Review

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# Plant pattern-recognition receptors

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**Plants are constantly exposed to would-be pathogens in their immediate environment. Yet, despite relying on innate immunity only, plants are resistant to most microbes. They employ pattern-recognition receptors (PRRs) for sensitive and rapid detection of the potential danger caused by microbes and pests. Plant PRRs are either surface-localized receptor kinases (RKs) or receptor-like proteins (RLPs) containing various ligand-binding ectodomains that perceive pathogen-associated molecular patterns (PAMPs) or damage-associated molecular patterns (DAMPs). In this review, I summarize our current knowledge of plant PRRs and their ligands, illustrating the multiple molecular strategies employed by plant PRRs to activate innate immune signaling to survive.**

## A two-tiered pathogen-detection system

Plants are sessile organisms that rely entirely on innate immune responses for defense against potential pathogenic microbes or pests. They lack specialized immune cells or organs and each cell has the potential capacity to trigger immune responses autonomously. Innate immune perception triggers both local and systemic responses, allowing a plant to fight off pathogens both in a rapid and localized manner and on an extended scale of time and space. For these purposes, plants employ a two-tier innate immune system that involves plasma membrane-localized and intracellular immune receptors [1,2].

Cell surface-localized immune receptors function as PRRs that perceive PAMPs or DAMPs of 'non-self' and 'self' origin, respectively. Currently known plant PRRs are either RKs, which have a ligand-binding ectodomain, a single-pass transmembrane domain, and an intracellular kinase domain, or RLPs, which share the same overall structure but lack an intracellular kinase domain. Because RLPs do not possess any obvious signaling domains in their short intracellular region, they most likely always function in conjunction with one or several RKs to transduce ligand binding into intracellular signaling. Importantly, PRR-triggered immunity (PTI) has the potential to fend off multiple microbes, pathogenic or not, due to the conserved nature of PAMPs (e.g., bacterial flagellin, fungal chitin) across species, genera, family, or class. Thus, PRRs can provide resistance to most non-adapted pathogens, as well as contribute to basal immunity during infection.

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In addition to PTI, plants rely on effector-triggered immunity (ETI). ETI employs intracellular immune receptors, which are most are nucleotide-binding site leucine-rich repeat (NBS-LRR) proteins, to perceive secreted virulence effectors directly or indirectly. These effectors (e.g., AvrPto, AvrPtoB) have been evolved initially by adapted pathogens to reprogram the host's physiology toward infectious compatibility, but their perception by NBS-LRR proteins betrays the pathogens in what is the result of a constant arms race between plants and their pathogens. Notably, NBS-LRRs are structurally related to mammalian NOD-like receptors (NLRs).

In mammals, both surface-localized [e.g., Toll-like receptors (TLRs)] and intracellular (e.g., NLRs) immune receptors have been shown to recognize PAMPs [3]. This is in contrast to plants, which seems to rely on plasma membrane-localized RKs or RLPs only to perceive PAMPs or DAMPs (Box 1). It is interesting to note that, as studied for many years in plants, it is now also apparent that mammalian NLRs also engage ETI [4,5].

Here I summarize our current knowledge on plant PRRs. I illustrate the multiple molecular strategies employed by plants to detect rapidly the multitude of potential invaders in their immediate surroundings – strategies essential for their survival. For details on the molecular immune signaling mechanisms triggered after PAMP perception in plants, readers are directed to recent reviews on this topic [6,7].

## Perception of bacteria

### *Multiple recognition of flagellin and elongation factor Tu*

The perception of bacterial flagellin by the LRR-RK FLS2 was the first plant PAMP/PRR pair to be characterized [8–10]. FLS2 recognizes flagellin via the direct binding of an immunogenic epitope defined by a conserved stretch of 22 amino acids, referred to as flg22 (Figure 1), located close to the N terminus of flagellin [11–13]. FLS2 was initially identified in the model plant *Arabidopsis thaliana* [8]. Flg22 seems to be recognized by most higher plants [14] and functional orthologs of FLS2 have already been identified in a wild relative of tobacco (*Nicotiana benthamiana*), rice (*Oryza sativa*), tomato (*Solanum lycopersicum*), and grapevine (*Vitis vinifera*) [15–18]. FLS2 from different species have revealed interesting differences in flg22 recognition specificities that may reflect the evolutionary histories of these species and their adaptation to their respective microbiota.

Flg22 binding to FLS2 leads to the instantaneous recruitment of the LRR-RK BAK1 (Figure 1), which acts as a coreceptor for flg22 and is required for the full activation of FLS2 and flg22-triggered immune signaling [9,13,19,20].

**Box 1. Similarities and differences between plant and animal PRRs**

- Plants seems to rely only on plasma membrane-localized PRRs to perceive PAMPs or DAMPs, in contrast to mammals, which employ both surface-localized and intracellular immune receptors to recognize PAMPs.
- Whereas animals have only a limited set of PRRs, plant genomes encode a large number of RKs and RLPs that are potential PRRs.
- Plants have uniquely combined ligand-recognition domains (e.g., LRR, LysM) directly with an intracellular kinase domain in the case of RK-type PRRs.
- Both plant and animal PRRs have evolved to perceive similar PAMP molecules (e.g., bacterial flagellin). However, both the epitopes recognized and the modular PRRs involved are distinct, indicative of convergent evolution.

Notably, it is becoming increasingly apparent that BAK1 and related SERK proteins associate with several additional LRR-RKs or LRR-RLPs and regulate their function [21], suggesting that they also act as coreceptors for other ligands.

Plants seem able to recognize multiple epitopes within flagellin [18,22,23]. A comparative genomic study of field-isolated *Pseudomonas syringae* strains revealed the 28-amino acid epitope flgII-28 to be under strong selective pressure, potentially to evade plant immune recognition [23]. flgII-28 induces immune responses in tomato, as well as in several Solanaceae species, but does not seem to be perceived by FLS2 (Figure 1), despite potential genetic interactions between flg22 and flgII-28 recognition in tomato [22]. Notably, mammals can also recognize different flagellin-derived epitopes, employing both extracellular and intracellular PRRs such as TLR5 and NAIP5/6 [24] (Box 1). However, plants do not seem able to perceive flagellin intracellularly [25], suggesting that the PRR for flgII-28 is a RK or RLP.

The perception of bacterial elongation factor Tu (EF-Tu) by the *Arabidopsis* LRR-RK EFR defines another well-studied plant PAMP/PRR pair (Figure 1). EFR directly recognizes the conserved N-acetylated epitope elf18 defined by the first 18 amino acids of EF-Tu [26,27]. Interestingly, the ability to perceive elf18 seems restricted to the plant family Brassicaceae [14]. Transgenic expression of *EFR* in another plant family (Solanaceae) confirmed that EFR confers elf18 perception and revealed that interfamily transfer of plant PRRs can be used to engineer disease resistance in crops [28].

Similarly to what has been recently discovered for flagellin, plants can perceive EF-Tu via an epitope other than elf18 (Figure 1). Indeed, treatment with the 50-amino acid epitope EFa50 derived from the central region of EF-Tu induces immune responses in rice via an as-yet-unknown PRR [29].

### *Complex recognition of peptidoglycans (PGNs)*

PGNs are a major constituent of bacterial cell walls and represent a classical PAMP recognized by insects such as *Drosophila melanogaster* [30]. Plants can also perceive PGNs [31,32] (Figure 1). In *Arabidopsis*, this perception involves two RLPs with lysine motif (LysM)-containing ectodomains, AtLYM1 and AtLYM3, which specifically bind PGNs [33]. PGN perception in rice involves the orthologous LysM-RLPs OsLYP4 and OsLYP6 [34]. PGN-induced responses in *Arabidopsis* also require the LysM-RK CERK1, which does not bind PGN itself [33]. Also, the tomato CERK1 orthologs Bti9 and SlLyk13 are required for full antibacterial immunity [35]. Thus, it is likely

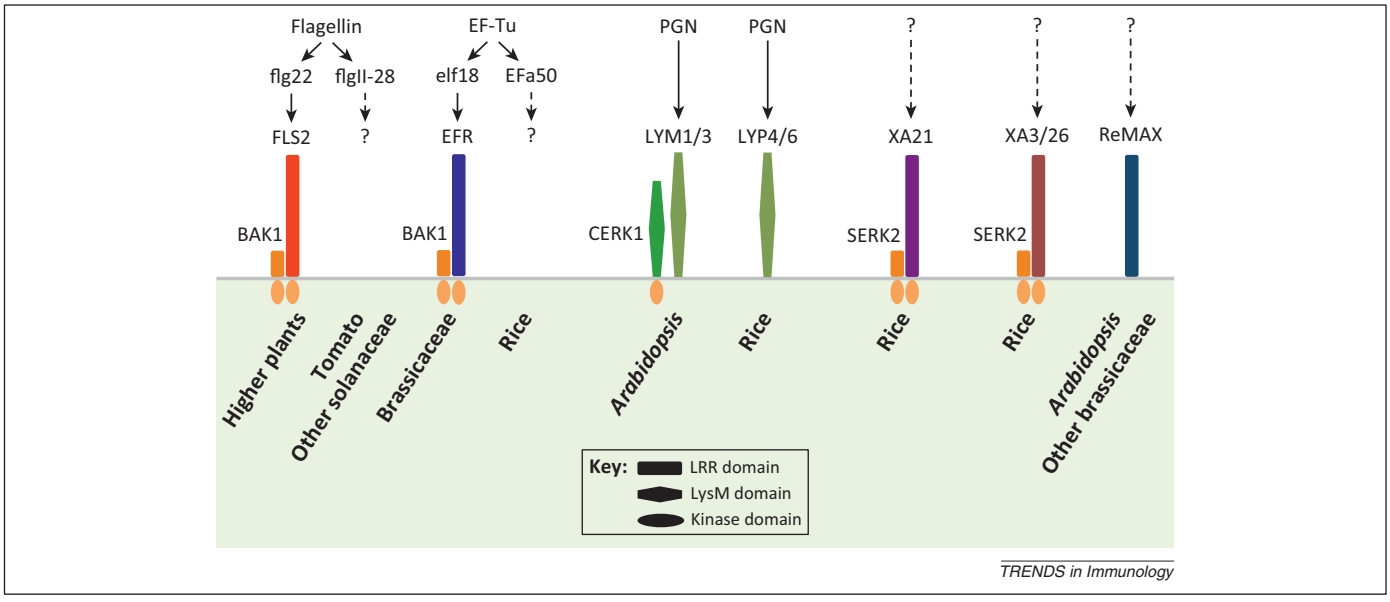


**Figure 1.** Recognition of bacteria by plant pattern-recognition receptors (PRRs). The conserved leucine-rich repeat receptor kinase (LRR-RK) FLS2 recognizes flagellin via the flg22 epitope. The flagellin-derived epitope flgII-28 is recognized in tomato and other Solanaceae via an as-yet-unknown PRR. The LRR-RK EFR perceives elongation factor Tu (EF-Tu) in Brassicaceae, whereas the EF-Tu-derived epitope EFa50 is recognized in rice by an as-yet-unknown PRR. Both FLS2 and EFR interact with the coreceptor LRR-RK BAK1 immediately upon flg22 or elf18 binding, respectively. Peptidoglycans (PGNs) bind to the *Arabidopsis* lysine motif receptor-like proteins (LysM-RLPs) LYM1 and LYM3, which may form a complex with the LysM-RK CERK1 on PGN recognition. In rice, PGNs bind to the LysM-RLPs LYP4 and LYP6. The rice LRR-RKs XA21 and XA3/26 interact with the LRR-RK OsCERK2 and confer resistance to *Xanthomonas oryzae* pv. *oryzae* via the recognition of as-yet-unknown pathogen-associated molecular patterns (PAMPs). The *Arabidopsis* LRR-RLP ReMAX perceives an enigmatic PAMP from xanthomonads that also induces immune responses in other Brassicaceae. Block arrows indicate direct binding; dashed arrows indicate lack of direct binding evidence, candidate PRR, or ligand.