A Synopsis of Different Plant LRR-RLKs Structures and Functionality

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Plant Defense Mechanism

As sessile organism plants are exposed to multiple environmental threats. Unlike animals, they lack mobile immune cells. Hence, to safeguard themselves from a range of pathogens, plants come by a multi-tiered innate immune system [1,2]. The first line of defense mechanism is the recognition of the pathogen by detecting pathogen-associated molecular patterns (PAMPs) or microbial-associated molecular patterns (MAMPs) which are either extracellularly exposed or secreted extremely conserved pathogen-derived molecules [1,3]. This recognition is achieved by a cognate plant cell-surface pattern-recognition receptor (PRR). Once the invading pathogen's microbial signature 'PAMP' is recognized by the PRR, the plant cell initiates signaling cascades via the mitogen-activated protein kinase (MAPK). This first line of the plant defense mechanism is referred to as pattern-triggered immunity (PTI) [4-8].

Pattern Recognition Receptors (PRRs)

PRRs are grouped into receptor-like kinase (RLK) and receptor-like protein (RLP). RLKs contain an extracellular domain, transmembrane domain, and intracellular kinase domain while RLPs lack kinase domain [6,7,9-11]. The number of RLKs and RLPs are much higher in plants compared to animals [12]. In *Arabidopsis* plant, around 410 RLKs and 170 RLPs have found so far, which is around 640 and 90 for rice consecutively [12-14]. Again, the number of RLKs is much higher than the number of RLPs. In the success of terrestrial plants, these high number of presence of RLKs and RLPs might have played a crucial role [15].

Based on the extracellular domain (ECD), RLKs and RLPs are again categorized into several subfamilies which include epidermal growth factor-like (EGF) domains, lysine motif (LysM) and leucine-rich repeat (LRR) [16]. Among these subfamilies, leucine-rich

repeat like kinase (LRR-RLKs) is the largest family in plant [15]. With over 200 members of LRR-RLKs in *Arabidopsis*, they play a great role in plant development and defense processes which includes symbiosis, wounding response, hormone perception, stem cell maintenance and cell proliferation [17].

Structure of Leucine-Rich Repeat Receptor-Like Kinase (LRR-RLK)

Plant LRR-RLKs are composed of a very specific consensus sequence LxxLxxLxLxxNxLSGxIPxxLGx, while x symbolizes non-conserved residues. This unique 24 amino acid sequence forms the beta sheet or beta turn which acts as protein-protein interaction surface. This unique motif forms a helical horse-shoe like structure in plant [18-21]. According to the recent studies, not all LRR-RLK domains composed of tandem arrays of multiple LRRs form horse-shoe like structure. Instead, some of them like plant brassinosteroid (BR) LRR form a right-handed superhelical structure which is different from solenoid conformation [19,22,23]. This unique GxIP sequence which form the helical structure is common in case if receptor-like protein kinase 2 (RPK2) [24], flagellin-insensitive 2 (FLS2) [25], BRI1-like receptor kinase 1 (BRL1) [26]. There is a notable difference in the size of LRR-RLK. Recent crystallographic structures reveal that this size varies from 21-19 LRRs. Recent studies showed that around 20-25 LRRs form this superhelical structure where inner surface and lateral side of the structure actively involves in binding with other proteins [25,27]. PGIP has 10 LRRs, SERK1 has 5 LRRs, HAESA has 21 LRRs, TDR/PXY has 22 LRRs, FLS2 has 29 LRRs, BRI1 has 25 LRRs, PSKR has 21 LRRs, RPK2 has 22 LRRs and TMK1 has 13 LRRs [28]. Small sized LRR-RLK is observed in AtBAK1 and OsSerk2 (Figure 1) which acts as a co-receptor for activation of PTI by PRR FLS2 and Xa21 respectively [25,29].

Figure 1: Cartoon structure of different LRR-RLK. C and N stands for C terminal and N terminal respectively.

Island domain in LRR-RLK

In LRRs, LRR-RLK stands between 1st to 322nd LRRs where there can be a spacer region at 4th to 5th LRR from the C terminal end of 30 to 70 amino acids known as island domain (ID) [9]. The ID is not likely for all the LRR-RLK and its sequence is not conserved

between species. These ID can interact with the PAMPs like BL with BRI1 [30] and PSK with PSKR [31,32] (Figure 2). Also, 2 ID were observed in the crystal structure of RPK2 which creates scaffold where the ligand binds [24]. This suggests the function of island domain as binding of LRR ectodomain with small ligands [28].

Figure 2: Island domain in BRI1 (left) and PSKR (right) [28].

Cys-pairs in LRR-RLK

Again, Cys-pairs which are placed between last LRR and transmembrane domain or near the start codon before LRR is another interesting extracellular domain in LRR-RLK [33]. Although

the function of the Cys-pair is not clear, the mutation of it showed a significant decrease in FLS2 activity while BRI1 and CLAVATA2 showed no effect [34]. Although Cys-Pairs in LRR-RLK is assumed to contribute towards trafficking, folding and binding, no strict decision can be drawn regarding the importance of it.

Conclusion

The above discussion shows, in spite of the fact that most of the LRR-RLKs share a common shape, a significant difference is observed in the case of other factors such as diameter, LRR numbers, the presence of the island domain and cys-pairs. All this play a pivotal role in different binding mechanism in PTI complex at the early stage of the plant defense mechanism. It is needless to say, to obtain a precise idea about the detail function and interaction of different domains, further investigation needs to be done on LRR-RLK conserved protein structures, motif compositions, and gene structures.

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