas oryzae* pv. *oryzae* (*Xoo*). Recently, Hou *et al.* (2019) [7] showed that Xoo infection through "SAPK10-WRKY72-AOS1" module stimulates the suppression of JA biosynthesis but increases *Xoo* susceptibility. When WRKY72 directly binds to the W-box promoter region of JA biosynthesis gene *AOS1,* it suppresses the tran-

scription by inducing DNA hypermethylation on the target site. This results in a reduction of endogenous JA level and induces *Xoo* susceptibility. This study showed that Abscisic acid (ABA)-inducible SnRK2-type kinase SAPK10 phosphorylates WRKY72 at Thr 129 that disrupts the DNA-binding ability of WRKY72 to cause suppression of *AOS1* and JA biosynthesis. Similarly, ORA59 and two functionally equivalent GCC-boxes have been reported to activate the JA/ET signaling pathways through a regulatory module along with MED25 that enables *AtACT* gene expression and Hydroxycinnamic Acid Amides (HCAAs) biosynthesis [8].

SA is another central phytohormone that plays a critical role in pathogen defense signaling pathway. SA is involved in diverse infection resistance mechanisms and is associated with a huge level of SA accumulation [9]. A recent study showed that novel salicylic inducible *Cyr1P4* and *Cyr1P5* promoters regulate the expression of *CYR1*, a CC-NB-LRR type candidate disease resistance gene in *Vigna mungo* [10]. Defense-related gene expression and SA-induced plant defense response are regulated by some WRKY DNA-binding proteins which are activated by enhanced protein phosphorylation [11].

JA and its methylated derivative, methyl jasmonate, play a critical role in plant defense against insect herbivores and microbial pathogens through Jasmonic biosynthesis pathway [12]. Many genes and Transcription Factors (TFs) influence the Jasmonic biosynthesis pathway. Van der Does *et al.* (2013) [13] showed that the JA signaling pathway downstream of the SCF^{COI1}-JAZ complex is inhibited by targeting GCC-box motifs in JA-responsive promoters *via* a negative effect on the transcriptional activator ORA59. A recent report showed that IbBBX24 regulates B-box (BBX) family TF. IbBBX24 binds to the JA signaling repressor *IbJAZ10* promoter which inhibits the repression of IbMYC2, a JA signaling activator [14]. This study showed that overexpression of IbBBX24 enhances the transcriptional activity of IbMYC2 resulting in increased Fusarium wilt resistance in sweet potato. Yeast one-hybrid screening using the *AtACT* promoter as bait showed that the key positive regulator ORA59 induces *AtACT* gene expression and HCAAs biosynthesis to confer JA/ET mediated plant defense responses [15].

ET is a crucial hormone for plant responses to microbial pathogens and the interaction of plants with beneficial microbes and insects. ET is involved in modulation of defense signaling pathways, including both JA and SA pathways. It is involved in the activities of mitogen-activated protein kinases and ET Response Factor (ERF) TFs during Initial ET signaling events [13]. A pathogen-induced ERF, TaPIE1, acts as a positive regulator to mediate wheat responses of ET, *Rhizoctonia cerealis*, and freezing stimuli. TaPIE1 overexpression can activate the expression of *POX2*, *P5CR*, and additional defense- and stress-related genes downstream of ET biosynthesis, which regulates physiological changes, finally leading to enhanced resistance to both *R. cerealis* and freezing stresses [16]. According to microarray analyses, the synergism of ET and JA mediated signaling on pathogen response is responsible for commonly induced clusters of genes [17, 18]. Investigation of *PR* gene promoters showed the presence of an 11-bp ET-responsive element, TAAGAGCCGCC, known as the GCC
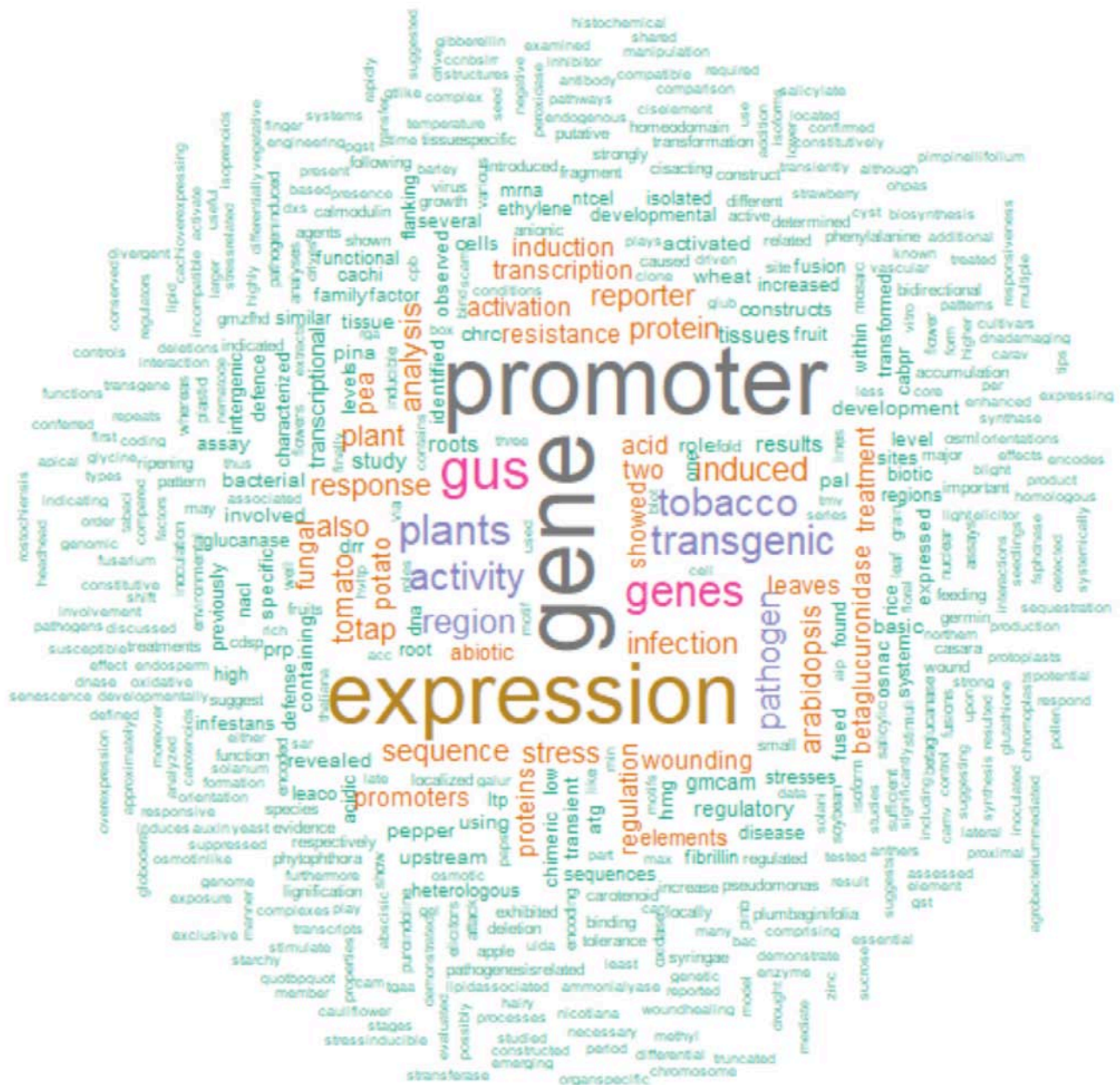
Fig. (1). Mined texts from the title and abstract sections of pathogen-induced promoter research articles are presented in the form of a Word cloud. (*A higher resolution / colour version of this figure is available in the electronic copy of the article*).

box [19-21]. The GCC-box required for the AtERF1 binding AtPDF1 gene in *Arabidopsis* has also been recognized as a JA-responsive element stating AtERF1 as a point of integration for both ET and JA signaling pathways [22, 23]. Broadly, ET-regulated defense responses depend on the outcome of interactions between multiple signals. ET biosynthesis is also known to be circadian regulated [24].

The role of Abscisic Acid (ABA) is ambiguous in plant defense pathways. It either induces or reduces defense responses based on the time of onset of the infection. A study devised to analyze the crosstalk between ABA and SA during the disease progression upon infection by *Xanthomonas oryzae* pv. *oryzae* (*Xoo*), the leaf blight pathogen, shed light on some interesting facts. It showed that exogenously administered ABA negatively regulates the defense mechanism

making rice hyper susceptible to *Xoo* infection, while chemical and genetic disruption of ABA biosynthesis and signaling led to enhanced resistance [4]. ABA acts negatively to promote the growth of the pathogen by interfering with classic defense hormone SA during the progression of the pathogen infection in the host plant [4, 25]. Disruption of the ABA signaling pathway proved to provide more pathogen resistance. ABA induces callose deposition at plasmodesmata limiting the accumulation and movement of *Bamboo mosaic virus* (BaMV), a potexvirus [25]. Histochemical analysis of pearl millet seedlings upon infection by the downy mildew pathogen *Sclerospora graminicola* advocated lignin and callose deposition as host structural responses enhancing resistance by restricting pathogen entry [26]. Studies have found that ABA is a significant hormone in fine-tuning responses concerning plant defense against a diverse range of

pathogens together with roles to play in several abiotic stresses. The relationship between pathogen dependent ABA level induction and transcriptional activation of ABA-responsive genes has been demonstrated in the report of Schmidt *et al.* (2008) [27]. In this study, a synthetic promoter was used, which is composed of multiple copies of the ABA-responsive element (ABRE) A2 and the coupling element CE3 of ABA-inducible barley gene *HVA1*. The induction of this barley gene was observed by the increased level of ABA and *C. beticola* infection in transgenic sugar beet leaves. The ABA-inducible promoter was found locally activated at the fungal infection sites when analyzed for the spatial pattern of promoter activity. Additionally, the expression of the basic leucine zipper TF AREB1 was also observed during drought stress and fungal infection in sugar beets. The same study also explained the reduction of promoter activity of phenylalanine ammonia-lyase (*BvPAL*) gene upon application of ABA, which is located on the -34 to +248 promoter region of *BvPAL* gene and necessary for the suppression of *BvPAL* expression by *C. beticola* [27].

The cross-talk between phytohormones is an important and interesting phenomenon that takes place during many pathogen infections and regulated by TFs. In a report [28], the role of WRKY8 was demonstrated in the defense response against TMV-cg through the direct regulation of expression of *ABI4*, *ACS6* and *ERF104* which may mediate the cross-talk between ABA and ET signaling during the TMV-cg–*Arabidopsis* interaction [28].

SA and ABA play roles in the tuning of plant defense pathways like RNAi. Although the known role of these phytohormones is that they exert antagonistic effects on various stress responses, it is still not clear that whether they play a similar role in RNAi silencing pathway. The overexpression of several SA related TFs like *AGO*, *DCL*, and *RDR* genes and availability of multiple binding sites for the identified TFs in the queried promoters were found in bamboo mosaic virus infection. Moreover, with respect to the expression of *AGO1* and *RDRs*, ABA and SA were found to have antagonistic effects because ABA induced these genes only when SA was mutant. However, the induction of AGO2 by ABA was found to be SA dependent, which explained the upstream activation of ABA than SA in the regulation of this gene [29].

2.2. Phytoalexins

Phytoalexins by definition are secondary metabolites of acidic nature secreted and accumulated briefly by plants in response to pathogen attack. Phytoalexins are known to have inhibitory effects against bacteria, fungi, nematodes, insects, animals as well as the plant itself [30, 31]. More than 350 phytoalexins have been chemically characterized in approximately 30 plant families including crop plants from Brassicaceae, Fabaceae, Solanaceae, Vitaceae, and Poaceae [32, 33]. Studies concerning accumulation, circulation, enzymology, and molecular aspects of phytoalexin synthesis term it as one of the components of an induced defense strategy. Its mode of action involves the lignification of cell walls, lytic enzymes like chitinases and glucanases, oxidizing agents, and diverse Pathogenesis-Related (PR) proteins of the undefined role [34]. Pathogenesis Related

Proteins (PRP) are the class of proteins that are generated by the plants in response against pathogen attack. A large number of cis-regulatory elements like W-box, GCC box, PR box and G-box have been reported to be involved in facilitating the expression of pathogen-induced *PR* genes [35-37]. Most of the promoters of *PR* genes contain GCC box with 5′ AGCC GCC sequence. Most of these are tobacco basic *PR* genes and also found in osmotin promoter. Similarly, *PRI-* and *PR2* genes contain W-box and are also present in tobacco *CHN50*, asparagus *AOPRI* and potato *PR-10*. Overexpression of the *GmPRP* gene in T2 transgenic tobacco and T2 soybean plants showed that it increased the resistance to *Phytophthora nicotianae* (*P. nicotianae*) and *P. sojae* which signified the importance of *GmPRP* promoter sequence [38]. A series of 5′-deletions of the *CAPIP2* promoter showed that novel *cis*-acting elements including GT1, MYB, RAV, and W-box play a critical role in inducing *CAPIP2* gene expression by *Pseudomonas syringae* pv. *tabaci*, SA, methyl jasmonate and ABA, NaCl and cold stress [39]. A recent research study showed that rapid changes in WRKY mRNA levels in response to a defined signal molecule indicated the critical role of WRKY1, 2 and 3 in a signal transduction pathway that leads from elicitor perception to PR1 gene activation in Parsely genome [40].

A *Zea mays* TF ZmWRKY79 was found to be highly correlated with the expression of Maize Terpenoid Phytoalexins (MTP) biosynthetic genes upon infection by *Fusarium graminearum*, phytohormone treatment, and multiple stresses. A transient overexpression study of ZmWRKY79 in maize was found to increase the expression of genes of MTP biosynthesis, ET, and JA biosynthesis together with scavenging of Reactive Oxygen Species (ROS) [41]. Most of the biosynthesis pathway genes for another major phytoalexin accumulated in response to fungal infection in *Nicotiana tabacum* and *Capsicum annuum* known as capsidiol were found to be transcriptionally induced by wounding in both WIPK/SIPK-dependent and -independent manners. Reporter gene analysis for the enzyme involved in capsidiol synthesis, *i.e.* 5-*epi*-aristolochene synthase (EAS) and the promoter of *EAS4* showed that two regions each 40–50 bp length were responsible for the activation of the *EAS4* promoter through wounding or by artificial activation of WIPK and SIPK [42]. As per the report of Ren *et al.* 2008, the induction of a mitogen-activated protein kinase (MAPK) cascade involving MPK3 and MPK6 is one of the earliest signaling events which occurs after a pathogen attack in *Arabidopsis* [43]. It was previously found that MPK3/MPK6 signaling activates camalexin biosynthetic genes. It has been reported that induction of camalexin, a characteristic phytoalexin of *Arabidopsis thaliana*, in *P. syringae* infected Arabidopsis plant, is dependent on the TF *WRKY33*. This TF binds directly to the promoter of *PAD3* which is the camalexin biosynthesis gene [44]. Mao *et al.* 2011 provided a critical finding bridging the connection of the signaling cascade that MPK3/MPK6 signaling causes phosphorylation of *WRKY33*, thus causing the camalexin production in *Arabidopsis* upon pathogenic infection [45]. This work demonstrated the crucial role played by WRKY33 in the stimulation of the camalexin biosynthesis pathway in response to the infection by the necrotrophic fungus *B. cinerea* and established WRKY33 as a target of MPK3/MPK6 signaling [46]. A

more detailed take on deciphering the molecular aspects would untangle the mode of action and disclose the intricacy of the action and metabolism of phytoalexin [33].

2.3. Melatonins

Melatonin is a universal molecule playing pleiotropic roles in plants as well as animals. It improves the stress tolerance in plants *via* a direct pathway involved in scavenging of ROS and indirect pathways by increasing the activity of antioxidant enzymes, photosynthetic efficacy, and concentration of metabolites [47]. Spraying of exogenous melatonin on leaves of *Arabidopsis* and tobacco induced PR genes together with some plant defense genes activated by SA and ET and showed enhanced resistance against the virulent bacterial pathogen *Pseudomonas syringae.* Similarly, *N*-acetylserotonin, unlike serotonin, also shows the same type of role inducing a series of defense genes [48]. Melatonin also acts as an important defensive molecule against pathogen attack. NPR1 and EIN1 are key signaling components that stimulated the defense response against Pseudomonas syringae in *Arabidopsis* and Tobacco under melatonin treatment [49]. Similarly, melatonin treatment increases the Differentially Methylated Regions (DMRs) associated genes that decrease the promoter methylation levels [50]. G-BOX BINDING FACTOR 1 (GBF1) negatively regulates pathogen-induced CAT2 expression and binds to the G-box-like element present in the intron of PHYTOALEXIN DEFICIENT 4 (PAD4) to positively regulate PAD4 transcription [51]. This enhances the pathogen resistance in Arabidopsis against *Pseudomonas syringae*.

2.4. Transcription Factors Having a Role in Modulating Disease Resistance of Plants

The TFs are the regulatory proteins that control the expression of the genes. During stress conditions like pathogen attack, the role of TFs influences the stress-responsive expressions and stress signaling networks of defense pathways. Synthetic promoters are considered more preferable to conventional ones for disease resistance. Through the gain of function and loss of function analysis of TFs, promoters can be modified for specific disease resistance in plants. Past research contributions have discovered several defense-related TFs like APETALA 2 (AP2), ET-responsive element (ERF), WRKY, basic leucine zipper (bZIP), myeloblastosis (MYB), myelocytomatosis (c-MYC)/ basic helix–loop–helix (bHLH), NAC (NAM, ATAF and CUC), and Whirly and homeobox (HB) proteins [52]. Zhang *et al.* (2019) [34] have identified a new MYB family member from apple which is MdMYB30. In this study, MdMYB30 is reported to be associated with *MdKCS1* gene promoter transcriptional activation and regulation of cuticular wax content and composition. MdMYB30 has also been reported to participate in disease resistance against bacterial strain Pst DC3000 *Botryosphaeria dothidea* [53]. In the defense signaling pathways, certain hormones and proteins play essential roles. JA is one of the important plant hormones that involve defense regulation against chewing herbivores and necrotrophic pathogens. The MYC- and ERF-type TFs in *Arabidopsis thaliana* regulate two antagonistic branches of the JA response pathway. Vos *et al.* (2019) [54] showed that ABA induction is essential for activation of the MYC-36 branch and suppression of

the ERF-branch of the JA pathway to increase the defense response against leaf-chewing *Pieris rapae* caterpillars. Similarly, ERF TFs regulate the JA/ET branch responses which involve the expression of defensins and resistance against necrotrophs [55]. MYC2 regulates wounding responses, insect resistance, and suppression of JA/ET-dependent innate immunity against necrotrophs through the JA/ABA branch responses [56, 57]. Recent studies showed that the ERF2-like promoter binding TF positively regulates the production of a phytoalexin, capsidiol, in *N. attenuata* which plays an important role in response to *A. alternata* infection [58]. WRKY family TFs bind to the W box region of the defense associated gene promoter [59, 60]. WRKY1 protein from parsley (*Petroselinum crispum*) binds to the W boxes of its native promoter as well as to that of *PcWRKY3* and the defense-related PR10-class marker gene *Pathogenesis-Related1-1* (*PcPR1-1*) which affects pathogen defense response [61]. In the jasmonate and ET signaling defense pathway, many TFs and regulatory genes are involved. ORA59 interacts with the GCC motif and controls the expression of genes that are synergistically induced by jasmonates and ET, whereas AtMYC2 interacts with the G-box promoter site and related sequences, and controls genes activated by jasmonate alone [62]. Deletion, point mutagenesis, and detection of cis-acting TF binding sites are the most commonly used approaches to construct transgenic promoters for disease resistance. There are several databases like PLACE, AtTFDB, AtcisDB, and AtRegNet which are available with plant-specific TF information [2]. These databases can extensively be used for constructing disease-resistant plant promoters.

3. WHAT IS COMMON IN THESE PROMOTERS?

Characterization of the promoter elements responsible for specific interactions holds interest in the field of molecular plant pathology [63]. The key lies in decoding the common factors in the promoter sequences which are pathogen-sensitive. Deciphering the underlying mechanism would certainly help in understanding the molecular programming of disease resistance and the role of such promoters in it. With the help of such information, researchers would be able to form better strategies for the development of disease-resistant crops. A study conducted by Andolfo, in the year 2019, [64] found that over-representation of a TC box-like motif and a thymine-rich motif in Mildew Locus O (*MLO*) genes was transcriptionally up-regulated when infected with Powdery Mildew (PM) fungi. The key regulation in terms of promoters lies in the transcriptional level which is regulated at several stages. Hence, understanding the orchestration of gene regulation poses a chief task in characterizing complex events, such as plant-pathogen interactions [65, 66], to have a clear vision about the common elements in a promoter that is already studied for the role it plays in acquiring resistance by the plants infected with pathogenic microbes. Various promoters of pathogen resistance genes have been reported to get induced while under the attack of a particular pathogen in the plant system. The list of promoters along with their Ids, sources, role in the pathogen attack, pathogen and their host information is summarized in Supplementary Table **S1**. Most of the inducible promoters were either found to be associated with pathogenesis-related genes or pathogen de-

fense genes. A few pathogen inducible promoters were also reported to be involved with important metabolic pathways.

Recent research outputs showed that various well-known fungi or viruses cause important diseases in several plants that involve pathogen inducible promoters. The report of Swartzberg *et al.* (2008) revealed that the infection of *Botrytis cinerea*, a necrotrophic fungus, which causes the botrytis bunch rot disease, induces precious leaf senescence by the expression of senescence-associated gene promoters (*SAG12_P1* and *At:SAG13_P1*) [67]. A number of promoters of pathogen responsive gene and pathogenesis-related protein class10 like (Pc:CMPG1b_P1, Pc:CMPG1b_P2, Pc:WRKY1_P1, Pc:WRKY1_P2, Pc:WRKY1_P3, Pc: WRKY1_P4, and Pc:WRKY1_P5) were reported to be induced upon infection by a fungal elicitor in *Petroselinum crispum*. These findings suggest the interaction between the elicitor-induced DNA binding proteins with elicitor response elements in the promoters of parsley *PR1* genes [68, 40]. The *Phytophthora infestans* race. that causes important diseases in citrus, infection in *Solanum tuberosom, citurs sinesis,* and *Malus x domestica* was reported to induce pathogen defense gene *prp1* promoter.

As discussed in the previous sections, the phytohormones regulated defense strategies play a significant role in plant-pathogen interaction. Phytohormones like SA, ABA, JA, and Gibberellic acid-mediated defense pathways are the key defense pathways in the plant defense system. The SA mediated defense pathway was induced by virus infections like TMV and PVY and here inducible promoters like glucanase, *PR2*, and *PR1*-a were found to control the respective gene expressions [69-72]. The induction of the ABA-mediated defense pathway by the infection of *Xanthomonas campestris pv.* and *Pseudomonas syringae* was identified to be regulated by inducible Lipid transfer protein LTP4 (Hv: LTP4.3_P1 promoter of *Hordeum H. vulgare* promoter). These pathogens cause important diseases like bacterial leaf streak or black chaff of barley, and bacterial canker, respectively [73, 74]. Another example of an inducible promoter is soybean calmodulin isoform-4 (*GmCaM-4*) promoter which was reported to be induced upon infection by *Pseudomonas syringae pv tomato* [74-76]. On the other hand, the inducible promoters regulate several other biosynthetic and structural metabolic pathways. The caffeic acid O-methyltransferase II gene promoter of *Nicotiana tabacum* induces the phenylpropanoid metabolism upon TMV infection in solanaceous plants. Additionally, Anthranilate N-hydroxycinnamoyl/benzoyl-transferase gene promoter of *Petroselinum crispum* regulates the phytoalexin biosynthesis and induces the biosynthesis upon infection by *Phytophthora megasperm* [77]. Thus, the pathogen inducible promoters regulate several plant-pathogen interactions like pathogen defense pathways as well as works for the regulation of other important biosynthesis pathways (Table **S1**). We used the PlantCare server to obtain the promoter elements by providing the FASTA sequences of the pathogen-induced promoters taken from the TransGene promoter database (Table **S1**). Table **S1** gives detailed information about these pathogen inducible

promoters that have been examined concerning the role of these promoters along with the regions of interest in plant resistance. The results from PlantCARE were processed to create a matrix and plot using circos (Fig. **2**). Several elements obtained from the server represent core promoter elements, such as CAAT-box and TATA-box, which were found to be more prominent among the other important elements such as Box_4, MYC, MYB, ABRE, ERE-motif, *etc*. The prominent presence of the core promoter elements is obvious as these are the common cis-acting elements in the promoters and enhancer regions. The role of other such noticeable elements that are involved mainly in plant growth hormone regulation and are key players in plant defense mechanisms is explained as follows:

The promoter elements known to be involved in wounding and pathogen response namely W-box, TC- rich repeats, WUN motif, Wound responsive element 3 (WRE 3), Box S [42] have also taken a key presence in the circos plot. Among these, W-box and WUN motifs showed a major presence, whereas WRE 3 and Box S have taken a backseat in the PlantCare analysis of the pathogen-sensitive promoters. MYC and MYB recognition sites, as well as as-1 motifs, are known to function as transcriptional activators in case of drought- and ABA-induced gene expression [78, 79], whereas ABA has key roles in pathogen resistance of the plants as previously mentioned. Box_4, G-Box, circadian, GT-1 motif and Sp 1 motifs are known as light-responsive elements and are components of the circadian rhythm [78, 80]. Circadian rhythms are evident biological alternations known to occur in 24-hours due to the internal transcriptional clock. Previously, only abiotic factors like light and temperature were credited as responsible for sending signals to the clock. Lately, research findings have shown a different perspective where developments in clock-defense signaling in plants have pointed towards the involvement of biotic factors, *i.e.* pathogens, as input signals to the circadian clock [81]. Studies have also demonstrated the capacity of the circadian clock to foresee likely attackers, and of redox signaling to regulate apt defense against pathogens [82]. Metabolic developmental processes like leaf movement and stomata opening obey circadian rhythm which correlates with the CO_2 assimilation rate affecting photosynthesis. It also makes sense as being an energy-consuming process, defense response in plants requires synchronization of signaling events with related physiological processes to produce an effective response of the plants against the pathogens in an enhanced way. On the other hand, promoter elements are known to be involved in ET response (ERE) and ABA-responsive element (ABRE) plays a role in circadian events confirming the link between the two [79]. The genes responsible for circadian rhythm and hormone-related genes were observed to be altered in *Paulownia* after *Paulownia* witches' broom (PaWB) phytoplasma infection [47]. The well-reserved presence of the JA response elements, such as CGTCA- motif and TGACG-motif, is prominent in the circus image. We also obtained probable TFs that are more likely to target the promoter sequences.

Fig. (2). A Circos plot showing the common important regulatory elements in pathogen-sensitive promoters. (*A higher resolution / colour version of this figure is available in the electronic copy of the article*).

4. SYNTHETIC PROMOTERS FOR RESISTANT PLANT VARIETIES

There are several databases available as resources of information on promoter sequences of crop varieties to create an experimental setup for generating pathogen-resistant plants. The PlantProm database (PPDB) is extensively used for the information on nucleotide sequences of rice and Arabidopsis promoter structures with cis-acting regulatory elements and experimentally verified transcription start sites [83, 84]. Athena and Osiris are also other resources of Arabidopsis and rice promoter sequences for systematic analysis [85, 86]. TGP database contains information on genomic DNA segments and certain expression patterns of reporter genes [2]. TGP is a very useful database for genetic engi-

neering research to develop pathogen-resistant and stress-tolerant plants as it contains verified experimental data of transgenic plants. Most of the plant promoters are comprised of a cap or transcription start, site; a CCAAT consensus sequence; and a TATA box. Usually, the synthetic promoters are designed for constitutive expression of the transgene by joining the upstream activation sequence of one promoter to a TATA box-containing region of another promoter [87]. To generate pathogen- or disease-resistant plants through mutation analysis, several promoters are extensively used. Some of these promoters are *INCURVATA2 (ICU2)* promoter (meristem-specific), EC1.2 promoter (embryo-specific), *YAO* promoter (young tissue-specific), *APETALA1 (AP1)* promoter (flower-specific), *SPOROCYTELESS (SPL)* promoter

(germline-specific), *Elongation Factor-1 (EF1)* promoter (germline- and meristematic cell-specific), *RIBOSOMAL PROTEIN S5 A (RPS5A)* promoter (egg cell- and meristematic cell-specific) and *AtU6–26* promoter [88]. Ochola *et al.* (2019) [89] engineered *PsAvr3b* promoter sequences by *in situ* substitution with promoter sequences from *Actin* (constitutive expression), *PsXEG1* (early expression), and *PsNLP1* (later expression) using the CRISPR/Cas9. Modified *PsAvr3b* driven by different promoters has shown different expression levels at different infection time points. This study has shown that appropriate editing in the *Avr* gene might help in the generation of improved crop variety with disease and pathogen resistance. CRISPR-Cas9-mediated genome editing in sucrose transporter gene promoters *SWEET11*, *SWEET13* and *SWEET14* and introduction into rice line Kitaake and the elite mega varieties IR64 and Ciherang-Sub1 have shown a quality broad-spectrum of resistance to the rice lines [90]. Liu *et al.* (2011) [91] showed a rapid *in-vivo* assay by fusing a synthetic promoter with Red Fluorescent Protein (RFP) reporter. The agrobacterium cultures with these constructs were infiltrated in Nicotiana tabacum leaves. Exposure of these leaves to bacterial pathogen and stress phytohormones has shown that the synthetic promoter confers inducibility of RFP reporter to bacterial pathogen and phytohormone response. Shokouhifar *et al.* (2019) [92] conducted a study on three synthetic promoters namely (1) synthetic promoter-D box-D box (SP-DD), (2) synthetic promoter-F element-F element (SP-FF) and (3) synthetic promoter-F element-F element-D box-D box (SP-FFDD) to see the response against two pathotypes of *Ascochyta rabiei* and two defense hormones, SA, and methyl jasmonate. In this study, the SP-FF promoter was found to be highly inducible to *A. rabiei* and methyl jasmonate phytohormone. The SP-DD promoter showed more sensitivity to SA, whereas the SP-FFDD promoter was found to be equally responsive to both pathotypes of *A. rabiei* that infers the complex nature of the box D *cis*-acting element.

5. THE CHOICE OF PROMOTER: INDUCIBLE *VS.* CONSTITUTIVE PROMOTERS

In the field of Applied Plant Biotechnology, the choice of the promoter depends on the expected outcome of the proposed study. However, in the crop improvement strategies, especially in the development of pathogen-resistant varieties, inducible promoters are preferred. A constitutive promoter may be active throughout all developmental stages and tissues of the plant, whereas an inducible promoter is only modulated by external stimuli of various biotic and abiotic factors [88]. Therefore, constitutive promoters can be exhausting for the crop plants exposed to biotic stress in the form of one or multiple pathogens risking the survival rate during a stressed condition, the metabolic processes, and other physiological mechanisms which are either halted or maintained in a very low expression rate to conserve metabolic energy to withstand the adversities.

In a comparative study between the constitutive promoter *35S* promoter of Cauliflower Mosaic Virus and the inducible *Actin 7* promoter of *A. thaliana* against the necrotrophic fungus, *Botrytis cinerea* showed *Actin 7* promoter as the better one. The use of *Actin 7* promoter rendered enhanced tolerance to the pathogen by expressing the 42 kDa endochitinase

gene of *Trichoderma hamatum* both in leaves and stems, whereas the *35S* promoter failed in providing adequate expression in the stems; the principal site of infection of the mold [93]. The *rolC* promoter of Agrobacterium rhizogenes was found to be induced by sucrose and considered as phloem-specific [94]. The systemic disease spread caused by the plum pox virus was found to be prevented by the expression of a self-complementary hairpin RNA using a rolC promoter without the prevention of the local infection [95]. Boni *et al.* (2017) stated that the negative effects caused by the constitutive expression of the *Ta-Lr34res* gene could be overcome *via* the use of pathogen-inducible promoter *Hv-Ger4c* in barley. *Ta-Lr34res* gene encodes for an ABC transporter that is known to provide resistance against multiple broad-spectrum fungal pathogens in wheat [96, 97]. Malnoy *et al.* (2003) showed that pathogen-inducible promoters *str246C* and *sgd24* can provide resistance against bacterial diseases by expressing the suitable transgene in a pathogen-responsiveness manner despite being less active than the *CaMV35S* promoter in pear (Table **S1**) [48, 67-78, 98-134]. These success stories give a vivid idea for the need to pick the right promoters for crop improvement strategies. Therefore, the selection of the promoters based on the ultimate goal of the crop improvement strategy is of first and foremost concern. However, studies entirely focused on the promoters or dissection of the promoter elements are very less and need a boost. It would help the scientific community to better understand the nature of the promoters, thereby helping in the choice of the promoters based on the expected outcome.

CONCLUSION

A detailed review of factors influencing the pathogen-induced promoters is presented to show the intricacy of the plant defense mechanism and the role of pathogen-induced genes and their promoters in it. Everything is intertwined and works in an array to produce the most effective resistance against the phytopathogens, thus minimizing the damage to the crop. Right from the plant defense signaling pathways involving phytohormones to other significant low molecular weight compounds like phytoalexin and melatonin, every component has an important part to play. An interesting connection between the light-sensitive promoter elements involved in circadian rhythm and the events leading to disease resistance by the plants has been observed. The role of the TFs like WRKY, and GT-1; cis-acting elements such as ABRE, MYC, and MYB; and the promoter elements dedicated to pathogen-sensitive expression namely W-box, G-box, WUN motif, and TC-rich repeats is found to be significant. Thus, dissecting the promoters of the pathogen sensitive genes to extract meaningful information may help in selecting suitable promoters and prove beneficial for devising crop improvement strategies.

LIST OF ABBREVIATIONS

Xoo	=	*Xanthomonas oryzae* pv. *oryzae*
SA	=	Salicylic Acid
JA	=	Jasmonic Acid
ET	=	Ethylene
ABA	=	Abscisic Acid
HCAAs	=	Hydroxycinnamic Acid Amides

EAS	=	5-*epi*-aristolochene Synthase
ERF	=	Ethylene Response Factor
BaMV	=	Bamboo Mosaic Virus
PR protein	=	Pathogenesis-related proteins
TF	=	Transcription Factor
MTP	=	Maize Terpenoid Phytoalexins
ROS	=	Reactive Oxygen Species
ERF	=	Ethylene Responsive Element
bZIP	=	Basic leucine zipper
MAPKs	=	Mitogen-Activated Protein Kinases
MYB	=	Myeloblastosis
c-MYC	=	Myelocytomatosis
bHLH	=	Basic helix–loop–helix
HB proteins	=	Homeobox proteins
MLO	=	Mildew Locus O
PM	=	Powdery Mildew
WRE 3	=	Wound Responsive Element 3
ERE	=	Ethylene response
ABRE	=	ABA-Responsive Element
PaWB	=	Paulownia *Witches'* Broom
PPDB	=	PlantProm Database
CRISPR	=	Clustered Regularly Interspaces Short Palindromic Repeats
Cas9 protein	=	CRISPR associated protein
RFP	=	Red Fluorescent Protein
GFP	=	Green Fluorescent Protein
SIPK	=	Salicylic Acid-Induced Protein Kinase
SP-DD	=	Synthetic Promoter-D box-D box
SP-FF	=	Synthetic Promoter-F element-F element
SP-FFDD	=	Synthetic promoter-F element-F element-D box-D box
WIPK	=	Wound-Induced Protein Kinase

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SUPPLEMENTARY MATERIAL

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