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Molecular Basis of Plant Recognition by Bacteria

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Plants are surrounded and infected by a diverse array of beneficial and pathogenic bacteria. To survive in this diverse environment, Plants employ multiple layers of sophisticated detection systems to distinguish pathogenic bacteria from beneficial bacteria and rapidly respond before these pathogens have a chance to cause serious damage to the plants. The most common and widely studied plant recognition involves the first line detection of pathogen-associated molecular patterns (PAMP) s or endogenous signals released after attack, so called danger-associated molecular patterns (DAMP) s via host pattern-recognition receptors (PRRs). Recognition of the pathogen by the host defense machinery has been studied using biochemical and genetic approaches and the paper reviews the molecular basis of the common recognition used by plants to perceive pathogenic bacterial attacks and how the hosts initiate efficient defense responses against its specific pathogens.

Key Words: Pathogen-associated molecular patterns (PAMP), Pattern-recognition receptors (PRR), Nucleotide binding leucine-rich repeat (NLR) proteins, Effectors, Plant innate immunity.

INTRODUCTION

Plants live in close contact with many different types of bacteria and phylogenetic diversity of plant-associated bacteria (PAB) can categorize in to three major groups as; commensals, mutualists and pathogens (Newton *et al.,* 2010). Among them only the bacterial pathogens can cause multiple plant diseases and harm to its host as plants being a source of food and/or shelter for these wide range of parasitic bacteria. Unlike other organism, being sessile organism plants cannot hide or escape when pathogens attacked, but like all other multicellular organisms, plants rely on their own innate immune system which is activated only after the recognition of an invading organism (Nürnberger *et al.*, 2004; Akira *et al.*, 2006; Spoel and Dong, 2012).

The innate immune system of plants can be divided into two layers of defense responses. Recognition of non-self molecules is an important first step towards an effective immune response and is enabled by pattern-recognition receptors (PRRs) in the host cells. These PRRs are able to recognize microbe-associated molecular patterns (MAMPs), which are also often referred to as pathogen associated molecular patterns (PAMPs) (Boller and Felix, 2009). The recognition of MAMPs/PAMPs by plant PRRs leads to so called PAMP-triggered immunity (PTI), which provides a first line of defense against most of the non-adapted pathogens (Jones and Dangl, 2006). In addition to non-self molecules, surface receptors can also recognize self-derived Damage-Associated Molecular Patterns (DAMPs) that are the result of wounding, initiating a similar immune response to PTI. Concurrently, pathogens have evolved ways to overcome this defense by producing effectors to

suppress PTI. Plant intracellular immune receptors can recognize this specific bacterial effectors and triggered effector-triggered immunity (ETI), the second layer of plant immunity, which was first defined as resistance (R-)/avirulence (Avr-) protein-dependent gene for gene specific resistance (Boller and He, 2009). Localized ETI leads to subsequent transmission of mobile signals to distal plant tissue, priming defense responses resulting in systemic resistance against future attack. Pathogen infection can also induce epigenetic modifications conferring trans-generational immunity. These two layers of the plant innate immune system function together and, as a result, the vast majority of bacteria are worked as nonpathogenic on most plants. This review is aims to summarize the recent discoveries in molecular mechanisms of plant recognition specifically to bacteria pathogen attacks, and their specifications.

PAMP Recognition by Pattern Recognition Receptors

Pathogen/microbe associated molecular patterns (P/MAMPs) are conserved molecules indispensable for the fitness of the pathogen/microbe and are not present in the host (Medzhitov and Janeway, 1997). PAMPs constitute the first layer of plant innate immunity, which recognized by plasma membrane-localized pattern recognition receptors (PRRs) and lacking of its recognition can lead to enhanced disease susceptibility. The group of bacterial PAMPs perceived by plants includes peptides. Examples for such peptides are peptidoglycan, bacterial lipopolysaccharides, ilongation factor Tu, bacterial flagellin, etc. (Postel and Kemmerling, 2009; Zhang and Zhou, 2010).

Peptidoglycan (PGN)

PGNs are building blocks of the bacterial cell wall and provide rigidity to the cell. In Gram-positive bacteria, PGN is present as a thick outer layer, and in Gram-negative bacteria, a thinner layer of PGN can be found between the two membranes. PGN consists of sugar chains that are formed by two alternating sugars, GlcNAc and *N*-acetylmuramic acid (MurNAc). These carbohydrate backbones are linked by short polypeptides, which are attached to the MurNAc lactyl group (Schleifer and Kandler, 1972). As receptors two LysM domain-containing, membrane bounds proteins called LYSM1 and LYSM3 do interact physically with PGNs.

Lipopolysaccharides

LPSs are glycol-conjugates present in the outer membrane of Gram-negative bacteria. They contribute to the structure of the bacterial envelope and offer protection against antimicrobial compounds. LPSs generally consist of a hydrophobic lipid moiety called lipid A, an oligosaccharide core domain, and a polysaccharide called the O-specific chain or O-antigen. LPSs of a wide range of bacterial species can elicit plant immune responses, such as callose deposition, nitric oxide production, production of reactive oxygen species, and increased expression of Pathogenesis Related (PR) genes (Dow *et al.*, 2000; Gerber *et al.*, 2004; Zeidler *et al.*, 2004; Silipo *et al.*, 2005, 2010; Desender *et al.*, 2006). Additionally, LPSs of several bacterial species suppress the hypersensitive response or induce resistance in plants (Van Wees *et al*., 1997; Erbs and Newman, 2012; Bakker *et al.*, 2007; Silipo *et al.*, 2010), although suppression of the hypersensitive response does not lead to increased susceptibility of the plant tissue (reviewed by Erbs and Newman, 2003). The recognition of LPS molecules from different species suggests that plants recognize LPSs through a common conserved domain.

As well as the most-conserved lipid A domain being able to trigger plant defense responses (Zeidler *et al.*, 2004; Silipo *et al.*, 2005, 2008; Madala *et al.*, 2011, 2012), the more variable core domain and O-antigen can also activate plant responses (Bedini *et al.*, 2005; Silipo *et al.*, 2005; Madala *et al.*, 2012). For many phytobacteria, the O-antigen consists of a rhamnan backbone (Molinaro *et al.*, 2009), and synthetic oligorhamnans that resemble this backbone induce defense responses in *A. thaliana*. Lipo-oligosaccharides (LPSs without the O-antigen) of *Xanthomonas campestris* trigger defense gene expression in *A. thaliana* in two phases, while treatment with the core domain leads to activation of the first phase and treatment with the lipid A domain triggers the second phase (Silipo *et al.*, 2005). Additionally, it has been shown that of the LPS of *Burkholderia cepacia*, the lipid 'A' domain and the core/O-antigen domain trigger distinct gene expression patterns in *A. thaliana* (Madala *et al.*, 2012). These data suggest that the two LPS domains are differentially recognized. However, how plants recognize LPS is still unknown.

Elongation factor Tu (EF-Tu)

Another MAMP that is recognized by plants is the bacterial elongation factor Tu (EF-Tu). EF-Tu was discovered as elicitor of defense responses in 2004, and shortly thereafter, the PRR responsible for EF-Tu recognition was identified and named EF-Tu receptor (EFR) (Kunze *et al.*, 2004; Zipfel *et al.*, 2006). Comprising 5–10% of the total protein content, EF-Tu is the most abundant protein in bacteria, where it mediates the entry of aminoacyl-tRNA into the ribosome complex and in this way facilitates protein elongation (Krab and Parmeggiani, 1998). EF-Tu is present in the bacterial cytoplasm making it unavailable for recognition by the EFR. Probably, the high abundance of EF-Tu results in

sufficient amounts of this protein for detection by the plant when bacteria die and lyse during plant infection. Additionally, there are some reports of surface-localized EF-Tu (Dallo *et al.*, 2002; Zipfel, 2008). In contrast to EF-Tu, which is widespread among bacteria, the presence of the EFR seems to be restricted to a small group of plants. This PRR has only been found in members of the Brassicaceae family, indicating that EF-Tu recognition has been acquired only recently during evolution (Kunze *et al.*, 2004). Interestingly, heterologous expression of *A. thaliana* EFR in the non-Brassicaceae plant species *Nicotiana benthamiana* and *Solanum lycopersicum* leads to the ability to recognize EF-Tu, which results in increased resistance to bacterial pathogens (Zipfel *et al.*, 2006; Lacombe *et al.*, 2010).

Flagellin

A MAMP in contrast to EF-Tu, which is recognized by the members of all groups of higher plants and the main subunit of the bacterial flagellum, named as flagellin (Felix *et al.*, 1999; Boller and Felix, 2009). The perception of flagellin in plants was discovered after treating cell cultures of tomato with boiled *P. syringae* pv. *tabaci* cells. The observed defense responses were the result of the highly sensitive recognition of a conserved N-terminal domain of flagellin by the plant PRR Flagellin Sensing 2 (FLS2) (Felix *et al.*, 1999; Gómez-Gómez *et al.*, 1999; Gómez-Gómez and Boller, 2000). In contrast with EF-Tu recognition, binding of the ligand to the receptor, leads to heterodimerization with BAK1, which is important for downstream defense signaling (Chinchilla *et al.*, 2007; Heese *et al.*, 2007; Segonzac and Zipfel, 2011). Furthermore, it has been shown that treatment with the peptide flg22, which contains the 22 corresponding amino acids of the conserved N-terminal domain of flagellin, also leads to strong defense activation (Felix *et al.*, 1999). As same as the EF-Tu recognition, the high abundance of the protein results in the requirement for only a small percentage of flagellin to be released for defense activation (Michiel *et al.*, 2013).

P/MAMP Recognition Determinants

The four PAMPs described above are very different in structure, come from different bacteria, and have different functions. However, when comparing them, they have a number of characteristics in common that make them suitable ligands for plant PRRs.

Firstly, they are widespread. PGN and EF-Tu can be found in all bacteria and LPS is present in all Gram-negative bacteria while flagellin is widespread among many bacterial species as well (Krab and Parmeggiani, 1998; Dow *et al.*, 2000; Yonekura *et al.*, 2002; Chevance and Hughes, 2008; Lee *et al.*, 2008; Silipo *et al.*, 2010).

Secondly, they are conserved. Almost the entire EF-Tu sequence shows over 90% sequence similarity among many different bacteria (Kunze *et al.*, 2004). Additionally, even though the exposed domain of flagellin is highly variable (from almost absent up to 1000 amino acid residues), the flagellin protein is highly conserved in the non-exposed domain of the protein (Felix *et al.*, 1999; Smith *et al.*, 2003; Bardoel and Van Strijp, 2011). In contrast, LPS is highly variable compared with the other four MAMPs. However, LPSs contain a more conserved part as well, which is the lipid A domain (Silipo *et al.*, 2010).

Thirdly, they are abundant. As major components of the bacterial cell wall, PGN is present at high levels to be the second most abundant polysaccharide in the world (Lee *et al.*, 2008; Silipo *et al.*, 2010). In addition, LPS molecules are spread around the surface of bacteria, which requires high numbers of these glycol-conjugates (Silipo *et al.*, 2010). Furthermore, both EF-Tu (5–10% of total bacterial protein) and flagellin (one flagellum can contain around 20 000 monomers) are present at relatively high levels (Krab and Parmeggiani, 1998; Samatey *et al.*, 2001; Chevance and Hughes, 2008).

Lastly and most importantly, they are essential, which explains why they are widespread and highly conserved. As the major components of the bacterial cell wall, PGN is indispensable for the viability of bacteria (Silipo *et al.*, 2010). Additionally, EF-Tu is required for protein formation, and it has been shown that inactivation of one EF-Tu-encoding gene is only possible if a second EF-Tu-encoding gene is present (Hughes, 1990; Krab and Parmeggiani, 1998). Furthermore, the LPS lipid A domain, together with a small part of the core domain, is required for bacterial growth (Raetz and Whitfield, 2002). By contrast, the production of flagella is not essential for bacterial survival, but pathogenic bacteria that are disturbed in their flagellum production are severely affected in their virulence (Feldman *et al.*, 1998; Schmitt *et al.*, 2001).

Hence, by targeting widely distributed indispensable microbial structures for recognition, plants are able to detect a wide range of microbes. The high abundance of the MAMPs described above might help the plant to detect the presence of even small numbers of microbes, and in this way an early infection can be arrested. The recognition of conserved sites enables plants to detect large groups of microbes with only a limited number of receptors. However, for pathogen survival, recognition is not desirable, and pathogenic microbes have therefore evolved ways to circumvent MAMP detection.

Pattern Recognition Receptors (PRRs) In Plants

FLS2

The first characterized PRR from plants was FLS2, a

leucine-rich repeat receptor-like kinase (LRR-RLK) that perceives a conserved peptide of bacterial flagellin (flg22) (Mazzotta and Kemmerling, 2011). FLS2 consists of an extracellular leucine-rich repeat domain with 28 repeats, a trans-membrane domain and a cytoplasmic kinase domain which can initiate phosphorylation-dependent signaling cascades (Boller and Felix, 2009). FLS2 was identified in a forward genetic screen based on flg22-induced root growth inhibition, in order to find flg22-insensitive mutants (Gomez- Gomez and Boller, 2000). This receptor shows structural similarities to animal pattern recognition receptors such as Toll and Toll-like receptors (TLR) from *Drosophila* and mammals, respectively. Together with their associated cytoplasmic kinases the TLR receptors resemble a similar modular structure as the LRR–RLKs (LRRs as recognition domains and cytoplasmic kinases as output domains).

The plant PRR FLS2 perceives the conserved, N-terminal, 22 amino acid peptide flg22 of the bacterial flagellin protein (Nürnberger *et al*., 2004). Flg22 recognition leads to several plant defense reactions, such as production of reactive oxygen species (ROS), activation of mitogen-activated protein kinases (MAPK), ethylene production, callose deposition at the cell wall and expression of defense-related genes leading to enhanced immunity as well as growth arrest (Boller and Felix, 2009). Pretreatment of *Arabidopsis* with flg22 induces resistance to the phytopathogenic bacterium *Pseudomonas syringae* pv. *tomato* strain DC3000 (*Pto*DC3000) (Zipfel, 2009). Based on homology modeling, the extracellular leucine-rich repeat region forms a predicted horse-shoe-like structure which is involved in direct binding of the peptide flg22 (Chinchilla *et al.*, 2006). Activation of the receptor by binding of its corresponding peptide ligand leads to internalization of FLS2 by endocytosis and further degradation by lysosomal and/or proteasome-related processes (Robatzek *et al.*, 2006).

Elongation Factor Receptor (EFR)

Another well studied receptor is the elongation factor receptor EFR, which can perceive the N-terminal acetylated peptide elf18 of the bacterial elongation factor Tu (EF-Tu). Activation of EFR leads to activation of similar defense responses as those triggered by flg22 (Zipfel *et al*., 2006). Activation of both FLS2 and EFR leads to identical calcium-associated plasma membrane anion channel opening as an initial step in the pathogen defense pathway, indicating that both signalling pathways rapidly converge at a very early stage of signaling (Jeworutzki *et al*., 2010). EFR was identified by a reverse genetic approach in a group of 28 flg22-induced receptor-like kinases from *Arabidopsis thaliana.* This indicates that PAMP perception leads to an alerted state of the plant represented by the activation of multiple receptors necessary for the perception of additional PAMPs. Proof of EFR function was provided by transient expression of *Arabidopsis* EFR in *Nicotiana benthamiana*, the latter not being responsive towards elf18 because of the lack of an EFR gene (Zipfel *et al.*, 2006).

As FLS2, EFR belongs to the LRR-RLK family XII and possesses 21 LRRs. Further analysis of the ligand binding site within the LRR domain was performed with chimeric receptors consisting of different parts of FLS2 and EFR. This led to the discovery of the importance of LRR1-6 and LRR19-21 for binding of elf18 and EFR dependent signaling (Albert *et al.*, 2010). For FLS2, the binding side for flg22 was narrowed down by mutational analysis to LRR 9 to 15 (Dunning *et al*., 2007). The impact of PAMP recognition on defense is supported by the fact that expression of EFR in *solanaceous* plants such as tomato and *N. benthamiana* leads to strongly enhanced resistance to a range of phytopathogenic bacteria from different genera (Lacombe *et al*., 2010).

*Le*EIX2

Apart from the two best PRRs, FLS2 and EFR, other interesting immune receptors were recently identified namely *Le*EIX2. The receptor *Le*EIX2 belongs to the receptor-like protein (RLP) family, and consists of extracellular LRR-repeats, a trans-membrane domain and a short cytoplasmic tail with unknown function (Boller and Felix, 2009). Recently, an interaction of the receptors *Le*EIX1 (closest homolog of *Le*EIX2) and BAK1 was shown to attenuate EIX responses indicating an inhibitory, potentially competitive effect of *Le*Eix1 on the receptor *Le*EIX2 (Bar *et al*., 2010). *Le*EIX2 was first identified as the fungal receptor in *Arabidopsis* (Wan *et al*., 2008; Miya *et al*., 2007) but later demonstrated to bacterial pathogens such as *Pseudomonas syringae* (Gimenez- Ibanez *et al*., 2009).

XA21

Another LRR-RLK-type PRR is XA21 from rice. It confers resistance against the bacterial pathogen *Xanthomonas oryzae* pv. *oryzae* in certain rice cultivars (Lee *et al*., 2009; Wang *et al*., 1998). XA21 was initially classified as a R protein because of the narrow spectrum of pathogens it can perceive. Recently it was shown that it perceives the PAMP Ax21 that might be involved in quorum sensing (Han *et al*., 2011). The minimal active fragment that was identified from Ax21 is the 17 amino acid tyrosine-sulfated peptide axYS22 (Lee *et al*., 2009). Ax21 contains all features of a typical PAMP, i.e. it is conserved within a class of microbes, necessary for its life style and not present in the host (Park *et al*., 2010b).

PEPR1 and PEPR2

Photo-affinity labeling and binding assays in tobacco (*Nicotiana tabacum*) cells expressing LRR-RLKs PEPR1 or PEPR2 proved that PEPR1 and PEPR2 are receptors for the damage-associated plant peptide *At*Pep1 (*At*Pep2-6 for PEPR1, or *At*Pep1 and 2 for PEPR2). PEPRs again belong to the class of LRR-RLKs. There is clear evidence of differential affinity of the two receptors and their cognate peptides to regulate innate immunity in plants. *At*Pep1 action on defense-related gene induction and enhancement of resistance to *Pto* DC3000 were partially reduced in single mutants of *PEPR1* and *PEPR2* and abolished completely in double mutants (Yamaguchi *et al*., 2010). By root growth inhibition assays and electrophysiological experiments, it was shown that only double mutants in *PEPR1* and its closest homologue *PEPR2* are fully insensitive to *At*Pep1 treatment (Krol *et al*., 2010). As known for other ligand binding LRR-RLKs, PEPR1 and PEPR2 are interacting with the small LRR-RLK BAK1 (BRI1-associated kinase) in yeast two-hybrid experiments. These *in vitro* interaction data are supported by *in vivo* formed *At*Pep1-induced phosphorylation- dependent BAK1 complexes with a protein corresponding to the expected size of PEPR1 or 2 (Postel *et al*., 2010; Schulze *et al*., 2010).

Wall Associated Kinases (WAK)

Another group of PRRs is the family of wall associated kinases (WAK). These kinases consist of an epidermal growth factor (EGF)-like motif on the extracellular part that can covalently bind cell wall components as pectin or oligogalacturonides (OGs) *in vitro* (Decreux *et al.*, 2006). OGs are homogalacturonic acids which are activators of plant defense, growth and development (Cervone *et al*., 1989). *WAK* genes are up-regulated upon pathogen or salicylic acid treatment (Hématy *et al*., 2009). With chimeric receptors consisting of parts of EFR and WAK1 it was shown that the extracellular WAK1 domain can activate the EFR kinase domain after OG treatment and *vice versa* (Brutus *et al*., 2010).

Erecta

Another candidate for sensing cell integrity could be ERECTA. This receptor belongs to the family of LRR-RLKs and is important for regulating developmental processes like inflorescence architecture, lateral organ shape, ovule development, stomata patterning, and transpiration efficiency (van Zanten *et al.*, 2009) but is also involved in plant defense. *ERECTA* was identified in a quantitative trait locus (QTL)-approach searching for the loci responsible for susceptibility to the soil born bacterium *Ralstonia solanacearum* in the *Arabidopsis* accession Landsberg *erecta* (L*er*) (Godiard *et al*., 2003).

Specific Plant Recognition

In nature, plants not only interact with pathogenic bacteria, they also abundantly form beneficial interactions with soil-borne bacteria. Classic examples of such mutualistic plant–bacteria associations are *Rhizobium* bacteria that fix atmospheric nitrogen for the plant (Spaink, 2000) and plant growth-promoting rhizobacteria that stimulate plant growth and suppress plant diseases (Lugtenberg and Kamilova, 2009; Van der Ent *et al*., 2009; Berendsen *et al.*, 2012; Zamioudis and Pieterse, 2012). As many MAMPs are widespread and conserved among microbes, beneficial microbes posses similar MAMPs as pathogens. For plants to benefit from the presence of these beneficial microbes, it is important to distinguish between pathogenic and beneficial microbes. However, like pathogens, many beneficial microbes have been shown to suppress host immunity to establish a successful relationship with their host (reviewed by Zamioudis and Pieterse, 2012).

Rhizobium bacteria form a symbiotic relationship with leguminous plants, and together they form nodules in which the bacteria fix atmospheric nitrogen. Plants recognize rhizobia initially as a threat, which leads to the elicitation of defense gene expression (Kouchi *et al.*, 2004; Lohar *et al.*, 2006; Zamioudis and Pieterse, 2012). Therefore, rhizobia need to avoid detection in a similar way to pathogens. *S. meliloti* produces flagellin molecules that do not elicit defense responses, and recently it was shown that the same is true for *Mesorhizobium loti* (Felix *et al.*, 1999; Lopez-Gomez *et al*., 2012).

Plant growth-promoting rhizobacteria (PGPRs) are non-symbiotic bacteria that can stimulate plant growth (Lugtenberg and Kamilova, 2009). Like rhizobia, PGPRs trigger PTI responses in plants (Bakker *et al.*, 2007; Van Wees *et al*., 2008). Hence, PGPRs should decrease the level of recognition by the host in order to minimize activation of host defenses (Millet *et al.*, 2010). Phase variation might be a strategy for PGPRs to minimize detection when colonizing roots. Phase I bacteria produce low amounts of flagellin and are found predominantly on the basal parts of the root. Phase II cells produce significantly higher amounts of flagellin and can be found mostly on secondary roots and root tips. Interestingly, phase I cells produce several extracellular enzymes, among which is AprA, which are not produced in phase II cells (Chabeaud *et al.*, 2001; Achouak *et al.*, 2004). The lower amount of flagellin in combination with the production of AprA in phase I cells suggests a role for phase variation in evading host immunity.

CONCLUSIONS

In recent years much progress has been made in

understanding the molecular basis and functional analysis of plant recognition receptors against their pathogens. The first pattern recognition receptor in plants was identified and it led to a paradigm shift in the plant defense field. Since then, multiple new PRR have been identified. Complex networks of receptors and partners as co-receptors, binding proteins and cytoplasmic proteins are formed to specifically initiate different defense pathways. Flagellin and lipopolysaccharides have been identified as common bacterial determinants or PAMPs that act as elicitors of defense responses in plant cells. The identification of more PRR candidates has also revealed a number of proteins with known functions in developmental processes. Interestingly, beneficial microbes appear to have evolved strategies via plant recognition to evade host immune responses that are very similar to those discovered in pathogenic microbes. Despite this progress, many questions still remain. What are the signaling proteins immediately downstream of immune receptor activation? What are the biochemical and structural changes in immune receptors that occur upon pathogen perception? Answers to these and other pressing questions will undoubtedly keep the field busy for years to come.

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