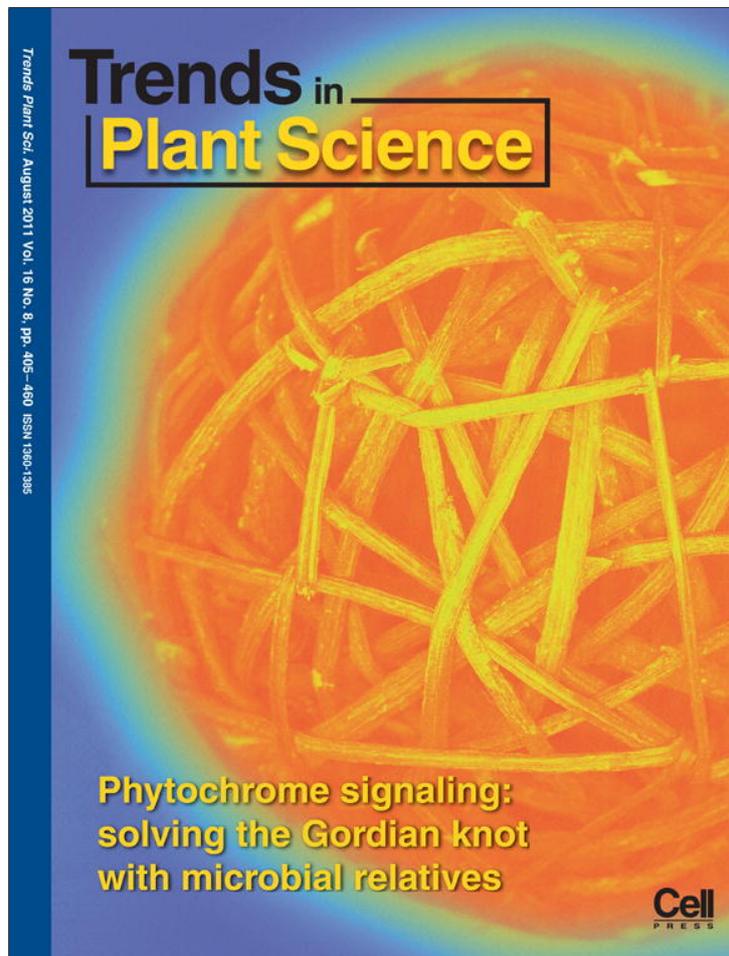


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# Innate immunity in rice

Xuewei Chen and Pamela C. Ronald

Department of Plant Pathology, University of California, Davis, CA 95616, USA

**Advances in studies of rice innate immunity have led to the identification and characterization of host sensors encoding receptor kinases that perceive conserved microbial signatures. Receptor kinases that carry the non-arginine-aspartate domain, are highly expanded in rice (*Oryza sativa*) compared with *Arabidopsis* (*Arabidopsis thaliana*). Researchers have also identified a diverse array of microbial effectors from bacterial and fungal pathogens that triggers immune responses upon perception. These include effectors that indirectly target host Nucleotide binding site/Leucine rich repeat proteins and transcription activator-like effectors that directly bind promoters of host genes. Here we review the recognition and signaling events that govern rice innate immunity.**

## Innate immunity

Rice (*Oryza sativa*) is the most important staple food because it feeds half of the world's population. It is also a model for molecular studies of other monocotyledonous species. The use of resistant cultivars is one of the most important factors used to control diseases that annually decrease global yields by 10–15% [1]. Studies of rice innate immunity are therefore of great interest both for advancing mechanistic knowledge of this important plant stress response as well as for advancing crop improvement.

One component of innate immunity is governed by the recognition of conserved microbial signatures (also known as pathogen- (or microbial-) associated molecular patterns (PAMPs or MAMPs)); by host sensors (also known as pattern recognition receptors (PRRs)) [2]. This immune response is called PAMP-triggered immunity (PTI). PAMPs are conserved among diverse strains or species of pathogens and are essential for survival or pathogenicity. For this reason, strains carrying mutations in these conserved microbial signatures are generally impaired in infection which limits their ability to spread in populations and cause epidemics [3].

A second type of innate immunity in plants, which is activated upon recognition of highly variable microbial molecules (known as effectors), is called effector-triggered immunity (ETI) [4]. Effectors are highly variable among strains of a pathogen species. Thus, compared with PTI, the resistance mediated by ETI is more specific and is predicted to be less durable [4]. A third type of immunity is systemic acquired resistance (SAR) that confers long-lasting protection against a broad spectrum of microorganisms. SAR requires the signal molecule salicylic acid (SA) [5].

In this review we describe recent advances in rice innate immunity, with a focus on PTI and ETI, including recognition of the pathogens and the signaling cascades resulting from this recognition.

## PAMP-triggered immunity

In animals, host sensors of conserved microbial signatures fall into the Toll-like receptor (TLR) class or the Nod-like receptor (NLR) family [6–8]. In plants, host sensors of conserved microbial signatures (also called PAMPs) are typically receptor kinases [6]. These host sensors detect lipopolysaccharides (LPS), peptides, chitin, double-stranded RNA, microbial DNA and other molecules of microbial origin [6]. Conserved microbial signatures such as the sulfated peptide Ax21, chitin, flagellin peptides and LPS have all been shown to trigger innate immune responses in rice [9–12].

### *Innate immunity mediated by Ax21–XA21*

The rice *Xa21* gene confers broad-spectrum resistance to diverse strains of *Xanthomonas oryzae* pv. *oryzae* (*Xoo*) [13]. *Xa21* encodes a receptor kinase carrying extracellular leucine-rich repeats (LRRs), as well as transmembrane (TM), juxtamembrane (JM) and intracellular non-RD (arginine - aspartate) kinase domains [14] (Table 1). In contrast to RD kinases that carry a conserved arginine immediately preceding the catalytic aspartate, non-RD kinases usually carry a cysteine or glycine in place of the arginine [14].

The non-RD motif is a hallmark of kinases associated with early signaling events in both plant and animal innate immunity [14]. In animals, both NLRs and TLRs activate inflammatory responses via association with non-RD kinases [14,15]. In plants, the *Arabidopsis* host sensors flagellin sensitive 2 (FLS2) [16] and elongation factor-Tu receptor (EFR) [17], rice XA21 [13], XA3/XA26 [18,19], Pid2 [20] (Table 1), tetraploid wheat (*Triticum. turgidum L ssp. dicoccoides*) Yr36 [21] and barley (*Hordeum vulgare*) Rpg1 [22] carry the non-RD motif. Genome analyses have revealed an approximately 10-fold greater number of non-RD receptor kinases in rice (328) than in *Arabidopsis* (35). These results suggest that rice has a vastly expanded capacity to recognize conserved microbial signature molecules. Confirmation of this hypothesis requires that such molecules be isolated and characterized. Receptor kinases that function in development fall into the RD class [14].

XA21-mediated immunity is activated upon recognition of a 194-amino acid protein designated Ax21 (activator of XA21-mediated innate immunity) [9] (Table 1). A sulfated 17-amino acid synthetic peptide (AxY<sup>S</sup>22) derived from the N-terminal region of Ax21 is sufficient for this activation

Corresponding author: Ronald, P.C. (pconald@ucdavis.edu).

**Table 1. Rice host sensors that recognize conserved microbial signatures**

Protein name	Protein class	Microbial molecule	Pathogen	Refs
XA21	LRR RLK, non-RD kinases	Sulfated Ax21	<i>Xoo</i>	[9,13]
CEBiP	LysM	Chitin	<i>M. grisea</i>	[10]
OsFLS2	LRR RLK, non-RD kinases	Flagellin	ND	[11,43,44]
XA3/XA26 <sup>a</sup>	LRR RLK, non-RD kinases	ND	<i>Xoo</i>	[18,19]
Pi-d2 <sup>a</sup>	SD-2b RLK, non-RD kinase	ND	<i>M. grisea</i>	[20]

<sup>a</sup>based on presence of non-RD motif, these RLKS are predicted to recognize conserved microbial signatures. ND = not determined.

and can directly bind to XA21. In contrast, peptides lacking the tyrosine sulfation are biologically inactive [9].

Ax21 is conserved in all sequenced *Xanthomonas* species including four strains that are pathogenic on rice: *Xoo* PXO99, *Xoo* KACC10331, *Xoo* MAFF311018 and *X. oryzae* pv. *oryzicola* BLS256 (*Xoc*). These results explain the observation made by breeders in the 1970 s that Xa21 confers broad spectrum resistance [23,24].

Ax21 is also present in pathogens of citrus (*X. axonopodis* pv. *citri* 306, *Xac*), tomato and pepper (*X. axonopodis* pv. *vesicatoria*, *Xav*), soybean (*X. axonopodis* pv. *glycines* 8ra, *Xag*), and *Brassica* and *Arabidopsis* [*X. campestris* pv. *campestris* 33919 (*Xcc*33919), 8004 (*Xcc* 8004) and B100 (*Xcc* B100)]. Ax21 is found outside the *Xanthomonas* genera in *Xylella fastidiosa* (the causal agent of phony peach disease, oleander leaf scorch and Pierce's disease, and citrus X disease) [9] and in the opportunistic human pathogen *Stenotrophomonas maltophilia*.

To elucidate the XA21-mediated signaling network, we identified proteins that interact with XA21 using co-immunoprecipitation and yeast two-hybrid (Y2H) assays [25–29]. We validated the interactions using co-expression of transcripts and phenotypic analyses [30]. These approaches contributed to a model for XA21 function (Figure 1).

These studies indicate that XA21 biogenesis occurs in the endoplasmic reticulum (ER) [31]. After processing and transit to the plasma membrane, XA21 binds to XA21 Binding Protein 24 (XB24) [28]. XB24 physically associates with the XA21 JM domain and uses ATP to promote phosphorylation of certain Ser/Thr sites on XA21, keeping the XA21 protein in an inactive state. Upon recognition of sulfated Ax21, the XA21 kinase disassociates from XB24 and is activated, triggering downstream defense responses [28]. Key components of the downstream response include mitogen-activated protein kinase 5 (MAPK5), which negatively regulates resistance to *Xoo* [30], MAPK12, which positively regulates resistance to *Xoo* [30], and XB3, a RING finger ubiquitin ligase [25], which is required for full activity of XA21 (Figure 1). The transcription factors OsWRKY62 and OsWRKY76 negatively regulate XA21-mediated resistance and interact with two other WRKYs in the same subclass [27,30,32]. XA21 binding protein 15 (XB15), a PP2C phosphatase, binds to XA21 and dephosphorylates XA21 to negatively regulate the XA21-mediated innate immune responses [26].

The phosphorylation state of XA21 is critical for XA21-mediated signaling. Phosphorylation of certain residues (likely those promoted by the XB24 ATPase) on the XA21 JM domain negatively regulates XA21 function, whereas phosphorylation on other residues (likely those

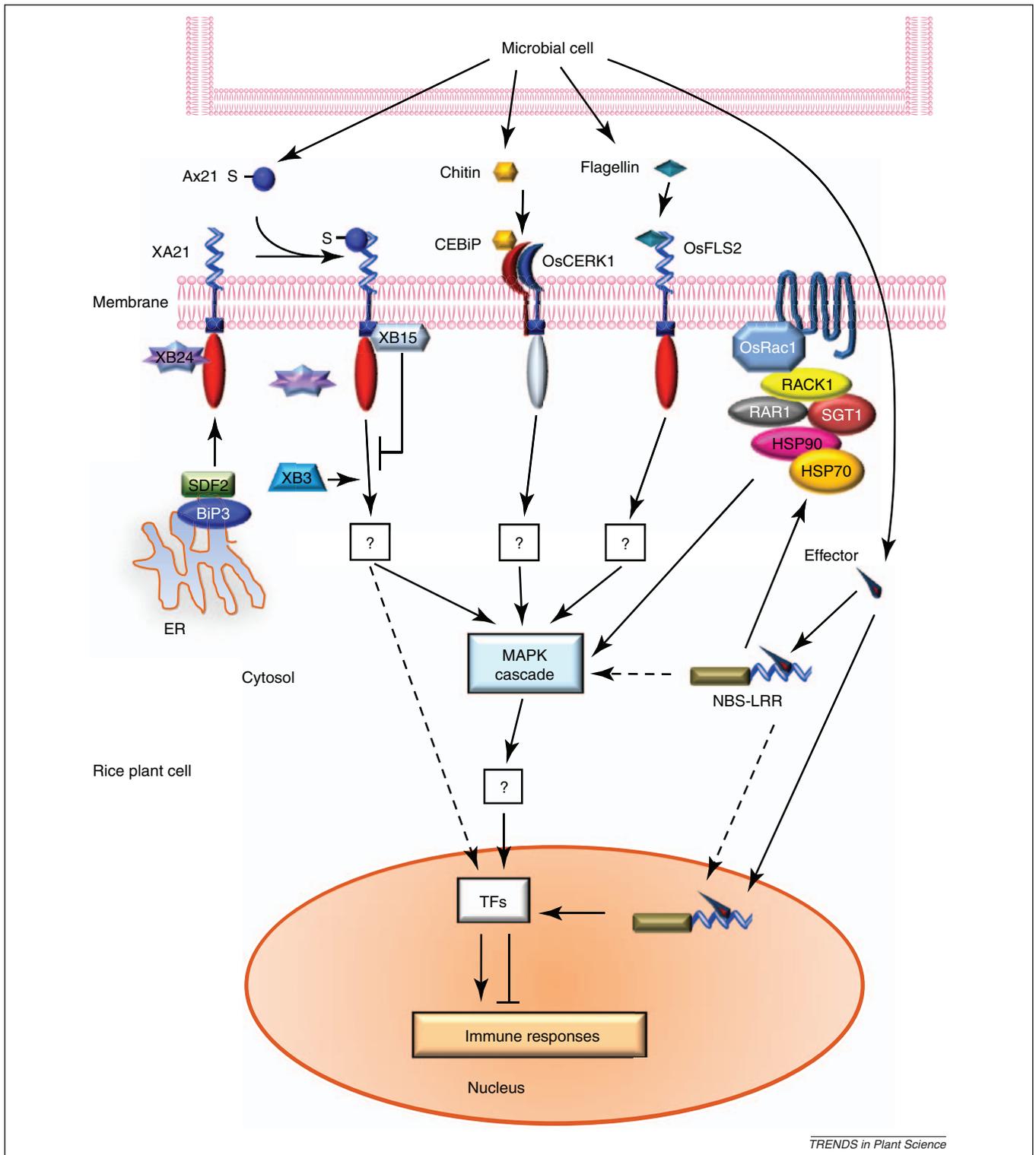
dephosphorylated by the XB15) are predicted to be required for activation of XA21 [26,28].

#### *Innate immunity mediated by chitin–CEBiP*

Chitin (a polymer of N-acetyl-D-glucosamine) is a major component of fungal cell walls that triggers various defense responses in both animals and plants [33]. The defense responses triggered by chitin perception in rice are similar to those in other plant species, including reactive oxygen species (ROS) generation, pathogenesis-related (PR) gene expression and biosynthesis of phytoalexins. The chitin elicitor binding protein (CEBiP) is a plasma membrane glycoprotein that contains two LysM domains but lacks an intracellular kinase [10]. Reduced expression of CEBiP in cultured rice cells results in a markedly decreased response to chitin, indicating that CEBiP plays an essential role in the perception and signal transduction of chitin. Chitin elicitor receptor kinase 1 (CERK1 also known as LysM-RLK1) is also a crucial component for chitin signaling in rice [34]. CERK1 and CEBiP form hetero- and homo-dimers in Y2H assays. CEBiP and CERK1 are present in a receptor complex immunoprecipitated from rice cells treated with chitin indicating that these proteins interact *in vivo* upon ligand recognition [34] (Figure 1). In cultured rice cells, the recognition of chitin elicitor induces a series of defense responses including the activation of MAPKs [35], ROS production, defense gene expression, phytoalexin production and the accumulation of phosphatidic acid (PA) [10,36,37]. PA is a signal molecule that is important for the plant response to both biotic and abiotic stresses [38].

The chaperone complex Hop/Sti-Hsp90 is required for CERK1 maturation and transport [39]. CERK1 belongs to the RD-class of kinases. The inability of CERK1 to mount defense responses in the absence of CEBiP indicates that CERK1 is a coregulator of the response rather than part of the key recognition and signaling components. In this respect, CEBiP is similar to XA21D, a receptor-like protein lacking a TM and kinase domain that is predicted to require a co-regulator for function [40]. A role for non-RD kinases has not yet been demonstrated for XA21D- or CEBiP-mediated defense responses.

Transgenic rice plants carrying a chimeric gene encoding the CEBiP extracellular domain, the XA21 intracellular JM and kinase domains, and the TM domain from either CEBiP or XA21, exhibit cell death accompanied by an increased production of reactive oxygen and nitrogen species after treatment with chitin [41]. Rice plants expressing the chimeric receptor exhibit necrotic lesions in response to chitin and become more resistant to the fungal pathogen, *Magnaporthe grisea* (*M. grisea*) [41]. These



**Figure 1.** Rice innate immunity signaling pathways [6,31,83,114]. Conserved microbial signatures are recognized by cell-surface host sensors (also called pattern recognition receptors) [28]. The XA21 sensor detects the sulfated Xoo peptide Ax21 that is secreted from bacterial cells. In the absence of infection, the XB24 ATPase physically associates with the XA21 JM domain, promotes autophosphorylation and keeps XA21 in an inactive state [28]. Binding of sulfated Ax21 to the XA21 LRR domain induces dissociation of XA21 from XB24 and activates the XA21 non-RD kinase domain [28]. XA21 phosphorylates downstream target proteins that have not yet been identified, as well as XB3 [25] that is hypothesized to activate a downstream MAPK cascade [92]. OsWRKY class IIA TFs are key regulators that control the downstream defense responses [6]. Dephosphorylation of XA21 phosphorylated residue(s) by the PP2C phosphatase XB15 attenuates the XA21-mediated immune response [26]. Proper biogenesis and localization of XA21 requires the ER chaperones stromal-derived factor-2 (SDF2) and Bip3 [29,31]. The LysM-containing, receptor-like protein CEBiP [10], which binds to chitin, partners with OsCERK1 (a LysM RLK with an RD kinase domain) to transduce the innate immune response [34]. The chaperone complex of Hop/Sti1-Hsp90 facilitates the maturation and transport of OsCERK1 [39]. Bacterial flagellin triggers OsFLS2-mediated immunity and signals through a MAPK cascade. Diverse microbial effectors are recognized by NBS-LRR and other proteins in the cytosol or the nucleus. NBS-LRR-mediated cytosolic signaling is hypothesized to be transduced through a MAPK cascade before nuclear localization [114]. The OsRac1 GTPase regulates NBS-LRR-mediated innate immunity through the RAR1-SGT1-HSP90-HSP70 cytosolic complex in rice [83]. The OsRac1 pathway activates the MAPK6-mediated MAPK cascade [53,54]. Pathogen effectors can also directly enter the nucleus to bind to NBS-LRR proteins to activate defense responses through regulation of TFs.

results demonstrate that generation and expression of chimeric host sensors is a viable strategy for engineering resistance [41].

#### Innate immunity mediated by flagellin–OsFLS2

Flagellin is the principal constituent of bacterial flagellum, and is present in large amounts on nearly all flagellated bacteria. Flagellin triggers the immune response in both animals and plants [6]. In plants, the conserved flg22 epitope triggers immunity in *Arabidopsis* seedlings carrying the host sensor FLS2 [16]. In animals, TLR5 serves as the host sensor of flagellin [42].

Flagellin also triggers the innate immune response in rice is mediated through OsFLS2, which the rice ortholog of FLS2 [11,43] (Table 1). OsFLS2-mediated defense responses in cultured rice cells are induced by flagellin isolated from an incompatible strain of *Pseudomonas avenae* but not from a compatible strain [11]. Thus, both XA21 and OsFLS2 serve as host sensors of conserved microbial signatures [6,9]. Flagellin from an incompatible strain of *Acidovorax avenae* also activates immune responses in rice, including H<sub>2</sub>O<sub>2</sub> generation, hypersensitive cell death and PR gene expression [44]. Such responses are also characteristic of *Arabidopsis* FLS2-mediated flagellin perception [45]. These results indicate that flagellin perception mediated by OsFLS2 in rice is similar to that mediated by FLS2 in *Arabidopsis*. It is still unknown whether OsFL2 recognizes the *P. avenae* or *A. avenae* flagellins directly.

#### Immunity triggered by LPS

LPS is present in most Gram-negative bacteria [46]. Widely known for its ability to induce septic shock in animals, LPS also triggers innate immune responses in plants [12]. Diverse bacterial LPS molecules, including those from plant pathogens and non-pathogens, are able to induce ROS generation, programmed cell death and defense gene

expression in rice cells [12]. Global analysis of gene expression profiles demonstrate that the rice LPS-triggered responses overlap with chitin-triggered responses [12]. These results suggest a convergence of signaling cascades that transduce both chitin and LPS signals. The rice LPS sensor has not yet been identified.

#### Effector-triggered immunity

In rice and other plant species, Nucleotide binding site/Leucine rich repeat (NBS-LRR) proteins perceive microbial effectors. Characterized rice NBS-LRR proteins include XA1 [47] that confers resistance to *Xoo*; Pita [48,49], Pib [50], Piz-t [51], Pikm [52], Pit [53,54], Pid3 [55], Pi2 [51], Pi5 [56], Pi9 [57], Pi36 [58], Pi37 [59], Pb1 [60] and Pia [61] that confer resistance to *M. grisea*; and Bph14 [62] that confers resistance to the brown planthopper (Table 2).

Four effectors produced by the rice blast fungus *M. grisea* have been characterized: AvrPita [49], AvrPiz-t [55], AvrPik/km/kp [56,57] and AvrPia [57]. All four effectors are small proteins with different structures that are recognized by the corresponding NBS-LRR proteins. AvrPita encodes a protein containing a zinc-metal protease motif [49]. AvrPiz-t contains a LxAR motif ([LI]xAR[SE][DSE]) and suppresses mouse BAX protein-mediated programmed cell death in tobacco leaves [63]. The amino acid sequences of AvrPik/km/kp and AvrPia show no similarity to known protein domains. These results are consistent with the theme that most fungal effectors are small novel secreted proteins generally lacking homology to known proteins [64].

Of these rice NBS-LRR proteins, Pita is the best characterized [48,49]. A single amino acid difference in the Pita leucine-rich domain (LRD) distinguishes resistant from susceptible alleles [48]. A far-western blot analysis showed that the LRD binds specifically to the *M. grisea* avirulence protein AvrPita [49]. Upon binding to AvrPita, Pita induces localized plant cell death, which is predicted to

**Table 2. Rice proteins that perceive variable microbial effectors**

Protein name	Protein class	Microbial molecule	Pathogen	Refs
XA1	NBS-LRR	ND	<i>Xoo</i>	[47]
Pita	NBS-LRR	AvrPita1 (a Zinc-dependent metalloprotease motif)	<i>M. grisea</i>	[48]
Pib	NBS-LRR	ND	<i>M. grisea</i>	[50]
Piz-t	NBS-LRR	AvrPiz-t	<i>M. grisea</i>	[51,63]
Pikm	NBS-LRR	AvrPikm	<i>M. grisea</i>	[52]
Pit	NBS-LRR	ND	<i>M. grisea</i>	[53,54]
Pid3	NBS-LRR	ND	<i>M. grisea</i>	[55]
Pi2	NBS-LRR	ND	<i>M. grisea</i>	[51]
Pi5	NBS-LRR	ND	<i>M. grisea</i>	[56]
Pi9	NBS-LRR	ND	<i>M. grisea</i>	[57]
Pi36	NBS-LRR	ND	<i>M. grisea</i>	[58]
Pi37	NBS-LRR	ND	<i>M. grisea</i>	[59]
Pb1	NBS-LRR	ND	<i>M. grisea</i>	[60]
Pia	NBS-LRR	AvrPia	<i>M. grisea</i>	[61,113]
Bph14	NBS-LRR	ND	brown plant hopper insect	[62]
XA27	two $\alpha$ -helix domains and a signal-anchor-like sequence	AvrXA27 (TAL effector)	<i>Xoo</i>	[67]
xa5 <sup>a</sup>	TFIIA transcription factor	Probable TAL effector	<i>Xoo</i>	[68,69,74,75]
xa13(Os8N3, OsSWEET11) <sup>a</sup>	Homolog of nodulin MtN3	pthXo1 (TAL effector)	<i>Xoo</i>	[70,72]
Os11N3 (OsSWEET14) <sup>a</sup>	Homolog of nodulin MtN3	AvrXA7 (TAL effector)	<i>Xoo</i>	[70–72]

<sup>a</sup>encoded by a recessive allele. ND = not determined

prevent *M. grisea* from spreading to adjoining rice cells [49]. The physical interaction between Pita and AvrPita is dependent on amino acid 918 located in the LRD of Pita [48]. Recently, a new locus, Ptr(t), was found to be essential for Pita-mediated signal recognition [65].

Three models are proposed for recognition of effectors by NBS-LRR proteins: the direct recognition, decoy and bait models [66]. In rice cells, the AvrPita–Pita interaction best fits the direct recognition model because AvrPita binds to Pita [49]. In general, however, it is still not clear how most effectors are recognized by their cognate NBS-LRR proteins.

There are some rice proteins that do not contain NBS or LRR domains but confer resistance to *Xoo*. These include XA27 [67], xa5 [68,69], xa13 (Os8N3 or OsSWEET11) [70,71] and Os-11N3 (OsSWEET14) [71,72] (Table 2). The corresponding effectors, AvrXA27, pthXo1 and AvrXA7, which trigger Xa27-, xa13- and Os-11N3-mediated resistance, respectively, belong to the transcription activator-like (TAL) transcription family of effectors [67,70,72]. The effector that triggers xa5-mediated immunity is also predicted to be a TAL transcription factor [73–75]. *Xanthomonas* TAL effectors contribute to disease or trigger defense by binding host DNA and activating effector-specific host genes [76]. For example, the TAL effector pthXo1 secreted by *Xoo* PXO99A directly binds to the promoter of OsSWEET11 and specifically activates transcription of OsSWEET11, presumably to induce sugar efflux to feed bacteria in xylem and/or the apoplast [71].

Recently, a cluster of rice genes encoding twelve germin-like proteins (OsGLPs) was shown to confer broad spectrum resistance to both rice blast disease caused by *M. grisea* and sheath blight disease caused by the fungus *Rhizoctonia solani* [77]. It will be of interest to determine whether these OsGLPs recognize effector protein(s) and if they can transduce defense responses similar to those observed for ETI.

### Signal transduction mediating rice innate immunity

#### *OsRac GTPase is required for both ETI and PTI*

The Rac GTPase (also called Rop GTPase) family belongs to the Rac superfamily of small GTPases [39]. Members of this superfamily process GTPase activity and are used for activation of protein kinases. In plants, Rac GTPases serve diverse functions in many important cellular activities, including polar growth, cell differentiation and stress responses [78]. Rice contains seven genes encoding Rac GTPases [79,80]. OsRac1, a small (~21 kDa) signaling G protein with GTPase activity, is involved in the immune response induced by the conserved microbial signature molecules, chitin and sphingolipid [81,82]. OsRac1 interacts directly with the NBS-LRR protein Pit and is required for Pit-mediated innate immunity to *M. grisea* [53]. OsRac1 functions through the RAR1-SGT1-HSP90-HSP70 cytosolic complex [83]. This process is reminiscent of the animal Nod1 and Nod2-mediated immunity, NLR proteins that also require (co-)chaperones containing HSP90 and SGT1 to transduce immunity [7,8]. The OsRac1 pathway activates the MAPK6-mediated MAPK cascade [53,54] (Figure 1). The immune responses regulated by OsRac1 include cell death, ROS production, activation of PR gene expression and phytoalexin production [84].

### MAPK cascades

MAPK cascades play important roles in transmission of extracellular signals to downstream components through protein phosphorylation [85]. A MAPK cascade minimally consists of three kinases: a MAPK, a MAPK kinase (MAPKK) and a MAPKK kinase (MAPKKK) [35]. Several MAPKs are predicted to play roles in plant immune responses mediated by PTI or ETI [86] as well as in other signaling events [87].

Seventeen MAPKs have been identified in rice [88]. Out of the five characterized MAPKs (OsWJMUK1, MAPK4, OsBWMK1(MAPK12), MAPK5 and MAPK6), three (MAPK5, MAPK6 and MAPK12) have been investigated as to how they regulate to plant defense responses [88]. Molecular, biochemical, and transgenic analyses demonstrated that MAPK5 is a positive regulator of abiotic stress tolerance but acts as a negative regulator of rice disease resistance [89]. MAPK5 also negatively regulates resistance to *Xoo* [30]. MAPK6 functions with the OsRac1-RAR1-HSP90-STG1 complex to transduce the signaling mediated by the NBS-LRR protein Pit (Figure 1) [53,54]. MAPK6 is also essential for the chitin-induced biosynthesis of diterpenoid phytoalexins in rice that act as toxins to restrict *M. grisea* infection [90]. These results indicate that MAPK6 is involved the MAPK cascades of both PTI and ETI in rice. MAPK12 is induced by *M. grisea* strains [91] and positively regulates the disease resistance to *Xoo* [30], supporting the view that a MAPK12-mediated MAPK cascade is involved in the innate immune responses to both *M. grisea* and *Xoo*.

Phylogenomics analysis led to the identification of eight additional MAPK cascade genes that are also predicted to regulate the rice stress response [92]. These data indicate that MAPKK Os02g54600 functions upstream of MAPK Os03g17700 to regulate stress responses. Six MAPKKKs (Os01g50370, Os05g46760, Os01g50400, Os01g50410, Os01g50420 and Os05g46750) are predicted to function upstream of the MAPK and MAPKK genes. Whether and how this MAPK cascade functions with MAPK5-, MAPK6- and MAPK12-mediated MAPK cascades remains to be determined.

### Transcription factors

ETI and PTI activate large-scale changes in expression of transcription factors (TFs) including the WRKY TF family. There are more than 100 WRKY TFs in the rice genome [93]. Based on the sequences of the WRKY domain, these WRKY TFs are classified into three groups and each group is divided into several subgroups according to their phylogenetic clusters [93]. Many are involved in rice innate immune responses. For example, WRKY45 (subgroup IIId), WRKY53 (subgroup IIIb) and WRKY89 (subgroup IIIb) are differentially expressed in response to *M. grisea* infection [94]. Four TFs in subgroups IIa (WRKY28, WRKY62, WRKY71 and WRKY76) specifically respond to *Xoo* infection and two of them (WRKY62 and WRKY76) have been shown to be involved in XA21-mediated innate immunity [30,32]. WRKY53 responds to both *M. grisea* and *Xoo*, and WRKY89 responds both to *M. grisea* and the white-backed planthopper *Sogatella furcifera* [95]. These studies support the view that some WRKYs are involved in

response to specific diseases whereas others might respond to multiple diseases.

TGA factors, a group of transcription factors that bind to the TGACG-motif essential DNA elements resulting in transcription activation, have also been shown to play an important role in defense responses. In *Arabidopsis*, TGA factors play dual roles: they act to repress PR gene expression under uninduced conditions but are required for NPR1-mediated, SA-mediated SAR response [96]. In rice, silencing of rTGA2.1 results in a moderately enhanced resistance to *Xoo* [97].

#### Expression of pathogenesis-related proteins

Following pathogen recognition and signal transduction, defense responses are activated that protect plants from infection. These responses include cell wall reinforcement, accumulation of antimicrobial secondary metabolites such as phytoalexins, and expression of PR proteins [98]. PR proteins are classified into 17 groups (PR1–PR17) based on their amino acid sequence, serological relationship and enzymatic activities [99]. In rice, only a few groups of PR genes, including PR1, PR8 and PR10, have been reported to be induced following bacterial or fungal infections [100–102]. Several studies propose that some PR genes are regulated pathogen species-dependently and some are not [100].

#### Crosstalk between hormone-mediated signaling and rice innate immunity

Brassinolide (BL), an important brassinosteroid regulating plant growth and development, also plays an important role in the rice defense responses [103]. BL-treated rice plants are resistant to *M. grisea* and *Xoo* [103]. In *Arabidopsis* at least four PRRs, FLS2, EFR, AtPEPR1 and AtPEPR2, directly interact and require the coregulatory receptor kinase BAK1 (BRI1 associated kinase 1)/SERK3 for full PTI-signal induction [104,105]. In addition to its essential role in BRI1-mediated brassinolide signaling, BAK1 is also required for FLS2- and EFR-mediated innate immunity indicating that dynamic membrane bound complexes mediate response to different extracellular signals.

A co-regulator such as BAK1 has long been hypothesized to be important for XA21-mediated signaling [40]. This hypothesis is supported by the fact that a natural variant of XA21 that only harbors an LRR domain, highly similar to that of XA21, lacks any domain for intracellular signal transduction. This natural variant is called XA21D and confers partial resistance to *Xoo* expressing Ax21 [40]. Similar to CEBiP, XA21D is required for recognition of conserved microbial signatures. Because XA21D is a predicted extracellular protein it probably requires a co-regulator(s) for intracellular signal initiation as has been shown for CERK1/CEBiP. Preliminary results indicate that one of the eleven rice SERK-homologs [106] is required for XA21-mediated immunity (Chen and Ronald, unpublished).

Other hormones such as abscisic acid (ABA), jasmonic acid (JA), and SA have also been shown to play important roles in rice immune responses [107–109]. For example, ABA enhances resistance to the brown spot-causing ascomycete *Cochliobolus miyabeanus* [107]. Exogenous appli-

cation of JA activates defense gene expression and local induced resistance in rice seedlings against *M. grisea* [109]. ABA interacts antagonistically with the SA signaling pathway in rice–*M. grisea* interactions [108].

#### Concluding remarks

Rice host sensors of conserved microbial signatures and NBS-LRR proteins are crucial for the rice innate immune response. Whereas host sensors recognize conserved molecules, NBS-LRR proteins recognize effector molecules that are highly variable among strains. The signals mediated by rice host sensors and NBS-LRR proteins are transduced through routes that include MAPK cascades and transcription factors. These signal cascades activate PR gene expression, cell wall reinforcement and accumulation of antimicrobial secondary metabolites, leading to immune responses (Figure 1).

The receptor kinases carrying non-RD domain, a newly recognized hallmark of kinases that function in innate immunity, are highly expanded in rice compared with *Arabidopsis* (104 in *Arabidopsis* and 419 in rice) [14]. Thirty-five of the 104 *Arabidopsis* (~34%) are receptor-like kinases; by contrast, 328 of the 419 rice non-RD kinases (~78%) are receptor-like kinases [14]. It will be of great interest to determine whether these non-RD receptor-like kinases bind to conserved microbial signatures and, if so, what types of molecules they recognize. Another important question is whether the characterized rice host sensors (XA21, XA3/XA26, Pid2 and OsFLS2) signal through common or overlapping pathways. Another important area of research is to determine if host sensors that lack intracellular non-RD kinase domains such as CEBiP and XA21D, function in partnership with non-RD kinases or if they transduce their signal through a different mechanism. Despite the importance of non-RD kinases in mediating rice innate immunity, few studies have addressed the mode of non-RD kinase activation [110]. Future research in this area will help elucidate the mode of action of this important class of proteins.

NBS-LRR genes (~500 predicted) are even more abundant in rice than the predicted host sensors of conserved microbial signatures [111]. It is not known if all of these NBS-LRR proteins recognize pathogen effectors or if they play a role in non-defense response pathways. Conversely, ~739 proteins are predicted to be secreted from *M. grisea* [112] but few have been shown to be important in the pathogen's interactions with rice [112].

Recent results indicate that other monocotyledonous species also use non-RD kinases to sense and respond to important pathogens. For example in wheat, the non-RD kinase-START gene (WKS1), *Yr36*, provides broad-spectrum resistance to stripe rust [21]. It is not yet known if components of the WKS1-signaling cascade that transduce *Yr36*-mediated resistance correspond to orthologous proteins in rice.

Finally, an important goal is to harness the knowledge garnered over the past 15 years of the rice innate immune response to engineer new resistance specificities. The effectiveness of this approach has already been demonstrated by the engineering of the CEBiP/XA21 chimeric receptor [41].

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