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Chitin Signaling in Plants: Insights into the Perception of Fungal Pathogens and Rhizobacterial Symbionts

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In addition to the *R* gene-mediated pathways of plant resistance to specific pathogens, plants have the capacity to recognize a number of microbial surface-derived molecules, which elicit a general immune response in both host and nonhost plants. These are known as pathogen-associated or microbe-associated molecular patterns (PAMPs/MAMPs), so named because they are presumed to contain a structure or a pattern that is absent from eukaryotic host molecules and allows the host to recognize a microbial (and potentially pathogenic) invader. Many PAMPs that have been identified are essential for microbial metabolism or for penetration and invasion of a host cell and are therefore broadly conserved among diverse microbial pathogens (Parker, 2003). These include lipopolysaccharides of Gram-negative bacteria, peptidoglycans from Gram-positive bacteria, eubacterial flagellin, and glucans, chitins, and proteins derived from fungal cell walls (Nürnberg and Brunner, 2002).

Chitin is a polymer of *N*-acetyl-D-glucosamine that is a major component of fungal cell walls and has been recognized as a general elicitor of plant defense responses for many years (Boller, 1995). Fungal infection induces the expression of chitinases in plant cells, and these chitin-degrading enzymes accumulate at the site of invasion. In addition to the direct effect of limiting fungal invasion by degrading the fungal cell wall, the resulting chitin fragments (chitooligosaccharides) also appear to function as elicitors of numerous downstream defense response genes. Interestingly, Nod factors, which are produced by rhizobia (symbiotic N_2 -fixing bacteria) and are essential for the induction of the nodulation process in legumes, are chitin-related molecules (lipochitooligosaccharides). The predicted Nod factor receptor proteins NFR1 and NFR5 in legumes are LysM domain-containing receptor-like kinases (LysM RLKs) (Limpens et al., 2003; Radutoiu et al., 2003). The LysM RLKs represent a relatively large plant-specific protein family present in nonlegumes and legumes (Zhang et al., 2007) and have been considered good candidates for playing a role in fungal chitin perception.

In this issue of *The Plant Cell*, Wan et al. (pages 471–481) show that LysM RLK1 is required for chitin signaling in *Arabidopsis*. The authors demonstrate that a mutation in *RLK1* blocks the induction of chitooligosaccharide-responsive genes and leads to enhanced susceptibility of plants to fungal pathogens. These results are similar to those reported recently by Miya et al. (2007), who also showed that LysM RLK1 (called CERK1 by these authors) is essential for the chitin response in *Arabidopsis*. Both of these studies provide strong evidence that LysM RLK1 is involved in the perception of chitin and that it plays a role in resistance to fungal diseases. The work of Wan et al. also provides interesting insights into the evolution of Nod factor signaling, suggesting that some elements of Nod factor perception and signaling, which is specific to legumes, may be derived from the more general system of fungal chitin perception.

Arabidopsis encodes five LysM RLKs (RLK1-5) that are similar to the Nod factor receptor proteins NFR1 and NFR5 in legumes, and Wan et al. obtained homozygous T-DNA insertion mutants of all five of these genes to study their potential role in chitin perception and signaling. The authors treated all of these mutants with a purified chitooligosaccharide (chitooctaose) and monitored the expression of several genes previously shown to be induced by such treatment. The *LysM RLK1* insertional mutant lacked any chitin induction of all tested genes, whereas the mutations in the other four *RLK* genes had no effect, suggesting a specific role for LysM RLK1 in chitin signaling. Whole-genome expression analysis using microarrays showed that of hundreds of genes regulated by chitooctaose (nearly 900 genes showing significant induction or repression in wild-type *Arabidopsis*), only a handful (33) were weakly induced or repressed in the *LysM RLK1* mutant, demonstrating that the chitin-responsive pathway in this mutant was almost completely blocked. This shows that *LysM RLK1* is critical for chitin perception and signal transduction.

Interestingly, Kaku et al. (2006) previously identified a LysM domain-containing receptor

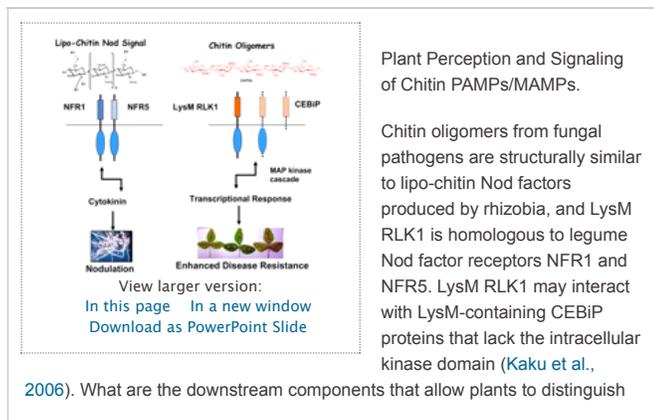
protein, called CEBiP, that is important for chitin perception in rice. However, CEBiP lacks an intracellular kinase domain, so it is unclear how it participates in signal transduction. The characterization of LysM RLK1 raises the possibility that CEBiP interacts, directly or indirectly, with LysM RLK1, although a homolog has not been identified in rice. *Arabidopsis* contains three CEBiP-like proteins, all of which similarly lack the kinase domain, so it will be of interest to determine if these proteins participate with LysM RLK1 in chitin perception and signaling.

Wan et al. next conducted experiments to determine if the *LysM RLK1* mutant was affected in its response to fungal pathogens, as would be expected if the chitin-responsive pathway plays an important role in pathogen defense. Mutant plants were found to be more susceptible to the biotrophic powdery mildew fungal pathogen *Erysiphe cichoracearum* and to the necrotrophic fungus *Alternaria brassicicola*. The effect was moderate rather than severe, but no effect was observed in response to a *Pseudomonas* bacterial pathogen, suggesting that the RLK1-dependent pathway may be induced specifically by fungal invaders but that it is only one of several pathways involved in defense against these pathogens.

To investigate potential overlap of RLK1-dependent signaling with other defense-related signaling pathways, *LysM RLK1* mutant and wild-type plants were treated with salicylic acid (SA), methyl jasmonic acid (MeJA), 1-aminocyclopropane-1-carboxylic acid (ACC), and the bacterial PAMP flagellin, and expression of known early-responsive genes to these treatments was monitored. Both the mutant and wild-type plants showed similar induction of *PR-1* by SA, *PDF1.2* by MeJA or ACC, and four selected early flagellin-responsive genes, suggesting that RLK1 operates independently of these other defense-related signaling pathways, at least in the early stages. However, microarray analysis suggested downstream convergence of signaling pathways induced by chitin and the bacterial PAMPs flagellin and EF-Tu, as the expression of a large number of genes (>400) was found to be upregulated by all three elicitors. In addition, exogenously applied chitooligosaccharides were found to enhance resistance of plants to subsequent challenge with both fungal and bacterial pathogens. These data support previous work suggesting that different PAMPs activate a common downstream pathway to induce pathogen resistance (e.g., [Asai et al., 2002](#)).

Since chitooligosaccharides also induce defense-related genes in legumes, the authors next investigated whether NFR1 and NFR5 in *Lotus japonicus* might be involved in general chitin signaling, in addition to their specialized roles in Nod factor signaling. Expression of selected chitooligosaccharide-responsive genes was similarly induced in response to chitooctose treatment in *L. japonicus* wild-type and *nfr1* and *nfr5* mutant plants, showing that these LysM RLKs do not participate in general chitin signaling. The similarity between these LysM RLKs suggests that they are evolutionarily related, but the NFR proteins appear to have evolved a specific function in Nod factor perception and signaling, as previously suggested ([Zhang et al., 2007](#)).

Previous work has identified several Leu-rich repeat RLKs in *Arabidopsis* as receptors for important bacterial-derived PAMPs, including the flagellin receptor FLS2 ([Gomez-Gomez and Boller, 2000](#)) and more recently the bacterial elongation factor EF-Tu receptor EFR ([Zipfel et al., 2006](#)). [Miya et al. \(2007\)](#) and [Wan et al. \(2008\)](#) provide important new information on fungal-derived PAMPs with the identification of LysM RLK1 as a component of chitin perception and signaling. In addition, the work suggests a potential evolutionary link between the recognition of pathogenic microbes and symbiotic beneficial microbes. It will be of great interest to determine how the plant can distinguish between a beneficial symbiont (rhizobia) and a detrimental pathogen (fungi) when the signals (lipo-chitin Nod factors and chitin elicitors) and initial perception mechanisms (LysM RLKs) are structurally very similar (see [figure](#)). What are the downstream components that allow divergence of these pathways to direct the appropriate responses in each case? Further investigation into the functions of other members of the LysM RLK family may provide additional clues as to how plants distinguish between beneficial versus pathogenic microbes.



2006). What are the downstream components that allow plants to distinguish

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Footnotes

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