

Editorial

Understanding Disease Resistance Signaling in Rice against various Pests and Pathogens

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Editorial

Rice is one of the major food crop for half of the world's population. The production of rice is influenced by various biotic and abiotic factors. Although over 100 species of insects have been reported as pests of rice, major pests that are of economic importance are the stem borers (*Chilosuppressalis*), the Brown Plant Hopper, (BPH) (*NilaparvatalugensStal*), Asian rice gall midge (*Orseoliaoryzae*) and rice bugs [1-3]. Rice blast (*Magnaportheoryzae*), bacterial blight (*Xanthomonasoryzae* *pv. oryzae*), are the most destructive fungal and bacterial diseases of rice [4,5]. A crucial step in plant defense is the timely perception of the stress in order to respond in a rapid and efficient manner. Present study reviews rice defense signaling pathway in disease resistance against blast, bacterial blight, BPH and Asian rice gall midge.

Molecular responses of plants are associated with the feeding way and tissue damage amount caused by different plant-pathogens/herbivore interaction [2]. Plants induce a multilayered immune system after recognition of non-self-molecules such as microbial-associated molecular patterns (PAMPs) from pathogenic organism and cease the growing pathogen by two effective ways of plant innate immunity which is called PAMP-Triggered Immunity (PTI) and Effector-Triggered Immunity (ETI). These PAMPs which include bacterial flagellin, Lipopolysaccharides (LPSs), Elongation Factor Tu (EF-Tu) and fungal chitin are perceived in plants *via* membrane-bound receptor known as Pattern Recognition Receptors (PRRs), which eventually results in activation of PTI [6-7]. PRRs typically consist of an extracellular Leucine-Rich Repeat (LRR) domain and an intracellular Receptor Like Kinases (RLKs) domain [8]. *Xa21*, a rice resistance (R) gene that confers resistance to diverse *X. oryzae pv. Oryzae* strains was considered a pattern recognition receptor [9]. In most cases, PTI is adequate to suppress disease development *via* hindering pathogen establishment. However virulent pathogens, escape PTI-based surveillance by transporting small effector proteins in the plant cells, which in turn cause effector triggered plant susceptibility. Second level of innate immunity which is known as Effector-Triggered Immunity (ETI) has been observed in plants. ETI, also known as R-gene-mediated resistance, or specific resistance, represents a more amplified form of resistance [10]. ETI is initiated through plant cultivar-specific recognition of microbial effectors. Specific recognition is generally mediated *via* resistance (R) gene

products carrying Leucine-Rich Repeats (LRRs), and is typically distinguished from PTI by elicitation of Hypersensitive Response (HR)-associated localized program cell death.

Majority of R genes cloned so far belong to the Nucleotide-Binding Site Leucine-Rich Repeat (NBS-LRR) or LRR Kinase super-families [7]. NBS-LRR gene family organized in large clusters of orthologous genes and comprised about 1500 genes in rice [11]. Examples of known NBS-LRR R genes include the *Xanthomonas* resistance gene *Xa1* in rice [12]. For example, most (22 out of 23) cloned functional blast resistant R genes and one cloned gene (*Xa1*) against bacterial blight in rice represents NBS-LRR domains [12-14]. The *Bph14* gene against brown-plant hopper also encodes CC-NB-LRR protein of the NB-LRR family [2]. Most of the R genes mapped against gall midge resistance in rice are also from NBS-LRR gene family [15-17]. Even though the recognition mechanisms and outcomes of PTI and ETI are different, the intermediate signaling pathways overlap [10]. After recognition, plant's constitutive basal defense mechanisms [12] initiates a diverse set of downstream signaling events, leading to an activation of complex signaling cascades such as rapid microbursts of Reactive Oxygen Species (ROS), callose deposition to strengthen the cell wall, ion channels and MAP kinase cascades, phytohormones like Salicylic Acid (SA), Jasmonic Acid (JA), Ethylene (ET) and transcriptional induction of defense related genes [18,19].

ROS

A virulent pathogen, successfully recognized by the action of disease resistance (R) gene products in plant, elicit a biphasic ROS accumulation that act as direct reactive substrates to kill pathogens, and to strengthen plant cell walls by *via* cross-linking of glycoproteins to obstruct further extension of the pathogen [20]. ROS commonly triggers and precedes programmed cell death and also functions as signal molecules for production of Pathogenesis-Related (PR) protein. In rice, OsRac1 GTPase complex, which is essential for PTI, participate in direct regulation of NADPH oxidase which in turn controls ROS production [21]. Enzymes generating ROS during the defense response include NADPH oxidase, peroxidase, oxalate oxidase and amine oxidase. The increase of Ca²⁺ concentration is an important factor in the development of Reactive Oxygen Intermediate (ROI) mediated cell death [22]. Ca²⁺ is a well-known secondary signal in numerous signaling pathways among eukaryotes. ROS induction has been implicated in rice against bacterial blight [23], blast [24] and gall midge resistance [25]. In rice-BHP interaction, Ca²⁺ influx is triggered by insect feeding as one of the earliest cellular event [26].

Mitogen-Activated Protein Kinase (MAPK) Cascades

MAP kinase signaling has been reported to be involved in both PTI and ETI plant defense pathways [27]. MAPK pathways are activated by pathogen attack and mediated by SA which subsequently result in

pathogenies-related protein expression. Seventeen MAPK genes have been identified in the rice genome, however the role of these *OsMPKs* in rice defense responses yet to be deciphered [28]. The *OsMAPKs* negatively regulates rice resistance to both the pathogens (blast and bacterial blight) [29]. *BWMK1*, the first cloned MAPK gene in rice interacts with AP2/EREBP family of Transcription Factor (TF) and phosphorylates ERFs *Pti4* and *OsEREBP*, pivotal step in regulating resistance to blast and bacterial blight disease [30]. Expression levels of four MAPK genes (*OsMPK5/12/13/17*) were found to be induced by Blast and BPH [31].

Hormone signaling

Plant hormones are typically divided in two groups; one groups is for growth hormones such as auxin, Gibberellic Acids (GAs), Brassinosteroids (BRs) and Abscisic Acid (ABA) and, the other group is for defense related hormones such as SA, JA and ET those are associated with the regulation of diverse array of biotic stress responses [32]. However in past few decades, the role of growth hormones in plant defense have been widely studied which regulate plant defense, either by themselves or in combination with the defense hormones [33]. Biotic stress responses are preferentially mediated by antagonism of SA and JA/ET pathways. SA pathway is mostly connected with responses to biotrophic pathogens, while JA and ET pathways generally act synergistically and are linked to defenses against necrotrophic pathogens and herbivorous insects.

Downstream of SA biosynthesis, the SA pathway in rice shares a typical redox protein, NPR1 (NON-EXPRESSOR OF PR1) [34]. NPR1 exists as dimeric inactive protein which gets activated by SA-pathway. Salicylic acid reduces the intermolecular disulphide bonds and releases monomeric NPR1, which is translocated to the nucleus from cytosol where it interacts with TGA TF to activate defense-related gene expression [34,35]. Jasmonic Acid (JA) and its derivatives such as Methyl Jasmonate (MeJA) are known as lipid-derived hormones that play multiple and important regulatory role which comprise the regulation of developmental and defense processes in plants [36]. The only jasmonate receptor identified to date is COI1 protein, an F-box protein, which binds to JAZ proteins, a negative regulator of JA-responsive genes, finally leading to ubiquitin-dependent degradation [37]. Other JA responsive genes include leucine aminopeptidase and Allene Oxidecyclase (AOC) those are crucial in the proper functioning of JA signaling. It has been reported that the JA signaling pathway negatively regulates rice resistance to BPH, while the transcription levels of genes that are known to function in the SA pathway are activated in the *Bph14*-mediated insect resistance following BPH feeding [38]. Rice-gall midge interaction showed up-regulation of SA pathway in HR+ and not in HR- mediated defense [39-41].

Transcription Factors (TFs)

Changes in gene expression and the reprogramming of the molecular defense machinery is regulated by the action of TFs. Among many different type of TFs available in plants, the most common TFs involved in plant defense mainly belong to six groups; WRKY, AP2/ERF, MYB, BZIP, MYC and NAC [42]. Among the WRKY TFs, *OsWRKY45* is known as second master regulator of SA pathway which functions parallel to NPR1 to mediate resistance to blast and bacterial blight diseases of rice [43]. *OsWRKY45* seems to be activated at least in part by an SA-dependent phosphorylation cascade controlled by

the *OsMPK4* and *OsMPK6*. *OsWRKY70* induction increases plant susceptibility in rice against BPH feeding [44]. *OsWRKY62* is a negative regulator of both types of plant immunity (PTI and ETI). AP2/ERF TFs constitutes ~163 members in rice and ~140 members in Arabidopsis [45]. *OsEREBP1* was reported to be induced in rice and bacterial pathogen, *Xanthomonas, oryzaepv, oryzae* (Xoo) interaction [29]. MYB15 and WRKY40 TFs may play important roles in the transcriptional regulation of carbohydrate metabolism in citrus-HLB interactions [46,47]. A number of NAC proteins such as OsNAC4 have been reported inducing HR and cell death by activating PR genes. NAC TFs (ONAC122 and ONAC131) in rice increased susceptibility to blast disease [48]. BZIP transcription factors are characterized by their basic leucine Zipper (bZIP) domain which is involved in DNA binding. Rice rTGA2.1 interacts with *OsNPR1* which has a negative impact on SAR by altering accumulation of PR genes in response to bacterial blight disease [49]. In contrast, *OsBZIP1* may play a positive role in the SA-dependent signal transduction after Blast infection [50]. BPH feeding could suppress *OsBZIP60* expression levels by introducing effector proteins which suggest that the BPH may protect itself that suppress stress responses and enhance susceptibility [31].

The present study summaries and presents an informal description of complex and comprehensive molecular mechanism of rice defense against several pests and pathogens. Plant defense and pathogen counter defense mechanisms evolved as a part of co-evolutionary race between plants and their natural enemies. In the past decades significant progress was made in elucidating the molecular mechanism and cross talk has been recognized between hormone-regulated and defense-signaling pathways. Future studies will be focusing more to understand the specific responses against different combinations of stress that could be controlled by different signaling pathways and may elucidate additional candidate disease resistance genes/pathways for crop protection and breeding programs.

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