Signaling and Communication in Plants

P. Vidhyasekaran

# Plant Innate Immunity Signals and Signaling Systems

## Bioengineering and Molecular Manipulation for Crop Disease Management

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## Bioengineering and Molecular Manipulation for Crop Disease Management

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P. Vidhyasekaran
Department of Plant Pathology
Tamil Nadu Agricultural University
Coimbatore, Tamil Nadu, India

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# Chapter 1
# Introduction


**Abstract** Several signals and signaling systems are involved in activation of plant immune system. Early and robust activation of plant immunity signaling systems triggers strong defense responses against pathogens. Enhancing disease resistance through altered regulation of these signaling systems has been shown to be an attractive technology for management of crop diseases. This book describes various bioengineering and molecular manipulation techniques to activate calcium ion influx–mediated immune signaling system, reactive oxygen species signaling system, nitric oxide signaling system, MAPK signal transduction system, salicylate (SA) signaling system, jasmonate (JA) signaling system, and ethylene signaling system. $Ca^{2+}$ signaling system involves voltage-dependent $Ca^{2+}$-permeable ion channels, cyclic nucleotide-gated channels, glutamate receptor-like ion channels, calcium transporters, calcium ion pumps, carriers, and $Ca^{2+}$ efflux channels, Bioengineering gene encoding glutamate receptor-like ion channel protein has been found to be a useful technology to develop disease resistant plants. The transgenic plants expressing the $H^{+}$-ATPase proton pump show enhanced resistance against viral, bacterial, and oomycete pathogens. Annexin is a $Ca^{2+}$-permeable transporter. The transgenic tobacco plants expressing the annexin gene show enhanced disease resistance. Calcium-dependent protein kinases (CDPKs) are $Ca^{2+}$ sensor proteins in transducing differential $Ca^{2+}$ signatures activating complex downstream responses. Transgenic plants overexpressing calcium-dependent protein kinase gene show enhanced disease resistance. Several G-protein genes have been cloned and used for engineering to develop transgenic plants expressing enhanced resistance against bacterial, fungal, and viral diseases. Cysteine-rich receptor-like kinases (CRKs) are connected to redox and ROS signaling. Transgenic plants overexpressing *CRK* genes show enhanced disease resistance by triggering enhanced ROS production. L-type lectin receptor kinases (LecRKs) have been exploited to develop transgenic disease-resistant plants. These transgenic plants show enhanced production of ROS and trigger defense responses against pathogens. Peroxidases in the cell wall can generate apoplastic $H_2O_2$ and transgenic plants overexpressing peroxidase gene show



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enhanced disease resistance. Super oxide dismutase gene has been engineered to activate ROS-mediated immune signaling for disease management. Fungal glucose oxidase gene has been engineered to develop disease-resistant plants. Expression of the fungal glucose oxidase gene leads to elevated production of $H_2O_2$ in the transgenic plants resulting in increased disease resistance. Nitric oxide (NO) signaling system can also be manipulated for disease management. GSNOR (S- nitroso glutathione reductase) has been exploited using antisense strategy to develop transgenic plants expressing resistance against oomycete and bacterial pathogens. Mitogen-activated protein kinases (MAPKs) are important components in the plant immune signal transduction system and they transduce extracellular stimuli into intracellular transcription factors. Technologies have been developed to utilize appropriate *MAPK* genes for developing disease-resistant plants. Plants do not have much endogenous SA and by increasing the SA content, defense genes can be activated. The endogenous SA level can be increased by engineering *ICS*, *IPL*, *PAD4*, *AtRBP-DR1*, *OsWRKY13*, *OsWRKY89*, and *SGT1* genes and the transgenic plants overexpressing these genes show enhanced accumulation of SA and disease resistance. *NPR1* gene is a master regulator of the SA-mediated induction of systemic acquired resistance (SAR). *NPR1* gene has been exploited to develop disease-resistant transgenic plants. Genes encoding phospholipases, lipoxygenases (LOXs), allene oxide synthase (AOS), allene oxide cyclase (AOC), and OPDA reductase (OPR) have been cloned and engineered to enhance jasmonate (JA) biosynthesis and JA accumulation activates plant immune system. Arachidonic acid isolated from microbes is an elicitor of plant defense responses. Bioengineering technology has been developed to make the plants themselves to produce arachidonic acid. The arachidonic acid-containing transgenic plants show increased levels of jasmonic acid. Developing transgenic plants constitutively producing arachidonic acid may be a potential approach to activate JA pathway for management of plant diseases. Some transcription factor genes have been engineered to manipulate JA signaling system for crop disease management. Under natural conditions endogenous ethylene content is very low in plants and its level is not sufficient to induce defense gene expression. Increase in ethylene biosynthesis induces enhanced defense responses. Transgenic rice lines overexpressing ACC synthase gene, *OsACS2*, have been generated and these transgenic plants show increased levels of endogenous ethylene and disease resistance. Several biotic and abiotic elicitors have been successfully utilized to activate the plant immune system for management of crop diseases. Laminarin manipulates the proton pump and triggers defense responses. Chitosan treatment inactivates $H^+$-ATPase resulting in membrane depolarization, which is involved in increasing $Ca^{2+}$ influx. Chitosan has been found to be highly effective in inducing resistance against oomycete, fungal, viral, and bacterial diseases. Thiamine treatment triggers $Ca^{2+}$ influx and induces $Ca^{2+}$-induced protein kinase C (PKC) activity. It effectively controls bacterial, fungal, and viral diseases of crop plants by activating $Ca^{2+}$ signaling system. BTH (benzo[1,2,3]thiadiazole-7-carbothioc acid S-methyl ester) is the most successfully developed commercial compound to manipulate ROS signaling system for management of viral, bacterial, and phytoplasma diseases and parasitic plants. Riboflavin is another compound which can be used to manipulate ROS and redox signaling system.

Menadione sodium sulphite (MSB) induces systemic resistance by activating redox signaling systems. The herbicide lactofen targets protoporphyrinogen oxidase, which in turn causes singlet oxygen generation. Singlet oxygen is involved in triggering ROS-mediated signaling system. Lactofen application provides significant control of fungal and oomycete diseases. Trifluralin, a dinitroaniline herbicide, induces disease resistance against several pathogens by manipulating redox signaling system. Glufosinate ammonium is a nonselective herbicide. It activates ROS-dependent SA signaling system and induces resistance against pathogens. Milsana activates ROS-mediated signaling system and is highly effective in controlling powdery mildew diseases in crop plants. β-Aminobutyric Acid (BABA) has been shown to induce disease resistance against various pathogens by triggering ROS production. Potassium dihydrogen phosphate induces systemic resistance by inducing a rapid generation of superoxide and hydrogen peroxide. Silicon is another potential tool to enhance defense responses by activating ROS signaling system. Manipulation of nitric oxide (NO) signaling by sodium nitroprusside (SNP) may be another potential approach to trigger plant immune system for effective crop management. Treatment of plants with BTH triggers SA signaling and causes the induction of a unique physiological state called "priming". BTH activates SA-dependent SAR in many crops and has been found to be useful in management of several crop diseases caused by oomycetes, fungi, bacteria, and viruses. N-cyanomethyl-2-chloroisonicotinamide (NCI) is another potential chemical that activates NPR1-dependent SA signaling system. CMPA (3-chloro-1-methyl-1H-pyrazole-5-carboxylic acid) is another compound, which activates SA signaling pathway. Tiadinil (3,4-dichloro-*N*-(2-cyanophenyl)-1,2-thiazole-5-carboxamide) is another potential chemical, which triggers SA signaling pathway by activating NPR1 gene expression. Probenazole and its metabolite BIT intervene in SA signaling system at SA accumulation stage as well as at NPR1 stage to trigger resistance against pathogens. BABA induces priming in the SAR induction pathway. The descendants of primed plants exhibit next-generation systemic acquired resistance. Azelaic acid stimulates the production of AZ11, a protein which helps prime the plant to build up its immunity by generating additional SA. An oligosaccharide product obtained from burdock (*Arctium lappa*) plant triggers production of methyl salicylate involved in SA signaling system and confers disease resistance. Yeast elicitor treatment activates SA signaling system and induces resistance against oomycete, fungal, and bacterial pathogens in many crop plants. Priming for JA-dependent defenses using hexanoic acid appears to be an effective tool for management of crop diseases. Ulvan is a potential activator of JA signaling pathway. Alkamides are fatty acid amides, which are commonly present in plants. N-isobutyl decanamide, the most highly active alkamide, has been shown to be a potential tool to manipulate enzymes involved in JA biosynthesis pathway. SA, JA, and ethylene signaling systems can be activated by using different rhizobacteria and the rhizobacteria trigger "induced systemic resistance".

**Keywords** $Ca^{2+}$ ion channels · $H^+$ - ATPase proton pump · Annexin · G-protein genes · ROS · NO · MAPK · NPR1 · gene · Chitosan · Laminarin · Thiamine · BABA · BTH · Probenazole · SAR · ISR

## 1.1 Signals and Signaling Systems Involved in Activation of Plant Innate Immune System

Plants are endowed with innate immune system, which has a high potential to detect and fight against viral, bacterial, oomycete, and fungal pathogens and protect the crop plants against wide range of diseases (Vidhyasekaran 2002, 2004, 2007a, b, 2014, 2015, 2016). The plant innate immune system is a sleeping system in unstressed healthy plants (Vidhyasekaran 2014). Specific signals are needed to activate the "sleeping" immune system. My earlier books (Vidhyasekaran 2014, 2015, 2016) described in detail the various signals and signaling systems involved in activating the sleeping giant. The first book (Vidhyasekaran 2014) describes the function of pathogen-associated molecular patterns (PAMPs)/Microbe-associated molecular patterns (MAMPs) as primary signals involved in activation of the sleeping plant immune system. PAMPs directly bind to plant pattern recognition receptors (PRRs) and the PAMP-PRR complex activates the plant immune system. This book (Vidhyasekaran 2014) describes the PAMP-PRR signaling complex and signal transduction system. Several second messengers are involved in delivering the information generated by the PAMP-PRR signaling complex to the proteins which decode/interpret signals to initiate defense gene expression. Calcium ion is an important second messenger. Calcium signatures are recognized by calcium sensors to transduce calcium-mediated signals into downstream events. G-proteins act as molecular switches in signal transduction system. MAPK cascades transduce extracellular stimuli into intracellular responses. Reactive oxygen species (ROS) and nitric oxide (NO) also act as second messengers in transmitting the PAMP signal (Vidhyasekaran 2014).

My second book (Vidhyasekaran 2015) describes plant hormone signaling systems including salicylate (SA), jasmonate (JA), ethylene (ET), abscisic acid (ABA), auxins, gibberellins, and brassinosteroids signaling systems involved in activation of the sleeping immune systems. Two forms of induced resistance, systemic acquired resistance (SAR) and induced systemic resistance (ISR) are recognized. SA signaling system is involved in SAR, while JA/ET signaling system is involved in ISR. This book (Vidhyasekaran 2015) also describes the plant hormones-modulated priming, histone memory for information storage gene priming, chromatin remodeling in priming, DNA methylation in trans-generational SAR, mobile signal complex, signal receptor complex, JAZ proteins, cross-talk between hormones, and phosphorelay signaling systems. My third book (Vidhyasekaran 2016) describes various bioengineering and molecular manipulation techniques to switch on PAMP-PRR signaling complex. Early and robust activation of PAMP-PRR signaling complex triggers strong defense responses. Bioengineering PRRs is a potential technology to awaken the quiescent plant innate immunity for effective management of crop diseases. The present book describes various bioengineering and molecular manipulation techniques to activale calcium ion influx–mediated immune signaling system, reactive oxygen species, redox and nitric oxide signaling systems, MAPK signal transduction system, SA, JA, and ET signaling systems for crop disease management.

## 1.2 Bioengineering Technologies to Activate Plant Immunity Signaling Systems for Management of Crop Diseases

Plant innate immunity can be activated by different biotic or abiotic elicitor signals (Vidhyasekaran 2014). The plant immune system uses several second messengers to encode information generated by biotic or abiotic elicitors and deliver the information to proteins which decode/interpret signals and initiate defense gene expression (Hwang and Hwang 2011; Vidhyasekaran 2014). Calcium ion is an important intracellular second messenger. It acts as a signal carrier and the calcium signaling is modulated by specific "calcium signatures". These calcium signatures result from the concerted action of channels, pumps, and carriers that shape temporally and spatially defined $Ca^{2+}$ elevations (Vidhyasekaran 2014). Cellular $Ca^{2+}$ signals are decoded and transmitted by a tool kit of $Ca^{2+}$ binding proteins that relay this information into downstream responses (Vidhyasekaran 2014). Several genes involved in the calcium ion influx–mediated immune signaling system have been exploited for management of crop diseases. Genes encoding calmodulin-binding protein (Wan et al. 2012), G-proteins (Li et al. 2005; Thao et al. 2007), glutamate receptor-like ion channel protein (Kang et al. 2006), $H^+$-ATPase proton pump (Abad et al. 1997; Pontier et al. 2002), calcium dependent protein kinase (CDPK) (Geng et al. 2013), and annexin (Jami et al. 2008) have been bioengineered to develop disease-resistant plants.

ROS signaling network plays a central role in launching the defense response (Vidhyasekaran 2014). NPR1, the transcriptional regulatory cofactor, is activated by redox signaling in plants and NPR1 is involved in triggering defense responses. *NPR1* gene has been used to develop transgenic plants using bioengineering technologies (Chern et al. 2001; Friedrich et al. 2001; Makandar et al. 2006). Cysteine-rich receptor-like kinases (CRKs) are connected to redox and ROS signaling (Vidhyasekaran 2014). Transgenic plants overexpressing *CRK* genes show enhanced disease resistance by triggering enhanced ROS production (Bourdais et al. 2015; Yeh et al. 2015). L-type lectin receptor kinases (LecRKs) have been exploited to develop transgenic disease-resistant plants. These transgenic plants show enhanced production of ROS and trigger defense responses against pathogens (Huang et al. 2014). Peroxidases in the cell wall can generate apoplastic $H_2O_2$ at neutral to basic pH in the presence of reductants in plant cells. It is possible to generate transgenic plants overexpressing peroxidase gene to overproduce peroxidase resulting in enhanced ROS accumulation. These transgenic plants show enhanced disease resistance (Choi et al. 2007). Super oxide dismutase gene has been engineered to activate ROS-mediated immune signaling for disease management (Guevara-Olvera et al. 2012; Rietz et al. 2012). Fungal glucose oxidase gene has been engineered to develop disease-resistant plants. Expression of the fungal glucose oxidase gene leads to elevated production of $H_2O_2$ in the transgenic plants resulting in increased disease resistance (Felcher et al. 2003; Maruthasalam et al. 2010). Nitric oxide (NO) signaling system can also be manipulated for disease management. GSNOR (S-nitroso glutathione reductase)

has been exploited using antisense strategy to develop transgenic plants expressing resistance against oomycete and bacterial pathogens (Rustérucci et al. 2007). Nitric oxide synthase (NOS) has been used to develop transgenic plants. The mammalian NOS isolated from rat brain has been shown to be a potential tool to develop transgenic plants expressing resistance against a wide range of pathogens (Altamiranda et al. 2008; Chun et al. 2012).

Mitogen-activated protein kinases (MAPKs) are important components in the plant immune signal transduction system and they transduce extracellular stimuli into intracellular transcription factors (Vidhyasekaran 2014). Technologies have been developed to utilize appropriate *MAPK* genes for developing disease-resistant plants. Bioengineering specific *MAPK* genes has been shown to induce disease resistance by triggering phosphorylation of transcription factors (Cheong et al. 2003). Some *MAPK* genes have been shown to regulate SA-mediated systemic acquired resistance (SAR) (Vidhyasekaran 2015). The cotton MAPK gene *GhMPK7* and the maize MAPK gene *ZmSIMK1* activate SA signaling system and transgenic plants overexpressing these genes show enhanced disease resistance (Shi et al. 2010; Wang et al. 2014).

Some MAPK genes (*BnMPK4* and *MK1*) trigger the JA-mediated signaling system and these genes have been exploited to develop transgenic plants expressing enhanced resistance against necrotrophic pathogens (Wang et al. 2009). The cotton MAPK genes *GhMPK16* and *GHMPK2* activate SA, JA and ET signaling complex and these genes have been engineered to develop disease-resistant transgenic plants (Zhang et al. 2011). Some mitogen-activated protein kinase kinase (*MAPKK*) genes have also been exploited to activate immune responses for crop disease management (Shen et al. 2010). Some MAPK genes negatively regulate the defense responses and these genes also have been exploited to develop disease-resistant plants by knocking-out these *MAPK* genes (Liu et al. 2011). MAPK gene can also be manipulated to trigger the immune responses by using the biocontrol agent *Trichoderma asperellum*. A MAPK, designated as *Trichoderma*-induced MAPK (TIPK), has been identified and characterized in the *Trichoderma*- induced disease-resistant cucumber plants. The *TIPK* gene has been cloned and cucumber plants overexpressing the *TIPK* gene show resistance against pathogen (Liu et al. 2011).

Salicylic acid (SA) signaling system is the most important signaling system activating plant innate immunity (Vidhyasekaran 2014, 2015, 2016). Plants do not have much endogenous SA. It has been suggested that by increasing the SA content, defense genes can be activated and diseases can be controlled (Vidhyasekaran 2015). Increased synthesis and accumulation of salicylic acid in plants result in increased expression of defense genes conferring resistance against pathogens. SA may be synthesized through the isochorismate pathway (Vidhyasekaran 2015). Isochorismate synthase (ICS) and isochorismate pyruvate lyase (IPL) are the key enzymes involved in biosynthesis of SA. SA is synthesized from chorismate, the end product of the shikimate pathway. Chorismate is converted by ICS to isochorismate, which is subsequently cleaved by IPL to yield SA (Vidhyasekaran 2015). The genes encoding ICS and IPL cloned from two different bacteria have been exploited to develop transgenic tobacco plants overexpressing both *ICS* and *IPL* genes. These transgenic plants show

enhanced accumulation of SA. The transgenic tobacco plants which show high accumulation of SA, show enhanced disease-resistance (Verberne et al. 2000). Several SA signaling regulator proteins are involved in SA production pathway. PAD4 is a key regulator protein acting at upstream of SA. PAD4 is required for amplification of weak signals to a level sufficient for activation of SA signaling. *PAD4* gene has been exploited to develop disease-resistant wheat plants (Makandar et al. 2015).

RNA-binding proteins (RBP) play important roles in post-transcriptional gene regulation by controlling splicing, polyadenylation, mRNA stability, RNA trafficking, and translation (Pallas and Gomez 2013; Marondedze et al. 2016). A RBP from *Arabidopsis thaliana*, AtRBP-defense related 1 (AtRBP-DR1), has been shown to be involved in plant immune responses. The *AtRBP-DR1* gene was cloned and exploited for developing disease-resistant plants. Transgenic *Arabidopsis* plants overexpressing *AtRBP-DR1* were developed (Qi et al. 2010). These transgenic plants show higher mRNA levels of *SID2*. The *SID2* gene encodes an isochorismate synthase, which is required for producing SA during immune responses (Wildermuth et al. 2001). Activation of the SA pathway by *AtRBP-DR1* overexpression was fully dependent on *SID2* (Qi et al. 2010). Overexpression of *AtRBP-DR1* led to high accumulation of SA and these transgenic plants show enhanced resistance to the bacterial pathogen *Pseudomonas syringae* pv. *tomato* DC3000 (Qi et al. 2010).

A camodulin binding protein, CBP60g, has been shown to be involved in activating SA biosynthesis (Wang et al. 2009; Vidhyasekaran 2015). *CBP60g* has been shown to bind to the promoter region of *SID2* (Wang et al. 2011). Transgenic *Arabidopsis* plants overexpressing *CBP60g* gene were developed and these transgenic plants showed elevated SA accumulation and increased expression of defense genes (Wan et al. 2012). The transgenic plants showed enhanced resistance against the bacterial pathogen *Pseudomonas syringae* (Wan et al. 2012).

Several transcription factors are known to take part in the regulation of SA signaling pathway (Vidhyasekaran 2015, 2016). The transcription factor genes *OsWRKY13* (Qiu et al. 2007, Cheng et al. 2015), *OsWRKY89* (Wang et al. 2007), and *NtWIF* (Waller et al. 2006) have been engineered to develop disease-resistant plants. Ubiquitin-proteasome pathway can be manipulated to trigger SA signaling system for crop disease management (Vidhyasekaran 2015). Transgenic tobacco plants expressing a ubiquitin-variant with Lys to Arg exchange in position 48 (ubr48) were developed (Becker et al. 1993). These transgenic tobacco plants showed enhanced resistance against *Tobacco mosaic virus* (Becker et al. 1993). The transgenic plants expressing the ubiquitin variant ubr78 contained elevated levels of SA compared to the control plants (Conrath et al. 1998). *SGT1* genes are required for SA accumulation and they have been engineered to develop disease resistant plants (Wang et al. 2008; Zhou et al. 2008).

*NPR1* gene is a master regulator of the SA-mediated induction of systemic acquired resistance (SAR) (Vidhyasekaran 2015). *NPR1* gene has been engineered to develop several transgenic crop plants including rice, tomato, citrus, carrot, and strawberry (Feng et al. 2011; Le Henanff et al. 2011; Chen et al. 2012; Dutt et al. 2015; Silva et al. 2015; Boscariol-Camargo et al. 2016; Molla et al. 2016; Joshi et al. 2017).

Jasmonic acid and their derivatives (JA) are important signal molecules detected in a wide spectrum of plant species (Vidhyasekaran 2015). They are involved in activation of plant immune system. The concentrations of JA in healthy unperturbed plant tissues are very low. Increased concentrations of JA are needed to activate the plant immune system and to induce "Induced systemic resistance (ISR)". JA concentration can be increased by enhancing the activities of the enzymes involved in JA biosynthesis. The key enzymes involved in the biosynthesis involve phospholipases, lipoxygenases (LOXs), allene oxide synhases (AOS), allene oxide cyclase (AOC), and OPDA reductase (OPR) (Vidhyasekaran 2015). The genes encoding these enzymes have been cloned and engineered to enhance the JA biosynthesis and JA accumulation activates plant immune system (Mei et al. 2006; Mene-Saffrané et al. 2003; Hwang and Hwang 2010; Hou et al. 2018). The transcription factor genes *OsMYC2* and *VvWRKY1* have been engineered to manipulate JA signaling system for crop disease management (Marchive et al. 2013; Uji et al. 2016).

Under natural conditions endogenous ethylene content is very low in plants and its level is not sufficient to induce defense gene expression (Vidhyasekaran 2015; Ravanbakhsh et al. 2018). Increase in ethylene biosynthesis induces enhanced defense responses. Hence several attempts were made to induce ethylene biosynthesis in plants for disease management. Transgenic rice lines overexpressing ACC synthase gene, *OsACS2*, have been generated and these transgenic plants show increased levels of endogenous ethylene. The transgenic lines overexpressing *OsACS2* show increased resistance to the rice blast pathogen *Magnaporthe oryzae* and the rice sheath blight pathogen *Rhizoctonia solani* (Helliwell et al. 2013).

ERF belonging to the APETELA2 (AP2)/ETHYLENE RESPONSIVE ELEMENT BINDING PROTEIN (EREBP) transcription factor family is the important group of transcription factors functioning downstream in ethylene signaling system (Vidhyasekaran 2016). Several *ERF* genes have been engineered to develop disease-resistant plants (Dong et al. 2015; Xing et al. 2017; Wang et al. 2018). EIN2 is a membrane protein that acts as the central regulator of ethylene signaling pathways. The rice plants overexpressing *OsEIN2* show enhanced resistance against the rice blast pathogen *Magnaporthe oryzae* (Yang et al. 2017).

## 1.3 Molecular Manipulation of Plant Immunity Signaling Systems Using Abiotic or Biotic Elicitors for Management of Crop Diseases

Several biotic and abiotic elicitors have been developed as commercial formulations to activate the plant immune system and induce disease resistance. Chitosan has been found to be highly effective in inducing resistance against oomycete, fungal, viral, and bacterial diseases (Algam et al. 2010; El-Mohamedy et al. 2014; Sunpapao and Ponsuriya 2014). Chitosan treatment inactivates $H^+$-ATPase resulting in membrane depolarization, which is involved in increasing $Ca^{2+}$ influx (Amborabé et al. 2008).

Thiamine treatment triggers $Ca^{2+}$ influx and induces $Ca^{2+}$-induced protein kinase C (PKC) activity. Thiamine treatment effectively controls bacterial, fungal, and viral diseases of crop plants by activating $Ca^{2+}$ signaling system (Ahn et al. 2005).

Many attempts have been made to manipulate the ROS signaling system to trigger host defense responses. BTH (benzo[1,2,3]thiadiazole-7-carbothioc acid S-methyl ester) is the most successfully developed commercial compound to manipulate ROS signaling system for management of viral, bacterial, and phytoplasma diseases and parasitic plants, which are difficult to be controlled by traditional chemical control methods (Walters et al. 2005; Mandal et al. 2008). BTH induces accumulation of ROS through activation of different signaling pathways (Faize et al. 2004; Cavalcanti et al. 2006; Lanteri et al. 2008). The induced ROS triggers several downstream events inducing expression of several defense genes (Faize et al. 2004; Deepak et al. 2006; Faoro et al. 2008; Schreiber and Desveaux 2008). BTH has been shown to induce several genes with potential roles in establishing reducing conditions following the oxidative burst induced by it (Faize et al. 2004; Deepak et al. 2006; Faoro et al. 2008). Thiol-based redox signaling has been suggested to contribute to the activation of a primed state in BTH-treated plants (Kużniak et al. 2014). BTH treatment, which induces redox conditions, activates *NPR1* (for non-expresser of PR gene 1) and induces resistance against pathogens (Chern et al. 2001; Zhu et al. 2003). *NPR1* gene is a master regulator of the systemic acquired resistance (SAR) in plants. NPR1 enhances the binding of transcription factors to the promoters of pathogenesis-related (*PR*) defense genes for activation (Chern et al. 2008; Mukherjee et al. 2010). BTH may activate the plant immune system by triggering accumulation of ROS, which may enhance the expression of NPR1, the key regulator of the long-lasting broad-spectrum defense responses. BTH treatment effectively controls several fungal, oomycete, bacterial, phytoplasma, and viral diseases in wheat, rice, barley, potato, bean, cucumber, lettuce, sunflower, oilseed rape, sugarcane, strawberry, Japanese pear, sugarbeet, blackgram, red clover and chrysanthemum (D'Amelio et al. 2010; Venkatesan et al. 2010; Romanazzi et al. 2013; Oliveira and Nishijima 2014).

Riboflavin is another compound which can be used to manipulate ROS and redox signaling system (Dong and Beer 2000). It induces $H_2O_2$ production. Riboflavin induces priming of defense responses and triggers systemic resistance against pathogens (Saikia et al. 2006). Menadione sodium sulphite (MSB) is a water-soluble addition compound of vitamin $K_3$. It is a ROS generator, readily undergoing cell-mediated one-electron reduction, producing superoxide radicals ($O_2^-$) and $H_2O_2$ (Hassan and Fridovich 1979). MSB treatment induces systemic resistance by activating redox signaling systems (Borges-Pérez and Fernandez-Falcon 1996). Some herbicides have been shown to act as plant innate immunity system activators. The herbicide lactofen targets protoporphyrinogen oxidase, which in turn causes singlet oxygen generation. Singlet oxygen is involved in triggering ROS-mediated signaling system. Lactofen application provides significant control of fungal and oomycete diseases (Graham 2005). Trifluralin, a dinitroaniline herbicide, induces disease resistance against several pathogens by manipulating redox signaling system (Bolter et al. 1993). Glufosinate ammonium is a nonselective herbicide. It activates ROS-dependent SA signaling system and induces resistance against pathogens (Ahn

2008). Milsana (*Reynoutria sachalinensis* formulation) activates ROS-mediated signaling system and is highly effective in controlling powdery mildew diseases in crop plants (Randoux et al. 2006). β-Aminobutyric Acid (BABA) has been shown to induce disease resistance against various pathogens by triggering ROS production. BABA-induced resistance is mostly based on priming of defense responses rather than on the direct activation of these defense responses. BABA has been shown to prime *RbohD* gene, which encodes a NADPH oxidase potentially involved in ROS production (Dubreuil-Maurizi et al. 2010; Pastor et al. 2013). Potassium dihydrogen phosphate induces systemic resistance by inducing a rapid generation of superoxide and hydrogen peroxide (Orober et al. 2002). Potassium phosphonate triggers ROS signaling system–mediated plant defense responses by rapidly releasing superoxide around the point of infection (Daniel and Guest 2006). Oxycom is a commercially available chemical containing reactive oxygen species. It acts as a plant innate immunity activator. Applications of Oxycom triggers plant immune system downstream of ROS (Blee et al. 2004). Several bacterial and fungal biocontrol agents have been shown to induce systemic resistance (ISR) against several plant pathogens in various crop plants. Some of the rhizobacteria activate the plant innate immune system by triggering the ROS signaling system. *Pseudomonas fluorescens* WCS374 is a potential tool to trigger ROS signaling system and confer resistance against pathogens (De Vleesschauwer et al. 2008). *Serratia plymuthica* ICI270, primes leaves for enhanced attacker-induced accumulation of ROS. It induces accumulation of ROS in leaves and induces systemic resistance (De Vleesschauwer and Höfte 2009). *Bacillus mycoides* elicits ISR by triggering ROS production. Silicon is another potential tool to enhance defense responses by activating ROS signaling system (De Vleesschauwer et al. 2009). Silicon treatment significantly alters the activity of lipoxygenase (LOX), which catalyzes the direct oxygenation of polyunsaturated fatty acids and produces $O_2^-$. Several silicon-based formulations are available for management of crop diseases (Sun et al. 2010). Manipulation of nitric oxide (NO) signaling by sodium nitroprusside (SNP) may be another potential approach to trigger plant immune system for effective crop management. SNP is a NO generator (Kobeasy et al. 2011; Thuong et al. 2015). SNP treatment triggered ROS and SA signaling systems (Thuong et al. 2015). Sodium nitroprusside applied as foliar spray effectively triggered host defense responses against *Peanut mottle virus* in peanut (Kobeasy et al. 2011).

Treatment of plants with BTH triggers SA signaling and causes the induction of a unique physiological state called "priming" (Camañes et al. 2012; Slaughter et al. 2012) BTH induces histone modifications, which may be involved in the gene priming (Jaskiewicz et al. 2011). The expression of the *WRKY* genes is enhanced in BTH-treated plants. BTH triggers NPR1-dependent chromatin modification on WRKY promoters to activate defense gene expression (Jaskiewicz et al. 2011). BTH activates SA-dependent SAR in many crops and has been found to be useful in management of several crop diseases caused by oomycetes, fungi, bacteria, and viruses. N-cyanomethyl-2-chloroisonicotinamide (NCI) is another potential chemical that activates NPR1-dependent SA signaling system. NCI activates SAR by stimulating the site between SA and NPR1. NCI has been found to be effective in inducing

resistance against *Tobacco mosaic virus* (TMV), *P. syringae* pv. *tabaci*, and *Oidium lycopersici* in tobacco and *Magnaporthe oryzae* in rice (Nakashita et al. 2002; Yasuda 2007).

CMPA (3-chloro-1-methyl-1H-pyrazole-5-carboxylic acid) is another compound, which activates SA signaling pathway. It acts in the SA signaling pathway between SA production and NPR1 activity. It protects rice from infection by rice blast pathogen *Magnaporthe oryzae* and bacterial blight pathogen *Xanthomonas oryzae* pv. *oryzae*. It enhances resistance of tobacco to *Pseudomonas syringae* pv. *tabaci* and *Oidium* sp. (Nakashita et al. 2003; Nishioka et al. 2005; Yasuda et al. 2003). Tiadinil (3,4-dichloro-*N*-(2-cyanophenyl)-1,2-thiazole-5-carboxamide) is another potential chemical, which triggers SA signaling pathway by activating NPR1 gene expression. It induces resistance against various fungal, bacterial, and viral diseases in tobacco and is practically used to control rice blast disease (Yasuda et al. 2004, 2006; Yasuda 2007). Probenazole (3-allyloxy-1,2-benzisothiazole-1,1-dioxide) and its metabolite 1,2-benzisothiazole-3 (2H)-one 1,1-dioxide (BIT, saccharin) are potential plant defense activators and both of them are known to induce SA accumulation and activate SA signaling system (Schreiber and Desveaux 2008). Probenazole/BIT intervenes in SA signaling system at SA accumulation stage as well as at NPR1 stage to trigger resistance against pathogens (Yoshioka et al. 2001; Park et al. 2007, 2009). The nonprotein amino acid β-aminobutyric acid (BABA) induces broad-spectrum resistance in a range of crops. BABA induces priming in the SAR induction pathway. The descendants of primed plants exhibit next-generation systemic acquired resistance (Slaughter et al. 2012). SA signaling system can also be activated using plant-derived products. Azelaic acid, a natural compound found in several plants, is a signal molecule triggering plant defense responses. Azelaic acid does not directly induce defense responses, but confers on the plants the ability to mount a faster and stronger defense response if and when the plant is attacked again. It does this by increasing the production of SA. Azelaic acid stimulates the production of AZ11, a protein which helps prime the plant to build up its immunity by generating additional SA (Jung et al. 2009). AHO (3-acetonyl-3-hydroxyoxindole) isolated from the extracts of *Strobilanthes cusia* is an activator of SA signaling system. When tobacco plants are treated with AHO, SA accumulates in the leaf tissues and induces disease resistance (Li et al. 2008). An oligosaccharide product obtained from burdock (*Arctium lappa*) plant triggers production of methyl salicylate involved in SA signaling system and confers disease resistance (He et al. 2006). *N*-Acyl-L-homoserine lactones (AHLs)–producing bacteria, which induce SA-dependent systemic resistance, have been shown to be potential tools for management of crop diseases (Schuhegger et al. 2006). Some of the rhizobacterial strains activate the plant innate immune system by triggering SA signaling system and they are widely used for management of crop diseases (De Meyer et al. 1999; Zhang et al. 2002; Tjamos et al. 2005). SA signaling system can be activated by some MAMPs (for Microbe-associated molecular patterns) for effective crop disease management. The MAMP yeast elicitor treatment activates SA signaling system and induces resistance against oomycete, fungal, and bacterial pathogens in many crop plants (Raacke et al. 2006; Tosun 2007).

Hexanoic acid is a nine carbon dicarboxylic acid that acts as an inducer of plant defenses by means of a priming mechanism (Vicedo et al. 2009). Priming results in a faster and stronger induction of defense mechanisms after pathogen attack (Conrath 2011; Po-Wen et al. 2013). Hexanoic acid primes JA biosynthesis pathway (Vicedo et al. 2009). Priming for JA-dependent defenses using hexanoic acid appears to be an effective tool for management of crop diseases (Djami-Tchatchou et al. 2017). Ulvan, a sulfated polysaccharide product isolated from green algae belonging to the *Ulva* genus is a potential activator of JA signaling pathway (Jaulneau et al. 2010). Ulvan treatment induces elevation of JA content in *Medicago truncatula*. It also induces the expression of well-known jasmonic acid-responsive genes including lipoxygenase, hydroxyproline-rich glycoproteins, proline-rich proteins, defensin and wound-induced protein (Jaulneau et al. 2010). Ulvan treatment induces biosynthesis of jasmonoyl-isoleucine (Staswick and Tiryaki 2004), which is involved in defense signaling (Wasternack and Hause 2013). Ulvan spraying has been shown to control several foliar diseases (de Freitas and Stadnik 2012, 2015; de Freitas et al. 2015).

Alkamides are fatty acid amides, which are commonly present in plants (Méndez-Bravo et al. 2011). N-isobutyl decanamide, the most highly active alkamide, has been shown to be a potential tool to manipulate enzymes involved in JA biosynthesis pathway. Alkamide treatment enhances the expression of genes encoding enzymes for jasmonic acid biosynthesis. It enhances the expression of lipoxygenase genes (*LOX2* and *LOX3*), allene oxide synthase gene (*AOS*), allene oxide cyclase2 gene (*AOC2*), and OPDA reductase3 (*OPR3*) gene. The alkamide has great potential to combat pathogens by triggering JA biosynthesis pathway (Méndez-Bravo et al. 2011).

Chitosan has been developed as a potential activator of JA signaling system to induce defense responses for crop disease management (Bueter et al. 2013). Chitosan triggers lipoxygenase activity and induces accumulation of jasmonic acid (Doares et al. 1995; Rakwal et al. 2002). Chitosan activates plant innate immune system and controls several crop diseases (Prapagdee et al. 2007; Li et al. 2009; Dafermos et al. 2012).

JA signaling system can be manipulated using some microbes for crop disease management. *Trichoderma* spp. are known to be involved in triggering 'induced systemic resistance' (ISR) in many plants (Harman et al. 2004; Vidhyasekaran 2004; Shoresh et al. 2010: Mathys et al. 2012; Martinez-Medina et al. 2013; Harel et al. 2014). *Trichoderma asperellum* T 203 induced systemic resistance against the foliar bacterial pathogen *Pseudomonas syringae* pv. *lachrymans* and reduced the angular leaf spot symptom development (Yedidia et al. 2003). The *Trichoderma* strain induced the expression of *Lox1* encoding lipoxygenase (LOX), the key enzyme in LOX pathway which is involved in biosynthesis of JA (Shoresh et al. 2005). It also induced the lipoxygenase pathway gene encoding hydroperoxide lyase (HPL) (Yedidia et al. 2003). *Trichoderma virens* is a commercially formulated biocontrol agent and it is effective in the control of *Rhizoctonia solani*, *Sclerotium rolfsii*, and *Pythium* spp. in several crop plants (Mukherjee and Kenerley 2010). It induces resistance against several crop diseases by activating JA signaling system (Djonovic et al. 2006). *Pseudomonas putida* strain BTP1 treatment primes tomato plants to activate two key enzymes of lipoxygenase (LOX) pathway, lipoxygenase (LOX) and

lipid hydroperoxidase (LHP) after challenge inoculation with the pathogen *Botrytis cinerea* (Akram et al. 2008). *P. putida* BTP1 induces ISR in bean against the gray mold pathogen *B. cinere*a (Ongena et al. 2002) and in cucumber against the root rot oomycete pathogen *Pythium aphanidermatum* (Ongena et al. 1999, 2000).

Ethylene signaling system can be activated by using different rhizobacteria (Leeman et al. 1995a, b; Ran et al. 2005a, b; Spencer et al. 2003). *Trichoderma asperellum* triggers ISR against several pathogens. Ethylene signal transduction pathway has been shown to be involved in the ISR induced by *T. asperellum* (Shoresh et al. 2005). *Pythium oligandrum* is a biocontrol agent which controls several soil-borne fungal and bacterial pathogens (Benhamou et al. 1997; Picard et al. 2000; Takenaka et al. 2003; Hase et al. 2006). *P. oligandrum* treatment induces biosynthesis of ethylene (Hase et al. 2006). *P. oligandrum* also activates ethylene signaling pathway. Activation of the ethylene-dependent signaling pathway is accompanied by increased expression of genes encoding ethylene receptors and ethylene-responsive transcription factors (Hase et al. 2006). Collectively these studies suggest that enhancing disease resistance through altered regulation of plant immune signaling systems will be an attractive technology for management of crop diseases.

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