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The Past, Present and Future of Plant Activator Targeting Salicylic Acid Signal Pathway

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The Past, Present and Future of Plant Activator Targeting Salicylic acid Signal Pathway

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Abstract: Plant activators have emerged as promising alternatives to conventional pesticides for crop disease management due to their unique mode of action. By priming the plant's innate immune system, these compounds can induce systemic acquired resistance against a broad spectrum of pathogens without directly inhibiting their proliferation. Key advantages of plant activators include prolonged defense activity, lower effective dosages, and negligible risk of developing pathogen resistance. Among the various defensive pathways targeted, the salicylic acid (SA) signaling cascade has been extensively explored, leading to the successful development of commercial activators like benzothiadiazole for widespread application in crop protection. While the action sites of many SA-targeting activators have been preliminarily mapped to different steps along the pathway, a comprehensive understanding of their precise mechanisms remains elusive. This review provides a historical perspective on plant activator development and outlines diverse screening strategies employed across multiple levels, from whole-plant bioassays to molecular and transgenic approaches. We expound on the intricate components, biological relevance, and regulatory circuits governing the SA pathway, while critically examining the structural features, bioactivities, and proposed modes of action of classical activators such as benzothiadiazole derivatives, salicylic acid analogs, and other small molecules. Insights from field trials assessing their practical applicability are also discussed. Furthermore, we highlight the current status, challenges, and future prospects in the realm of SA-targeting activator development globally, with a focus on recent endeavors in China. Collectively, this comprehensive review aims to synthesize existing knowledge and provide a roadmap for future research toward developing more potent and mechanistically understood plant activators that fortify crop immunity against disease.

Keywords: plant activator; salicylic acid signal pathway; systemic acquired resistance; plant resistance; action mechanism

1. Introduction

Systemic acquired resistance (SAR) represents an inducible, whole-plant immune response in which localized exposure to a pathogen or an elicitor confers long-lasting, broad-spectrum resistance against subsequent infections [1,2]. This phenomenon underscores the remarkable ability of plants to adapt and fortify their defenses in the face of potential threats [3]. At the heart of SAR lies the salicylic acid (SA) signaling cascade, a pivotal molecular pathway that orchestrates a multifaceted defense program upon activation [4–6]. Central to this pathway is the accumulation of pathogenesis-related proteins (PRs) and antimicrobial phytoalexins, accompanied by the potentiation of enzymes involved in oxidative burst and other frontline defense responses (Figure 1) [7,8]. Over the past decades, intensive research has gradually unraveled the intricate network architecture, key components, and regulatory mechanisms governing the SA pathway [8]. Critical players such as the harpin-binding protein (HrBP1), enhanced disease susceptibility proteins (EDS1 and EDS5), the master regulator nonexpressor of pathogenesis-related genes 1 (NPR1), *WRKY* transcription factors, and the *PRs* themselves have been identified as essential signaling hubs, amplifiers, and executors of the SA-mediated resistance response [9–11]. This expanding molecular blueprint has paved the way for targeted interventions aimed at priming plant immunity (Figure 2) [12]. Capitalizing on this knowledge, researchers and agrochemical companies have actively pursued the development of synthetic "plant activators" compounds capable of stimulating the SA pathway and conferring robust, broad-spectrum disease resistance without directly targeting pathogens [13].

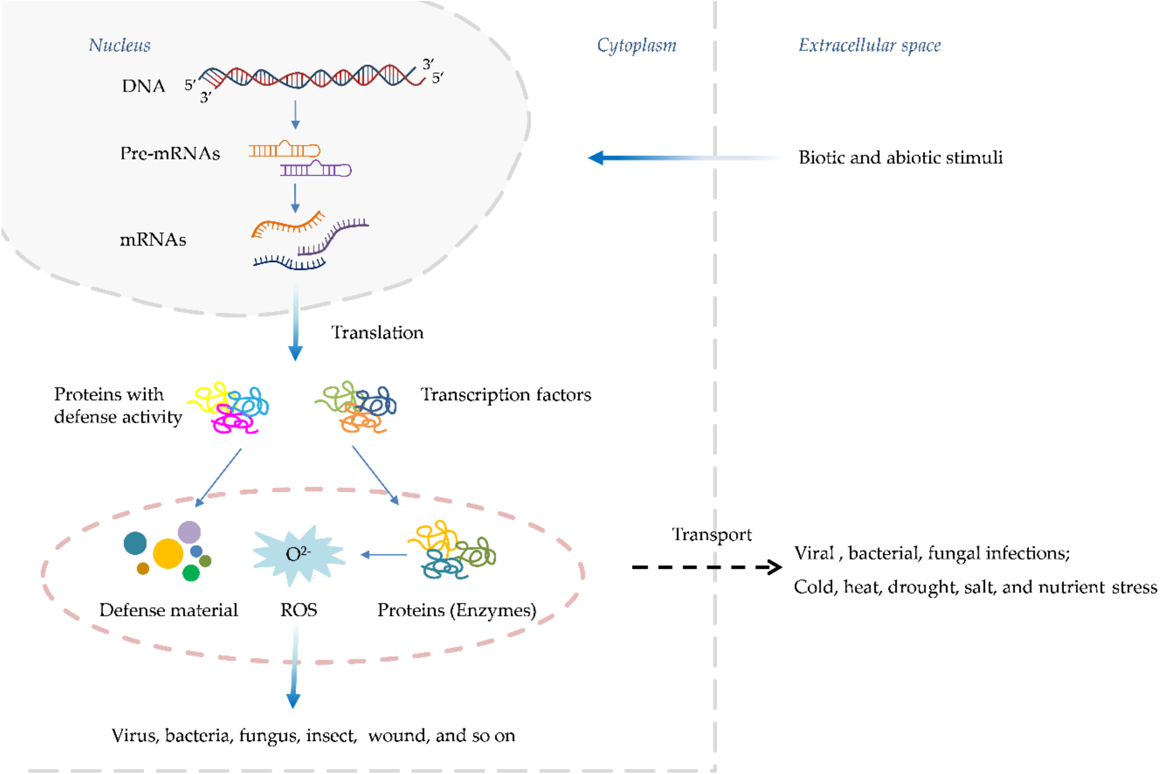

Figure 1. The genetic basis of plant defense responses.

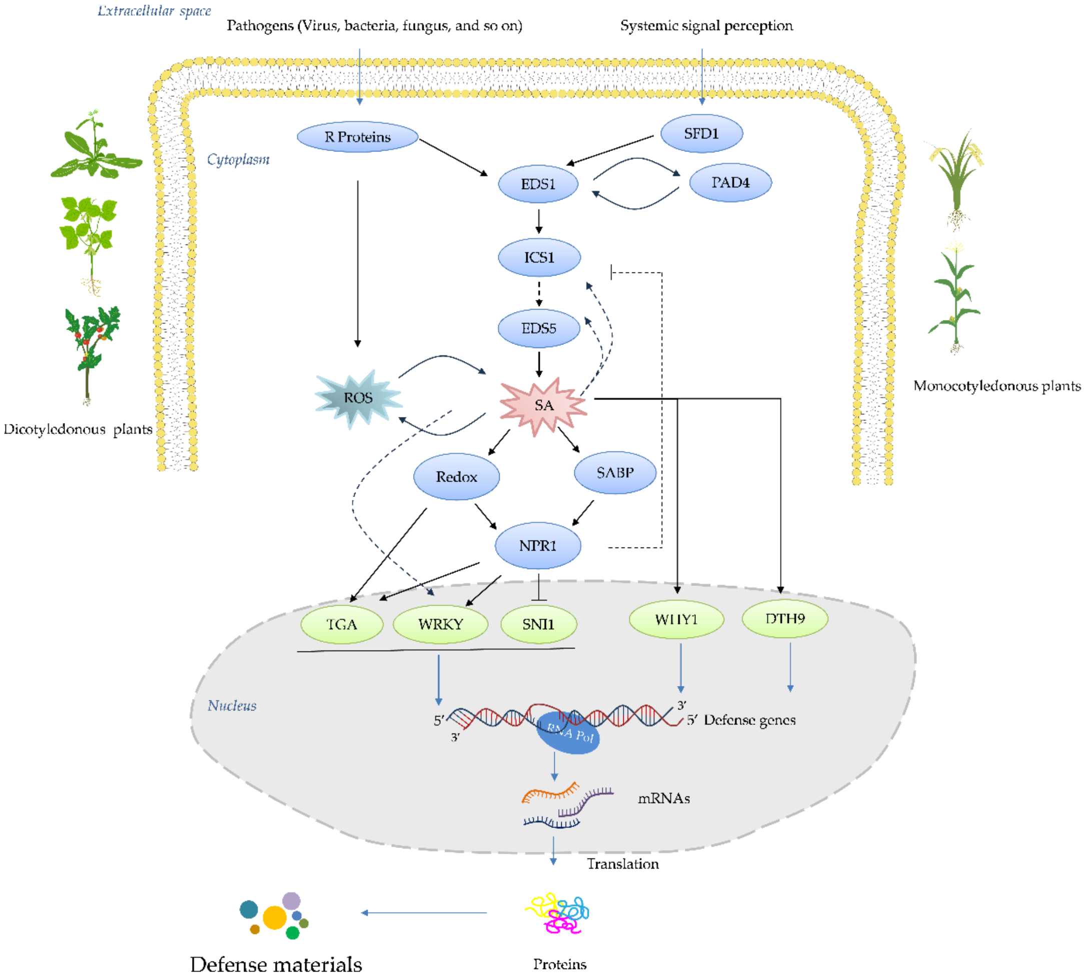

Figure 2. SA signal pathway and some related regulatory elements in the pathway.

SAR inducible, whole-plant immune response in which localized exposure to a pathogen or an elicitor confers long-lasting, broad-spectrum resistance against subsequent infections [14]. This remarkable ability of plants to "immunize" themselves against potential threats was first reported by Ross in 1961, who observed that localized infection of tobacco leaves with tobacco mosaic virus (TMV) prevented the systemic spread of the same virus upon subsequent inoculation [15]. Subsequent pioneering work by Malamy, et al. [16] and Métraux, et al. [17] demonstrated that SAR is mediated by a long-distance signal produced at the initial infection site, which travels through the vascular system and activates defense responses in distal, uninfected parts of the plant. This seminal finding paved the way for intensive research aimed at elucidating the molecular underpinnings of SAR.

A major breakthrough came when Gaffney, et al. [18] and Malamy, Carr, Klessig and Raskin [16] identified the SA as a crucial signaling molecule required for the establishment of SAR. Exogenous application of the SA or its synthetic analogs was found to be sufficient to induce SAR responses in various plant species. Concurrently, Ward, et al. [19] reported the pivotal role of PR proteins, a suite of antimicrobial proteins whose expression is tightly regulated by the SA pathway, in manifesting SAR. Further dissection of the SA signaling cascade identified key regulatory components such as the transcriptional co-activator *NPR1* [20,21], which acts as a master regulator of SAR by orchestrating the expression of *PR* genes and other defense responses upon perception of the SA signal. Subsequent studies unveiled additional players, including the *EDS1* and *PAD4* lipase-like proteins [22,23], which function upstream of the SA biosynthesis, and the transcription factor family of *WRKY*, which acts downstream of *NPR1* to regulate *PR* gene expression [24,25]. The elucidation of the SA-mediated SAR pathway has profound implications for crop protection strategies [26]. By harnessing our understanding of this endogenous defense mechanism, researchers have developed synthetic "plant activators" that can prime the SA pathway and confer broad-spectrum disease resistance without directly targeting pathogens [27]. This approach offers several advantages over conventional pesticides and has led to the successful commercialization of activators like benzothiadiazole for widespread use in agricultural systems [28]. These activators offer several advantages over conventional pesticides, including prolonged defense activation, lower effective dosages, reduced environmental impact, and a negligible risk of developing pathogen resistance [29]. Consequently, numerous the SA-targeting activators, such as benzothiadiazole derivatives, have been successfully commercialized and widely adopted for crop protection globally [30]. Importantly, plant activators have also served as invaluable chemical probes, facilitating the elucidation of SA pathway's intricate mechanisms and associated physiological phenomena [31]. In this comprehensive review, we trace the historical evolution of plant activator development and elucidate the current understanding of the SA signaling pathway's architecture and regulation. Furthermore, we critically examine the structural features, bioactivities, proposed modes of action, and field performance of classical and emerging SA-targeting activators (Figure 3). Finally, we highlight the current challenges and future prospects in this burgeoning field, with a particular emphasis on recent endeavors undertaken in China to advance the development of more potent and mechanistically understood plant activators that can fortify crop immunity against diseases.

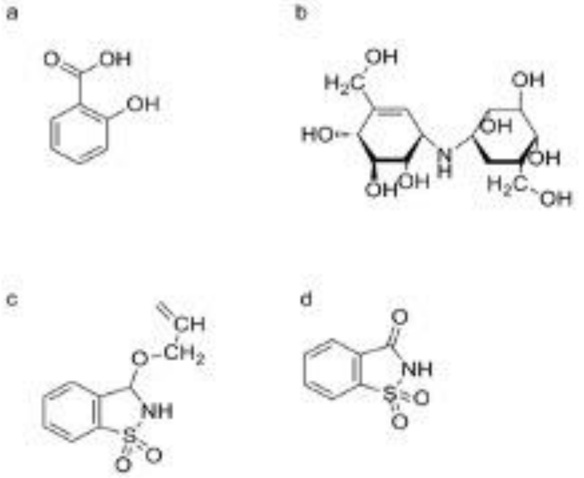

Figure 3. SA and some molecules act in SA upstream in SA signal pathway. (a) SA. (b) VMA. (c) PBZ. (d) BIT.

2. Plants Receptors Trigger an Immune Response

Plants possess cell-surface pattern recognition receptors that can detect danger signals from pathogens or the host itself, triggering an immune response [32]. One subgroup of these receptors is the leucine-rich repeat receptor-like proteins (*LRR-RLPs*), which play a crucial role in plant immunity [33]. However, the mechanisms underlying ligand recognition and activation of *LRR-RLPs* have remained elusive. In a recent study, researchers reported in *Nicotiana benthamiana*, the crystal structure of the *LRR-RLP RXEG1* which recognizes the *XEG1* xyloglucanase enzyme from the pathogen *Phytophthora sojae* [33]. The structure revealed that RXEG1 recognizes XEG1 primarily through its amino-terminal and carboxy-terminal loop-out regions. RXEG1, a receptor-like protein in plants, recognizes the pathogen XEG1 (a glycoside hydrolase secreted by Phytophthora) through interactions primarily involving its amino-terminal and carboxy-terminal loop-out regions. This structural insight highlights the specific regions of RXEG1 that are crucial for pathogen recognition, helping to understand the molecular mechanisms behind plant immunity and pathogen evasion strategies [34]. These loops bind to the active site groove of XEG1, inhibiting its enzymatic activity and suppressing *Phytophthora* infection in *N. benthamiana*. Binding of *XEG1* promotes the association of *RXEG1's LRR* domain *RXEG1* (*LRR*) with the co-receptor *BAK1*, also an LRR-type protein, through

RXEG1 (ID) and the last four conserved *LRRs* [35]. This association triggers RXEG1-mediated immune responses (Figure 1). Structural comparisons of apo-RXEG1 (LRR), XEG1–RXEG1 (LRR), and XEG1–BAK1–RXEG1 (LRR) complexes showed that XEG1 binding induces conformational changes in the N-terminal region of RXEG1 and increases structural flexibility in BAK1-associating regions of RXEG1 (LRR), the RXEG1, characterized by its leucine-rich repeat domain known as RXEG1 (LRR) [36]. These changes allow RXEG1 to undergo a fold-switching mechanism, facilitating the recruitment of BAK1 (LRR). It brassinosteroid-insensitive 1-associated receptor kinase 1, is characterized by its leucine-rich repeat domain (LRR). This domain is crucial for its interactions in plant signaling pathways, particularly in immune responses and development processes. This association triggers *RXEG1*-mediated immune responses. These changes allow a fold-switching of RXEG1, facilitating the recruitment of brassinosteroid-insensitive 1-associated receptor kinase 1 (BAK1 (LRR), which is essential for initiating downstream signaling cascades in plant defense and development pathways. Chen et al [36] reveal a conserved mechanism of ligand-induced heterodimerization of an LRR-RLP with BAK1 and suggest a dual function for LRR-RLPs in plant immunity direct ligand recognition and co-receptor recruitment for signaling.

The study investigates the role of BIR2, also known as BAK1-interacting receptor-like kinase 2, plays a significant role in plant immune responses by interacting with BAK1 (LRR) and other proteins to regulate signaling pathways involved in defense against pathogens. Meanwhile BIR2 is a receptor-like kinase that recognizes the fungal cell wall protein AVRY567 to initiate PTI responses in *N. benthamiana* [37]. The E3 ubiquitin ligases SNIPER2a and SNIPER2b target BIR2 for degradation via the 26S proteasome pathway, negatively regulating PTI [38,39]. BAK1 associates with BIR2 upon AVRY567 recognition and protects BIR2 from SNIPER2a/b-mediated degradation [40]. Knock-down of *BAK1* leads to enhanced degradation of BIR2 by SNIPER2a/b, compromising AVRY567-triggered PTI responses [41]. The kinase activity of BAK1 is required for its protective role against BIR2 degradation [38]. BAK1 appears to protect BIR2 by phosphorylating it, preventing SNIPER2a/b from ubiquitinating and targeting it for degradation [42]. This study uncovers a novel function for the co-receptor BAK1 in stabilizing receptor-like kinase BIR2 by protecting it from E3 ligase-mediated degradation [43]. This stabilization allows BIR2 to properly initiate and sustain pattern-triggered immune responses upon recognition of the fungal AVRY567 protein in *N. benthamiana* [38].

A summary of the key points regarding the past, present, and future of plant activators targeting the SA signal pathway:

Early research identified chemicals like SA, 2,6-dichloroisonicotinic acid (INA), and benzo (1, 2, 3) thiadiazole-7-carbothioic acid *S*-methyl ester (BTH) as activators of the SA signal pathway [44]. These compounds were found to induce SAR, a broad-spectrum resistance against pathogens, by mimicking the effects of pathogen infection [45]. Studies showed that these activators stimulate SA biosynthesis and signaling, leading to the expression of *PR* genes and other defense responses [46]. Current research focuses on understanding the molecular mechanisms by which these activators regulate the SA pathway and identifying new activators with improved efficacy and specificity [47]. Natural compounds like plant extracts, essential oils, and metabolites are being explored as potential the SA pathway activators with reduced environmental impact [48]. Advanced techniques like transcriptomics, proteomics, and metabolomics are being employed to elucidate the complex signaling networks and identify key components targeted by activators [49]. Activators are being tested for their ability to prime plant defenses against various biotic and abiotic stresses, leading to enhanced crop productivity and sustainability [50].

Future research aims to develop more potent and selective the SA pathway activators with minimal side effects on plant growth and development [51]. Targeted approaches like structure-based drug design and chemical genomics may facilitate the discovery of novel activators with specific modes of action [52]. Integration of activators with other defense-priming strategies, such as induced systemic resistance (ISR) and RNA interference (RNAi), could provide more robust and durable resistance against pathogens (Figure 2) [53]. Exploring the potential of activators in modulating plant-microbe interactions and facilitating beneficial symbioses is an emerging area of interest [54]. Field trials and commercial development of activators as biostimulants or plant

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protection products are expected to increase, promoting sustainable agriculture practices [55]. In summary, plant activators targeting the SA signal pathway have played a crucial role in enhancing plant immunity, and ongoing research aims to develop more effective and targeted activators for improved crop protection and productivity [56].

2.1. The Past of Plant Activators

Plant activators, plant inducers, and plant elicitors are compounds known to induce SAR in plants, thereby generating disease resistance without directly inhibiting the proliferation of pathogens [57,58].

2.1. The Usage of Plant Activators

Plant activators play a crucial role in enhancing plant defense mechanisms against a wide array of pathogens [59]. Unlike traditional fungicides, which directly target and kill pathogens, plant activators stimulate the plant's own immune system, enabling it to resist infections more effectively [60]. Plant activators were initially developed as pesticides to prevent rice blast [61]. For instance, Probenazole (PBZ) was widely applied to control rice blast in Japan in the last century [60,62]. In addition to their use in pest control, plant activators have also served as chemical probes in studying the mechanisms of plant resistance reactions [63]. The recent study discusses the creation of new 5-(thioether)-N-phenyl/benzyl-1, 3, 4-oxadiazole derivatives. These compounds were synthesized and evaluated for their antibacterial properties, showing significant activity against various bacterial strains. The study also explored the antibacterial mechanism, revealing that these derivatives disrupt bacterial cell membranes and inhibit essential enzymes, highlighting their potential as effective antibacterial agents [64]. The research by Ouyang, et al. [65] focuses on the design and synthesis of novel pyrazole derivatives containing oxime esters group. These compounds were evaluated for their antiviral activities, showing significant protective ability. The study also explores the structure-activity relationships to understand how modifications inducing plant host resistance as antiviral agents.

2.1.1. Screening Methods of Plant Activators

The screening of plant activators involves several methodologies to identify compounds that effectively enhance plant resistance [66]. One common approach is using living plants combined with symptom or disease severity observation, where plants are treated with potential activators and then exposed to pathogens; the reduction in disease symptoms indicates the efficacy of the activators (Table 1) [67]. Additionally, the detection of effector markers from the SA signaling pathway is employed, using techniques such as quantitative PCR or Western blotting to measure the expression levels of key markers like PRs, which indicate the activation of the pathway (Table 2) [68,69]. Determining action sites using transgenic or mutant plants is another vital method; genetically modified plants with specific mutations or transgenic expressions help pinpoint where and how activators interact with the plant's defense mechanisms (Table 3) [70]. Molecular biology screening models further enhance these methods by employing high-throughput techniques such as gene expression profiling, proteomics, and metabolomics to comprehensively analyze the effects of potential activators at the molecular level [71]. Together, these screening methods provide a robust framework for identifying and understanding the mechanisms of effective plant activators [72,73].

Table 1. The screening model of the living plant against many phytopathogens.

Plants	Plant species	Pathogen names	Evaluation index	References
Cucumber	No mention	*Colletotrichum lagenarium* (Paserini) Ell. & Halst	Infected leaf area	[292,293]

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Tobacco	*N. tabacum* cv. Xanthi nc	TMV	Lesion size	[294]
	N. tabacum cv. Xanthi nc	*Oidium lycopersici*	Lesion size	[119]
	N. tabacum cv. Xanthi nc	*Pst*	CFU or disease severity	[290]
	N. tabacum cv. Xanthi nc	*Cercospora nicotianae*	Infected leaf area	[290,295]
	N. tabacum cv. Xanthi nc	*Peronospora tabacina*	Infected leaf area	[290]
	N. tabacum cv. Xanthi nc	*Erwinia carotovora*	Length of infected stem	[290,296]
	N. tabacum cv. Xanthi nc	*Phytophthora parasitica*	Disease severity	[297]
	A. thaliana	*Peronospora parasitica* pv. Emwa	Disease severity	[171,299]
Rice	*Oryza sativa* cv. Aichiasahi	*M. grisea*	Lesion number	[178,298]
	O. sativa cv. Aichiasahi	*X. oryzae* pv. *oryzae*	Lesion length	[202]

Table 2. The markers in SA or JA signal pathway and the related methods.

Plant	**Signal pathways**	**Effector markers**	**Methods**	**References**
Tobacco	SA	SA (free SA)	Organic solvent extract coupled with HPLC	[178,301]
		SA (total SA)	Methanol extract coupled with the high-performance liquid chromatographic	
		SA (SAG)	Methanol extract coupled with the high-performance liquid chromatographic	[18]
Tobacco	SA	*PR-1*	Northern blotting	[302]
		PR-1	Western blotting	[172]

	SA	*PR-2*	Northern blotting	[302]
	SA	*PR-3*	Northern blotting	[303]
	SA	*PR-4*	Northern blotting	[304]
	SA	*PR-5*	Northern blotting	[155]
Arabidopsis	SA	*PR-1*	Northern blotting,	[170]
	SA	*PR-2*	Northern blotting,	[170,305]
	SA	*PR-5*	Northern blotting,	[170] [122]
Tomato	SA	*β*-1, 3-glucanase	Western blotting	[306]
Tobacco	JA	*PDF1.2*	Northern blotting,	[307]

Table 3. The transgenics plant or mutant gene and their corresponding the detection methods.

Transgenics or mutants	**Plants**	**Action sites**	**Signal pathways**	**References**
NahG transgenics	Tobacco	SA level	SA	[9,170,294,308,310]
SABP2-silenced transgenic	Tobacco	SA level	SA	[111]
nim mutant	*A. thaliana*	Downstream of SA	SA	[299]
npr1 mutant	*A. thaliana*	Downstream of SA	SA	[20]
etr1 mutant	*A. thaliana*		ET	[312]
ein2 mutant	*A. thaliana*		ET	[313]
jar1 mutant	*A. thaliana*		JA	[314]

2.1.2. Interaction Study of Target-Plant Activator

The study of interactions between plant activators and their targets involves understanding the SA signal pathway, which plays a crucial role in plant immunity [74]. This pathway is significant for its role in SAR, a defense mechanism that provides long-lasting protection against a broad spectrum of pathogens [4]. When a plant activator targets the SA pathway, it typically enhances the production and accumulation of SA, which in turn activates downstream defense genes, such as PRs [75]. These proteins bolster the plant's immune response, making it more resistant to subsequent pathogen attacks [74]. The interaction studies often focus on how activators influence key components of the SA pathway, including *NPR1*, a regulatory protein that controls the expression of defense genes, and *EDS1*, which is involved in signaling processes leading to SAR [76]. By using techniques such as gene expression analysis, protein-protein interaction assays, and mutant plant studies, researchers can elucidate how specific activators modulate the SA pathway, thereby providing insights into their bioactivity and potential effectiveness as plant defense enhancers (Table 4) [77].

Table 4 The proteins physically interacted with SA.

Table 4. Proteins interacting with SA in plant systems.

Proteins interacted with SA	Sources	Ligands	References
Catalase	*N. tabacum*	^{14}C-SA	[315]
Methyl esterase	*N. tabacum*	^{3}H-SA	[316,317]
Carbonic anhydrase	*N. tabacum*	^{3}H-SA	[318]
A protein with ankyrin repeat and BTB/POZ domain	*A. thaliana*	Genetics/T-DNA mutant	[319]
CUL3 adapter protein	*A. thaliana*	Genetics/NPR1 paralog	[320]
CUL3 adapter protein	*A. thaliana*	Genetics/NPR1 paralog	[320]
Ascorbate peroxidase	*N. tabacum*	^{3}H-SA	[321]
E2 subunit of α-ketoglutarate dehydrogenase 2	*A. thaliana*	4-azido SA, SPR	[322]
Glutathione *S*-transferase 2	*A. thaliana*	4-azido SA, SPR	[1]
Glutathione *S*-transferase 8	*A. thaliana*	4-azido SA, SPR	[321]
Glutathione *S*-transferase 10	*A. thaliana*	4-azido SA, SPR	[322]
Glutathione *S*-transferase 11	*A. thaliana*	4-azido SA, SPR	[93]

2.2. Plant Activators against the SA Signal Pathway

Plant activators against the SA signal pathway play a crucial role in enhancing plant immunity by inducing various components upstream or downstream of the SA signal pathway [4,78].

2.2.1. HrBP1

So far, rarely research reported HrBP1 and its biology function [79]. HrBP1 was firstly isolated from a cDNA library of *Arabidopsis thaliana* [9]. This protein was found to locate in the plant cell wall [80]. Activated HrBP1 can prime many signal pathways containing with SA, ethylene (ET), and so on [80]. HrBP1 was participated in forming of the ion channel locating at the plant cell wall with the role of the signal transduction [81]. So far, the sequence of HrBP1 from various species indicated that HrBP1 is very evolutionarily conserved [82]. Harpins are secreted by gram-negative phytopathogenic bacteria harboring the hypersensitive response and *pathogenicity* (*hrp*) gene cluster, which were controlled by the secretion channel of three types [83,84]. These proteins possess the characteristics of glycine- or cysteine- rich, thermal stability and proteinases stable. Harpin was firstly isolated from *Erwinia amylovora*, and identified as an hypersensitivity (HR)-elicitor, then it was also identified from *E. chrysanthemi*, *Pseudomonas syringae*, *Ralstonia solanacearum*, and *Xanthomonas*, and named to hrpNEch, hrpZ, popA, and harpin-like Hpa1 [85–87]. Spraying harpins on the fruit or leaf of apple tree can enhance plant resistance, and then reduce the disease severity of the fruit infected by *Penicillium expansum* [88]. For citrus black spot caused by *Guignardia citricarpa*, spraying harpins on the fruit of citrus can reduce the number of the lesion and pycnidia of the pathogen [89]. Spraying harpins on tomato leaf can enhance the activity of POD, and reduce the disease severity caused by *phytophthora infestans* and *Ps. syringae pv. tomato* [90]. Pretreated harpin can reduce the numbers of lesions in citrus leaf cauased by *X. axonopodis pv. citrumelo* and *X. axonopodis pv. Citri* [91]. Postharvest application of harpin can reduce the size of lesion in hami melons inoculated with *Trichothecium roseum* [92]. In addition, spraying harpin can promote the growth of plant and increase production during the early growth stage of plants [93]. For the blue mold of apple fruit caused by *Pe. expansum*, pretreated harpin can intensify cell wall density. The morphological observation found that tannin vacuoles and appositions were accumulated in the epidermal and hypodermal cells, and the growth of mycelial was delayed [94]. Harpins can elicit the alkalinization of plant cells and generate a reactive oxygen species (ROS) burst, and induce plant cell apoptosis when the plant host was infected by the pathogens [95]. Harpin Psph can induce the expression of *HIN1* gene, which belongs to tobacco *PR* gene, as well as the gene of *8-kD salicylic acid-responsive mitogen-activated protein kinase* (*MAPK*) [84]. Meanwhile, harpin can activate plant the SA signal pathway by inducing *PR-1* mRNA and increasing the SA amount [96]. Spraying *Ps. syringae pv. Syringae* 1.3 S on apple peel can induce the accumulation of *PR-1a, PR-2, PR-5*, and *PR-8* [97]. Meanwhile, harpin cannot activate plant the SA signal pathway for *NahG* transgenic *A. thaliana* and *nim1* mutants plant [98]. The latter is defective in responding to methyl jasmonate or ethylene dependent signal pathway. These results indicated that Harpin act in the upstream of SA in the SA signal pathway [99]. Harpin can bind the HrBP1 to form a protein-protein complex. A study speculated that the complex was changed in the spatial structure, then activate the SA signal pathway [100]. HrpZpss can bind the cell wall of tobacco suspension cell or living cell of tobacco leaf, but was failure to bind the protoplasm without cell wall. These results indicated the action site located on the plant cell wall [100].

2.2.2. Validamycin A and Validoxylamine A (VMA)

These antibiotics, derived from the bacterium Streptomyces hygroscopicus var. limoneus, are known to induce SAR in plants [101]. They function by triggering the SA pathway, leading to increased resistance against a variety of pathogens [46]. VMA, whose chemical name is ([1S-(1α, 4α, 5β, 6α]-1, 5, 6-trideoxy-4-O-β-D-glucopyranosyl-5-(hydroxymethyl)-1-[[4, 5, 6-trihydroxy-3-(hydroxymethyl)-2-cyclohexen-1-yl]amino]-D-chiro-inositol-1L-(1, 3 , 4/2, 6)-2, 3-dihydroxy-6-hydroxymethyl-4-[(1S, 4R, 5S, 6S)-4, 5, 6-trihydroxy-3-hydroxymethylcyclohex-2-enylamino] cyclohexyl-3-D-glucopyranoside), is an aminoglucoside compound. The first aminoglycoside, streptomycin was isolated from Streptomyces griseus in 1943; neomycin was isolated from Streptomyces fradiae. This antibiotic was very effective against (Figure 2b) [46,102]. Validoxylamine A (VAA), whose chemical name is ([1S-(1α, 4α, 5β, 6α)]-1, 5, 6-trideoxy-5-(hydroxymethyl)-1-[[4, 5, 6-trihydroxy-3-(hydroxymethyl)-2-cyclohexen-1-yl] amino]-D-chiro-inositol), is an aglycon of VMA [103]. The mechanism of inhibiting pathogens for VMA and VAA involves two types of action: direct inhibition and induction of plant resistance. For instance, VMA can inhibit the growth of fungi in vitro by decreasing trehalase activity [104].

In addition, pretreated by VMA and VAA can reduce disease severity in tomato and cabbage infected by Ps. solanacearum, Xanthomonas campestris pv. campestris and Fusarium oxysporum f. sp. Lycopersici [105]. These results indicated that VMA and VAA possess the inductive activity [106]. VMA and VAA can accumulate the effector marker in the SA signal pathway in tomato leaf, such as PR-1, PR-2, and PR-5. The inductive effect of two compounds is similar to that of BTH [107]. VMA and VAA can also enhance the amount of free SA from the sprayed leaves and the upper leaves in tomato. For the treatment of above two compounds, the amount of free SA in the upper leaves is significantly higher than that of sprayed leaves [108]. Comparing with the content of SA in the upper leaves, the induction ability of VMA and VAA is significantly higher than that of PBZ treatment [109]. Above results indicated that VMA and VAA act at the upstream of SA in the SA signal pathway [106]. The study by Yang, et al. [110] which exhibited significant antiviral activity against the pepper mild mottle virus (PMMoV). Among these, compound A32 showed superior efficacy compared to the standard antiviral agents. The study also included a 3D-QSAR model to understand the structure-activity relationships, indicating the potential of these compounds for further antiviral development. The study of bioassays exposed that many of the title compounds exhibited moral inhibitory activities against TMV in vivo condition [111]. The study explores the creation and antibacterial properties of new benzofuran derivatives that include disulfide groups [112]. These compounds demonstrated significant antibacterial activity against various strains, and mechanistic studies revealed their ability to disrupt bacterial cell walls and interfere with protein synthesis. This research highlights the potential of these novel derivatives as effective antibacterial agents. Bai, et al. [113] study describes the creation of new antiviral compounds by combining indole and 4, 5-dihydro-1H-pyrazoline structures. These novel agents were tested against the potato virus Y (PVY), showing significant antiviral activity. Notably, one compound, D40, exhibited superior curative and protective effects compared to the commercial antiviral agent Ningnanmycin, enhancing key defense enzyme activities and regulating the carbon fixation pathway in plants. Zhang, et al. [114] indicated that some novel mesoionic pyrido [1, 2-a] pyrimidinone compounds featuring a dithioacetal group showed significant insecticidal activity against bean aphids and white-backed planthoppers. However, their effect on disease resistance is not addressed. In particular, compound 34 demonstrated superior insecticidal properties with an LC_{50} value of 2.80 μg/mL, outperforming the commercial insecticide trifluoropyrimidine. The study suggests that these compounds act on nicotinic acetylcholine receptors, highlighting their potential as new insecticidal agents. Nonetheless, their role in inducing resistance in plants remains unexplored.

2.2.3. Probenazole (PBZ)

PBZ is a synthetic plant activator widely used in agriculture, especially in Japan, to control rice blast disease [115]. It works by stimulating the SA pathway, which enhances the plant's natural defense mechanisms and increases resistance to the rice blast pathogen [116]. PBZ, whose chemical name is 3-allyloxy-1, 2-benzisothiazole-1, 1-dioxide, was developed as fungicides by Meiji Seika (Janpan) Co., Ltd (Figure 2c) [117]. During the 70-90s of the last century, PBZ was developed as plant protective agent (trade name: *Oryzaemat*e) by Meijiseika *Co.,* Tokyo, Japan, and widely used to prevent and control rice blast and rice bacterial blight in Asia [118]. It can induce the plant resistance against TMV, Pst, and *Oidium SP.* [119].

PBZ can up-regulate some defense-related genes of rice host, such as *peroxidase* (*POD*) and *chitinase* and *PR* genes [120,121]. It can also induce the mRNA accumulation of *PR-1*, *PR-2*, and *PR-5* in *A. thaliana* leaves, and the amount of *PR-1* is increased in the manner of dose dependent [26,122]. PBZ also enhance the activity of defense-related enzymes, such as phenylalanine ammonia-lyase (PAL), POD, and PBZ cannot induce the SA accumulation and up-regulate *PR-1* mRNA for *Salicylate hydroxylase* (*NahG*) transgenic *A. thaliana* and the signaling mutants *npr1-1* [60,123,124]. Meanwhile, PBZ did not exhibit an inductive effect on *NahG* transgenic tobacco [125]. These results indicated that PBZ can act upstream of SA in the SA signaling pathway (Figure 3). 1, 2-Benzisothiazol-3(2H)-1, 1-dioxide (BIT), also known as Saccharin, was identified as the active metabolite of PBZ [60]. BIT is found using a cultured parsley cells combined with spectrophotometric measurement of coumarin [126]. Then, spraying BIT can inhibit the growth of Pst tomato DC3000 in *A. thaliana* leaves (Figure 2d) [122]. Soil drench using BIT can also enhance the plant resistance against tobacco, cucumber and bean infected with TMV*, Colletotrichum lagenarium, Uromyces appendiculatu* [44]. BIT can accumulate total SA in plant host, and up-regulate the *mRNA* of *PR-1*, *PR-2*, and *PR-5* in plant leaves [122,127]. Interestingly, PBZ can induce *PBZ1* mRNA, namely *PR-10* mRNA, but BIT be failure at the gene for rice suspension cells [128]. In addition, *PBZ1* mRNA can be induced by rice blast fungus, but not correlated with the resistance of rice blast [129].

2.2.4. (D, L)-3-Aminobutyric Acid (BABA)

BABA is a non-protein amino acid that induces resistance in plants by activating the SA pathway [130]. It primes the plant's immune system, leading to a faster and stronger defense response upon pathogen attack. BABA was firstly found to increase resistance of pea plants for the oomycete *Aphanomyces euteiches* [131]. Then, BABA was found to induce plant resistance against many plant diseases, such as many fungal, bacterial, and viral pathogens [132]. BABA can accumulate the intercellular fluid extract from *N. tabacum cv. Xanthi-nc* leaves, which was identified as PRs [133]. It can increase the amount of P14a. P14a is a type of peptidylglycine α-amidating monooxygenase (PAM), an enzyme that catalyzes the conversion of glycine-extended peptides to their amidated forms, which are often crucial for their biological activity. P14a likely refers to a specific PAM isoform or variant involved in a particular biological process or the pathway realated with β-1, 3-glucanase and chitinase in tomato plant leaves, and it enhance the activity of these enzymes [134]. For un-sprayed leaf, the amount of *PR-1* mRNA was enhanced by BABA treatment; the inductive effect indicated that BABA is a systematic inducer [135]. Nevertheless, BABA cannot enhance plant resistance for *NahG* transgenic tobacco infected by TMV [60]. The result indicated that BABA act at the up-stream of SA in the SA signal pathway. In addition, many studies represent that BABA is also involved with HR or direct inhibitory effect against pathogens [60,136].

2.2.5. Imprimatins

These synthetic compounds are known to enhance plant immunity by activating the SA pathway [46]. Imprimatins increase the levels of SA and promote the expression of defense-related genes, thereby boosting the plant's resistance to pathogens [46]. After plant being infected by the pathogens, the level of SA always increases and reaches at 10-20 fold for generating plant defence response [137]. Salicylic acid glucosyltransferase (SAGT) is responsible for transforming SA to its inactive metabolites, 2-O-beta-D-glucose and SA glucose ester [138,139]. So, SAGT possess the role of decreasing the SA level and maintaining a homeostasis of the SA amount in the plant host. A model system of the suspension cultured cells of A. thaliana infected with the bacterial pathogen Pst DC3000 avrRpm1 was used to screen the molecules with the characteristic of only strengthening plant resistance but not triggering plant resistance [140]. Imprimatins A and B were finally screened from above model system (Figure 3a to f), and these compounds can increase the SA level in A. thaliana plant after inoculated by the bacterial avirulent strain or the virulent strain, then generate a strong plant resistance [141]. At an effective concentration of inducing plant disease resistance, imprimatins compounds can block the activity of SAGT mutants in vitro (Figure 4). The results indicated that SAGT can competitively bind with imprimatins to SA [142].

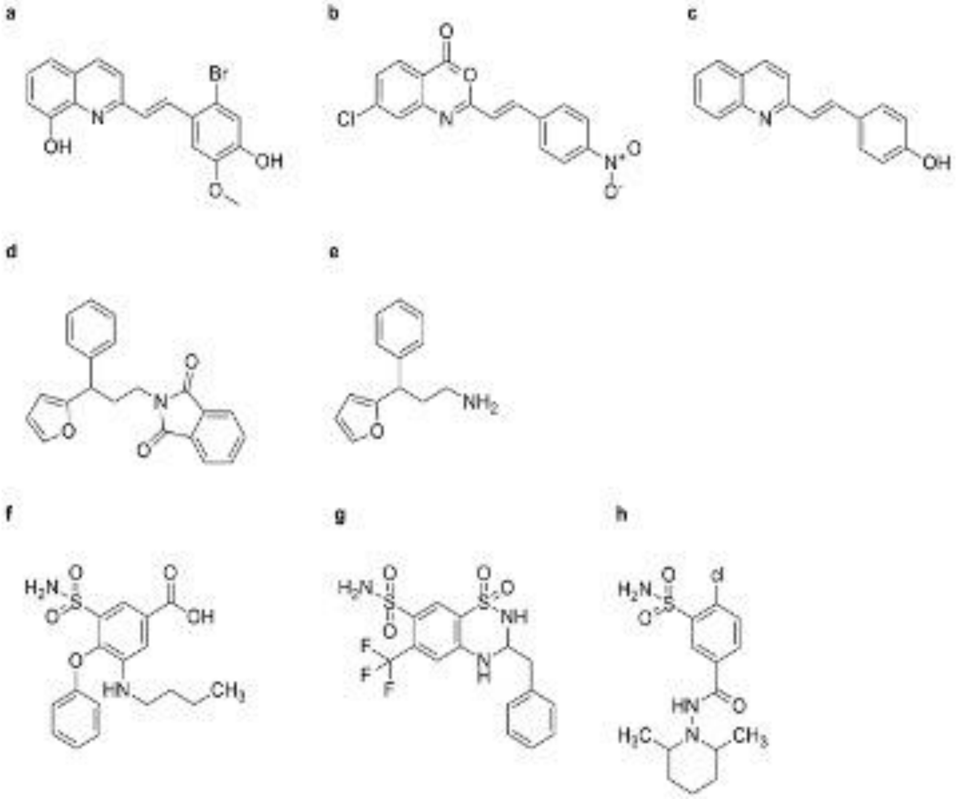

Figure 4. The molecule structure of Imprimatins and diuretics compounds. (a) Imprimatins A1. (b) Imprimatins A2. (c) Imprimatins A3. (d) Imprimatins B1. (e) Imprimatins B2. (f) Bumetanide. (g) Bendroflumethiazide. (h) Clopamide.

2.2.6. Diuretics

Certain diuretic compounds have been found to act as plant activators by inducing the SA pathway [143]. These compounds enhance the plant's defense responses, making them more resistant to various diseases. Three diuretics of 3-(butylamino)-4-phenoxy-5-sulfamoylbenzoicacid (Bumnide, MBT) (Figure 3f). 3-benzyl-1, 1-dioxo-6-(trifluoromethyl)-3, 4-

dihydro-2H-1, 2, 4-benzothiadiine-7-sulfonamide (Bendroflumethiazide, BFM) (Figure 3g), and 4-chloro-N-(2, 6-dimethyl-1-piperidyl)-3-sulfamoyl-benzamide (Clopamide, CLP) (Figure 3h), were screened via the model system of suspension cultured cells above described [144]. These compounds can promote cell death caused by Pst *avrRpm1* in a concentration-dependent manner, but their effects were weaker than that of SA. Three compounds can enhance the resistance of *A. thaliana* seedlings against Pst *avrRpm1* and Pst. After *A. thaliana* seedlings infected by Pst, three diuretics can accumulate *PR-1* mRNA [145]. Differing from the action mechanism of imprimatins A and imprimatins B, MBT and BFM can inhibit the activity of SAGT, and then SA is allowed to be degraded by SAGT. Nevertheless, CLP cannot nearly inhibit SAGT [146]. These upstream activators are crucial for the activation of the SA pathway, which is essential for the plant's immune response. By inducing the production and accumulation of the SA, these compounds help to strengthen the plant's defense mechanisms, providing long-lasting protection against a wide range of pathogens.

3. Plant Activators Acted in the Downstream of SA in the SA Signal Pathway

3.1. Downstream Activators

Downstream activators play critical roles in enhancing the SA signaling pathway, which is essential for plant immunity [74].

3.1.1. Benzothiadiazole (BTH)

BTH, also known as acibenzolar-S-methyl, is a synthetic analog of SA that acts downstream in the SA signaling pathway [147]. It mimics SA's effects, inducing the expression of defense genes and enhancing disease resistance.

BTH, chemically named *S-methyl benz* [1, 2, 3] *thiadiazole-7-carbothioate*, was first reported by Schurter, et al. [148,149] (Figure 5a). Subsequent studies by schurter and colleagues systematically explored various bioassay models of plant activators, finding that the cucumber-colletotrichum lagenarium model was superior in resistance response and experimental stability compared to other plant-pathogen models such as cucumber/*Ps. lachrymans*, wheat/*E. graminis*, and tomato/*Ph. infestans* [150]. Field and greenhouse trials confirmed BTH's high protective activity, leading to its development by *Novartis/Syngenta* under the trade name "*Bion*" [151,152]. BTH is metabolized by salicylic acid binding protein 2 (SABP2) into acibenzolar, its active form, which induces SAR in various plants including *A. thaliana*, tobacco, tomato, cucumber, wheat, sunflower, rice, maize, cotton, and soybean against multiple pathogens like TMV, turnip crinkle virus, wheat powdery mildew, *Peronospora sparsa*, *Ps. syringae*, *F. oxysporum*, *Sclerotinia sclerotiorum*, and cucumber mosaic virus [44,153-164]. BTH also inhibits nematode reproduction, specifically *Meloidogyne incognita*, when root-dipped [165]. For wheat infected by *E. graminis*, BTH spray can reduce pathogen proliferation at multiple stages of infection [166]. In tomatoes, BTH increases root cell wall density, reducing *F. oxysporum* entry [167]. In strawberries, BTH pretreatment increases phenolic compounds in leaves infected by powdery mildew [168]. For sugar beet roots infected by Beet necrotic yellow vein virus (BNYVV), BTH accumulates β-1, 3-glucanase and class IV chitinase in cortical and endodermis cells [169]. BTH induces accumulation of *PR-1, PR-2,* and *PR-5* mRNA in *A. thaliana* leaves [170]. It also stimulates the expression of resistance-related genes in wheat [171]. Proteomic analyses, such as two-dimensional gel electrophoresis coupled with mass spectrometry, have shown that BTH up-regulates the SA pathway-related proteins in *Arctic bramble* and induces PAL and PRs expression in rice [171]. BTH induces *PR* genes in ethylene-response and methyl jasmonate-insensitive mutant plants, indicating that BTH operates independently of JA and ET pathways [141]. BTH also accumulates *PR-1* gene expression in *NahG* transgenic tobacco, suggesting its action is downstream of SA (Figure 6,7) [172]. For BTH's action mode, acibenzolar can induce *PR-1a* gene in SABP2-silenced tobacco, confirming SABP2 as a metabolic target [173]. In rice, BTH pretreatment up-regulates *OsWRKY45* and *OsWRKY13*, transcription factors responsible for *PRs* gene expression [173,174]. This indicates that acibenzolar, the active form of BTH, induces *WRKY* transcription factors to regulate *PRs* genes, although the precise regulatory mechanism remains unclear [174].

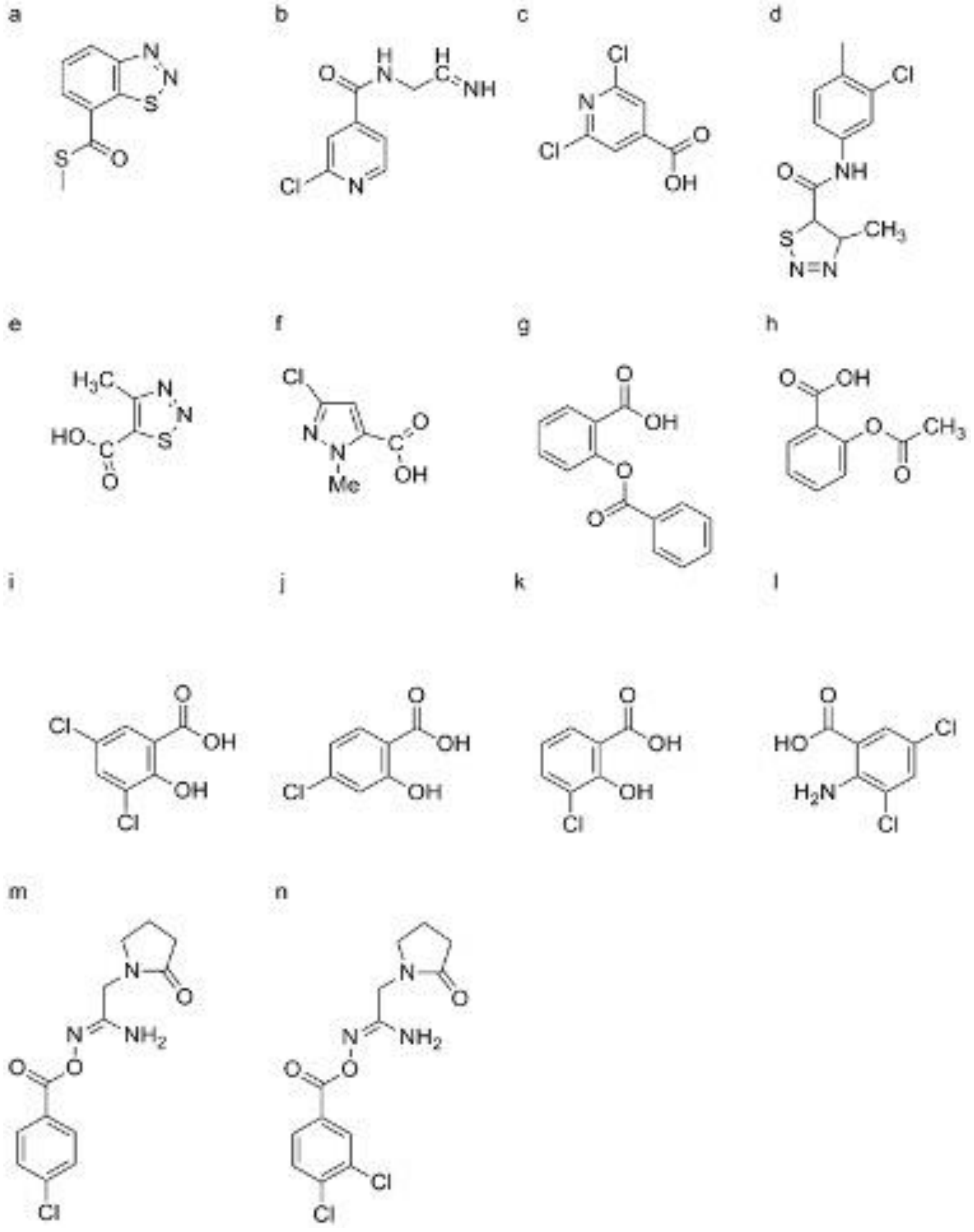

Figure 5. Some molecules act in SA downstream in SA signal pathway.

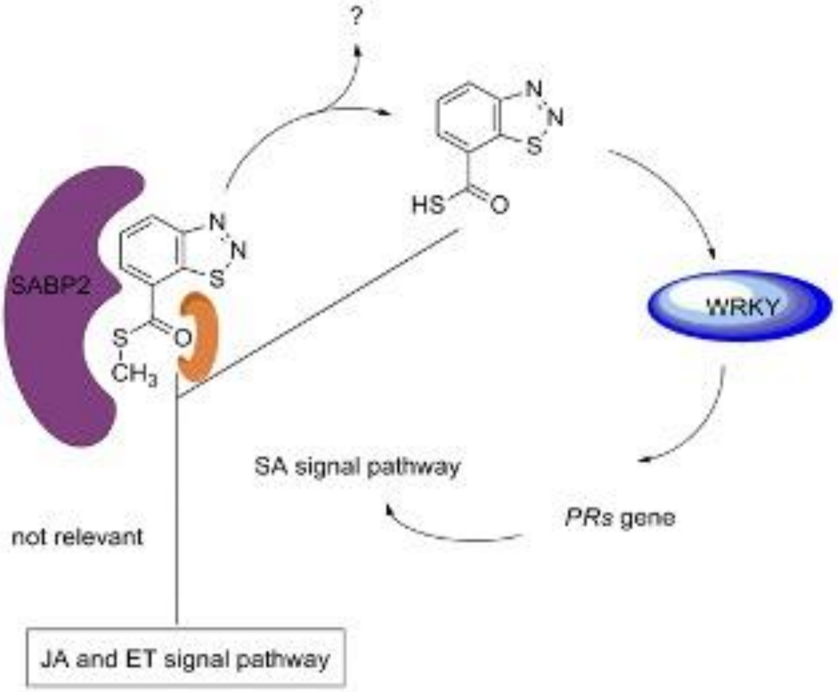

Figure 6. The action mechanism of BTH.

3.1.2. N-Cyanomethyl-2-Chloroisonicotinamide (NCI)

NCI was first synthesized and identified for its protective activity against the rice/Pyricularia grisea model (Figure 5b) [175]. Subsequent studies have demonstrated NCI's broad-spectrum protective efficacy against various pathogens in multiple plant species, including Ps. syringae pv. tomato (Pst) and Xanthomonas oryzae [176]. Remarkably, NCI's protective activity against Py. grisea is significantly higher than that of PBZ [44]. Pretreatment with NCI significantly reduces lesion sizes in NahG transgenic tobacco plants infected by TMV and Oidiopsis lycopersici [177,178].

Additionally, the derivatives of NCI, such as N-methyl-2-chloroisonicotinamide and N-propargyl-2-chloroisonicotinamide, exhibit superior protective activity against rice blast [179]. NCI is known to induce the accumulation of mRNAs for the defense-related genes of PR-1, PR-2, and PR-5 in A. thaliana leaves without altering the levels of SA [177]. Similarly, NCI pretreatment induces these PRs genes in both wild-type and NahG transgenic tobacco leaves [180]. In rice leaves, NCI can also induce the expression of PR-10 (PBZ1 gene), and enhances PAL activity [126,181]. Importantly, pretreatment with NCI does not alter the levels of free and total SA in tobacco leaves. These findings indicate that NCI acts downstream of SA in the SA signaling pathway (Figure 7) [182]. Recent studies supported NCI’s role as an effective plant activator. For instance, research has shown that NCI can enhance resistance in a range of crops, contributing to sustainable agricultural practices by reducing the reliance on traditional chemical pesticides [183]. The recent study about the precise molecular mechanisms of NCI’s action and its integration into plant immune networks continue to be areas of active investigation [184].

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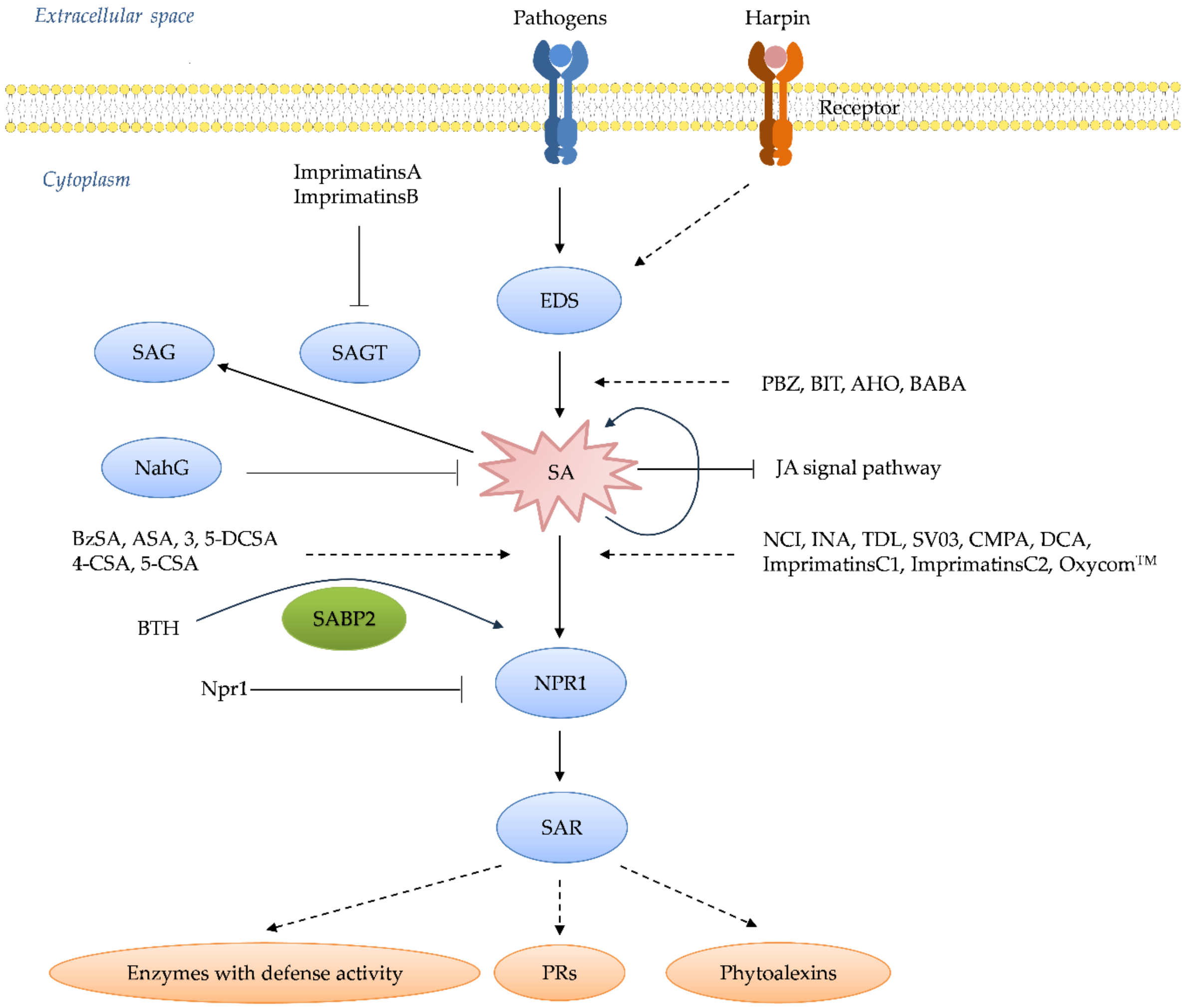

Figure 7. The action sites of some plant activators against SA signal pathway.

3.1.3. 2,6-. Dichloroisonicotinic Acid (INA)

INA, a derivative of isonicotinic acid, exhibits notable resistance-inducing properties in various plant species (Figure 5c) [184]. Originally observed in cucumber infected with C. lagenarium, subsequent studies have extended its protective effects to a wide array of plant-pathogen interactions [185]. These include defense responses in tobacco against TMV, A. thaliana against Pst, sugar beet against Cercospora beticola, rose against Sphaerotheca pannosa, barley against E. graminis f. sp. Hordei, and soybean against Sc. sclerotiorum, among others [186]. Field trials with INA have demonstrated its efficacy in enhancing resistance against pathogens such as Uromyces appendiculatus in beans and Alternaria macrospora in cotton seedlings [187]. Furthermore, INA treatments have shown positive effects on seed germination and plant growth, as evidenced by increased shoot and root lengths in INA-treated tomato seeds [188]. Mechanistically, INA elicits the accumulation of PRs gene, including PR-1, PR-2, and PR-5 in A. thaliana and a broader spectrum of PRs gene in tobacco plants [189]. It also induces PRs gene expression in rice, soybean, and tomato, enhancing the activity of defense enzymes such as chitinase and β-1, 3-glucanase [190]. Additionally, INA treatments have been associated with the upregulation of antioxidative enzymes like ascorbate peroxidase (APX) and catalase (CAT), contributing to enhanced defense responses in plants [191]. Furthermore, INA has been shown to accumulate intercellular washing fluid (IWF) in sugar beet leaves, leading to increased defense against pathogens such as C. beticola [192]. At a molecular level, INA primes SAR in tobacco plants by inducing PRs genes in NahG transgenic plant, thereby inhibiting TMV replication without altering the SA content [60]. However, this priming effect is impaired in A. thaliana mutants lacking functional NPR1 or NIM1 protein. Ramadass et al., [61] highlighted the essential role of these proteins in SAR signaling, suggesting the involvement of INA in the SA signaling pathway between SA and NPR1. Indeed, INA has been demonstrated to bind to SABP in vitro, potentially activating the SA signaling cascade [193,194]. Furthermore, affinity chromatography studies have identified INA's interaction with BTH-binding protein kinase (BBPK), implicating it as a potential target protein for INA-mediated signaling [194]. These findings underscore the need for further investigation into the precise mechanisms by which INA activates the SA signaling pathway and its interactions with key regulatory proteins like SABP and BBPK (Figure 7) [195].

3.1.4. Tiadinil (TDL)

N-(*3-chloro-4-methylphenyl*)*-4-methyl-1, 2, 3-thiadiazole-5-carboxamide*, is the another name of TDL was introduced by Nihon Nohyaku Co., Ltd., and registered as a commercial pesticide for combating rice blast disease in Japan in 2003 (Figure 5d) [196]. Upon application, TDL undergoes conversion into its active metabolite, 4-methyl-1, 2, 3-thiadiazole-5-carboxylic acid (SV03), which serves to prime plant SAR (Figure 5e) [197]. Although TDL does not directly inhibit pathogen proliferation *in vitro*, the bioassays have demonstrated its efficacy in inducing resistance against rice blast and inhibiting the proliferation of pathogens of viral disease, bacterial disease, gray blight and anthracnose of tea tree [196,198]. Moreover, TDL has been shown to enhance the production of certain plant volatiles, indirectly suppressing herbivorous mites [199]. At the molecular level, TDL induces the expression of genes involved in the SA signaling pathway in tobacco leaves without altering the SA levels, suggesting its action downstream of the SA pathway [200]. Similarly, SV03 induces the accumulation of *PR-1a, PR-2,* and *PR-5* mRNA in *NahG* transgenic tobacco leaves, and exhibits efficacy in inhibiting Pst proliferation and reducing lesion size in tobacco leaves infected with TMV [176, 201]. These findings underscore the potential of TDL and its active metabolite SV03 as effective tools for enhancing plant resistance against various pathogens, providing insights into their mode of action within the SA signaling pathway (Figure 7) [202].

3.1.5. 3-chloro-1H-pyrazole-5-carboxylic acid（CMPA）

A pyrazole derivative, CMPA, can reduce the disease symptoms of rice bacterial leaf blight in a dose-dependent manner, but it did not inhibit the proliferation of *X. oryzae*. CMPA can induce *PBZ1* mRNA in rice and tobacco, then activate SAR. Nevertheless, CMPA cannt induce SA accumulation in tobacco (Figure 5f,7) [203–205].

3.1.6. Benzoylsalicylic acid (BzSA) and acetylsalicylic acid (ASA)

Endogenous SA serves as a key regulator of the SA signaling pathway, influencing SAR against various plant pathogens [206]. External application of SA, particularly during early disease stages or at the seedling stage, has been shown to confer protective effects against a wide range of plant diseases caused by viruses, bacteria, and fungi [207]. This exogenous SA treatment induces the upregulation of PRs genes in tobacco, enhancing resistance against pathogens such as TMV [208,209]. Similarly, in tomato leaves, SA treatment followed by inoculation with Cladosporium fulvum leads to the accumulation of mRNA related to the SA signaling pathway, including extracellular PR-1, intracellular β-1, 3-glucanase, extracellular β-1, 3-glucanase, extracellular chitinase, and extracellular PR-4 [210]. Furthermore, SA plays a pivotal role in regulating R-gene mediated local disease resistance mechanisms [74]. As a derivative of SA, benzoylsalicylic acid (BzSA), also known as 2-(benzoyloxy) benzoic acid, has been isolated from the seed coats of Givotia rottleriformis (Figure 5g) [211]. Spraying BzSA has been demonstrated to reduce lesion number and size in tobacco leaves infected with TMV [212]. Moreover, BzSA treatment induces the accumulation of PR-1 and PR-5 mRNA and upregulates the expression of MYB and WRKY genes in both wild-type tobacco and transgenic NahG tobacco (Figure 7) [213]. Comparative analyses have revealed that BzSA exhibits higher efficacy in regulating marker genes of the SA signaling pathway and inhibiting TMV proliferation compared to SA and ASA (Figure 5h) [214]. Furthermore, injection of tobacco plants with ASA and benzoic acid derivatives has been shown to induce PRs mRNA expression and enhance tobacco resistance to TMV [215]. These findings underscore the potential of SA derivatives such as BzSA and ASA as effective tools for enhancing plant resistance against pathogens, offering valuable insights into their mechanisms of action and their applications in agricultural disease management strategies (Figure 7) [216].

3.1.7 3,5-. dichlorosalicylic acid (3, 5-DCSA), 4-chlorosalicylic acid (4-CSA), and 5-chlorosalicylic acid (5-CSA)

3, 5-DCSA, 4-CSA, and 5-CSA have demonstrated the ability to enhance disease resistance in tobacco against TMV infection, with reduction rates in lesion size of 70.0±16.0%, 76.0±11.0%, and 66.0±9.0%, respectively (Figure 5i-k) [217]. However, their potency in inducing disease resistance is slightly weaker compared to that of SA, which achieves a reduction rate in lesion size of 80.3±7.2% [218]. These SA analogs also exhibit the capability to accumulate PR-1 in tobacco leaves, albeit with slightly lower induction effects than SA [219]. These chlorinated derivatives of SA offer potential advantages over SA itself, such as increased stability, prolonged activity, and reduced phytotoxicity (Figure 7) [220]. However, their effectiveness and mechanisms of action may differ, and further research is needed to fully understand their potential as plant activators targeting the SA signal pathway [47].

3.1.8. Dichloroanthranilic acid (DCA)

DCA, identified through screening using the late/sustained up-regulation in response to Hyaloperonospora parasitica (LURP) cluster as a defense gene marker in A. thaliana, has been found to enhance disease resistance against virulent strains of the oomycete Hpa and Ps. syringae DC3000 (Figure 5l) [221]. DCA induces the accumulation of PR1 and WRKY70 mRNA in plants, but does not lead to the SA accumulation [222]. Notably, DCA's inductive effect is independent of the NPR1-mediated pathway in npr1 mutants of A. thaliana but is blocked by the WRKY70 mutant, indicating its action downstream of SA in the SA signaling pathway, distinct from other compounds such as BTH, NCI, and INA [221].

3.1.9. Imprimatins C1 and Imprimatins C2

Analogous to SA, imprimatins C1 and imprimatins C2 induce cell death in *Arabidopsis* cells infected with avirulent *Pst-avrrpm1*, demonstrating concentration-dependent effects similar to SA (Figure 5m,n) [117]. These compounds, collectively referred to as "imprimatins C" molecules, induce the accumulation of *PR-1* mRNA in both wild-type and *salicylic acid-induction deficient 2* (*sid 2*) mutant *A. thaliana* seedlings, independent of pathogen infection [142]. However, pretreatment with imprimatins C1 fails to induce the SA accumulation in *A. thaliana* cells, suggesting their action on the downstream of SA in the SA signaling pathway, without activating SA biosynthesis through positive-feedback cycles (Figure 7) [142].

3.1.10. Oxycom™

Oxycom™, a form of peracetic acid, has been observed to elicit a robust resistance response against numerous plant pathogens, particularly affecting leaf, berry, and root diseases [223,224]. For example, pretreatment of tobacco leaves with Oxycom™ has been shown to reduce symptoms caused by Pst infection, with its protective efficacy surpassing that of SA [225]. Furthermore, Oxycom™ demonstrates a distinct ability compared to exogenous SA, significantly enhancing the expression of PR-1a, PR-1g, and PR-3a mRNA in tobacco leaves [226]. Pretreatment with Oxycom™ induces resistance against various pathogens in NahG transgenic tobacco, indicating its action downstream of SA in the SA signaling pathway [178]. Moreover, Oxycom™ has been found to rapidly induce the phosphorylation of Salicylic Acid-Induced Protein Kinase (SIPK) within 1 hour of treatment [227]. There appears to be a correlated dynamic trend between the expression of PR-1a mRNA and SIPK phosphorylation, suggesting that certain defense genes associated with SA signaling pathway may be mediated by SIPK [228]. These findings underscore the potential of Oxycom™ as an effective inducer of plant defense mechanisms, offering insights into its mode of action and its significance in plant disease management strategies (Figure 7) [229].

4. Activators with Unclear Action Sites

Activators with unclear action sites represent a group of compounds that have demonstrated the ability to enhance plant defense mechanisms against pathogens [230,231]. However, the exact pathways through which they exert their effects remain ambiguous [232]. There are some examples of plant activators with unclear or unknown action sites within the SA signaling pathway from previous research. Laminarin is a β-1, 3-glucan derived from brown algae that has been shown to induce defense responses in various plants (Table 1). While laminarin is known to activate the SA pathway, its exact point of action remains unclear. Some studies suggest it may act upstream of the SA biosynthesis, while others propose it acts downstream or in parallel with the SA signaling pathway [233]. Chitosan, a deacetylated derivative of chitin, can induce the SA accumulation and activate defense-related genes in plants [234]. However, the molecular mechanisms by which chitosan triggers the SA pathway are not fully understood [235]. Some researchers suggest it may interact with plant receptors to initiate signaling cascades leading to the SA biosynthesis, while others propose it acts through modulating ROS levels [235]. Hexanoic acid is a natural compound found in plants and has been reported to activate the SA pathway and induce resistance against pathogens [236]. However, the specific targets of hexanoic acid within the SA signaling network remain unclear (Table 2). Some studies suggest it may act upstream of the SA biosynthesis, while others propose it affects downstream components like *NPR1* [74]. Azelaic acid is a dicarboxylic acid produced in plants during pathogen infection and has been shown to induce the SA accumulation and the defense responses [237]. However, the precise mechanisms by which azelaic acid activates the SA pathway are not well understood [2]. Some researchers suggest it may act through modulating lipid-derived signaling molecules, while others propose the direct effects on SA biosynthesis or downstream signaling components [238]. Riboflavin (vitamin B2) has been reported to induce resistance against pathogens in various plants, potentially through activating the SA pathway [239]. However, the specific targets and mechanisms by which riboflavin modulates the SA signaling cascade remain unclear, with some studies suggesting it may act through modulating cellular redox status or interacting with unknown receptors [240]. These examples elucidate that while many compounds have been identified as potential activators of the SA signaling pathway, their precise action sites and molecular mechanisms are often not well characterized [241]. Further research is needed to elucidate the specific targets and modes of action of these activators within the complex the SA signaling network [242].

4.1. 3,4-. dichloro-2′-Cyano-1, 2-Thiazole-5-Carboxanilide (Isotianil)

Isotianil, initially considered a derivative of PBZ, was discovered through the screening of isothiazole compounds by Bayer CropScience AG, and further developed in collaboration with the Japanese company Sumitomo Chemical Co., Ltd., as a plant activator (Figure 8a) [119, 142]. Demonstrating notable efficacy, Isotianil exhibits protective activity against various rice diseases, including rice blast and bacterial leaf blight [243]. Remarkably, even at very low dosages, isotianil can sustain elevated resistance levels for extended durations [29]. Its inductive capacity surpasses that of PBZ and TDL [244]. Isotianil enhances the abundance and activity of defense-related enzymes such as lipoxygenase and PAL. Additionally, it induces the expression of OsWRKY45, a transcription factor responsible for PR gene expression [245].

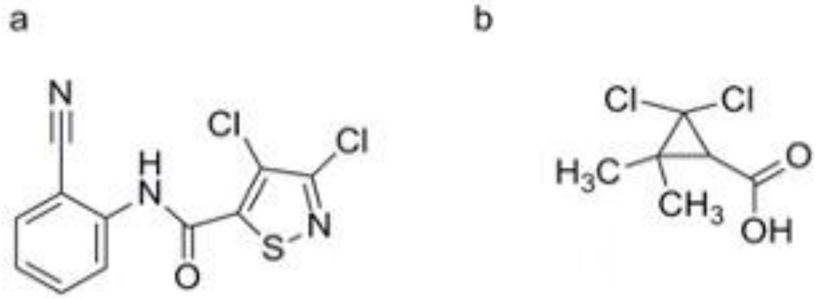

Figure 8. The molecule structrue of Isotianil (a) and DDCC (b).

4.2. Polypeptide-Product

Polypeptide-product, namely "Pen", as a water soluble substances, was isolated from Pe. chrysogenum in 1990s [246]. Foliar spraying or soil drench with "Pen" can induce the plant resistance against many pathogens [247]. The pretreated "Pen" can increase the resistance level of many fruits and vegetables for P. viticola, U. necator, V. inaequalis, P. infestans, C. lagenarium, P. cubensis, and P. destructor, and reduce disease severity [248]. When the acidic dry mycelium extract or the neutralized dry mycelium extract were drenched the roots of melon plants, the treatment can also enhance the resistance level against F. oxysporum f. sp. melonis [249]. These two dry mycelium extracts can increase POD activity of plant host (Figure 5). Polypeptide-product can accumulate the mRNA of many defense genes in the cotton leaves, such as PR-1a, PR-1b, PR-2, PR-3, PR-4, PR-5, and so on. Nevertheless, the acurate action site of Polypeptide-product remains unclear [249].

4.3. β,γ-. Methyleneadenosine 5′-Triphosphate (AMP-PCP)

AMP-PCP, which is a non-hydrolysable analogue of ATP, can enhance tobacco resistance against Pst and TMV [250]. AMP-PCP can accumulate PR-1, PR-2, and PR-5 in tobacco Xanthinc leaves [251]. Massively used AMP-PCP can inhibit the concentration of extracellular ATP (eATP) [252]. Nevertheless, increasing concentration of ATP can block the expression of PR-1 mRNA [253]. So, a lower concentration or deletion status of eATP can prime plant SAR. The action mechanism may be involved with two aspects: 1) ATP block SA synthesis; 2) ATP promote SA degradation. These two aspects lead to SA reduction. So, as an antagonist of ATP, AMP-PCP can be used for plant activator to activate the SA signal pathway [250].

4.4 2, 2-dichloro-3, 3-Dimethylcyclopropane Carboxylic Acid (DDCC)

DDCC has shown promise in preventing rice diseases caused by *Piricularia oryzae* and *Pyriailaria oryzae* (Figure 8b) [254]. Studies have demonstrated that root drenching with DDCC enhances the activity of POD in rice leaves inoculated with *Pi. oryzae* [255]. Moreover, pretreatment with DDCC can induce the production of melanin compounds at infection sites by *Pi. oryzae*, effectively inhibiting the growth of pathogens [256]. Furthermore, DDCC has been found to significantly accumulate phytoalexins, specifically momilactones A and B, in inoculation sites and surrounding tissue in rice leaves infected by *Py. oryzae*. Interestingly, these momilactones were scarcely detected in healthy rice leaves [257]. Momilactones A and B exhibit direct inhibitory effects on fungal growth *in vitro*, with ED_{50} values of 4.8 and 0.9 ng ml^{-1}, respectively (Figure 6). Additionally, these compounds promote hyphal disruption in liquid media, suggesting their role as specialized defense materials against pathogens [258]. However, the precise action mechanism of DDCC remains elusive and requires further investigation [259].

4.5 Hyaluronic Acid (HA)

HA, a linear, unbranching polyanionic disaccharide produced by bacteria, consists of alternately joined glucuronic acid (GlcUA) and N-acetyl glucosamine (Glc-NAc) units through β-1-3 and β-1-4 glycosidic bonds [260]. Recent studies have highlighted its potential as a plant activator, showcasing its ability to enhance protective activity and mitigate disease severity in various plant species [261]. For instance, cucumber infected by C. orbiculare, Ps. syringae pv. lachrymans, tomato infected by Pst, Xanthomonas axonopodis pv. vesicatoria, and pepper infected by CMV have all shown improved resistance upon HA treatment [262]. Interestingly, while HA does not directly inhibit these pathogens in vitro, its application can induce SAR in plants. Furthermore, investigations using a tobacco model with transgenic PR-1a promoter-GUS and PDF1.2 promoter-GUS genes have revealed that HA strongly up-regulates these genes [263]. This observation suggests that HA activates both the SA and JA-mediated signaling pathways, distinguishing it from other known plant activators [262]. This dual activation of the SA and JA pathways by HA underscores its potential as a versatile tool for enhancing plant defense mechanisms against a wide range of pathogens [264].

5. The Development of Plant Activator against the SA Signal Pathway in the World at Present

5.1. Plant Activators Developed in China in Recent Years

In recent years, significant strides have been made in China in researching pesticides and plant protection. For example, researchers have synthesized a series of derivatives based on benzo-1, 2, 3-thiadiazole-7-carboxylic acid, with notable findings (Figure 9a) [265]. One such derivative, benzo-1, 2, 3-thiadiazole-7-carboxylic acid 2-(2-hydroxybenzoxyl) ethyl ester, demonstrated the ability to substantially elevate hydrogen peroxide (H_2O_2) levels and enhance the activity of PAL in taxus chinensis suspension cell cultures [266,267]. Moreover, novel derivatives of benzo-1, 2, 3-thiadiazole carboxylic esters were synthesized, showing promising control efficacy against a spectrum of bacteria and fungi in crops like cucumber, rice, and maize (Figure 9b) [268]. Subsequent research focused on synthesizing benzo-1, 2, 3-thiadiazole-7-carboxylate derivatives containing fluorine, revealing that derivatives with specific functional groups displayed substantial protective activity against pathogens like E. cichoracearum and C. lagenarium (Figure 9c)[268]. Additionally, novel thiadiazole derivatives incorporating thiazole or oxadiazole moieties were synthesized, demonstrating inducible protective activity against pathogens, as reported by Gan, et al. (Figure 9d,e) [269]. Notably, our research group developed an amino phosphonate compound containing benzo-1, 2, 3-thiadiazole, named dufulin, which exhibited superior protective activity across various crops under greenhouse and field conditions (Figure 9f) [269]. Dufulin showed inhibitory effects on the replication of TMV and southern rice black-streaked dwarf virus, while also enhancing the expression of PR-1a mRNA in tobacco leaves and the activity of PAL, POD, and polyphenol oxidase (PPO) in rice leaves or rice suspension cells [9]. Furthermore, the novel pyrimidine-like compound 5-(cyclopropylmethyl)-6-methyl-2-(2-pyridyl) pyrimidin-4-ol (PPA) emerged as a promising plant activator, exhibiting similar inhibitory effects to BTH against A. thaliana disease caused by Ps. syringae pv. maculicola strain (Figure 9g). PPA was found to accumulate mRNA of various genes related to the SA signal pathway in A. thaliana leaves, while also promoting H_2O_2 accumulation in intracellular sites inoculated with the pathogen, suggesting a novel mechanism of action [270, 271]. Finally, 3-acetonyl-3-hydroxyoxindole (AHO), a derivative of isatin isolated from Strobilanthes cusia, demonstrated efficacy in reducing lesion number and size caused by TMV and E. cichoracearum (Figure 9h). AHO was found to induce the accumulation of PR-1a mRNA in N. benthamiana cv. Xanthinc leaves and increase the SA content and PAL activity (Figure 7). However, AHO pretreatment did not lead to the accumulation of SA and PR-1a in NahG transgenic tobacco, suggesting a complex interaction with the SA signal pathway [272].

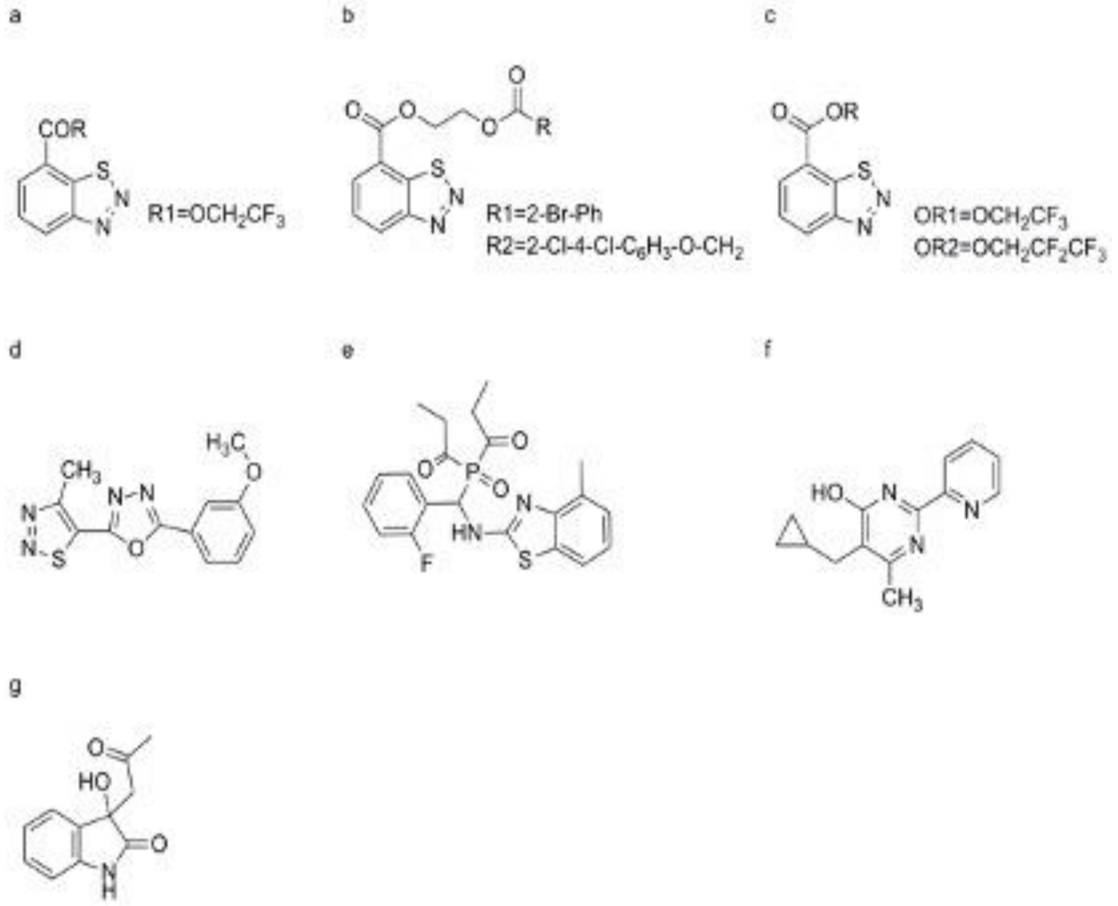

Figure 9. The plant activators targetting plant SA signal pathway by developed in China.

5.2. Limited Understanding of Molecular Targets

Recent research has made significant strides in finding and understanding the molecular targets of plant activators. However, the advancements are crucial for improving plant resistance and the rational design of new activators [113].

1) Discovery of plant activators with novel structures: Some key bioactive compounds like withaferin-A and withanolide-D were identified from *Withania somnifera*, which can target specific pathways to inhibit nuclear factor kappa-B, enhancing dopaminergic D2 receptor activity and providing insights into their molecular interactions and potential as stress modulators and immune boosters in plants [273].

2) Discovery of new targets for plant activators: Some studies have demonstrated that silencing certain susceptibility genes (*S* genes) like *REM1.3* using virus-induced gene silencing (VIGS) in plants can enhance resistance to pathogens such as *P. infestans*. This technique has been effective in crops like potato and soybean, revealing crucial targets for genetic modifications to improve disease resistance [274]. By detecting pathogen-associated molecular patterns (PAMPs), it has been found that Pattern Recognition Receptors (PRRs) and Nucleotide-binding Leucine-rich Repeat Receptors (NLRs) play a significant role in plant immune systems [275]. Advances in understanding these receptors have led to the identification of new molecular targets that can be manipulated to bolster plant defenses against a broad spectrum of pathogens [276].

3) Discovery of new mechanisms in plant resistance responses: Recent work highlights the role of Long non-coding RNAs (lncRNAs) in regulating plant immune responses [277–279]. For instance, silencing specific lncRNAs has led to increased resistance to fungal pathogens of tea leaf spot, providing new molecular targets for enhancing crop resistance [280–282].

4) New research methods for studying the targets of plant activators: CRISPR/Cas9 was used to edit *miR482b* and *miR482c* in tomatoes, which showing the promising results in increasing resistance

to *P. infestans* [283]. At present, this method can identify and modify some critical genetic components involved in plant immunity, paving the way for targeted genetic enhancements [284,285].

5) The crosstalk between the SA signaling pathway and jasmonic acid (JA) signaling pathways and their synergistic role in disease resistance. At present, the interplay between these two pathways has been further elucidated, revealing how their modulation can influence plant responses to biotic stress [286]. Targeting these pathways and crucial nodes would help in designing activators that fine-tune plant immune responses for better protection against pests and diseases [287].

6) New approaches for the development of plant activators: At present, the integration of synthetic biology with traditional breeding techniques has led to the development of new plant activators [288]. These technologies enable precise modifications at the molecular level, enhancing the efficacy and specificity of plant defense mechanisms [289]. These studies collectively underscore the importance of identifying precise molecular targets for the development of effective plant activators, which can significantly enhance crop resilience and yield [290].

6. Future of Plant Activators

6.1. Action Mechanism of Plant Activators

In the past and present, many researchers have developed numerous plant activators targeting the SA signal pathway. However, several unresolved issues require further investigation:

Firstly, while the action sites of some plant activators have been identified upstream or downstream of SA in the SA signal pathway, the precise action mechanisms and targets of these activators remain unclear. For example, while SABP2 converts BTH into acibenzolar, the mechanism by which acibenzolar activates the SA signal pathway and its target are not fully understood [173,174].

Secondly, certain plant activators with diverse molecular structures can target the same protein to induce plant resistance. Therefore, it is speculated that the precise action mechanisms of these activators may differ. For instance, Imprimatins A and B target SAGT, but the spatial sites of interaction in SAGT may vary between two compounds [142].

Lastly, some plant activators can trigger the SA signal pathway while also activating other signal pathways or directly inhibiting microorganisms. Thus, these compounds possess diverse functions in the plant host, and their precise mechanisms require further study. Examples include BABA, HA, and so on [131,263,264].

6.2. Metabolism Mechanism of Plant Activators

The active components and metabolism mechanisms of certain plant activators remain unclear. Some activators are converted into specific metabolites within the plant host, which then induce plant resistance. However, other activators retain disease resistance activity without clear elucidation of their action and metabolism mechanisms. Examples include PBZ and its metabolite BIT, TDL, and its metabolite SV03 [291].

6.3. Screening Models of Plant Activators

The use of models such as the *PR-1a* or *PDF1.2* gene promoters linked with *GUS* gene has proven effective in screening plant activators, as well as *CaBP22* promoter linked with the *GUS* gene. These models offer advantages in stability and accurate intracellular localization [263]. Moving forward, constructing the models with the promoters of crucial genes upstream of the *GUS* gene could aid in screening the action sites of plant activators.

6.4. Discovery of Lead Compound Based on Novel Action Target

At present, we had not an accurate information of the action target of many plant activators, except for SABP and SAGT [138–140,173,193–195]. So, we are unable to design a rational structure template against molecular target. Next step, we should study the action target for these plant activator, and screen novel lead compound from nature.

7. Conclusion

The future of plant activators holds exciting prospects for advancing our understanding of plant defense mechanisms and revolutionizing crop protection strategies. By elucidating the action mechanisms, metabolism, and screening models, and discovering lead compounds based on novel targets, researchers can harness the full potential of plant activators to mitigate crop losses and ensure global food security in the face of evolving biotic stresses.

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