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Review

Join the green team: Inducers of plant immunity in the plant disease sustainable control toolbox

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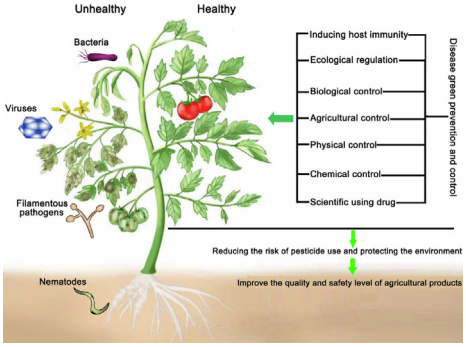
HIGHLIGHTS

- To overcome the major challenges of global food security and environmental and social problems caused by the extensive use of chemical pesticides, developments of modern green sustainable management strategies are urgently needed for the control of crop diseases.
- A deeper understanding of the principles of plant immunity and induced host immunity offers potentials for reducing the use of chemical pesticides and paves the way for sustainable agriculture.
- The sustainable environment-friendly disease prevention and control technologies based on plant immunity inducers are comprehensively summarized in this review.
- The significance of the application of plant immunity inducers for plant disease control is systematically summarized.
- By focusing on research advances of plant immunity inducers, this review offers future perspectives of plant immunity inducers and provides a theoretical reference for researchers.

GRAPHICAL ABSTRACT

Diverse environment-friendly technologies are applied in sustainable prevention and control of crop diseases. Inducing host immunity, ecological regulation, biological control, agricultural control, physical and chemical control, and scientific drug use are utilized to control crop diseases and ensure the safety of agricultural production, agricultural product quality and protect agricultural ecological environment.



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ABSTRACT

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Crops are constantly attacked by various pathogens. These pathogenic microorganisms, such as fungi, oomycetes, bacteria, viruses, and nematodes, threaten global food security by causing detrimental crop diseases that generate tremendous quality and yield losses worldwide. Chemical pesticides have undoubtedly reduced crop damage; however, in addition to increasing the cost of agricultural production, the extensive use of chemical pesticides comes with environmental and social costs. Therefore, it is necessary to vigorously develop sustainable disease prevention and control strategies to promote the transition from traditional chemical control to modern green technologies. Plants possess sophisticated and efficient defense mechanisms against a wide range of pathogens naturally. Immune induction technology based on plant immunity inducers can prime plant defense mechanisms and greatly decrease the occurrence and severity of plant diseases. Reducing the use of agrochemicals is an effective way to minimize environmental pollution and promote agricultural safety.

Aim of review: The purpose of this work is to offer valuable insights into the current understanding and future research perspectives of plant immunity inducers and their uses in plant disease control, ecological and environmental protection, and sustainable development of agriculture.

Key scientific concepts of review: In this work, we have introduced the concepts of sustainable and environment-friendly concepts of green disease prevention and control technologies based on plant immunity inducers. This article comprehensively summarizes these recent advances, emphasizes the importance of sustainable disease prevention and control technologies for food security, and highlights the diverse functions of plant immunity inducers-mediated disease resistance. The challenges encountered in the potential applications of plant immunity inducers and future research orientation are also discussed.

Contents

Introduction

The world currently faces huge challenges, including rapid population growth, climate change, food security, environmental degradation, and pandemic diseases caused by pathogens [1]. It is expected that the global population will swell to 10 billion in 2050. Global food security will become an important issue for the 21st century because food demand is expected to increase 70%-100% by 2050 [2]. Crops are continuously subjected to all kinds of stresses, which threaten the survival of crops and cause significant yield and quality losses in crops [3,4]. Biotic stresses such as pathogens, pests, and competition, represent the major limiting factors for crop production (Fig. 1). Among them, plant pathogens and pests are responsible for 5 major crop yield losses worldwide (wheat 10.1–28.1% rice 24.6–40.9%, maize 19.5–41.1%, potato 8.1–21.0%, and soybean 11.0–32.4%) [5].

Plant diseases caused by bacterial, fungal, viral, and nematode pathogens frequently result in huge yield and quality declines in crops, especially in developing countries, and cost the global economy more than $220 billion every year [5,6]. Firstly, plant bacterial disease is a common disease in agricultural production. Huanglongbing (HLB) is a severe citrus bacterial disease that seriously harms citrus production worldwide. The bacterial pathogen *Candidatus* Liberibacter spp. is thought to cause HLB that severely affects tree health, citrus fruits development, ripening, and quality. HLB was responsible for up to 2.22 billion tons of oranges losses in the United States from 2017 to 2018 [7]. Secondly, plant fungal diseases are the largest group of plant diseases. Rice blast caused by the fungal pathogen *Magnaporthe oryzae* is a destructive disease and is responsible for up to 30% of rice yield losses worldwide. The metric value of these losses is enough to feed 60 million people [8]. Presently, 88% of the global wheat plants are susceptible to stripe rust caused by *Puccinia striiformis*, and yield losses inflicted by this pathogen are nearly 5.47 million tons annually, which is equivalent to an economic loss of $979 million [9]. Thirdly, plant viral pathogens are harmful to crops [10], and around 1484 plant virus species are identified by the ICTV (International Committee on Taxonomy of Viruses) in 2019. Viruses cause a major portion of plant diseases and have a global cost of more than $30 billion annually [1,11]. For example, cassava mosaic begomovirus infection causes cassava crop yield losses of 25 million tons annually [6]. Finally, to date, over 4100 species of plant-parasitic nematodes are described [12]. Plant-parasitic nematodes can be harmful to various crops, such as, soybean, rice, corn, and wheat. Losses caused by plant parasitic nematodes are estimated at $80 billion annually [12]. Rice is infected by over 200 plant nematodes at various stages of development and the parasitic nematode diseases of rice are becoming more and more serious. They account for an estimated US$16 billion in the world's rice losses each year [13]. Therefore, in order to decrease the losses caused by diseases, it is important to develop effective disease prevention and control technologies.

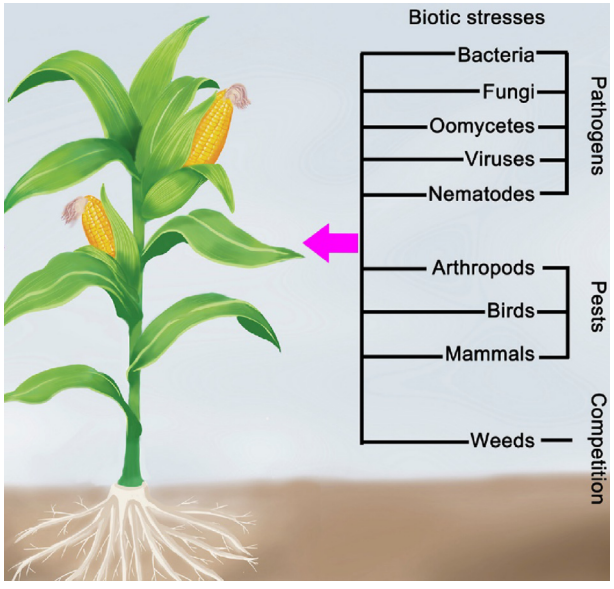


Fig. 1. Crops are subject to all kinds of biotic stresses. Biotic stresses are composed of pathogens (bacteria, fungi, oomycetes, viruses, and nematodes), pests (arthropods, birds, and mammals) and competitive weeds.

Currently, chemical pesticides are the primary means for controlling crop diseases and they are often considered indispensable to secure the global food supply. However, besides increasing the cost of agricultural production, the extensive use of agrochemicals caused many environmental and societal problems. Firstly, pesticide exposure poses a direct threat to human health and the indiscriminate use of agrochemicals caused pesticide residues in food [14], which increase food safety risks. Secondly, the indiscriminate use of agrochemicals kills large numbers of non-target organisms, destroying agricultural biodiversity and the balance of the ecosystem. Thirdly, the indiscriminate use of agrochemicals leads to pesticide residues in soil and water, which affects farmland ecological security. Finally, chemical pesticides have also caused the development of resistant strains of pathogens and pests, which prompts more pesticide utilization, aggravating the problem. Not surprisingly, chemical pesticides have been banned by Europe in postharvest stone fruit [15]. Therefore, research and development of new technologies of plant disease control, while minimizing chemical pesticides, is urgently needed to facilitate the transformation from traditional chemical control to modern green control of plant disease, which is safer for human health and the environment. Therefore, in this study, we outline the various strategies of sustainable prevention and control and future perspectives of this approach with a major focus on the inducers of plant immunity.

The principles of plant immunity

The development of inducers to promote plant protection in agriculture has been facilitated by the remarkable progress that we have made in our understanding of the molecular mechanisms of plant defense. Plants possess a two-tiered immunity defense system [16]. According to the standard Zig-Zag model, the first branch uses cell surface-anchored pattern recognition receptors (PRRs) that identify conserved pathogen-associated molecular patterns (PAMPs), causing PAMP-triggered immunity (PTI) [17,18]. PRRs trigger Ca^{2+} signaling, reactive oxygen species (ROS) production, activation of protein kinases, such as, calcium-dependent protein kinases (CPKs) and mitogen-activated protein kinase (MAPK) cascades, and ultimately transcriptional reprogramming to activate PTI responses. To counteract PTI, pathogens evolved various effector proteins and deliver them into the host to alter plant physiology to suppress PTI, resulting in effector-triggered susceptibility (ETS) [19]. The other branch of plant innate immunity utilizes intracellular immune receptors (nucleotide-binding (NB) leucine-rich repeat (LRR) receptor (NLR) proteins) to recognize these effectors, causing effector-triggered immunity (ETI), which is accompanied by rapid cell death termed hypersensitive response (HR), and thus locally restricts pathogens spread [18,20]. Although PTI and ETI have often presented as two distinct immune signaling pathways, recent studies indicate that these pathways share components and work synergistically to resist pathogen infections (Fig. 2) [21–23]. Although antiviral immunity conceptions are gen-

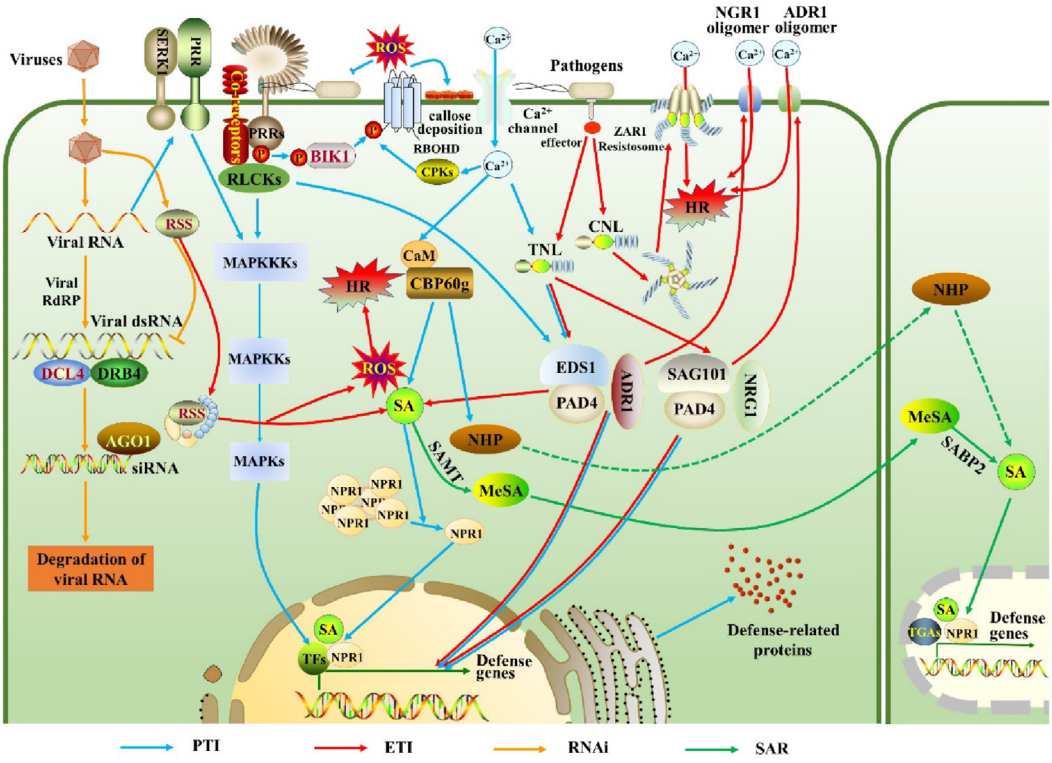


Fig. 2. Diagram of the four modes of plant immune system: PTI, ETI, SAR, and RNAi.

erally excluded from the classic Zig-Zag model of plant innate immunity [24], recent studies suggest that PTI also plays an important role in antiviral defense in plants [25,26]. Viral double-stranded RNAs (dsRNAs) are considered as the PAMPs of viral pathogens. RNA silencing (RNAi) that recognizes dsRNAs may function similarly to PTI and play an important role in immune defense responses against viral pathogens (Fig. 2) [24,27]. Viruses have evolved viral suppressors of RNAi (VSRs), such as coat proteins (CPs) as effector proteins to suppress RNAi-mediated defense responses, effectively triggering ETS [24]. Plant then developed R proteins that recognize VSRs or effectors to confer ETI against viral pathogens. Thus, the RNAi-based PTI and the *R* gene-based ETI form the two layers of immunity that constitute plant antiviral innate immunity.

In addition to local resistance conferred by the plant's innate immunity in local tissue, plants also evolved induced systemic resistance (ISR) and systemic acquired resistance (SAR) that protect systemic or uninfected tissues (Fig. 2). SAR can be activated plant-wide by local pathogen infection. In contrast to ETI, which is often race-specific and confers resistance to avirulent pathogens, SAR results in a long-lasting and broad-spectrum systemic resistance to a wide range of pathogens, making it an attractive candidate for plant protection in agriculture. PTI, ETI, and SAR are all associated with the production of the plant defense hormone salicylic acid (SA) [28]. SA also induces the expression of genes involved in RNAi, thereby activating RNAi [29]. The modes of action of PTI, ETI, SAR, and RNAi are briefly described in Fig. 2. Overall, these four branches of plant immunity partially overlap and work additively or synergistically to protect the host from various pathogens (Fig. 2). For example, SAR and ISR in Arabidopsis had an additive effect on resistance to *Pseudomonas syringae* pv. *tomato* DC3000 (*Pst* DC3000) [30]. Various biomolecules that are capable of priming plant defense can be employed as inducers of plant immunity in agriculture. Thus, understanding the principles of plant immunity and the genetic and molecular mechanisms of disease resistance and induced host immunity offers great potential for reducing the use of agrochemicals and paving the way for sustainable agriculture [31].

Strategies for sustainable prevention and control of crop diseases

The purpose of sustainable prevention and control of crop diseases is to ensure agricultural product quality and environmental safety while maximizing yield primarily by decreasing the use of agrochemicals. It involves prioritization of environment-friendly technologies and approaches such as biological control, agricultural control, physical and chemical control with natural products, activation of host immunity, and scientific drug use to control crop diseases combined with ecological regulations (Fig. 3). These approaches promote standardized crop production and enhance the safety and quality of agricultural products, while reducing the risks of pesticide use and protecting the ecological environment. Among these approaches, disease control through the activation of plant immunity by applying inducers of plant immunity has become popular recently and is a promising sustainable strategy for the future.

Mode of action of plant immune inducers

Plant immunity inducers have negligible direct bactericidal, antifungal, or antiviral activities; however, they can stimulate the plant immune system. We propose new insights on the mode of action of plant immunity inducers (Fig. 4). Our action model schematically illustrates the key points of three components (recognition or detection, signal transduction, or activation, or modulation, and defense response or effective resistance) of inducer-triggered defense. Briefly, the recognition or detection of inducers by plant cell-surface receptors or intracellular receptors

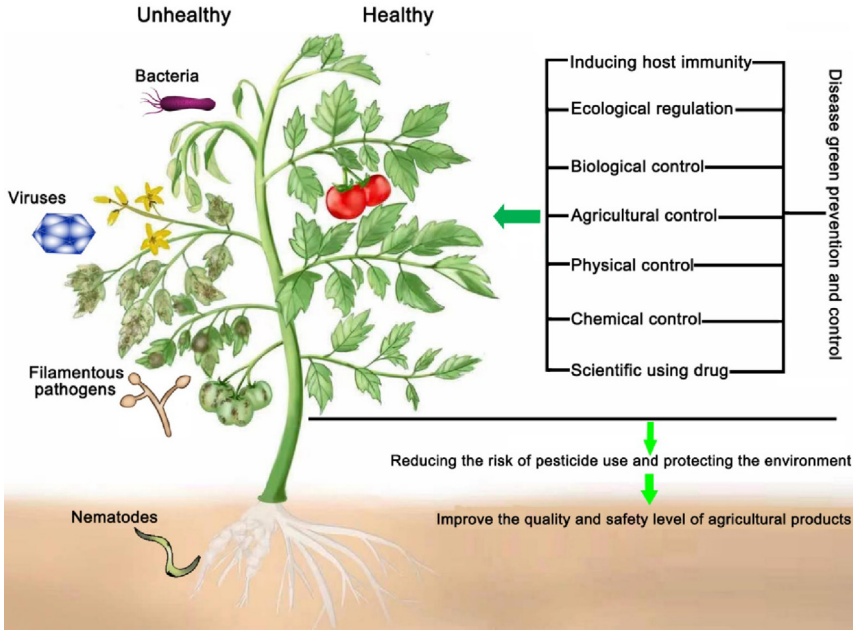


Fig. 3. Diverse environment-friendly technologies are applied in sustainable prevention and control of crop diseases. Inducing host immunity, ecological regulation, biological control, agricultural control, physical and chemical control, and scientific drug use are used to control crop diseases and ensure the safety of agricultural production, agricultural product quality and protect agricultural ecological environment.

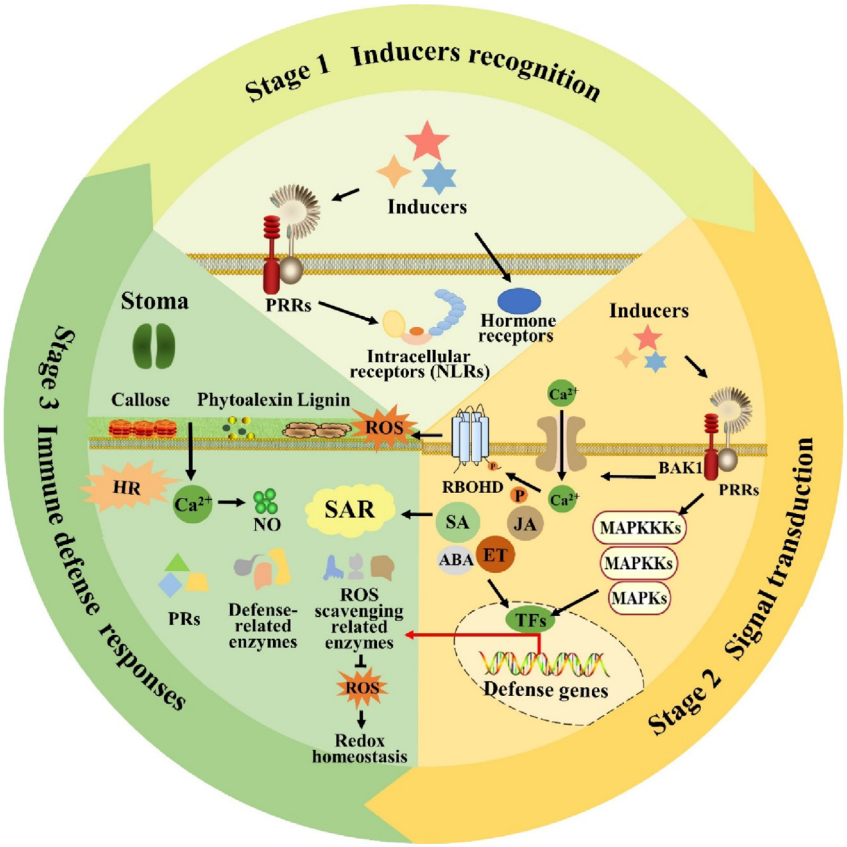


Fig. 4. A diagram for the mode of action of plant immunity inducers. Firstly, plant immunity inducers are recognized by the plasma membrane receptors or intracellular receptors, such as pattern-recognition receptors (PRRs) and hormone receptors. Next, the receptors work in conjunction with some proteins to transmit immune signals downstream via the multiple signal transduction pathways, such as, Ca^{2+}, MAPK, phytohormones (like ABA, ET, JA, SA), and protein phosphorylation (like phosphorylating RBOHD). Finally, the signal downstream triggers the multiple disease-related immune responses, which result in the increased resistance to various pathogens.

Table 1
Oligosaccharides that show immune inducer activity in various plant species.

Oligosaccharides inducers	Source	Plants	Disease	Pathogen	Application	Defense responses
Chitin [32,33]	Fungal cell wall	Rice, Barley, Strawberry	Rice blast, Gray mold, Fusarium head blight	*Magnaporthe oryzae*, *Fusarium graminearum*, *Botrytis cinerea*	Spray	Induce phytoalexins formation, cell death, accumulation of ROS, MAP kinase activation, PR genes, chitinase activity, PAL activity, callose deposition, stomatal closure, accumulation of NO
Oligogalacturonides [34]	Plant cell wall	Wheat	Powdery mildew, Gray mold	*Pectobacterium carotovorum* sp. *carotovorum* SCC1, *Botrytis cinerea*, *Blumeria graminis* f. sp. *Tritici*	Spray	Induce defense-related genes, phosphorylation of MPK3 and MPK6, production of ROS and NO, OXO activity, PO activity, SA signaling pathway
Laminarin [35,36,37]	Brown algae	Tobacco, Grapevine	Bacteriosis, Tobacco mosaic disease, Downy mildew, Olive leaf spot	*Erwinia carotovora* subsp. *Carotovora*, *Plasmopara viticola*, *Tobacco mosaic virus*, *Fusicladium oleagineum*	Add elicitor to cell culture, Syringe, Spray	Accumulation of PR proteins, release of H_2O_2, stimulation of PAL and LOX activity, increase level of SA, plasma membrane depolarization, induce defense-related genes
Curdlan [38,39]	*Alcaligenes faecalis* var. *myxogenes*	Potato, Tobacco	Late blight, Tobacco mosaic disease	*Tobacco mosaic virus*, *Phytophthora infestans*	Infiltration, Spray	Expression of defense-related proteins, increase accumulation of SA, induce PAL, GLU and CTN activity, extracellular alkalinization response, H_2O_2 and NO burst, induce stomatal closure, inhibition of stomatal opening
Sucrose [40,41]	Plant	Rice, Lupin	Fusarium wilt, Rice blast	*Fusarium oxysporum*, *Magnaporthe oryzae*	Spray, Add to the medium	Induce defense-related genes, PAL activity, level of isoflavonoids Anthocyanin accumulation, activation of PR genes
Trehalose [42]	Plant	Wheat	Wheat powdery mildew	*Blumeria graminis* f.sp. *tritici*	Spray	Induce defense-related transcription factor, PR protein, PAL activity, PO activity, accumulation of ROS,
Chitosan [43,44]	Crustacea	Rice, Phaseolus Vulgaris, Grapevine	Powdery mildew, Bacterial leaf blight, Bacterial leaf streak	*Tobacco necrosis virus*, *Erysiphe necator*, *Xanthomonas oryzae* pv. *Oryzae*, *Xanthomonas oryzae* pv. *Oryzicola*	Spray, Add to the bacterial solution	Disrupt cell membranes, induce PAL, POX and PPO activity, callose deposition, increase synthesis of polyphenols and abscisic acid content
Cellodextrins [45]	Plant	Grapevine	Gray mold	*Botrytis cinerea*	Add elicitor to cell culture	Induce defense-related genes, induction of oxidative burst and cytosolic calcium variation, phytoalexin accumulation
Algino-oligosaccharides [46,47]	Seaweed	Soybean, Rice	Rice blast	*Pseudomonas aeruginosa*, *Magnaporthe grisea*	Spray	Induce PAL, POD, CAT activity, accumulation of phytoalexin
Sulfated fucan oligosaccharides [48]	Seaweed	Tobacco	Tobacco mosaic disease	*Tobacco mosaic virus*	Add elicitor to cell culture	Induce PAL activity, PR genes, accumulation of phytoalexin and SA, release of H_2O_2
Ulvans [49,50]	Macroalgae	Medicago truncatula, Common bean, Grapevine, Cucumber, Wheat	Bean rust, Angular leaf spot, Septoria tritici blotch	*Colletotrichum trifolii*, *Erysiphe polygoni*, *Erysiphe necator*, *Sphaerotheca fuliginea*, *Uromyces appendiculatus*, *Pseudocercospora griseola*, *Zymoseptoria tritici*	Spray	Induce defense-related genes, ROS metabolism and octadecanoids
Carrageenans [51]	Rodophyta	Tobacco	Tobacco mosaic disease	*Tobacco mosaic virus, Botrytis cinerea, Pectobacterium carotovorum*	Spray	Induce OXO, PAL activity, jasmonic acid related genes and the accumulation of several phenylpropanoid compounds

is the beginning of the immunity responses. The receptors, together with some proteins such as BAK1 (BRI1-associated receptor kinase 1), transfer signals to downstream players through the multiple signal transduction pathways, including MAPK, phytohormones, and protein phosphorylation. Finally, the downstream signal triggers multiple defense responses such as cellular Ca^{2+} inflow, NO synthesis, ROS production, HR, SAR, defense/pathogenesis-related (PRs) proteins, callose and phytoalexin accumulation, lignin deposition, stomatal closure, and SA production, enabling plants to enhance resistance against various pathogens. To avoid the excessive accumulation of ROS-caused oxidative stress during infection by pathogenic microorganisms, several inducers also promote the activities of several ROS scavenging related-enzymes and regulate redox balance. A great diversity of compounds and natural products involved in plant immunity are deployed as inducers of plant immunity as discussed below.

Oligosaccharides (OGAs)

The oligosaccharides implicated in plant disease resistance are generated by the enzymatic degradation of polysaccharides. These oligosaccharides normally function as PAMPs or DAMPs, which are recognized by PRRs to activate plant immunity. Their activities are highly dependent on not only their degree of polymerization (DP) but also the dose. As shown in Table 1, various kinds of oligosaccharides, such as chitin and alginates, have been confirmed to act as immune inducers and consequently activate plant defense responses. The chemical structures of various oligosaccharides are shown in Fig. 5.

β-glucans

The first identified active oligosaccharides that functioned as inducers were β-glucans, which triggered defense responses of plants through the activation of phenylalanine ammonia-lyase (PAL) activity. β-glucans are widely found in the cell walls of plants and fungi. β-1,3-/ β-1,6-Glucans have been extensively explored for several decades because of their involvement in plant disease resistance [52]. Laminarin, a β-1,3-glucan, isolated from brown algae, has an average DP of 25–33 glucose units and up to three β-glucose branches in position 6. It can induce multiple defense responses in tobacco plants. However, induced defense by laminarin is slower than other β-1,3-glucans with lower DP (2–10) [38]. Application of laminarin to tobacco plants triggers a strong enhancement of Phe ammonia-lyase, caffeic acid O-methyltransferase, and lipoxygenase activities, as well as accumulation of SA. As a result, PR proteins have been accumulated, which lead to the activation of resistance to *Erwinia carotovora* [35]. Sul-

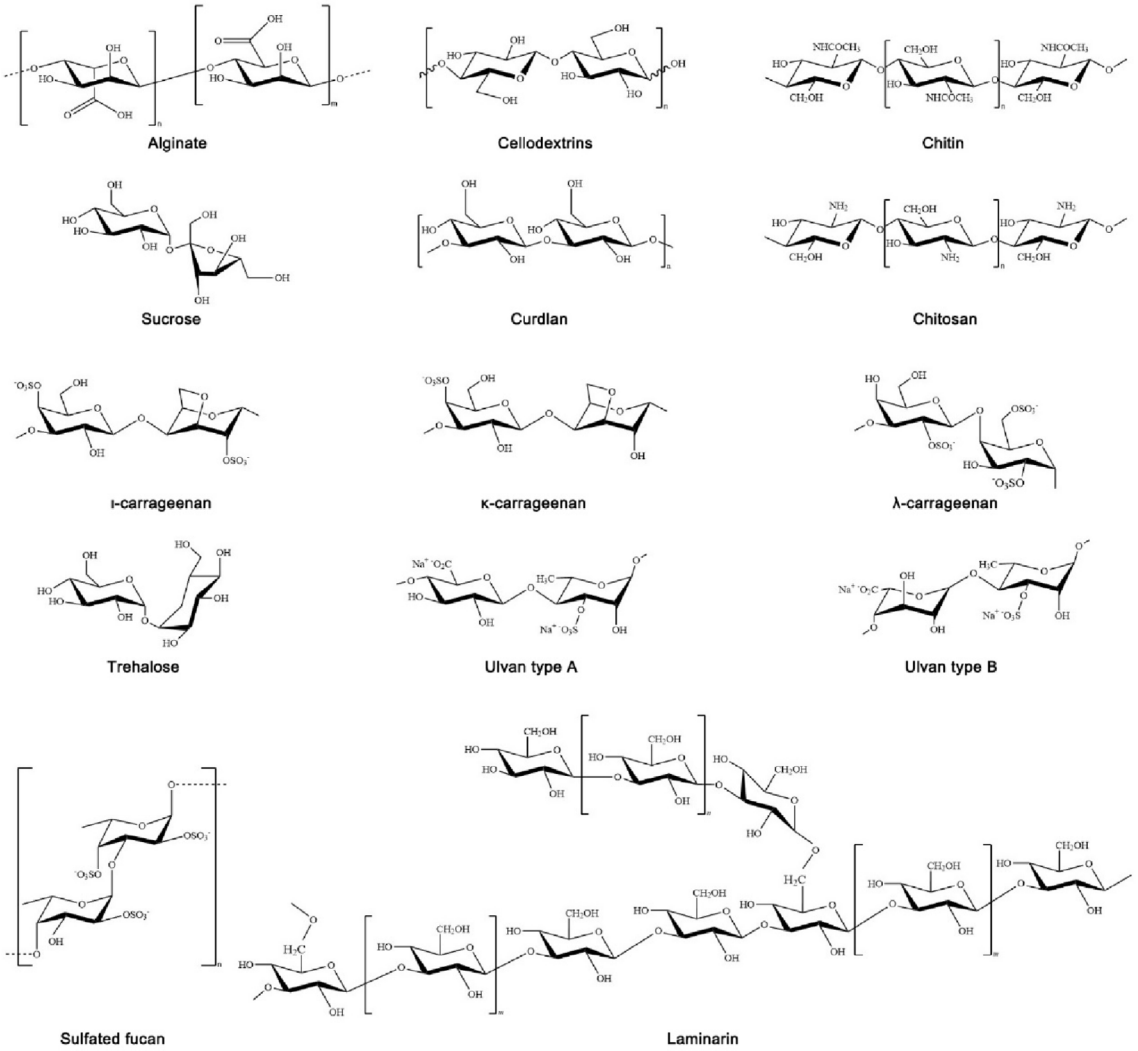


Fig. 5. Chemical structures of oligosaccharides with immune inducer activities.

fated β-1,3-glucan, but not β-1,3 glucan, induced the SA-mediated defense pathway against TMV in Arabidopsis and tobacco plants [36].

Chitin

Chitin is also found in the cell walls of fungi and is one of the best characterized PAMPs [53]. The receptors for chitin have also been identified in various plants. The chitin elicitor receptor kinase 1 (CERK1) is crucial for chitin elicitor signaling in Arabidopsis [54]. In rice, fungal chitin can be recognized by the LysM-RLP Chitin elicitor-binding protein (CEBiP) which is a specific chitin receptor [55]. Exogenous application of chitin could trigger typical PTI by binding to the chitin elicitor receptor, which could lead to enhanced resistance against pathogens in various crops, including rice, wheat, cotton, oilseed rape, and strawberry [56].

Chitosan

Chitosan found in zygomycete cell walls is a deacetylated derivative of chitin [57]. Chitosan has been proven to induce strong defense responses against fungal pathogens in various plant species. Chitosan oligomers can induce chitinase activity in melon plants. Exogenous application of chitosan oligosaccharides to wheat plants induces lignin deposition and increases the levels of phenolic acids [58]. Moreover, DP also affects the biological activity of chitosan. Chitosan oligomers with a DP ranging between 7 and 10 are usually the most active plant immunity inducers [59].

Alginates

Alginate oligomers are produced by the depolymerization of alginates. Alginate oligomers with DP between 2 and 10 have been shown to exert PAMP function to induce defense responses in various plant species. The algino-oligosaccharides induced defense responses by stimulating phytoalexin accumulation and antimicrobial activity on *Pseudomonas aeruginosa* [46]. In Arabidopsis, treatment with alginate oligosaccharide triggered a strong resistance against *Pst* DC3000 through the SA signaling pathway [60].

Oligogalacturonides

Some oligosaccharides derived from plant cell walls during a pathogen infection are considered DAMPs and could induce defense responses [61]. Oligogalacturonides (OGs) are examples of DAMPs that stimulate plant immunity and are oligomers of alpha-1,4-linked galacturonosyl residues released from plant cell walls upon partial degradation of homogalacturonan. OGs have been shown to induce resistance against pathogen infections by inducing ROS production, phytoalexins, callose deposition, nitric oxide (NO), and pathogenesis-related proteins [61]. OGs could also trigger nitrate reductase (NR)-dependent fast and long-lasting NO generation together with an increased NR activity and transcript level of *NR* gene, which lead to the enhanced ROS accumulation and the defense genes *PER4* and a *β-1,3-glucanase* expression against *Botrytis cinerea* in Arabidopsis [62]. Moreover, a novel oligosaccharide, mannan oligosaccharide (MOS) hydrolyzed from locust bean gum, has great potential as a plant immunity inducer for managing plant disease. Treatment of tobacco or rice with MOS led to increased intracellular Ca^{2+}, MAPK cascades, ROS, SA and JA-dependent signaling pathways, activation of defense-related genes, and the accumulation of four phytoalexins. MOS signaling induces multiple defense responses against *Phytophthora nicotianae* and *Xanthomonas oryzae* in tobacco and rice, respectively [63]. Recently, Poaceae-specific cell wall-derived oligosaccharides, namely the tetrasaccharide 3^1-β-D-Cellotriosyl-glucose and the trisaccharide 3^1-β-D-Cellobiosyl-glucose, have been shown to bind the immune receptor OsCERK1 and lead to the activation of strong immune responses against *M. oryzae* infection in rice [64]. Thus, oligosaccharides are effectively used as inducers of plant immunity in many crops.

Proteins and peptides

Some immune-inducing proteins derived from pathogens (bacteria, fungi, and oomycetes) have been shown to trigger plant immune systems to increase resistance to various pathogens. Here are some examples.

Bacterial proteins- harpins

Plant disease resistance can be induced by a protein from the fire blight bacterial pathogen *Erwinia amylovora*. This protein was named the hypersensitive protein (harpin) [65]. Harpin is a glycine-rich and heat-stable protein. Harpins can serve as inducers of HR, activate defense responses, and promote plant growth against a broad array of pathogens by regulating multiple signaling pathways in a range of non-host plant species (Fig. 6) [66]. The HrpN of *E. amylovora* is the first identified harpin protein and can trigger resistance. Since then, multiple harpins have been identified from various Gram-negative plant-pathogenic bacteria [67]. Similarly, Hpa1, another harpin protein, is produced by *X. oryzae* [68]. Exogenous application of Hpa1 increases resistance against bacterial blight, rice blast, sheath blight, and TMV in various plant species and improves plant growth [69–71]. Recently, harpins have been categorized into four major groups (Hpa1, HrpN, HrpW1, and HrpZ1) based on domain structures and protein similarity; A fifth group of harpins includes unclassified harpins [72]. The details of the mechanism of harpins-induced plant immunity against pathogens are shown in Fig. 6.

Fungal proteins

Several immunity-inducing proteins derived from fungi could also trigger plant innate immunity. PevD1, a novel immune-inducing protein isolated from *Verticillium dahliae*, is a pathogen-secreted protein. Treatment of plants with PevD1 induced HR, extracellular-medium alkalization, H_2O_2 production, phenolics metabolism, callose deposition, and lignin synthesis, and caused necrotic lesions, ultimately leading to SAR, and enhanced resistance to a viral pathogen [73]. PevD1 also triggered plant immunity through the up-regulation of *PR* genes, cell wall modifications, metabolite deposition, JA signaling, and Ca^{2+}-responsive pathways, enhancing resistance against *Pst* DC3000 and *B. cinerea* [74]. Pathogens secrete a range of cell wall-degrading enzymes (CWDEs) to invade plants, and CWDEs also act as inducers of immune responses. VdPEL1, a novel immune inducing protein isolated from *V. dahlia,* is a pectate lyase with pectin hydrolytic activity, which has been shown to trigger cell death in plants [75]. Purified VdPEL1 protein induced defense responses and systemic resistance in cotton and tobacco, which resulted in increased resistance to *B. cinerea* and *V. dahliae* infection [75]. A secreted protein elicitor MoHrip1 isolated from *M. oryzae* can induce the events of defense responses, including callose deposition, H_2O_2 production, and alkalization of the extracellular medium, and activation of SA and gibberellin (GA) signaling [76,77]. MoHrip1 enhanced systemic resistance to blast fungi in rice and tobacco while promoting plant growth.

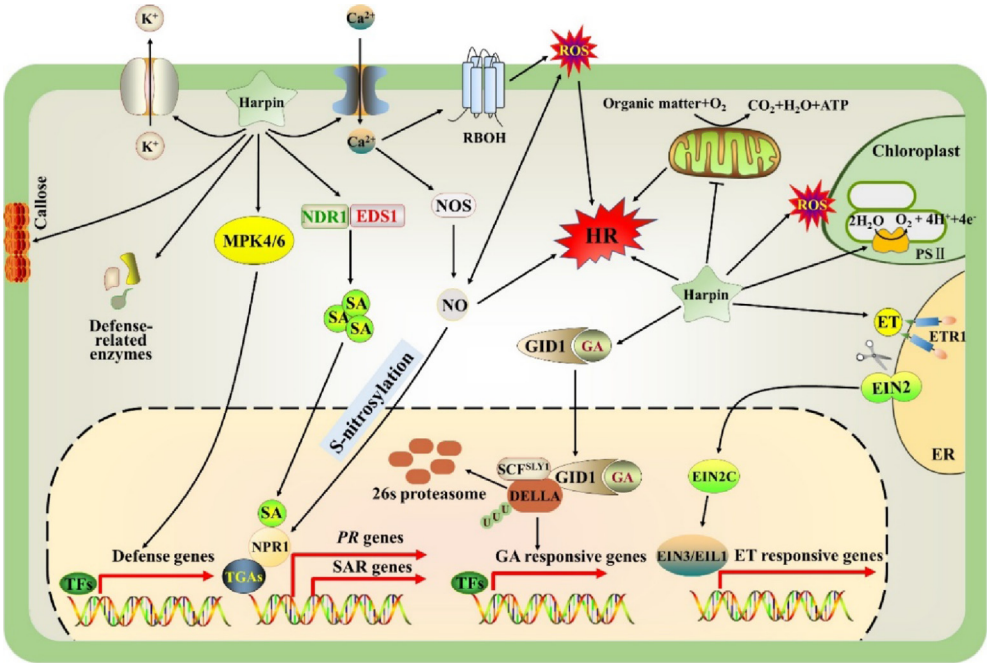


Fig. 6. A schematic model of harpin-induced plant immunity. Harpins activate plant immunity and promote plant growth by regulating multiple signaling pathways. The exogenous application of harpins promotes K^+ efflux, induces extracellular alkalization, and Ca^{2+} influx, and activates the RBOH and NOS, which result in the production of ROS and NO, respectively. NO and ROS promote each other to regulate HR. In addition, harpin treatment interferes with the function of mitochondria and inhibits the respiration of plants, which result in HR. Harpins also enhance plant immunity by promoting MAPK signal cascades, defense-related enzyme activities, and callose deposition. The application of harpins could activate the expression of *NDR1* and *EDS1*, promote SA synthesis, activate SA signal transduction pathway, and induce the expression of *PR* genes and SAR-related genes. Furthermore, harpins can also regulate the accumulation of ethylene (ET). ET binds its receptor ETR1 to activate the C-terminal domain of EIN2 and regulate the transcription factor EIN3 / EIL1, thereby enhancing the expression of ET signaling pathway genes, activating plant immunity, and promoting plant growth. Harpin treatment can induce the synthesis of GA. GA binds its receptor GID1 to promote the binding of GID1 to the DELLA protein, a negative regulator of GA signaling pathway, resulting in the conformational change of the DELLA protein. Then the conformational change of DELLA protein interacts with SCF^{SLY1} and leads to the poly-ubiquitination of DELLA protein. Finally, DELLA is degraded by 26S proteasome. Therefore, the repression by DELLA protein is removed, and then the expression of GA signaling pathway genes and plant growth are promoted. In addition, harpins can also increase photosynthetic efficiency and promote plant growth, which enhance plant resistance to pathogens infection.

Oomycete proteins

Immune-inducing proteins secreted by oomycetes have also been shown to trigger plant defense responses. Elicitins are structurally conserved extracellular proteins that are secreted by *Pythium* and *Phytophthora* pathogen species and act as oomycete PAMPs [78]. Elicitins induce HR and systemic resistance in various plants [78]. Recent studies suggest that elicitins can be recognized by immune receptors and activate broad-spectrum resistance. The receptor-like protein ELR from the wild potato mediates the perception of the elicitin from *Phytophthora*, and this receptor-like protein potentially promoted resistance against several oomycete [79]. Moreover, cryptogein secreted by *Phytophthora cryptogea* could induce an intense defense response in tobacco plants consisting of HR and SAR [80]. In addition, cryptogein also induces multiple signal transduction events in plants, including ROS and NO production, MAPK activation, cell death, lipid peroxidation, and LOX gene transcription [81]. A list of plant diseases managed by applying immune-inducing proteins in various plant species are summarized in Table 2.

Glycoproteins

The application of some pathogen glycoproteins could trigger host immune responses (Table 3). The first reported glycoprotein was identified in *Phytophthora megasperma*. This glycoprotein could trigger defense-related phytoalexin production [107]. Following this discovery, various pathogen glycoproteins have been identified and applied as elicitors that induce host defense responses. BcGs1, a glycoprotein isolated from *B. cinerea*, has been shown to act as an elicitor that activated hormone signal pathways, HR and H_2O_2 production in tomato and tobacco leaves, elevated the expression of the defense genes *PR-1a*, *tomato protein kinase 1* (*TPK1b*) and prosystemin [47]. These events lead to strong resistance against *B. cinerea*, *Pst* DC3000 and TMV in systemic leaves [47]. Moreover, GP-1, a novel glycoprotein has also been demonstrated to induce immunity in tobacco plants. Exogenous application of GP-1 triggered defense responses, including Ca^{2+} influx, oxidative burst, HR, callose apposition, PCD, increase in NO, and stomatal closure as well as the activation of SA and JA defense pathways and the systemic accumulation of PR proteins in *Nicotiana benthamiana*, which led to the enhanced resistance to TMV [108].

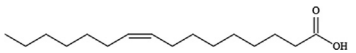
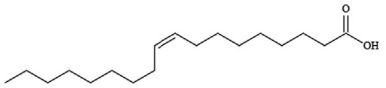
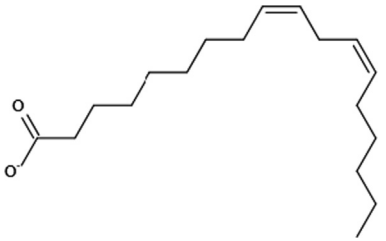
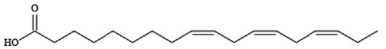
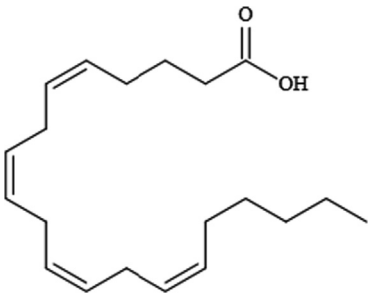
Peptides

Several peptides derived from pathogens and plants also act as inducers of plant defense and activate PTI. One of the first identified peptides is Pep13 (13 amino acid residue peptide, VWNQPVRGFKVYE) from *Phytophthora sojae*, which can induce the expression of defense marker genes against potato and parsley late blight diseases [90]. Flg22 (QRLSTGSRINSAKDDAAGLQIA) isolated from *P. aeruginosa* is a conserved 22 amino acid sequence at the *N*-terminal of bacterial flagellin. Exogenous application of Flg22 to tomato, potato, and Arabidopsis plants induced ROS accumulation and biosynthesis of ethylene. At the same time, a higher concentration of Flg22 can elicit necrosis or HR [91]. Flg22 isolated from *Xanthomonas campestris* pv. *campestris* (QQLSSGKRITSASV-

Table 2
Various proteins and peptides that enhanced resistance to a broad range of pathogens in different plant species.

Proteins	Source	Plants	Disease	Pathogen	Application	Defense responses
HrpN [82]	*Erwinia amylovora*	Tobacco		*Botrytis cinerea*	Spray, Transgenic	SAR pathway, promote plant growth, resistance-related genes expression, SA-dependent and JA/ET-dependent defense pathways, enhance superoxide production
Hpa1 [68–71]	*Xanthomonas oryzae*	Rice, *Pinellia ternata*	Bacterial blight, Rice blast, Sheath blight, Tobacco mosaic disease	*Xanthomonas oryzae, Magnaporthe grisea, Thanatephorus cucumeris, Tobacco mosaic virus*	Seed soak, Spray	Promote plant growth, hydrogen peroxide signal transduction, induce an increase in defense-related enzyme activity, increase the expression of disease resistance-related genes, increase the content of hydrogen peroxide, phenolics, and callose, reduce the content of malondialdehyde
PevD1 [73,74]	*Verticillium dahlia*	Tobacco, Cotton	Verticillium wilt, Tobacco mosaic disease	*Botrytis cinerea, Pseudomonas syringae* pv. *tomato* DC3000, *Tobacco mosaic virus*	Leaf injection	Hypersensitive response (HR), hydrogen peroxide production, extracellular-medium alkalization, callose deposition, phenolics metabolism, and lignin synthesis, cause necrotic lesions, induce SAR; trigger innate immunity and to result in the up-regulation of pathogen-related genes, metabolite deposition, cell wall modifications, JA signaling and Ca^{2+}-responsive pathways
PEL1 [75]	*Verticillium dahlia*	Tobacco, Cotton		*Botrytis cinerea, Verticillium dahlia*	Leaf syringe-infiltration	Cell death, accumulation of ROS, defense-related genes expression, callose deposition
Hrip1 [77,83]	*Magnaporthe oryzae, Alternaria tenuissima*	Rice, Tobacco	Rice blast, Tobacco mosaic disease	*Magnaporthe oryzae, Tobacco mosaic virus*	Spray, Leaf infiltration	Hydrogen peroxide production, callose deposition, alkalization of the extracellular medium, activation of SA signaling pathway, the gibberellin (GA) pathway, promote plant growth, enhance systemic resistance, hypersensitive response, NO production, SAR pathway, defense-related genes expression
HpaXpm [84]	*Xanthomonas phaseoli* pv. *manihotis* HNHK	Tobacco	Tobacco mosaic disease	*Tobacco mosaic virus*	Leaf injection, Foliar spray	Hypersensitive response, NPR1 gene expression, promote plant growth
PopW [85]	*Ralstonia solanacearum*	Tobacco	Tobacco mosaic disease	*Tobacco mosaic virus*	Spray	Hypersensitive response, SAR, induce expression of *PR* genes, H_2O_2 burst, activity of defense-related enzymes, increase tobacco yield, improve tobacco foliar quality
ELR [79]	*Solanum microdontum*	Potato	Potato late blight	*Phytophthora infestans,* oomycete plant pathogens	Transgenic	
Cryptogein [78,81]	*Phytophthora cryptogea*	Tobacco		*Phytophthora parasitica*	Leaf infiltration	Hypersensitive response, SAR, ROS and NO production, mitogen-activated protein kinase (MAPK) activation, cell death, lipid peroxidation and LOX gene transcription, cell wall modifications
BcGs1 [47]	*Botrytis cinerea*	Tobacco, Tomato	Tobacco mosaic disease, Gray mold	*Tobacco mosaic virus, Botrytis cinerea*	Injection	Induce hypersensitive response, up-regulation the PR genes, prosystemin elicitor
Gp-1 [86]	Streptomyces	Tobacco	Tobacco mosaic disease	*Tobacco mosaic virus*	Leaf spray	Induce HR, PCD, H_2O_2 and Ca^{2+}, induce elevated NO levels, stomatal closure, accumulation of callose, activation of defense-related genes
GhGLP2 [87]	Wheat cell wall	*Gossypium hirsutum L.*	*Verticillium* wilt, *Fusarium* wilt	*Verticillium dahliae, Fusarium oxysporum.*	Root drench	Induce PDF and PR genes expression, up-regulation the antioxidant enzyme. callose deposition, lignin formation
PLCP [88]	Papaya cell	Citrus	Citrus yellow shoot	*Liberbacter asianticum jagoueix*	Leaf spray	Activate the expression of SA related genes, induce PR genes expression, cell death, conduct MAPK signaling, activation the G-protein coupled receptors
GhLecRK-2 [89]	Fungal cell wall	Cotton	*Verticillium* wilt	*Verticillium dahliae*	Spray, Add to the bacterial solution	Activate WRKY gene
Pep13 [90]	*Phytophtora sojae*	Potato, parsley	late blight disease	*Phytophtora infestans*	Cell treatment	Function as a PAMP for the activation of innate defense reactions, expression of defense-related genes,
flg22 [91]	*Pseudomonas aeruginosa, Xanthomonas campestris* pv. *campestris*	Tomato, tobacco, potato,		*Pseudomonas syringae* pv. *tomato* DC3000	Cell treatment, Spray	Induce a visible alkalinization, oxidative burst, elicit necrotic or hypersensitive response, Induction of ethylene biosynthesis
CAPE1 [92]	Tomato	Tomato, Arabidopsis		*Pseudomonas syringae* pv. *tomato* DC3000	Spray	Induce H_2O_2 formation; induce the expression of genes involved in the stress response, defense response, innate immune response, bacterial defense, and systemic acquired resistance
LTP4 [93]	Grapevine cell suspension	Grapevine		*Botrytis cinerea*	Leaf infiltration	
Zea mays immune signaling peptide 1 (Zip1) [94]	Maize	Maize		*Ustilago maydis*	Leaves soaking	SA accumulation, expression of defense genes,
Phytosulfokines (PSKs) [95]	*Solanum lycopersicum*	Tomato		*Botrytis cinerea*	Spray	Promote the binding between calmodulins (CaMs) and the auxin biosynthetic YUCCAs (YUCs), increase cytosolic [Ca2 +] facilitate the auxin accumulation
SAMP [96]	Australian finger lime	Citrus	Huanglongbing	*Candidatus* Liberibacter asiaticus	Pneumatic trunk injection, spray	Induce the expression of defense response genes, promote plant growth

Table 3
Unsaturated fatty acids with immune inducer activities in different plant species.

Unsaturated fatty acid	Chemical structures	Source	Plant	Disease	Pathogen	Application	Defense responses
Palmitoleic acid (16:1) [97,98]		*Solanum melongena* L.	Eggplant	*Verticillium* wilt	*Verticillium dahliae*	Transgenic	
		Lycopersicon esculentum Mill.	Tomato	Powdery mildew	*Erysiphe polygoni* DC. edmund. Salm.	Transgenic	
Oleic Acid (18:1) [99]		Soybean (*Glycine.* max (L.) Merr.)	Soybean	Soybean phytophthora root rot	*Pseudomonas syringae* pv. *glycinea*, *Phytophthora sojae*	Transgenic, Glycerol application	NO accumulation, induction of cell death and PR-1 expression, increased GTPase activity, SA accumulation, express pathogenesis-related genes, R gene expression, production of reactive oxygen species (ROS)
Linoleic acid (18:2) [100–102]		Avocado fruits	Avocado	Anthracnose	*Colletotrichum gloeosporioides*	Ethylene treatment	Production of reactive oxygen species (ROS)
		Bean	Bean	Bean gray mold	*Botrytis cinerea*	Bacterial liquid treatment	
Linolenic acid (18:3) [101,103]		Rice	Rice	Rice blast	*Magnaporthe grisea*	Transgenic	Oxidative burst, JA signaling pathway, expression of disease-related genes
		Bean	Bean	Bean gray mold	*Botrytis cinerea*	Bacterial liquid treatment	
		Petroselinum crispum	Parsley		*Phytophthora sojae*	Elicitor treatment	
Arachidonic acid (20:4) [104–106]		*Mortierella hygrophila*	Potato	Late blight, Common scrab, Rhizoctonoise	*Phytophthora infestans*, *Macrosporium solani*, *Alternaria solani*, *Rhizoctonia solani*, *Actinomyces scabes*, *Pectobacterium phytophthorum*	Foliar spray	Reconstruction of the cell ultrastructure, increase the amounts of certain enzymes and protective substances, a decrease in sterol content, redirection of isoprenoid biosynthesis from sterol derivatives toward sesquiterpenoid phytoalexins, appearance of signal molecules, oxidative burst
		Mortierella hygrophila	Tomato	Macrosporiose of leaves, Septariose of leaves, Black bacterial blight of leaves	*Phytophthora infestans*, *Alternaria solani*, *Macrosporium solani*, *Septoria lycopersici*, *Xanthomonas vesicatoria*, *Meloidogyne incognita*	Foliar spray	
		Mortierella hygrophila	Suger beet	Cercosporose		Foliar spray	
		Mortierella hygrophila	Vine plants	Powdery mildew		Foliar spray	
			Laminaria digitata		*Laminariocolax tomentosoides*		

DAAGLAIS) can also induce plant immunity. Spraying Arabidopsis plants with Flg22 enhanced resistance to *Pst* DC3000 [109].

In addition, peptides isolated from plants can also induce plant immunity. In response to pathogen infection or other stressors, the expression of *PR* genes encoding proteins or peptides with antimicrobial activities will be induced [110]. Among a total of 17 families of PR proteins or peptides, PR1, PR2, and PR5 are apparently induced by the plant defense hormone SA and are associated with plant defense against biotrophic and abiotic trophic pathogens [111]. A peptide named CAPE1, derived from PR-1b, was discovered in tomato plants after wounding or wounding plus methyl-JA treatment. Exogenous application of its Arabidopsis homolog AtCAPE1 induces resistance to *Pst DC3000* in Arabidopsis plants. Non-specific lipid transfer proteins (LTPs) belong to the PR15 family. One of the type I LTPs VvLTP4 was purified from grapevine cell suspension. Exogenous application of VvLTP4 provided better protections to grapevine plants against *B. cinerea* than JA alone, with the VvLTP4-JA providing the best protection [93]. Immune signaling peptide 1 (Zip1) is a 17-aa peptide isolated from maize leaves. Soaking maize leaves with Zip1 can induce SA production in maize, in which case, the resistance of maize to *Ustilago maydis* was significantly improved [94]. Phytosulfokines (PSKs) are a kind of sulfated tyrosine-containing pentapeptides, which are ubiquitous in higher plants. Spraying PSKs on tomato plants could enhance the binding activity between calmodulins and auxin biosynthetic YUCCAs (YUCs), resulting in auxin accumulation and activating auxin-mediated immunity to *B. cinerea* [95]. Multiple injections of MaSAMP, a heat-stable peptide isolated from Australian finger lime, suppresses the citrus greening disease [96]. MaSAMP exhibited strong bacteria-killing activity, promoted the expression of plant defense genes including *PR* genes, and activated SAR [112]. As shown in Table 2, a list of plant diseases managed by applying proteins and peptides are summarized.

Unsaturated fatty acids

Several unsaturated fatty acids, such as oleic acid (18:1), linoleic acid (18:2), linolenic acid (C18:3), and arachidonic acid (C20:4), serve as signaling molecules. They induce natural, systemic, and durable resistance to diseases in plants [104,113]. Oleic acid and linoleic acid could stimulate protein kinase C-mediated activation of NADPH oxidase, resulting in ROS accumulation [113]. In soybean, oleic acid induces defense responses and enhances resistance to bacterial and oomycete pathogens [99]. Arachidonic acid acts as an inducer to promote defense responses against pathogens [104]. Arachidonic acid was found to strongly trigger oxidative bursts and induced resistance in *L. digitata* [106]. Future studies on the perception and signaling pathway of these unsaturated fatty acids will help us gain a better understanding on how they activate plant defense. Table 3 shows a comprehensive list of plant diseases managed by the application of unsaturated fatty acids in various plant species.

Plant hormones and functional analogs

Salicylic acid (SA)

SA plays an important role in establishing plant immunity. It could serve as an endogenous plant signal to trigger defense

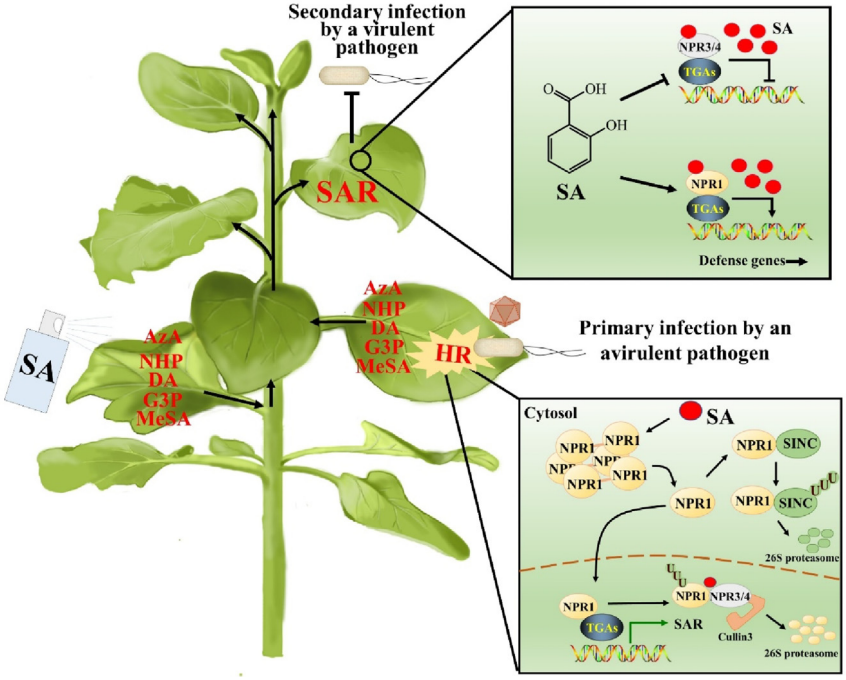


Fig. 7. Salicylic acid (SA)-mediated systemic acquired resistance (SAR). The level of SA in plants is low without pathogen infections. A local infection by an avirulent pathogen results in an increased level of SA, which will also increase NPR1 protein level. NPR1 targets substrates for ubiquitination and degradation through the formation of SA-induced NPR1 condensates (SINCs). SINCs are enriched with proteins involved in cell death. Therefore, SA activates NPR1 to induce SAR and NPR1 promotes cell survival to prevent the spread of cell death. In response to different levels of SA in the center of the infection zone and neighboring cells, NPR3 and NPR4 function as adaptors for Cullin 3 E3 ligase for the degradation of NPR1 to maintain optimal levels of NPR1 to achieve localized cell death during effector-triggered immunity (ETI). Glyceol-3-phosphate (G-3-P), azelaic acid (AZA), diterpenoid dehydroabietinal (DA), N-hydroxypipecolic acid (NHP) or one or more NHP metabolites, and methyl-SA (MeSA) function as mobile signals for SAR. Activation of SAR provides resistance in the entire plant to a secondary infection by a virulent pathogen in systemic leaves. It was proposed that the binding of SA to NPR3/NPR4 removes its transcriptional repression of defense-related genes. In the meanwhile, it was also proposed that SA binds NPR1 to activate the expression of defense-related genes. Accumulation of SA in the cytoplasm promotes the conversion of the oligomeric NPR1 into its monomers, which then migrate to the nucleus. NPR1 binds to TGAs to promote the expression of defense-related genes and increase resistance against pathogen infections.

responses and establish both local and systemic resistance against various pathogens [114]. The levels of SA increase at local leaves during a primary infection and infected plants generate a transportable signal that is critical for SAR establishment (Fig. 7). NPR1 and NPR3/NPR4 served as SA receptors that play important roles in SA- mediated local and systemic resistance [115,116]. The details of the mechanism of SA-mediated local and SAR against pathogens are shown in Fig. 7. Various defense-related stimuli could induce SA production in both local and systemic tissues, and the application of SA could trigger SAR. SA is synthesized from chorismate through two independent pathways in plants, either via PAL in the cytoplasm or via isochorismate synthase 1 (ICS1) in the chloroplast [117]. Generally, ICS1 is believed to be responsible for most pathogen-induced SA biosynthesis in plants like Arabidopsis [118], as SA induced by pathogen infections is dramatically decreased when the ICS1 pathway is blocked. However, the PAL pathway also contributes to SA biosynthesis and defense response. Knockdown of *ZmPAL* expression via VIGS led to increased sensibility to sugarcane mosaic virus (SCMV) in maize, symptom severity and virus replication, and reduced SA and PR proteins accumulation. In addition, the increase in endogenous SA production is positively correlated with the resistance to hemibiotrophic and biotrophic plant pathogens [119]. With the knowledge that SA is essential for plant immunity induction, foliar application of SA has been successfully utilized to trigger plant resistance to a broad array of pathogens, such as viruses, bacteria, nematodes, and fungi (Table 4). Exogenous SA treatment in maize reduced SCMV accumulation and enhanced maize's resistance to viral infection [124]. Tomatoes pretreated with SA showed elevated resistance against tomato yellow leaf curl virus (TYLCV) infection by regulation of the expression patterns of ROS-related genes and *PR* genes [86]. Our study shows that treatment with JA followed by SA in *N. benthamiana* triggers the strongest systemic resistance to TMV [125]. In addition, our studies suggest that glutathione is required for both local and systemic resistance against viral pathogens through differential regulation of SA signaling and ROS [10]. The exogenous application of SA also enhances plant resistance to fungal infection. Treatment with 200 μM SA increased the endogenous levels of SA, antioxidant activities, and the expression of SA marker genes in soybean seedlings. However, SA treatment did not affect the mycelial growth of *Fusarium solani*, suggesting that SA induces resistance to *F. solani* in soybean seedlings [123]. Similarly, SA pretreatment could enhance the resistance of tomato plants to the fungal pathogen *Fusarium oxysporum*. Foliar treatment with 1.5 mM SA could significantly enhance the activities of defense enzymes, NO production, and the expression of defense genes in tomato plants. However, NO synthase inhibitors or NO scavengers significantly decreased these parameters. Foliar treatment with SA also increased physiological parameters like shoot and root length, etc. [121] The results showed that cross-talk between SA and endogenous NO plays a significant role in improving the resistance against *F. oxysporum* in tomato plants [121]. Treatment of rice seedlings with 2 mM SA induces resistance to bacterial blight by regulating the activities of antioxidant enzymes and photosystem II [129]. Exogenous SA can activate SA signaling and participate in *xa5*-mediated resistance to bacterial blight by upregulating *OsNPR3.3* and *TGAL11* [122]. Exogenous application of SA by soil drench, foliar spray, or trunk injection induced citrus systemic resistance to HLB [128]. SA is also involved in protecting plants against nematode pathogens. SA-deficient Arabidopsis mutants showed increased susceptibility to the beet cyst nematode. Application of SA in wild-type Arabidopsis exhibited enhanced resistance to *Heterodera schachtii* [126]. In conclusion, exogenous SA treatment induces local and systemic resistance that is a safe and effective means to resist the infection of various pathogens.

Benzothiadiazole S-methylester (BTH)

BTH, is also referred to 1,2,3-benzothiadiazole-7-thiocarboxylic acid-S-methyl-ester (ASM), is a synthetic analog of SA and is one of the most commonly used immunity inducers in crops. BTH does not exhibit a direct suppression effect on plant pathogens tested *in vitro*; however, it has been found to trigger strong defense responses against a diverse range of pathogens, including TMV, *E. carotovora*, *Cercospora nicotianae*, *M. oryzae*, *Phytophthora parasitica*, and *P. syringae* pv. *tabaci* in various important crops [133,138]. Exogenous application of BTH in common bean plants increased the accumulation of receptor-like kinases and PR proteins, and resistance to common bean rust caused by *Uromyces appendiculatus* [182]. In addition, treatment with BTH markedly enhanced the H_2O_2 content and total antioxidant capacity, increased the activities of defense-related enzymes, reduced the content of malondialdehyde and delayed fruit ripening, and induced strong resistance against *Colletotrichum musae* in banana plants [130].

BTH can trigger SAR, induce the expression of PR genes, and enhance resistance against TMV and *Peronospora tabacina* in salicylic acid-deficient *NahG* transgenic lines [133]. Also, in Arabidopsis, BTH stimulates the *PR* gene expression and triggers NPR1-dependent SAR. However, in rice, the WRKY family transcription factor OsWRKY45 but not rice ortholog of Arabidopsis NPR1 is required for BTH-induced resistance to rice blast disease [138]. Knockdown of *OsWRKY45* in rice significantly reduced the BTH-induced resistance levels against *M. oryzae* and *X. oryzae* pv. *Oryzae* [138]. However, when BTH was sprayed on Arabidopsis seedlings multiple times, the biomass of these plants was reduced [183]. Therefore, precaution should be taken if BTH is repeatedly applied on the same plant with short intervals to prevent detrimental effects on plant growth. In addition to BTH, some other immunity inducers, such as PBZ and Tiadinil, partly triggered strong resistance to rice blast, via the OsWRKY45 signaling pathway [184]. A comprehensive list of diverse plant diseases managed by treatment with BTH in various plant species is summarized. BTH is suitable for agricultural crop protection and has been commercialized as an effective agrochemical (Table 4).

2, 6-dichloroisonicotinic acid and N-cyanomethyl-2-chloro isonicotinic acid

2, 6-dichloroisonicotinic acid (INA) induces similar defense responses as SA, but it does not increase the content of SA and can still induce SAR in *NahG* transgenic plants [185,186]. Therefore, it is regarded as a functional SA analog that works downstream of SA. Like SA, INA has been shown to inhibit ascorbate peroxidase (APX) and catalase activity and also induce ROS accumulation [187]. Exogenous application of INA triggers strong resistance in a large number of plants, such as tobacco, beans, pepper, pear, cucumber, rice, and Arabidopsis against various pathogens [141,144]. INA could enhance defense against bacterial spot disease in tomato plants through regulation of the defense-related genes [145].

N-cyanomethyl-2-chloro isonicotinic acid (NCI) is another potential immunity inducer, which was recognized as a potent immunity inducer for the control of rice blast disease [147]. NCI did not show antifungal activity on *M. oryzae in vitro* even when a high dose (1100 μM) was employed. However, NCI-induced resistance is long-lasting in rice. NCI also induced a strong resistance against various pathogens in tobacco plants, and increased the expression of *PR* genes [147]. In *NahG* transgenic tobacco plants, NCI also induces the expression of *PR* genes [149]; therefore, NCI-triggered immune responses do not require the accumulation of SA; Moreover, NCI-triggered resistance is independent of the

Table 4
Various plant hormones and functional analogs showing immune inducer activity in different plant species.

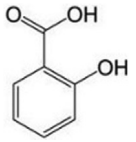
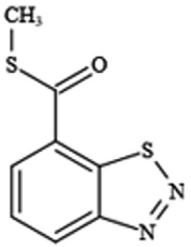
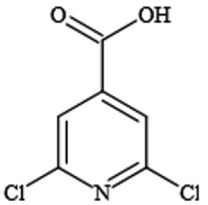
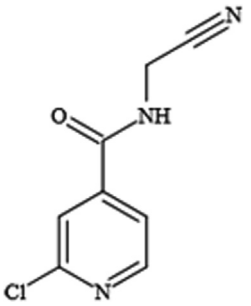
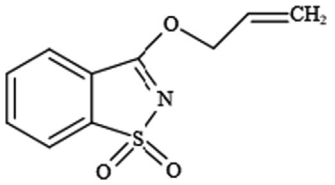
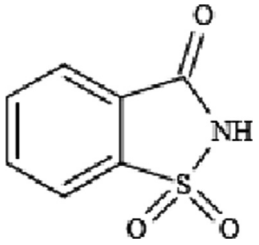
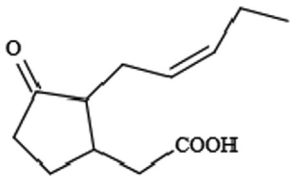
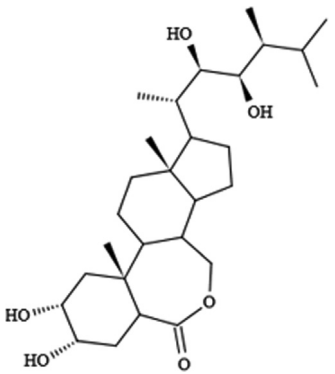
Chemical names	Chemical structures	Plant/Pathogen interaction	Application	Defense responses
Salicylic acid (SA)		Pakchoi/*Plasmodiophora brassicae* [120]	Application directly to the soil	Induce the activities of antioxidant and resistance-related enzymes, abilities of osmotic regulation, and ROS scavenging-related genes, defense-related genes, lignin accumulation, improve photosystem II activity.
		Tomato/*Fusarium oxysporum* [121]	Foliar spray	
		Rice/*Xanthomonas oryzae* pv. *Oryzae* [122]	Foliar spray	
		Soybean/*Fusarium solani* [123]	Foliar spray	
		Maize/*Sugarcane mosaic virus* [124]	Foliar spray	
		Tomato/*Tomato yellow leaf curl virus* [86]	Foliar spray	
		Nicotiana benthamiana/*Tobacco mosaic virus* [125]	Foliar spray	
		Arabidopsis thaliana/*Heterodera schachtii* [126]	Add to the medium	
		Tomato/*Ralstonia solanacearum* [127]	Seed soak	
		Orange/*Candidatus* Liberibacter asiaticus [128]	Foliar spray, soil drench, trunk injection	
		Rice/*Xanthomonas oryzae* pv. *oryzae* [129]	Soil drench	
Benzothiadiazole S-methylester (BTH)		Banana/*Colletotrichum musae* [130]	Fruit treatment	Enhance the activities of defense-related enzymes, including chitinase, phenylalanine ammonia-lyase, peroxidase, and polyphenol oxidase, increase the content of hydrogen peroxide and total antioxidant capacity, reduce malondialdehyde content, SA signaling pathway, trigger NPR1-dependent SAR
		Tomato/*Fusarium oxysporum* f.sp. *radicis-lycopersici* (FORL), *Clavibacter michiganensis* subsp. *Michiganensis, Bemisia tabaci* [131,132]	Foliar spray	
		Tobacco/*Tobacco mosaic virus, Cucumber mosaic virus, Cercospora nicotianae, Erwinia carotovora, Phytophthora parasitica, Pseudomonas syringae* pv. *Tabaci* [119,133,134]	Foliar spray	
		Arabidopsis thaliana/*Turnip crinkle virus, Pseudomonas syringae* pv. *tomato* DC3000, *Hyaloperonospora* arabidopsidis, *Peronospora parasitica* [135,136]	Foliar spray	
		Grapefruit/*Xanthomonas citri* subsp. *citr* [137]	Spray	
		Rice/*Magnaporthe oryzae*, *Xanthomonas oryzae* pv. *oryzae* [138,139]	Foliar spray	
2,6-dichloroisonicotinic acid (INA)		Tobacco/*Tobacco mosaic virus*, *Cercospora nicotianae*, *Peronspora tabacina*, *Phytophthora parasitica* var. *nicotianae*, *Pseudomonas syringae* pv. *tabaci* [140,141]	Injection into leaves	Induce SAR, inhibit catalase and ascorbate peroxidase (APX) activity, induce ROS accumulation, mediate defense-related effects upon interaction with NPR1-related proteins, control several TGA transcription factors, promote NPR1-NPR3 interactions, reduce the binding affinity of SA to NPR3 and NPR4 by competing with SA
		Cucumber/*Colletotrichum lagenariunm*, *Cercospora nicotianae*, *Peronospora tabacina*, *Phytophthora parasitica* var. *nicotianae*, *Pseudomans syringae* pv. *tabaci* [140,142]	Foliar spray	
		Arabidopsis thaliana (Ler)/*Hyaloperonospora arabidopsidis* [143,144]	Soil drench	
		Arabidopsis thaliana (Col-0)/*Pseudomonas syringae* pv. *tomato DC3000* [143,144]	Foliar spray	
		Tomato/*Xanthomonas perforans* [145]	Seed soak	
		Soybean/*Phytophthora sojae* [146]	Root drench	
		Hamlin sweet orange/*Candidatus* Liberibacter asiaticus [128]	Foliar spray	
N-cyanomethyl-2-chloro isonicotinic acid (NCI)		Oryza sativa/*Pyricularia oryzae*, *Xanthomonas oryzae* pv. *oryzae* [147]	Root drench	Induce SAR, enhance the expression of PR genes, induces expression of PR1, PR2 and PR5
		Tobacco/*Tobacco mosaic virus*, *Oidium lycopersici*, *Pseudomans.syringae* pv. *tabaci* [140,148]	Soil drench	

Table 4 (*continued*)

Chemical names	Chemical structures	Plant/Pathogen interaction	Application	Defense responses
Probenazole (PBZ)		Tobacco/*Tobacco mosaic virus*, *Pseudomonas syringae* pv. *tabaci*, *Oidium* sp. [149]	Foliar spray	SA accumulation, expression of several pathogenesis related (PR) genes, accumulation of PR proteins, hypersensitive reaction, accumulation of fungicidal substances, amplification of superoxide production
		Rice/*Magnaporthe grisea*, *Xanthomonas oryzae* pv. *oryzae* [150,151]	Spray	
		Arabidopsis/*Pseudomonas syringae* pv. *tomato* DC 3000, *Peronospora parasitica* Emco5 [152]	Spray, Leaf injection	
Saccharin		Wheat/*Blumeria graminis* f.sp. *tritici*, *Zymoseptoria tritici* [153,154]	Foliar spray	Expression of pathogenesis-related genes, SA signaling pathway, JA signaling pathway, deposition of callose, induce an increase in defense-related enzyme activity
		Arabidopsis thaliana/*Pseudomonas syringae* pv. *tomato* DC3000 [153]	Foliar spray, Root drench	
		Soybean/*Phakopsora pachyrhizi* [155]	Foliar spray, Root drench	
		Rice/*Magnaporthe grisea*, *Xanthomonas oryzae* [155]	Foliar spray	
		Tobacco/*Tobacco mosaic virus* [156]	Soil drench	
		Cucumber/*Colletotrichum lagenarium* [156]	Soil drench	
		Green bean/*Uromyces appendiculatus* [156]	Soil drench	
		Broad bean (Vicia faba)/*Uromyces viciae-fabae* [157]	Soil drench, Foliar paint	
		Barley/*Blumeria graminis* f.sp. *hordei* [158]	Foliar spray, Soil drench	
Jasmonic acid (JA)		*Nicotiana benthamiana*/*Manduca sexta* [159]	Foliar spray	Induce oxidative bursts, phytoalexin accumulation, pathogenesis-related proteins accumulation, lignification, cell wall stiffening, decrease malondialdehyde, enhance lipoxygenase and phenylalanine ammonia-lyase, induce resistance-related enzymes, defense-related genes, induce alkaloids and phenolic acids, induce the production of secondary metabolites and volatile compounds, induce the formation of defensive structure, modulate stomatal opening, tendril coiling, root growth inhibition, anther development, fruit ripening, tuber formation, seed germination, senescence, plant responses against wounding.
		Oryza sativa/*Magnaporthe oryzae* [160]	Root drench	
		Arabidopsis thaliana/*Botrytis cinerea* [161]	Foliar spray	
		Vitis vinifera/*Botrytis cinerea* [162]	Fruit infiltration	
		Solanum tuberosum/*Phytophthora infestans* [163]	Root drench	
		Triticum aestivum/*Powdery mildew* [164]	Foliar spray	
		Actinidia chinensis/*Botryosphaeria dothidea* [165]	Fruit infiltration	
		Amygdalus persica/*Rhizopus stolonifera* [166]	Fruit injection	
		Vigna mungo/*Mungbean yellow mosaic India virus* [167]	Foliar spray	
		Arabidopsis thaliana/*Plasmodiophora brassicae* [168]	Root drench	
		Arabidopsis thaliana, Nicotiana benthamiana, Nicotiana glutinosa, Nicotiana tabacum, Capsicum annum, Solanum lycopersicum/*Cucumber mosaic virus, Tobacco mosaic virus, Turnip crinkle virus* [169]	Seed spray	
		Saccharum officinarum/*Pratylenchus zeae, Helicotylenchus spp* [170]	Root drench	
		Solanum lycopersicum/Root-knot nematodes [171]	Seed spray	
		Phaseolus vulgaris/*Sclerotinia sclerotiorum* [172]	Foliar spray	
		Pennisetum glaucum/*Sclerospora graminicola* [173]	Seed treatment, Foliar spray	
Brassinosteroids		Tobacco/*Tobacco mosaic virus*, *Pseudomonas syringae* pv. *tabaci*, *Pseudomonas syringae* pv. *tomato* DC3000, *Oidium* sp. [174–176]	Spray	Induce systemic resistance, BDR-signaling pathway, H_2O_2 production, ROS burst, upregulate nitric oxide (NO) production, promote abscisic acid (ABA) biosynthesis, activate pathogenesis-related genes
		Rice/*Magnaporthe grisea*, *Xanthomonas oryzae* pv. *oryzae* [174]	Soil drench	
		Barley/*Fusarium culmorum* [177]	Spray	
		Tomato/*Botrytis cinerea*, *Meloidogyne incognita* [178,179]	Leaflet soak	
		Arabidopsis thaliana/*Cucumber mosaic virus* [180,181]	Spray	

accumulation of SA but depends on AtNPR1 in Arabidopsis [148]. Treatments with INA and NCI were used to manage plant diseases in various plant species (Table 4).

Probenazole (PBZ)

PBZ, a benzisothiazole derivative, was first identified as a plant immunity inducer through screening for chemicals that could trigger resistance against *M. oryzae* in rice. PBZ did not show strong inhibition of conidial germination and mycelial growth against *M. grisea*; however, PBZ-induced antifungal resistance in rice is long-lasting. PBZ induced a strong resistance to protect a large number of plants from various pathogens, such as bacteria, viruses, and fungi [149,188].

Treatment with PBZ or its active metabolite, BIT (1, 2-benzisothiazol-3 (2H)-one 1,1-dioxide), did not induce the expression of *PR-1* gene in *NahG* transgenic or *npr1* mutant plants. PBZ- and BIT-mediated defense responses seem to require SA and NPR1. Moreover, further evidence also suggests that PBZ and BIT act as immunity inducers by activating a site upstream of the point of SA accumulation [150]. Other modes of action have been observed for PBZ; for example, probenazole treatment can alter metabolic pathways leading to resistance to *M. grisea* in rice [151]. Application of PBZ in rice affected metabolic profiles by changing 54 metabolites. SA, shikimate, γ-aminobutyrate, and other resistance-related primary and secondary metabolites were significantly up-regulated [151]. PBZ has been commercially used against rice blast and bacterial leaf blight under the name Oryzemate® (developed by Meiji Holdings, CO., Ltd. Japan) [143]. Despite PBZ's extensive use over many years, the development of probenazole resistance in target pathogens has not been promising as of yet [149]. Table 4 shows that the application of PBZ was used to manage plant diseases in various plant species.

Saccharin

Saccharin (1,1-dioxo-1,2-benzothiazol-3-one) is an active metabolite of PBZ. Saccharin has been identified as an inducer of SAR in both dicots and monocots against various pathogens, (Table 4) [155,158]. Saccharin works through the upregulation of SA signaling and activation of the expression of *PR* genes in tobacco and Arabidopsis [149,152]. Pretreatment with saccharin enhanced the expression of multiple defense-related genes in wheat seedlings and resulted in increased resistance to powdery mildew [153]. Saccharin had no direct inhibitory effect on the hemibiotrophic pathogen *Zymoseptoria tritici*. However, foliar application of saccharin conferred protection against *Z. tritici* in wheat plants, through elicitation and induction of *LOX* and *PR* genes [154]. Saccharin triggered defense responses in barley, by increasing the activity of cinnamyl alcohol dehydrogenase (CAD), against *B. graminis* f.sp. *hordei* [158]. In addition, the effectiveness of saccharin as an inducer of SAR against soybean rust (SBR), caused by the fungus *Phakopsora pachyrhizi*, in soybean plants was also reported [155].

Jasmonic acid (JA)

While SA triggers defense responses against biotrophic pathogens, JAs have long been thought to mainly promote defense responses against necrotrophic pathogens and herbivores. Methyl-jasmonate (MeJA) and isoleucine conjugate (JA-Ile) are derivatives of fatty acids and are collectively called jasmonates (JAs). More recently, evidence indicates that JA-Ile plays a significant role in JA signal transduction in response to environmental stress [189]. JA-Ile can bind to the JA-receptor, coronatine insensitive 1 (COI1), which encodes an F-box protein. The interaction between JA-Ile and COI mediates the ubiquitin-dependent degradation of Jasmonate Zinc finger Inflorescence Meristem (ZIM)-domain (JAZ) repressors, which leads to the activation of JA-responsive gene expression controlled by several transcription factors (TFs) such as MYCs, NAC, WRKY, and ethylene response factor (ERF) [190,191]. A volatile methyl ester of JA, methyl jasmonate, also participates in plant immunity. Exogenous application of MeJA induces oxidative bursts, phytoalexin accumulation, the accumulation of PR proteins, lignification, and cell wall stiffening, which result in a strong resistance against pathogens in various plant species [172,192]. Treatment with MeJA in Arabidopsis increased the transcript levels of defense genes, and contributed to the host resistance against several necrotrophic pathogens [193]. Exogenous application of MeJA in *Phaseolus vulgaris* increased pathogenesis-related protein activities and induced resistance to the necrotrophic fungus [172]. Recently, several studies suggested that JA also plays an important role in plant defense against biotrophic or hemibiotrophic pathogens [160,194]. In rice, JA-mediated defense pathways enhance resistance to the hemibiotrophic rice blast fungus *M. oryzae* [160]. Application of MeJA in *Vigna mungo* reduced the levels of malondialdehyde, enhanced the expression of lipoxygenase, phenylalanine ammonia-lyase and defense-related genes, and decreased expression of the coat protein of the Mungbean Yellow Mosaic India Virus (MYMIV), implying that MeJA is also effective against viruses [167].

Interestingly, a bacterial phytotoxin from *P. syringae*, named coronatine, has also been shown to induce typical jasmonate-induced defense responses. The 6-substituted 1-oxoindanoyl isoleucine conjugates which are the structural mimics of coronatine have been designed and synthesized [195]. Among these conjugates, 1-oxo-indanoyl-L-isoleucine methyl ester has been reported to increase the activity of defense-related enzymes and trigger a strong resistance to downy mildew [143,173]. Another molecule, a 6-ethyl indanoyl isoleucine, named coronalon, is established as an efficient inducer of various jasmonate-induced defense responses in various plant species [195]. Additional synthetic JA mimics also triggered jasmonate pathways and defense responses against pathogen infection in various plants [143]. Thus, JA mimics are also employed to elicit plant resistance against various pathogens in agriculture. Table 4 shows a list of plant diseases managed via the application of JA and JA mimics in various plant species.

Brassinosteroids (BRs)

Increasing evidence implies BRs play important roles in plant defense responses. Perception and signal transduction of BRs are dependent on the plasma membrane receptor kinase BRI1 (BR receptor) and BRI1-ASSOCIATED KINASE 1(BAK1), which is the BR coreceptor. BRI1-EMS-SUPPRESSOR 1 (BES1) and BRASSINAZOLE RESISTANT 1 (BZR1) function as major transcription factors, which trigger BR defense responses and crosstalk with other hormones signals in response to pathogen infections in plants [176,180]. BR-induced resistance to various pathogens was observed in multiple plant species (Table 4) [196]. Wild-type tobacco treated with the most active BR brassinolide (BL) exhibited enhanced resistance to *Pseudomonas syringae* pv. tabaci and powdery mildew [174]. Further studies indicate that the crosstalk between BR and ethylene (ET) plays a significant role in plant defense responses. Foliar applications of BR and ET in *N. benthamiana* enhanced resistance to *Pst* DC3000. At the same time, the applications of BRZ (brassinazole, a specific BR biosynthesis inhibitor) abolished the ET signal and triggered resistance to *Pst* DC3000, suggesting that BR is connected with ET-induced resistance to *Pst* DC3000 [176]. In addition, exogenous BL enhanced resistance against rice blast and rice bacterial blight diseases [174].

BR also could induce resistance to viral pathogens in various plant species. Treatment with BL increased *N*-gene-mediated resistance to tobacco mosaic virus (TMV) [174]. Recent studies also confirmed that exogenous application of BRs increased tobacco resistance to TMV while treatment with BRZ reduced plant resistance [197]. Applications of BR enhance systemic resistance against viral pathogens through regulation of ROS production in *N. benthamiana* [175]. BR-induced anti-viral defense responses, include increased NO biosynthesis and H_2O_2 accumulation, which are required to regulate the expression of defense-related genes. BR treatment increased NO accumulation and enhanced Arabidopsis resistance against cucumber mosaic virus (CMV) [181,198]. However, pretreatment with NO scavenger (PTIO) or nitrate reductase (NR) inhibitor (tungstate) abolished the production of NO and appeared to compromise plant resistance [180]. Moreover, BR-induced resistance to virus infection involved antioxidant system by increasing the activities of antioxidative enzymes [196,198].

Other types of inducers

Vitamin B1

Increasing evidence indicates that vitamins could act as inducers of resistance and also enhance crop yield [199], which may be the keys to improving agricultural productivity and enhancing food security [200]. Thiamine, also known as vitamin B1, is the first identified B type vitamin. This article will focus on the significance of vitamin B1 in plant disease resistance. Increasing evidence has verified that thiamine could function as an immune inducer of systemic, broad-spectrum, long-lasting resistance to various pathogens in multiple plant species (Table 5). Exogenous application of thiamine increased rice resistance against leaf blight [201,243] and root-knot nematodes by increasing lignification and H_2O_2 generation [203], treatment with thiamine also triggered rice resistance to sheath blight disease in rice by boosting the total accumulation of phenolics accumulation, H_2O_2 content, and the activities of PAL and superoxide dismutase (SOD) [202]. In tobacco plants, thiamine can also induce systemic resistance to viral pathogens, such as pepper mild mottle virus (PMMoV), by increasing the expression of *PR* genes [201]. In cucumber plants, it also provided resistance to powdery mildew (*Sphaerotheca fuliginea*) and anthracnose (*Colletotrichum lagenarium*) [201]. Moreover, thiamine treatment triggered resistance against *Pst* DC3000 in Arabidopsis [201]. In *Capsicum annuum* plants, vitamin B1-induced defense responses and systemic resistance against TMV infection were associated with the antioxidant system and pathogenesis-related proteins by increasing the activities of Polyphenol Oxidase (PPO), PAL, and Peroxidase (POD) [207]. In soybean plants, the exogenous thiamine application enhanced resistance to root rot caused by *Macrophomina phaseolina* [244]. In grapevine, thiamine treatment triggered multiple defense responses including callose deposition, H_2O_2 production, upregulation of defense-related genes, phenolic compound accumulation, and HR, which resulted in increased grapevine resistance to downy mildew [206].

Inorganic salts

Spraying of inorganic salts significantly reduced pathogen infection in multiple plant species [245]. Several inorganic salts, such as silicates, bicarbonates, phosphites, chlorides, and phosphates, have been shown to be able to alleviate the severity and symptoms of various fungal diseases in multiple plant species [245]. This paper will focus on the significance of phosphates in plant disease resistance (Table 5). Increasing evidence suggests that phosphates could act as immune inducers of systemic resistance to various pathogens. The phosphate salts K_2HPO_4, K_3PO_4, $NH_4H_2PO_4$, and KH_2PO_4 showed antifungal properties [245]. Since dibasic and tribasic phosphate salts play important roles in systemic resistance to anthracnose in greenhouse cucumber [199], the efficacy of phosphates in disease resistance of crops has received attention. Moreover, phosphate salts provided long-lasting protection to cucumber plants because the induced-systemic resistance in newly developed leaves was still effective for five weeks after the exogenous treatment. Further studies also confirmed the exogenous application of K_3PO_4 or K_2HPO_4 in the lower leaf surface induced systemic resistance against the four fungal diseases of cucumber: powdery mildew, anthracnose, gummy stem blight, and scab, in larger greenhouse assays [209]. In addition, foliar sprays of K_2HPO_4 or KH_2PO_4 induced local and systemic resistance to powdery mildew in field-grown nectarine, mango trees, and grapevines [211]. In cucumber plants, foliar application of phosphate can also trigger systemic protection against powdery mildew [246,247]. In bean plants, exogenous application K_2HPO_4 or KH_2PO_4 stimulated the activities of defense-related enzymes and enhanced resistance to *Uromyces appendiculatus* [248]. Spray application of K_2HPO_4 in cucumber plants resulted in cell death along with a rapid generation of H_2O_2 and superoxide with increased levels of free and conjugated SA, indicating that foliar application of K_2HPO_4 on cucumber plants leads to activation of defense mechanisms similar to those initiated by necrotizing microbes and viruses that trigger SAR [210].

Non-protein amino acids

β-aminobutyric acid (BABA), a non-protein amino acid was recognized as a plant immunity inducer in 1963. Application of BABA was reported to protect about 40 different plant species against various pathogens and pests (Table 5) [249]. However, this broad-spectrum disease resistance is dependent on different defense mechanisms. BABA primes defense reactions modulated by SA and the master regulator of SA signaling NPR1 against the bacterial leaf pathogen *P. syringae*. In addition, BABA primes defense mechanisms that operate independently of SA and NPR1 based on cell-wall-related defense primed by abscisic acid (ABA) against some fungi and oomycetes [219]. Recently a new defense mechanism determined that the iron deficiency induced by BABA could increase plant resistance was reported [250]. More recently, the study provided evidence that the BABA receptor IBI1 which encodes an aspartyl-tRNA synthetase senses BABA in Arabidopsis [251]. The binding of BABA to the L-Asp-binding domain of IBI1 results in priming its alternative defense activity. Although BABA is generally considered as a synthetic plant immune inducer, recent studies have unequivocally recognized BABA as an endogenous plant metabolite synthesized by many different plant species [252].

Pipecolic Acid (Pip), another non-protein amino acid, is a lysine decomposition product, which has been shown to be a critical metabolite in the SAR pathway. After inoculation with pathogenic bacteria, Pip accumulated significantly in the exudates of infected leaves and petioles. Exogenous application of Pip to roots can induce the synthesis of the phytoalexin camalexin, Pip, and SA, initiating the expression of early defense-related genes. Besides, the *ald1* mutants lacking Pip have been shown to be defective in SAR and resistance induced by BABA. These results indicate that Pip ensures effective local resistance and SAR through defense responses amplification, positive regulation, and initiation of SA biosynthesis (Table 5) [239]. The flavin monooxygenase FMO1 converts Pip to N-hydroxypipecolic acid (NHP), which plays an essential role in SAR [253]. A recent study provide evidence that one or more NHP metabolites acts as a mobile signal for SAR [254].

Table 5
Other types of inducers showing immune inducer activity in different plant species.

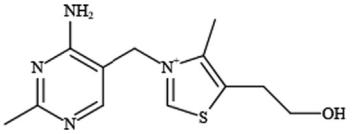
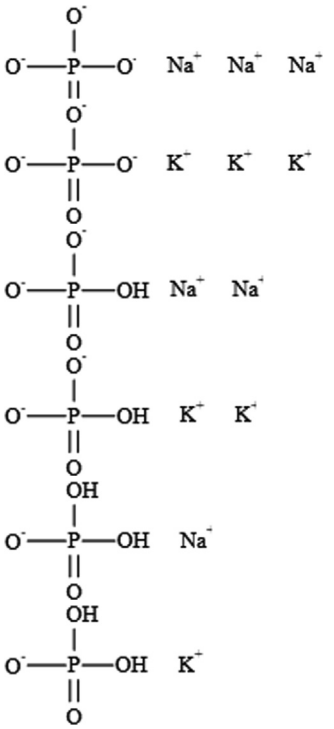
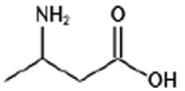
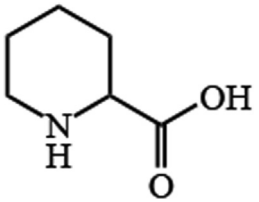
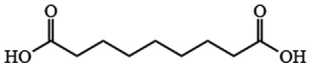
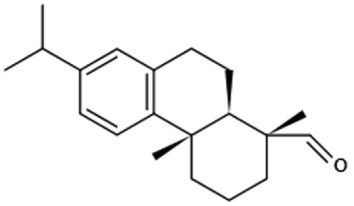
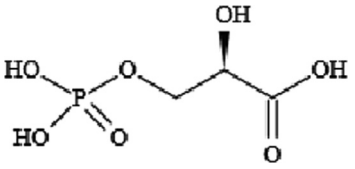
Chemical names	Chemical structures	Plant/Pathogen interaction	Application	Defense responses
Vitamin B1 (Thiamine)		Rice/*Magnaporthe grisea, Xanthomonas oryzae, Rhizoctonia solani, Meloidogyne graminicola* [201–203]	Spray, Root drench	SAR, expression of pathogenesis-related (PR) genes, ROS, HR, callose, phytoalexins, SA signaling pathway, JA signaling pathway, up-regulation of protein kinase C activity, Ca^{2+}-dependent signaling pathway, higher hydrogen peroxide content, total phenolics accumulation, phenylalanine ammonia lyase (PAL) activity and superoxide dismutase (SOD) activity
		Cucumber/*Colletotrichum lagenarium, Sphaerotheca fuliginea* [201]	Spray	
		Arabidopsis thaliana/*Pseudomonas syringae* pv. *tomato* DC3000 [201]	Spray	
		Tobacco/*Pepper mild mottle virus* [201]	Spray	
		Soybean/*Macrophomina phaseolina* [204]	Stem base syringe	
		Barley/Aphids [205]	Add to nutrient solution, Seed soak, Spray, Volatile treatments	
		Pea/Aphids [205]	Add to nutrient solution, Seed soak, Spray, Volatile treatments	
		Grapevine/*Plasmopara viticola* [206]	Spray	
		Capsicum annuum/*Tobacco mosaic virus* [207]	Spray	
Phosphate salts		Cucumber/*Colletotrichum lagenarium, Cladosporium cucumerinum, Dydimella bryoniae, Sphaerotheca fuliginea, Pseudomonas lachrymans, Erwinia tracheiphila, Tobacco necrosis virus, Cucumber mosaic virus* [208–210]	Spray	Activate phenylalanine ammonia lyase (PAL), peroxidase and lipoxygenase, cell death, generation of superoxide and hydrogen, a local and systemic increase in free and conjugated salicylic acid (SA) levels peroxide, trigger the activity of defense-related enzymes
		Grape/*Uncinula necator* (Schw.) Burr. [211]	Spray	
		Mango/*Oidium mangiferae* [211]	Foliar spray	
		Nectarine/*Sphaerotheca pannosa* [211]	Foliar spray	
		Rice/*Magnaporthe grisea* [212]	Foliar spray	
		Tomato/*Fusarium oxysporum* f. sp. *lycopersici* (Sacc) [213]	Spray	

Table 5 (*continued*)

Chemical names	Chemical structures	Plant/Pathogen interaction	Application	Defense responses
β-Aminobutyric acid		Apple/*Alternaria alternate, Penicillium expansum* [214,215]	Fruit injection	Improve CHT, POD, GLU and PAL activity, accumulation total phenols, flavonoids content, production of phenolics, peroxides, accumulation PR-proteins callose and lignin, induce HR response, improve PPO and POX activity, increase H_2O_2 content, regulate ROS metabolism, accumulation SA content
		Arabidopsis thaliana/*Alternaria brassicicola, Botrytis cinerea, Peronospora parasitica, Pseudomonas syringae* pv. *tomato* [216–219]	Foliar spray	
		Artichoke/*Sclerotinia sclerotiorum* [220]	Foliar spray	
		Barley/*Blumeria graminis* f.sp. *hordei* [221]	Foliar spray	
		Basil/*Peronospora belbahrii* [222]	Foliar spray	
		Citrus/*Citrus Huanglongbing* [223]	Foliar spray	
		Chinese cabbage/*Alternaria brassicicola* [224]	Foliar spray	
		Cucumber/*Colletotrichum lagenarium* [225]	Foliar spray	
		Grape/*Botrytis cinereal, Penicillium Digitatum, Plasmopara viticola* [226–228]	Foliar spray, Fruit injection	
		Jujube/*Alternaria alternata* [229]	Foliar spray	
		Lettuce/*Bremia lactucae* [230]	Foliar spray	
		Mango/*Colletotrichum gloeosporioides* [231]	Foliar spray	
		Peaches/*RhizopusRot* [232]	Fruit injection	
		Potato/*Fusarium sulphureum, Phytophthora infestans* [233,234]	Foliar spray	
		Brassica napus/*Verticillium longisporum* [235]	Root drench	
		Soybean/*Aphis glycines* [236]	Soil drench	
		Tobacco/*Tobacco mosaic virus* [237]	Foliar spray, Root drench	
		Wheat/*Brevicoryne brassicae* [238]	Soil drench	
Pipecolic Acid (Pip)		*Arabidopsis thaliana/Pseudomonas syringae* [239]	Root treatment	Synthesize the phytoalexin camalexin, Pip, and salicylic acid and primes plants for early defense gene expression
Azelaic acid		*Arabidopsis thaliana/Pseudomonas syringae (Pma*DG3*)* [240]	Spray	SAR, SA signaling pathway
Dehydroabietinal (DA)		*Arabidopsis thaliana,* tobacco, tomato/*Pseudomonas syringae* pv. *maculicola* ES4326 (*Pma*), *Pseudomonas syringae* pv. *tomato* DC3000 [241]	Leaves infiltration	SAR, SA signaling pathway, expression of pathogenesis-related genes
Glycerol-3-phosphate (G3P)		*Arabidopsis thaliana,* soybean/*Pseudomonas syringae* pv. *tomato* DC3000 [242]	Spray	SAR

Azelaic acid, glycerol-3-phosphate, and dehydroabietinal

Besides MeSA and NHP, Azelaic acid (AzA), glycerol-3-phosphate (G-3-P), and dehydroabietinal (DA) have been shown to serve as a mobile signals in SAR [110]. Bacterial infection can induce the accumulation of AzA in Arabidopsis and enhance local and systemic resistance to *P. syringae*. Further, exogenous spraying of AzA primes the accumulation of SA and induces local and systemic resistance (Table 5) [240]. In addition, some researchers suggest that SAR induced by AzA requires G3P. AzA acts upstream of G3P in this pathway and can promote G3P accumulation [255]. G3P is a phosphorylated sugar derivative, which is ubiquitously found. As a conserved metabolite, it is an essential precursor for the biosynthesis of glycerides. Increasing intracellular G3P level or exogenous spraying of G3P can stimulate SAR in Arabidopsis and soybean and increase the resistance to *Pst* DC3000 (Table 5) [242]. DA is a C_{20} diterpene, is a SAR activator via the SA signaling pathway. Infiltration of purified DA into leaves can systematically induce SA accumulation in Arabidopsis. *NPR1*, *FMO1*, and *DIR1*, are key genes of biologically induced SAR, were also upregulated after being induced by DA. DA-induced SAR can be further enhanced by AzA (Table 5) [241].

Characteristics of induced plant immunity

Armed with the knowledge of induced plant immunity, immunity-related compounds and inducers can be employed for local and systemic resistance against various pathogens. As illustrated in Fig. 8, induced immunity in plants has several superior characteristics compared to other modes of resistance [240,256]. The following are some of the characteristics defining these induced plant defenses.

Broad-spectrum property

While ETI triggers pathogen race-specific resistance, immunity inducers that are frequently based on SAR usually trigger broad-spectrum resistance against a wide range of pathogens. Different inducers can trigger resistance to the same disease; on the other hand, the same inducing factor can also induce resistance to different diseases. For example, BTH triggers disease resistance in multiple plant species against various pathogens [257]. Therefore, induced plant immunity is generally non-specific and broad-spectrum, making it easier to use one inducer to prevent multiple diseases in agricultural applications [256].

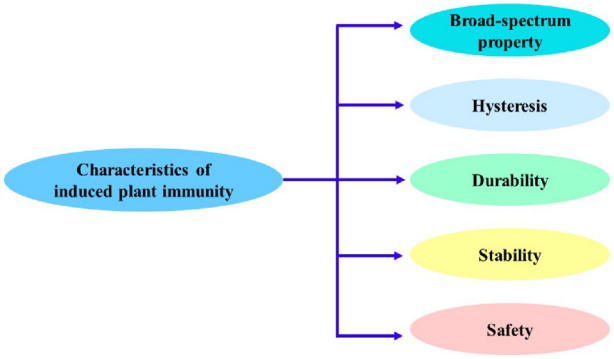


Fig. 8. Characteristics of induced plant immunity.

Hysteresis

A lag period is required from inducer treatments to the optimal deployment of immune function. This period of hysteresis is the time required for the plant to mount an "immune response" or gene sensitization to the stimulus. The length of this lag period is related to the type of inducers, the method of induction, and the plant species. It can be as short as a few hours or as long as a few days. For example, brassinosteroids induce the production of ROS and nitric oxide in *N. benthamiana* to enhance their resistance to TMV, and it takes 12 h from the start of the induction treatment to the activation of immune responses [175].

Durability

Once the induced immunity is established, it can be maintained for a sufficient amount of time. The persistence period is dependent on inducing factors and plant species. For instance, pretreatment of potato tubers with arachidonic acid (AA) induced resistance against the potato late blight, and this resistance is retained for 2–3 months [104]. Exogenous application of NCI induced resistance against rice blast disease that lasted for 30 days [147]. Foliar application of the inorganic salt, monopotassium phosphate (KH_2PO_4) induced resistance to *Sphaerotheca fuliginea* for up to 21 days [258]. Application of probenazole (PBZ) resulted in induced rice resistance to leaf blast disease, which completely controlled and blocked this disease for 40–70 days [188].

Stability

Plant immunity inducers provide resistance against pathogen infection by priming plant immunity. Since pathogens are not directly affected by the inducer, there is no risk of pathogens directly developing resistance to the inducers in contrast to pathogens evolving resistance to fungicides and pesticides. Therefore, plant-inducing immunity is a stable means of disease prevention [256,259].

Safety

Most chemical and biological plant immune inducers have no major adverse effects on humans, animals, and the environment. Their mechanisms determine that most inducers will not be metabolized and produce toxic substances in plants. Arysta Life Science (ALS) and the Institute of Plant Protection (IPP) in China launched the Green Tea Project in 2015 and conducted multiple trials of controlling tea plant diseases using plant immune inducers worldwide. The results showed that induced defense proteins of plant immunity could effectively control plant diseases and they do not persist in the environment [259]. In conclusion, controlling plant diseases using plant immunity inducers is an environmentally friendly green disease prevention technology.

Commercialization of plant immunity inducers

Because of the obvious advantages of using plant immunity inducers for pathogen control in crop protection, numerous biological and abiotic agents capable of triggering host defense against various pathogens in different plant species have been commercialized. Many of them can also regulate the physiological processes of plants to stimulate growth and development and strengthen productivity. Inducers such as BTH, PBZ, INA, NCI, MeJA, tiadinil (TDL), and ZhiNengCong (ZNC), as commercialized products, have been successfully used as agrochemicals for controlling plant diseases [260,261]. ZNC is the crude extract of an endophytic

Table 6
Plant immunity inducers that have obtained a pesticide registration certificate worldwide.

Species	Source	Function
Messenger [265]	EDEN Co., Ltd. of USA	Fungicide
Benzothiadiazole (BTH) [130]	Novartis (now Syngenta) Co., Ltd. of Swiss	Fungicide
KeyPlex humic acid [256]	KeyPlex Co., Ltd. of USA	Plant growth regulator
Probenazole (Oryzemate) [149]	Meiji Seika Kaisha Co., Ltd. of Japan	Fungicide
Serenade *Bacillus subtilis* [256]	AgraQuest Ltd. of USA	Fungicide
Laminarin [256]	Goemar Ltd. of France	Fungicide
Oxycom [256]	Redox Chemicals Co., Ltd. of USA	Fungicide
Chitosan [266]	Ukseung Chemical Co., Ltd. of the Republic of Korea	Plant growth regulator, antistaling agent fungicide
Actigard [256]	Syngenta Co., Ltd. of Swish	Fungicide
NCI [147]	Nippon Kayaku Co., Ltd. of Japan	Fungicide
Pyraclostrobin [256]	BASF Chemical Co., Ltd. of Germany	Plant growth regulator, fungicide
Plant activate protein [256]	Beijing Fenghui Huanong Biological Science and Technology Co., Ltd. of (Institute of Plant Protection, CAAS)	Plant growth regulator
Trans-Abscisic Acid (S-ABA) [256]	Chengdu Institute of Biology, Chinese Academy of Sciences	Plant growth regulator
ATaiLing (PeaT1) [267]	Institute of Plant Protection, CAAS	Antiviral agent
Amino oligosaccharide [256]	Hainan Zhengye Zhongnong High-tech Co., Ltd. and Dalian Kaifei Chemical Co., Ltd.	Immunity-inducer, fungicide
Methiadinil (thiazide induced amine) [256]	Nankai University	Activator, antiviral agent
Lentinan [256]	Beijing Yoloo Pesticides Co., Ltd. and Shandong Shengpeng Pesticides Co., Ltd.	Plant growth regulator, antiviral agent
Validamycin [256]	Zhejiang Tonglu Huifeng Bioscience Co., Ltd.	Fungicide
Matrine [256]	Beijing Multigrass Formulation Co., Ltd. and Inner Mongolia shuaiqi	Insecticide
ZhiNengCong (ZNC) [261]	Shandong Pengbo Bio-technology Co., Ltd and Shandong Agricultural University	Immunity-inducer
Tiadinil (TDL) [264,268]	Nihon Nohyaku Co., Ltd.	Immunity-inducer, fungicide
Amistar 250 SC [269]	Syngenta Co., Ltd. of Swish	Fungicide
Biosept 33SL (grapefruit extract) [269]	Cintamani Poland	Fungicide
Timorex Gold 24 EC [270]	S.T.K. Stockton Group Ltd. of Israel	Fungicide
Goëmar BM 86® [271]	Goëmar of France	Plant growth regulator, fungicide
Kelpak SL [272]	Kelp Products (Pty) Ltd. of South Africa	Plant growth regulator, fungicide
Serifel (*Bacillus amyloliquefaciens* MBI600) [273]	BASF SE of Germany	Fungicide

fungus, *Paecilomyces variotii*, and it has been widely used as an immune inducer on various crops in China. ZNC functions as a new, efficient, environmentally friendly immune inducer, enhancing plant resistance against *Pst* DC3000 [262]. Further studies have shown that ZNC could trigger strong plant defense responses, such as RNA silencing, H_2O_2 and SA accumulation, which enhanced tobacco resistance to Potato X virus (PVX) infection at low concentration by positively regulating RNA silencing via the SA signaling pathway [261]. TDL serves as a rice blast control agent triggering innate defense responses of rice against rice blast [263]. It can also activate the expression of resistance genes in tobacco plants and can be metabolized to produce 4-methyl-1,2,3-thiadiazol-5-formic acid, which induces disease resistance [264]. To date, several inducers have obtained a pesticide registration certificate and have also served as agrochemicals for controlling plant diseases in crop protection worldwide (Table 6).

Conclusions and perspectives

This paper provides a comprehensive review on sustainable prevention and control of crop diseases, the principles of plant immunity, inducers of plant immunity for pathogen control and their potential crop protection. Although immune inducers have the advantages mentioned above, they still have some drawbacks. For example, some inducers have high costs, making it difficult to put them into large-scale production. Most of the data on inducers in plant immunity were obtained in small-scale indoor experiments, without considering other factors in the field. In addition, some inducers take a long time to execute their immune function after application. Some outstanding questions need to be addressed despite these exciting advances in the research of immune inducers.

Firstly, novel and better plant immunity inducers still need to be explored. Integration of prior knowledge of inducers will deeply promote the discovery and research of novel and better inducers of plant immunity for pathogens control. Some novel and emerging biotechniques, such as, computer-aided design, molecular modeling and more recently artificial intelligence can create novel and better inducers. The research and development of inducers is becoming important in the development direction of new biological crop protective agents and will rapidly turn into a new and promising industry with remarkable prospects for development.

Secondly, the activation mechanism of several plant immunity inducers in crop disease resistance and their modes of action are unknown. Therefore, further studies must be carried out to clarify the target, receptor recognition, key activation sites, signaling transduction, and the activation mechanism of inducers, because elucidating the activation mechanism of inducers for improving crop disease resistance is the core scientific issue in formulating crop disease control strategies and the molecular basis for the design of plant immunity inducers as pesticides.

Thirdly, because different inducers activate plant defense through different pathways and mechanisms, the feasibilities of combining multiple inducers or elicitors remains to be explored for potential additive synergetic benefits in inducing a broader spectrum of durable resistance. Next, the industry must focus on developing plant immunity inducers that are safe, eco-friendly, and inexpensive for commercial utilization. In particular, the potential residual effects of the elicitors, especially less visible impacts, must be broadly defined and tested to ensure that they are indeed ecologically friendly. For example, it is becoming increasingly clear that soil microbiome is critical to their resilience,

and it is a good idea to test whether the inducers impact the microbiome. Inducer-based technologies are especially important for modern agriculture due to recent concerns about food security and the overall wellness of the environment. It is also important to note that governments worldwide are enacting policies that limit the use of agrochemicals, causing a massive gap in the agricultural industry and plant disease management. Both factors have caused the demand of inducers to increase in the comprehensive prevention and control of crop, fruit, and vegetable diseases. There is no doubt that this will expedite the development of safe and efficient plant immunity inducers.

Recently, the research and application of inducers have made major breakthroughs in the green disease prevention and control technologies. Improving crop resistance by immune-inducing technology based on plant immunity inducers is an ideal method for disease green prevention and control and opens new avenues for plant protection. Among the plant immunity inducers, different types of plant hormones and functional analogs provide excellent prospects in the prevention and control of agricultural diseases. Overall, the application of plant immunity inducers for pathogen control plays an important role in the movement to provide ecological and environmental protection, sustainable development of agriculture, as well as food security.

Compliance with ethics requirements:

This article does not contain any studies with human or animal subjects.

Declaration of Competing Interest

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

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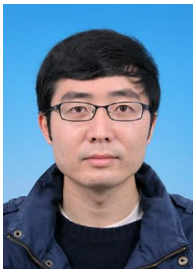

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