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Origin and diversification of leucine-rich repeat receptor-like protein kinase (*LRR-RLK*) genes in plants

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Abstract

Background: Leucine-rich repeat receptor-like protein kinases (LRR-RLKs) are the largest group of receptor-like kinases in plants and play crucial roles in development and stress responses. The evolutionary relationships among *LRR-RLK* genes have been investigated in flowering plants; however, no comprehensive studies have been performed for these genes in more ancestral groups. The subfamily classification of *LRR-RLK* genes in plants, the evolutionary history and driving force for the evolution of each *LRR-RLK* subfamily remain to be understood.

Results: We identified 119 *LRR-RLK* genes in the *Physcomitrella patens* moss genome, 67 *LRR-RLK* genes in the *Selaginella moellendorffii* lycoplyte genome, and no *LRR-RLK* genes in five green algae genomes. Furthermore, these *LRR-RLK* sequences, along with previously reported *LRR-RLK* sequences from *Arabidopsis thaliana* and *Oryza sativa*, were subjected to evolutionary analyses. Phylogenetic analyses revealed that plant *LRR-RLKs* belong to 19 subfamilies, eighteen of which were established in early land plants, and one of which evolved in flowering plants. More importantly, we found that the basic structures of *LRR-RLK* genes for most subfamilies are established in early land plants and conserved within subfamilies and across different plant lineages, but divergent among subfamilies. In addition, most members of the same subfamily had common protein motif compositions, whereas members of different subfamilies showed variations in protein motif compositions. The unique gene structure and protein motif compositions of each subfamily differentiate the subfamily classifications and, more importantly, provide evidence for functional divergence among *LRR-RLK* subfamilies. Maximum likelihood analyses showed that some sites within four subfamilies were under positive selection.

Conclusions: Much of the diversity of plant *LRR-RLK* genes was established in early land plants. Positive selection contributed to the evolution of a few *LRR-RLK* subfamilies.

Keywords: *LRR-RLK* genes, Functional divergence, Gene structure, Motif, Positive selection

Background

All living organisms sense and conduct signals through cell surface receptors. In plants, many such cellular signaling transductions are mediated by receptor-like kinases (RLKs). The largest group of plant RLKs is the leucine-rich repeat RLK family (*LRR-RLK*) [1]. *LRR-RLKs* contain three functional domains: an extracellular domain (ECD) that perceives signals, a transmembrane domain that anchors the protein within the membrane, and an intracellular kinase domain (KD) that transduces the signal downstream via autophosphorylation, followed by subsequent phosphorylation

of specific substrates [2]. The *LRR-RLK* ECD contains varying numbers of LRR repeats, and LRR diversity enables *LRR-RLKs* to sense a variety of ligands, including small molecules, peptides, and entire proteins [3]. On the other hand, the *LRR-RLK* KD is common in protein kinases, and contains 12 conserved subdomains that fold into a similar three-dimensional catalytic core with a two-lobed structure [4, 5]. Previous investigations demonstrated that all conserved residues in these subdomains play essential roles in enzyme function [4, 5].

LRR-RLKs function in a wide array of plant processes. Some *LRR-RLKs* are involved in the control of plant growth and development; for example, CLV1 is involved in controlling meristem development [6, 7], RUL1 is involved in secondary growth [8], SERK1 is involved in microsporogenesis

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