Chitin receptor-mediated activation of MAP kinases and ROS production in rice and Arabidopsis

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ABSTRACT

Rapid induction of plant immune responses is essential to inhibit colonization and invasion by pathogens. Plants can recognize pathogen-associated molecular patterns (PAMPs) including fungal chitin and bacterial flagellin using pattern-recognition receptors (PRRs), which trigger the intracellular activation of mitogen-activated protein kinase (MAPK) cascades and the production of reactive oxygen species (ROS). MAPK activation and ROS production play pivotal roles in the induction of robust immune responses. Recent investigation of chitin- and flagellin-mediated immune signaling revealed that receptor-like cytoplasmic kinases (RLCKs) connect PRR-mediated pathogen recognition to MAPK activation and ROS production. In addition, although the MAPK cascade is mediated by 3 sequentially activated protein kinases, MAPK kinase kinase (MAPKKK), MAPK kinase (MAPKK), and MAPK, how MAPKKKs are activated downstream of PRRs in plants has not been identified until recently. In this review, we summarize recent findings of RLCK-mediated MAPK activation and ROS production in rice and Arabidopsis.

Plant immunity is induced by the perception of pathogen-associated molecular patterns (PAMPs) by plasma membrane-localized pattern-recognition receptor (PRRs). Based upon protein structures, PRRs are classified into two groups, receptor-like kinases (RLKs) and receptor-like proteins (RLPs). Both RLKs and RLPs contain an extracellular ligand-binding domain. In addition, RLKs contain a cytoplasmic kinase domain that probably interacts with intracellular component to transmit the ligand recognition signals.

Chitin, which serves as a PAMP, is a major component of fungal cell walls, which are the first structure to physically contact host plant cells. To protect against infection of fungal pathogens, plants develop the PRRs for chitin perception. In rice, the glycosyl phosphatidylinositol-anchored RLP CEBiP is the chitin receptor, with an extracellular lysin motif (LysM) domain. The LysM domain of CEBiP directly binds to chitin and subsequently associates with the LysM-RLK OsCERK1. The cytoplasmic kinase domain of OsCERK1 interacts with the receptor-like cytoplasmic kinase (RLCK) OsRLCK185. Upon chitin perception, OsCERK1 phosphorylates OsRLCK185, which triggers intracellular immune responses in rice. In Arabidopsis, 2 LysM-RLKs AtCERK1 and AtLYK5 form a chitin receptor complex. AtLYK5 unlikely possesses the kinase activity, because it lost the amino acid residues essential for the kinase activity. AtCERK1 is activated through its homodimerization followed by autophosphorylation. The autophosphorylation of AtCERK1 is essential to induce chitin-triggered immunity. Similarly to OsCERK1, AtCERK1 phosphorylates the RLCK PBL27 to activate intracellular immune responses.

OsCERK1 and AtCERK1 are also involved in the perception of bacterial peptidoglycan. Recognition of chitin triggers the intracellular activation of mitogen-activated protein kinase (MAPK) cascades and the rapid production of reactive oxygen species (ROS). Each MAPK cascade is mediated by three sequentially activated protein kinases; each MAPK is activated via phosphorylation by a MAPK kinase (MAPKK), which follows after phosphorylation of MAPKK by a MAPK kinase (MAPKKK). Very recently, we and another group revealed the molecular mechanism by which MAPKKKs are activated downstream of chitin receptors. In this review, we introduce recent progress in PRR-mediated MAPK activation in rice and Arabidopsis.

Arabidopsis MAPK cascade in chitin signaling

There are 80 and 75 MAPKKKs in Arabidopsis and rice, respectively. The MAPKKKs are classified into two subfamilies, MEKK-like kinases and Raf-like kinases. Recently, we found that AtMAPKKK5, a member of MEKK family, is phosphorylated by PBL27, but only when AtCERK1 phosphorylates PBL27. PBL27 phosphorylated 6 Ser / Thr residues in the C-terminal domain of AtMAPKKK5. Alanine substitution mutants of these residues did not complement the Atmapkkk5 mutation, suggesting that AtMAPKKK5 is activated directly by PBL27-mediated phosphorylation. These findings provided the first evidence for a link between a PAMP receptor and MAPK cascades in plants.
The Atmapkk5 mutations compromised chitin-induced activation of the MAPks AtMPK3 and AtMPK6. Two MAPKKs, AtMKK4 and AtMKK5, are immediate upstream components of AtMPK3 and AtMPK6 in PAMPs signaling. In fact, AtMAPKKK5 interacts with and phosphorylates AtMKK4 and AtMKK5, suggesting a phospho-signaling pathway consisting of AtCERK1 – PBL27 – AtMAPKKK5 – AtMKK4/AtMKK5 – AtMPK3/AtMPK6.16

Bimolecular fluorescence complementation experiments showed that the interaction between PBL27 and AtMAPKKK5 occurs at the plasma membrane (PM), whereas AtMAPKKK5 interacts with AtMKK4 and AtMKK5 mainly in the cytosol (Fig. 1). In addition, AtMAPKKK5 disassociates from PBL27 in response to chitin exposure. Based upon these observations, we propose a model in which AtMAPKKK5 disassociates from PBL27 after PBL27 phosphorylates AtMAPKKK5 at the PM, and then AtMAPKKK5 interacts with and phosphorylates AtMKK4 and AtMKK5 in the cytosol (Fig. 1). These activation processes may apply to many receptor-mediated MAPK signaling pathways.

**OsRLCK185-mediated MAPK activation in rice**

As mentioned above, OsCERK1 phosphorylates OsRLCK185 in response to chitin.4 Because chitin-induced activation of OsMPK3 and OsMPK6 was suppressed by silencing of OsRLCK185, it was thought that OsRLCK185 might transmit the signals to downstream MAPks through phosphorylation of MAPKKKs. Recently, we found that OsMAPKKK18, the rice ortholog of AtMAPKKK5, is phosphorylated by OsRLCK185 (Fig. 2).17 OsMKK4 functions as a main MAPK for OsMPK3 and OsMPK6 in chitin signaling,18 which plays a crucial role in reprogramming antimicrobial metabolite synthesis. In fact, OsMAPKKK18 interacted with and phosphorylated OsMKK4, indicating a signaling pathway consisting of OsCERK1 – OsRLCK185 – OsMKK4 – OsMPK3 / OsMPK6 (Fig. 2).17 These data revealed a conservation of chitin signaling between rice and Arabidopsis. In addition, OsMAPKKK24 (OsMAPKKK24) was also reported to be phosphorylated by OsRLCK185.19 As found in PBL27-mediated phosphorylation of AtMAPKKK5, phosphorylation of OsRLCK185 by OsCERK1 positively regulates the phosphorylation of OsMAPKKK24 by OsRLCK185. It was also reported that OsMAPKKK24 contributes to chitin-induced immune responses and resistance to rice blast fungus infection.19 Thus, OsRLCK185 regulates MAPK activation through phosphorylation of at least OsMAPKKK18 and OsMAPKKK24 in rice chitin-induced immunity.

**Rac/Rop GTPase-mediated chitin signaling**

Plant Rac/Rop small GTPases are a plant-specific Rho family of small GTPases, which are regulated by shuttling between a GDP-bound inactive form and a GTP-bound active form. The shuttling is mediated by two regulatory factors, GDP/GTP exchange factors (GEFs) and GTPase-activating proteins (GAPs). Previous studies indicated that OsRac1, one of 7 rice Rac/Rop GTPases, plays important roles in chitin-induced immune responses, including ROS production, lignification, and expression of immune-related genes (Fig. 2).20-23 OsRacGEF1, which was identified as the GEF for OsRac1, belongs to a plant-specific ROP nucleotide exchange (PRONE)-type GEF family. OsRacGEF1 interacts with the cytoplasmic domain of OsCERK1, and is directly phosphorylated by OsCERK1,24 indicating that another chitin signaling pathway consisting of OsCERK1 – OsRacGEF1 – OsRac1 is also present in rice. Thus, it is likely that OsCERK1-mediated
immunity operates by at least two pathways that branch at OsRLCK185 and OsRacGEF1 (Fig. 2).

Expression of a constitutively active form of OsRac1 enhances MAPK activation.25 OsRac1 interacts with OsRACK1, a rice homolog of human Receptor for Activated C-kinase 1 (RACK1) that serves as an adaptor protein for multiple protein-protein interactions.26 An Arabidopsis ortholog of OsRACK1 functions as a scaffolding protein linking heterotrimeric G proteins and MAPK cascade.27 Because OsRac1 functions immediately downstream of heterotrimeric G protein in rice,28 it is conceivable that the OsRac1-OsRACK1 module may be positively involved in the activation of MAPK cascades in a different way than OsRLCK185 (Fig. 2).

OsRac1 positively regulates ROS production via interaction with the N-terminal region of the PM-localized NADPH oxidase OsRbohB (Fig. 2),29,30 indicating that the interaction of OsRbohB with OsRac1 somehow enhances oxidase activity. Silencing of OsRLCK185 also reduced chitin-induced ROS production.4 In Arabidopsis, the RLCK BIK1 associates with the RLK-type flagellin receptor FLS2 and its co-receptor BAK1.31,32 Upon perception of a flagellin-derived peptide, flg22, BIK1 is phosphorylated by the FLS2 / BAK1 complex, and it subsequently phosphorylates the N-terminal region of AtRbohD to induce ROS production.33,34 BIK1 also contributes to ROS production in chitin signaling, although the in vitro phosphorylation of BIK1 by AtCERK1 was very weak.10 Therefore, OsRLCK185 may regulate rice Rboh activity in a similar manner as BIK1.

**Independent regulation of MAPK activation and ROS generation mediated by the PRR-RLCK modules**

AtCERK1-associated PBL27 regulates the activation of the MAPK cascade by phosphorylation of AtMAPKKK5.16 However, PBL27 is not involved in chitin-induced ROS production.10 ROS production is likely mediated by BIK1, which is also required for flg22-induced ROS production, but it is not involved in MAPK activation.35,36 Thus, it seems plausible that each RLCK is responsible for MAPK activation or ROS production in Arabidopsis. If so, there are two possibilities. One is that each receptor complex contains multiple RLCKs, and has the ability to induce both MAPK activation and ROS production. Another is that there are at least two different PRR – RLCK complexes, and each complex is responsible for MAPK activation or ROS production.

Recent studies on spatio-temporal dynamics and interaction patterns of PRR complexes have provided tools to understand the molecular mechanisms of separatable regulation of MAPK activation and ROS production. Arabidopsis LLG1, a glycosyl-phosphatidylinositol (GPI)-anchored protein, constitutively associates with FLS2 and forms a complex with BAK1 after stimulation with flg22.37 llg1 mutations inhibited flg22-induced phosphorylation of BIK1, which resulted in the suppression of the ROS production. However, the mutations did not affect MAPK activation. These data suggest that LLG1 may modulate the activities of BIK1 itself in the receptor complex with multiple RLCKs or the BIK1-containing complex regulating only ROS production.

In contrast to LLG1, mutations in IOS1, an LRR-RLK interacting with FLS2 and BAK1, compromised flg22-induced MAPK activation but not the ROS production.38 Thus, IOS1 and LLG1 have the opposite functions on MAPK activation and ROS production in spite of their interaction with FLS2, supporting the possibility that MAPK activation and ROS production may be independently regulated by different RLCKs in a single complex or multiple complexes with different RLCKs. Because IOS1 also interacts with AtCERK1 and regulates chitin-induced MAPK activation, it would be interesting to test whether IOS1 associates with the PBL27-containing receptor complex. Understanding of the molecular mechanisms by which LLG1 or IOS1 regulates ROS production or MAPK activation, respectively, may

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**Figure 2.** (A) possible model of MAPK activation and ROS production in rice chitin signalling. In response to chitin, OsCERK1 phosphorylates OsRLCK185 and OsRacGEF1. OsRLCK185 phosphorylates OsMAPKKK18 and OsMAPKKK24, leading to the activation of OsMPK3 and OsMPK6 through OsMKK4. OsRacGEF1 activates OsRac1, leading to the activation of OsCCR1 and OsRbohB. OsRac1 also interacts with OsRACK1, which might connect heterotrimeric G protein and MAPK cascade.
provide an insight into separatable signaling pathways mediated by the PRR-RLCK modules. In addition, because BIK1 regulates ROS production in chitin signaling, it is an intriguing question to ask whether PBL27 and BIK1 exist in the same or different AtCERK1 complexes.

In contrast to the observation in Arabidopsis, OsRLCK185 regulates both MAPK activation and ROS production in rice chitin signaling. Additionally, different RLCKs such as OsRLCK57, OsRLCK107, OsRLCK118, OsRLCK176 and BSR1 were reported to play roles in these immune responses.39–41 However, how these RLCKs activate MAPKKKs and/or Rbohs remains to be identified. Further investigation of the protein dynamics of PRRs and RLCKs in plant cells is required to fully understand PRR-mediated MAPK activation and ROS production.

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